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Cranial osteology and reassessment of the historically collected South African gorgonopsians FMNH UC 1513 (*Lycaenops* cf. *L. angusticeps*) and AMNH FARB 5537 (*Lycaenops angusticeps*)

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Abstract: *Lycaenops* contains one of the most anatomically complete gorgonopsian specimens (AMNH FARB 2240) known and is thought to represent one of the more taxonomically diverse forms, with several species historically attributed to it. Despite this, many species in this complex, aside from the type species, *L. ornatus*, are not well defined, requiring substantial revisions. At present, *Lycaenops* likely represents a 'waste-basket taxon', as an overly generic morphological grouping that includes any medium-sized gorgonopsians with a reduced postcanine series, long snout, slender skull arches, and moderate to minor cranial pachyostosis. Here we provide a reassessment of the cranial osteology for two specimens previously assigned to *Lycaenops* including AMNH FARB 5537, the holotype of '*L. angusticeps*', and FMNH UC 1513, the holotype of '*Scymnognathus major*' that was later assigned to '*L.* cf. *L. angusticeps*'. Furthermore, FMNH UC 1513 has never been comprehensively assessed, with the original description being both brief and dated. Our anatomical and phylogenetic assessment of both specimens support their assignment to *Lycaenops*. We suggest that '*L. angusticeps*' be regarded as a nomen dubium and refer FMNH UC 1513 to a yet to be described *Lycaenops* species pending a more comprehensive study of variation (e.g., differing proportions of the snout among other characteristics) within the genus.

INTRODUCTION

Gorgonopsians are a clade of early-diverging predatory therapsids that perhaps appeared as early as the Cisuralian and persisted to the end of the Lopingian, with a global fossil record known from Africa, Russia, India, China, and recently the island of Mallorca, Spain (Sigogneau 1970; Sigogneau-Russell 1989; Ray and Bandyopadhyay 2003; Kammerer 2016; Liu and Yang 2022; Matamales-Andreu et al. 2024). The group famously contains the most abundant terrestrial predators of the late Permian with members ranging in size from *Aelurosaurus wilmanae*, with a basal skull length of 10.7 cm, to *Inostrancevia alexandri*, with a basal skull length of 53.0 cm, and likely occupying a variety of ecological guilds potentially analogous to living carnivore families (e.g., Felidae; Sigogneau-Russell 1989; Singh et al. 2024; Mann and Sidor in press). Historically, gorgonopsian alpha taxonomy and systematics have been chaotic, with the lack of taxonomic resolution having been attributed to a few factors, including the extreme taxonomic over-splitting by early therapsid researchers and the high degree of cranial homomorphism exhibited by gorgonopsians (Gebauer 2007; see Kammerer 2016 for detailed discussion). Currently, we are in a renaissance of research on gorgonopsians with many new in-depth studies published in the last decade (e.g., Kammerer 2014, 2015, 2016, 2017; Kammerer and Masyutin 2018; Kammerer et al. 2015, 2023; Bendel et al. 2023 among others). Most notably, the presence of a reliable phylogenetic framework for gorgonopsians (Kammerer 2016, and derivatives) provides a useful tool for assessing interrelationships and other evolutionary patterns among the group (e.g., Bendel et al. 2022; Sidor and Mann 2024).

Even the most well-known gorgonopsian genera have questionable species level diversity. Arguably, this is true of one of the most anatomically complete members of Gorgonopsia,

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Lycaenops ornatus, for which the holotype, AMNH FARB 2240, consists of both a well-preserved cranium and nearly complete postcranial skeleton that was described by Colbert in his comprehensive 1948 monograph. Despite Colbert's impressive monograph, the *Lycaenops* species complex represents one of the most complicated areas of gorgonopsian systematics, and past attempts at revisions have produced unsatisfactory results for this genus (Gebauer 2007; Sigogneau 1970). At present, *Lycaenops* can be considered a 'wastebasket' taxon in need of a substantial revision.

Here we provide an incremental step towards a full revision by contributing a revised differential diagnosis for the genus and updated descriptions and anatomical interpretations of two historically important fossils of *Lycaenops*. The first of these is FMNH UC 1513, the holotype of '*Scymnognathus major*' described in a brief and dated note (Olson and Broom 1937) and later assigned to '*L.* cf. *L. angusticeps*' by Sigogneau (1970), despite never having studied the specimen in person. In order to better understand the assignment of FMNH UC 1513 to '*L.* cf. *L. angusticeps*' (Sigogneau 1970), we also provide a new description and reassessment of the holotype of '*Lycaenops angusticeps*', AMNH FARB 5537. Finally, we provide an updated phylogenetic analysis introducing the two specimens of *Lycaenops* reviewed in this paper (FMNH UC 1513 and AMNH FARB 5537) to the recently published analysis of Mann and Sidor (in press), which recovered NHCC LB178 and the holotype of *L. ornatus*, as a *Lycaenops* node.

MATERIALS AND METHODS

The specimens, including '*Lycaenops* cf. *L. angusticeps*' (FMNH UC 1513), the holotype of '*Lycaenops angusticeps*' (AMNH FARB 5537), a referred skull of '*Lycaenops angusticeps*' (AMNH FARB 5535), a potentially new species of *Lycaenops* from Zambia (NHCC LB 178), and the holotype of the species, *Lycaenops ornatus* (AMNH FARB 2240), were analyzed using comparative anatomical methods. We also compared these specimens to a variety of *Gorgonops*ian specimens and casts housed in various museums across North America and the United Kingdom. Measurements of anatomical features were done using digital calipers and a tape measure (see Table 1). All specimens were photographed with a Nikon D700 Camera using an AF-S NIKKOR 24–85mm lens or a Canon 5DS with a Canon MP-E 65mm Macro lens. Photographs were processed using Adobe Photoshop CS6 and final figures were assembled using Adobe Illustrator CS6.

To assess the phylogenetic position of the new species described below, we conducted a phylogenetic analysis under the parsimony framework using the recent *Gorgonops*ian-focused matrix of Mann and Sidor (in press). Using the phylogenetic software Mesquite 3.2, we modified this matrix with the new addition of two taxa: '*Lycaenops angusticeps*', AMNH FARB 5537, and '*Lycaenops* cf. *L. angusticeps*', FMNH UC 1513 (see associated nexus file). The resulting modified matrix consisted of 29 operational taxonomic units (OTUs) and 52 characters, all of which are discrete-state and with 6 ordered characters: 11, 14, 26, 28, 31, 50. The parsimony analysis was performed using PAUP v4.0b10 (Swofford 2002). We performed a branch-and-bound search. Maxtrees were set at 10,000 and automatically increased by 100. Multistate characters were treated as polymorphic. To assess support of internal nodes, bootstrap values were calculated from a fast stepwise addition using 10,000 replicates.

Institutional Abbreviations: AMNH, American Museum of Natural History, New York, USA; FMNH, Field Museum of Natural History, Chicago, USA; NHCC, National Heritage Conservation Commission, Lusaka, Zambia.

Table 1. Comparative skull measurements of *Lycaenops* species considered in this paper (FMNH UC 1513, AMNH FARB 5537, AMNH FARB 2240, NHCC LB178). Measurements taken in mm.

	FMNH UC 1513				AMNH FARB 5537				AMNH FARB 2240				NHCC LB178			
	length	width	height	number	length	width	height	number	length	width	height	number	length	width	height	number
Basal Skull	344				275				179				227			
Total Skull	350				289				206				235			
Snout	190	47.21	120		179	43.8	96.8 (left side)		120.5	50.7	68.4 (left side)		106	53.25	76.89	
Jugal	144.4		38.9		157		27.3		90.2		25.7		89.18		11.18	
Preparietal	15.93	9.13			12.6	2.7			32.9	25.5			18.44	12.21		
Mandibular Symphysis			88.46				72				50.2				55.09	
Postcanines				4				4				4				3

SYSTEMATIC PALAEONTOLOGY

Clade SYNAPSIDA Osborn, 1903

Order THERAPSIDA Broom, 1905

Infraorder GORGONOPSIA Seeley, 1894

Family GORGONOPSIDAE Lydekker, 1890

Genus *Lycaenops* Broom, 1925

Holotype: AMNH FARB 2240, a virtually complete, slightly deformed, skull and associated postcranial skeleton (Colbert 1948).

Horizon and Locality: Permian, *Cistecephalus* Assemblage Zone (AZ) (originally reported by Broom 1925 as upper *Endothiodon* Zone), Lower Beaufort series, Karoo System, along railway line, about 2 miles south of Biesjespoort Railway Station, South Africa. Collected by Robert Broom.

Revised Differential Diagnosis: Medium-sized (up to ~34.4 cm basal skull length) non-rubidgiene gorgonopsians diagnosed by the following unique combination of characters: A long snout similar in proportions to *Arctops*, but not as long as the condition seen in *Cyonosaurus*; posterior process of the maxilla is highly elongated, terminating at the level of the postorbital bar; postorbital bar bears a brow-ridge dorsolaterally however, is still thin and lacking significant pachyostosis, falling between the range of conditions observed in *Cyonosaurus* (thinner) to *Gorgonops* (thicker). The jugal narrow below the postorbital bar shared with at least *Cyonosaurus*, *Inostrancevia*, and the rubidgiene *Sycosaurus*. The postfrontal invades the parietal border unlike *Smilesaurus* and *Arctops*, but similar to some rubidgienes. Possesses three or four postcanines as in *Arctops* and *Inostrancevia*, but differs from *Smilesaurus* which has two or fewer, and further differs from *Nochnitsa*, *Viatkogorgon*, *Sauroctonus*, *Cynariops*, *Gorgonops*, *Aelurosaurus*, *Cyonosaurus*, and *Arctognathus* all of which have five or more. The palatal bosses of the pterygoid are reniform in shape differing from the delta shaped bosses present in *Eriphostoma*, *Gorgonops*, *Viatkogorgon*, *Sauroctonus*, and

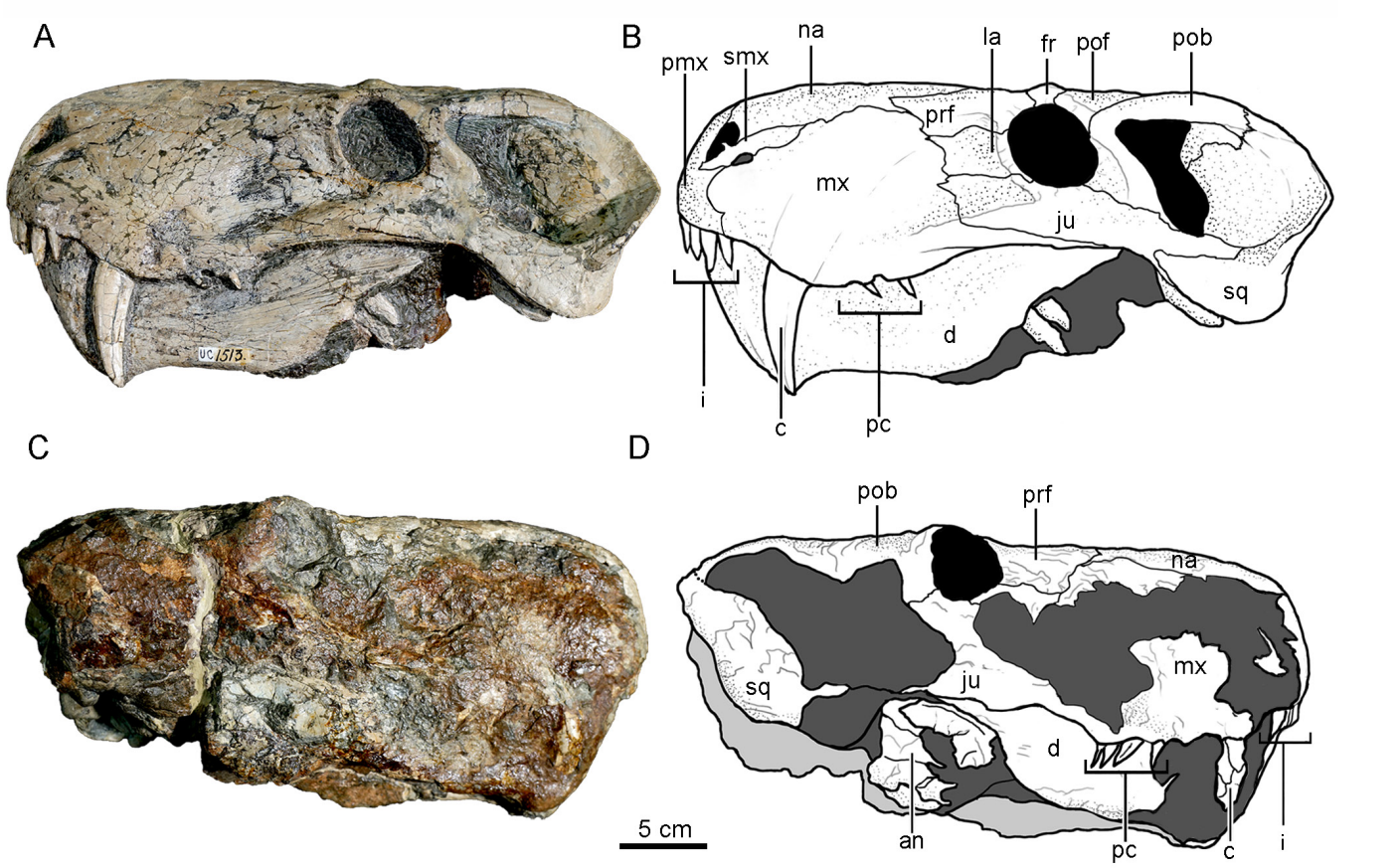

Figure 1. Cranium of FMNH UC 1513. A, photograph of right side of skull in lateral view; B, line drawing of right side of skull in lateral view; C, photograph of left side of skull in lateral view; D, line drawing of left side of skull in lateral view. In the illustrations, black indicates natural skull openings, dark grey indicates matrix, and light grey indicates out of view sections of the skull. Abbreviations: c, upper canine; d, dentary; fr, frontal; i, incisor; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pc, postcanine; pmx, premaxilla; pob, postorbital; pof, postfrontal; prf, prefrontral; smx, septomaxilla; sq, squamosal.

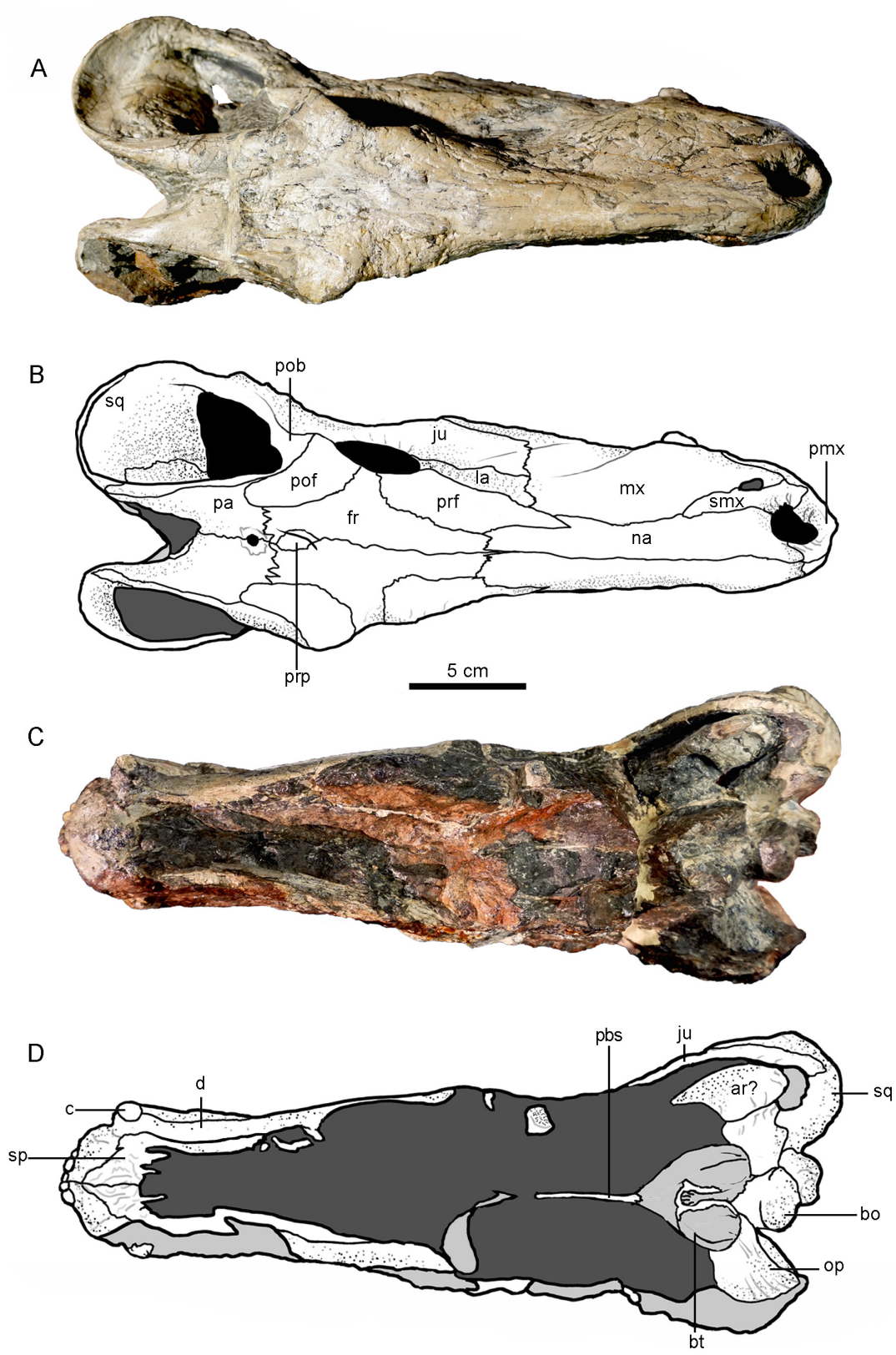

Figure 2. Cranium of FMNH UC 1513. A, photograph in dorsal view; B, line drawing in dorsal view; C, photograph in ventral view; D, line drawing in ventral view. In the illustrations, black indicates natural skull openings, dark grey indicates matrix, and light grey indicates out of view sections of the skull. Abbreviations: ar, articular; bo, basioccipital; bt, basal tuber; c, upper canine; d, dentary; fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pbs, parabasisphenoid; pc, postcanine teeth; pmx, premaxilla; pob, postorbital; pof, postfrontal; prf, prefrontal; prp, preparietal; smx, septomaxilla; sp, splenial; sq, squamosal.

Phorcys, and the weakly-developed single ridge present in *Inostrancevia*.

Comments: Prior to this study, Sigogneau-Russell (1989, p. 93) provided the most recent diagnosis for *Lycaenops*; however we recognize that this diagnosis is out of date and requires substantial revision including consideration for the current state of gorgonopsian research. The diagnosis provided in this paper is based on the current knowledge of *Gorgonops*ian systematics, but is still preliminary and would benefit from further anatomical research of the *Lycaenops* species complex.

Lycaenops sp.

(Figs. 1–3)

1937 *Scymnognathus major*, Olson and Broom
1970 *Lycaenops* cf. *L. angusticeps*, Sigogneau
1989 *Lycaenops* cf. *L. angusticeps*, Sigogneau-Russell
2007 *Lycaenops* cf. *L. angusticeps*, Gebauer

Material: FMNH UC 1513, a well-preserved skull including most of the mandible, and cranium. The left side of the specimen is virtually complete, while the right side is damaged, distorted, and less well-prepared.

Horizon and Locality: Permian, *Cistecephalus* AZ (originally reported by Olson and Broom 1937, as *Endothiodon* Zone), Lower Beaufort Series, Karoo Basin, Brakwater Farm area, NE of Murraysburg, west of Victoria Road, ¾ of a mile south of river crossing, Murraysburg, South Africa. The specimen was recovered on a Walker Museum expedition led by A. S. Romer and P. C. Miller in 1929.

Comments: The specimen was originally designated as the type specimen for '*Scymnognathus major*' by Olson and Broom (1937), but Sigogneau (1970) recognized '*Scymnognathus*' as no longer valid and divided the genus into *Gorgonops*, *Lycaenops*, and *Aelurognathus* (Gebauer 2007). The most recent assignment of FMNH UC 1513 as '*L.* cf. *L. angusticeps*' by Sigogneau (1970) was based on limited research and outdated descriptions of the specimen. Having never personally observed the specimen, she noted several differences between FMNH UC 1513 and '*L. angusticeps*,' including a shorter and higher snout in the former based on the original description, compromising an accurate diagnosis of the specimen. Gebauer (2007), who also did not observe the specimen personally, followed Sigogneau (1970) and Sigogneau-Russell (1989) in referring the specimen to the species '*L.* cf. *L. angusticeps*'.

We agree that FMNH UC 1513 is referable to the genus *Lycaenops*, but do not support assignment to the species '*L. angusticeps*' as suggested by Sigogneau (1970). Furthermore, we recognize that FMNH UC 1513 might represent a previously unrecognized species of *Lycaenops* that can be diagnosed by a unique combination of large size; jugal relatively tall under orbit (compared to other *Lycaenops* species); dentary tall and massive at symphysis; a higher snout; and a small diamond-shaped preparietal, which is shared with '*L. angusticeps*' but differs from *L. ornatus*, and NHCC LB178 (Colbert 1948: fig. 2; Levy 2023: fig. 6). FMNH UC 1513 (snout length (SL) = 190 mm; basal skull length (BSL) = 344 mm; snout proportion (SP) = 55.2%) might be

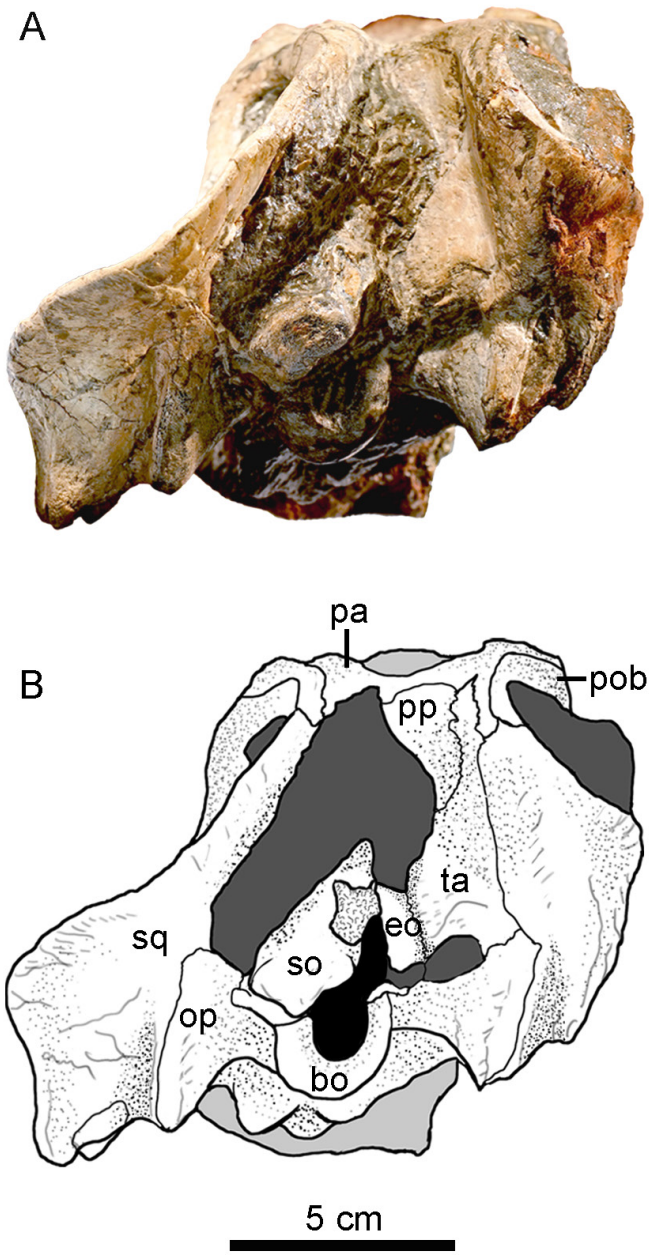

Figure 3. Occiput of FMNH UC 1513. A, photograph in occipital view; B, line drawing in occipital view. In the illustrations, black indicates natural skull openings, dark grey indicates matrix, and light grey indicates out of view sections of the skull. Abbreviations: bo, basioccipital; eo, exoccipital; op, opisthotic; pa, parietal; pbs, parabasisphenoid; pp, postparietal; so, supraoccipital; sq, squamosal; ta, tabular.

further differentially diagnosed by a uniquely shorter snout length compared with the species *L. ornatus* (SL = 120.5 mm, BSL = 179 mm, SP = 67.3%), and '*L. angusticeps*' (SL = 179 mm, BSL = 275 mm, SP = 65.1%), but still longer than the ratio seen in NHCC LB178 (SL = 106 mm, BSL = 227 mm, SP = 46.7%). Because most therapsids elongate their snout throughout ontogeny (Krone et al. 2019), it is unlikely that the observed differences in snout proportions are ontogenetically related as FMNH UC 1513 represents the largest skull of those examined in this study and perhaps is the largest known that is referable to the genus. Currently we recognize the need for further revisions of the *Lycaenops* species complex, and at present we refrain on providing any formal diagnosis. We also recognize that the aforementioned features may have overlap with other currently unrevised species of *Lycaenops*.

Description

Preservation: Few gorgonopsian skulls, among historically collected materials housed in North American collections, are as anatomically complete, well-preserved, and well-prepared as FMNH UC 1513 (Fig. 1A, B). Despite the nature of preservation, over preparation has likely removed most of the original 'pustular' cranial ornamentation and cranial ridges, such as the small interorbital ridge, that are observed in other gorgonopsians of similar size (e.g., *Arctops*, Mann and Sidor in press; *Gorgonops*, Sidor et al. 2023). The right side of the specimen (Fig. 1C, D) is not as well-preserved as the left and is slightly weathered, in addition to being unprepared in areas. Nevertheless, the right side of the skull possesses a number of anatomical features that are not present on the left side and thus both sides of the skull aid in the description of this specimen. Taphonomic distortion is present mostly in the form of lateral compression, more so on the right side as aforementioned. The left side of the skull has a well-preserved snout with the premaxilla, maxilla, septomaxilla, nasal, and near-complete marginal dentition (Fig. 1A, B). In left lateral and dorsal views (Fig. 2A, B) the majority of the skull bones can be seen. The left mandible only preserves the dentary. The right mandible preserves the dentary and the angular as well, though the dentary is less well-preserved on this side whereas the angular is much better preserved, showing the shattered remains of the reflected lamina. The occiput (Fig. 3) is preserved, though the exoccipitals and supraoccipital are distorted and partially covered in matrix, more so on the left side, largely obscuring the left tabular. The robust basioccipital is bordered dorsolaterally by a portion of the displaced supraoccipital.

Cranium: The snout of FMNH UC 1513 (Fig. 1A, B) appears long and high, although not as proportionally long as in '*L. angusticeps*'. The slope of the snout at the anterior margin is less steep and more gently rounded than that of most gorgonopsians (Sigogneau-Russell 1989; Kammerer 2016), and the dorsal margin of the snout displays a gradual dorsal sloping in a posterior direction. In this specimen there are five incisors and a canine present on both sides, and the postcanines are represented by two teeth and two tooth roots (four total) on the left side and three teeth on the right side. The anteroventral margin of the maxilla is gently curved similar to *Arctops* (Kammerer 2017), and does not possess a significant 'step' as seen in *Arctognathus curvimola* (Kammerer 2015). Starting at the I5-C diastema, the maxilla slopes ventrally as it approaches the canine, reaching its greatest depth just posterior to the root of the canine before sloping dorsally posterior to the postcanines. The greatest height of the snout is 120 mm which occurs in the C-PC1 diastema.

The septomaxilla is an elongate, cleaver-shaped bone that reaches posterodorsally from the front of the snout. The preserved septomaxilla on the left side (Fig. 1A, B) shows a similar horizontal orientation as that of other non-rubidgeine gorgonopsians (Colbert 1948: fig. 1; Sidor and Mann 2024: fig. 2; Mann and Sidor in press: fig. 2), and is posteriorly angled significantly compared to most rubidgeines (Kammerer 2016: fig. 2). The transverse lamina of the septomaxilla is thin and elongate, extending medially into the nasal opening, best viewed anteriorly, though it is well-worn and poorly preserved. The septomaxillary foramen is present directly posterior to the ventral edge of the septomaxilla.

The ascending process of the premaxilla is long and thin and forms the anterodorsal margin of the external nares (Fig. 2A, B). On the lateral surface, the premaxilla-maxillary suture has a distinct, concave shape with the dorsal aspect of the suture sitting roughly over the midpoint of I4 and the ventral aspect appearing to split the alveoli for I5 (Fig. 1A, B). This replicates the condition seen in other *Lycaenops* species (e.g., *L. ornatus*, Colbert 1948) and appears to be unique to this genus. The premaxilla is short and restricted to the most anterior end of the snout. A short triangular process extends dorsally, wedging between the septomaxilla and the maxilla. The premaxilla comprises the majority of the anterior and ventral portions of the external narial opening.

The maxilla is long, deep, and displays a posteriorly extending process wedging beneath the jugal and terminating under the postorbital bar (Fig. 1A, B). Scattered across the lateral surface are the maxillary foramina. They are more concentrated and smaller anteriorly and along the ventral margin, though they are largely overprepared. The posterior process of the maxilla is highly elongate reaching to the level of the mid postorbital bar, extending ventrally under the jugal and contributing significantly to the zygoma. The elongate posterior process of the maxilla appears to be shared widely among the specimens of *Lycaenops* examined

in this paper (e.g., *L. ornatus*, NHCC LB178, AMNH FARB 5537 '*L. angusticeps*'). This condition is somewhat unusual, as in most gorgonopsians the posterior process of the maxilla terminates well before the postorbital bar and the jugal is responsible for the majority of the ventral margin of the zygoma (Sigogneau-Russell 1989; Kammerer 2016). In *Lycaenops*, the elongated posterior process of the maxilla may serve as support for the overall elongated and expanded snout. The maxilla bears a pronounced lateral bulge surrounding the root of the canine (Fig. 1A, B), which produces a wide convexity beginning at the ventral margin of the canine alveolus. This convexity extends dorsally and somewhat posteriorly towards the low boss of the prefrontal. This bulge represents the widest part of the snout (Fig. 2A, B). Posterior to this swelling, the maxilla is concave, particularly above the C-P1 diastema and as it approaches the maxillary-jugal suture. Dorsally, between the canine bulge and the nasal, the maxilla is also shallowly concave. The maxilla contacts the nasal dorsally at an anteroventrally sloping angle.

The nasals are roughly rectangular in dorsal view and possess an expansion anteriorly, just posterior to the external nares, and a double scarf joint with the prefrontal posteriorly, anterior to the frontal-nasal suture (Fig. 2A, B). The nasals are remarkably slender, similar to *L. ornatus* and AMNH FARB 5537, but this condition is not true for all *Lycaenops* and does not carry through other gorgonopsians (Colbert 1948: fig. 2; Kammerer 2016). The suture with the prefrontal is variable between species but no others appear to have a double scarf joint. Its lateral margin begins at the prefrontal suture, and slopes to meet at the apex of the dorsal edge of the septomaxilla. The nasal-frontal suture is strongly interdigitated. A small process lies in between the frontal and prefrontal representing the posterior-most extension of the nasal. Dorsolaterally to this process there is a smaller process that wedges in between the prefrontal and maxilla and creates the lateral aspect of the double scarf joint. The anterior suture with the ascending process of the premaxilla is "M"-shaped where it bifurcates, and possesses a small medial triangular process that points anteriorly. The nasal contributes to the posterior dorsal wall of the naris.

The dentition of FMNH UC 1513 is well-preserved with five incisors and one canine present, and spaces for 4 postcanine teeth. This matches the observed dental formula in *L. ornatus* (AMNH FARB 2240) and AMNH FARB 5537 (I5-C1-PC4), although there is possibly space for a fifth postcanine in the former (Sigogneau-Russell 1989). This differs slightly from the postcanine count in NHCC LB178, which appears to have space for less than four post canines in the tooth row (Levy 2023: figs. 8, 19). The preservation of the specimen with the mandible in a closed position prevents any description of the dentary teeth. The position of the mandible does however show a tight dental occlusion with the visible teeth of the maxilla and premaxilla being closely associated with the dentary. Most noteworthy of the dentition of FMNH UC 1513 is the robust canine, which appears more pronounced than that of *L. ornatus* (Colbert 1948: fig. 1). The left canine is the better preserved. It appears to be in its original position, and shows an overall height of 69 mm, though we note the canine is heavily worn at the tip and that it likely extended slightly further, just beyond the mandibular protuberance. The right canine is highly worn and broken at approximately its mid-length. The canines are slightly recurved and ziphodont showing well-preserved steak knife-like rounded serrations visible only on the posterior edge of the tooth similar to other species of *Lycaenops* and *Arctops* (Colbert 1948; Mann and Sidor in press). The posterior incisors are more recurved towards the posterior end of the tooth row. The anterior incisors are the most worn and lack most of the tooth crown. The postcanines are relatively small and exhibit only slight recurvature. Apart from the canines, all dentition is too worn to distinguish the presence of serrations.

Similar to most gorgonopsians (Sigogneau-Russell 1989; Kammerer 2016), the prefrontal (Figs. 1, 2A, B) of FMNH UC 1513 is elongate and trapezoidal, lying above the lacrimal and extending well anteriorly beyond the other bones of the orbit. This region is slightly pachyostosed forming a low boss. The frontal-prefrontal suture is strongly interdigitated, similar to *Arctops umulunshi* (Mann and Sidor in press: fig. 4A).

The lacrimal (Fig. 1A, B) is rectangular and strongly concave, participating in the antorbital depression. The lacrimal slightly invades the prefrontal along the midpoint of the lacrimal-prefrontal contact. The lacrimal-jugal suture is relatively straight and terminates in a thin circumorbital process at the anteroventral margin of the orbit. At the orbital margin, the lacrimal is raised relative to the rest of the bone. The overall shape of the lacrimal is similar to other *Lycaenops* species (e.g., *L. ornatus*, Colbert 1948) but is notably longer and possesses a more pronounced circumorbital process. In general, this morphology is similar to what is seen in mid-sized gorgonopsians such as *Arctops* (Kammerer, 2017; Mann and Sidor in press: fig. 2).

The jugal (Fig. 1A, B) is convex on the lateral surface, robust and elongate, forming the ventral portion of the orbit. Its greatest height is observed at the posteroventral corner of the orbit. Relative to other species of *Lycaenops* (Colbert 1948; Sigogneau-Russell 1989), the jugal height beneath the orbit is tall and more closely resembles the condition found in *Arctops umulunshi* (Mann and Sidor in press: fig. 2A). Posteriorly, the jugal wedges between the postorbital bar and the squamosal, contributing to the anteroventral wall of the temporal fenestra. On its posterior aspect, the

jugal is bisected by the anterior process of the squamosal forming a double-scarf joint in a similar fashion to most non-rubidgiene gorgonopsians (e.g., *Cyonosaurus*, Olson 1937; *Gorgonops*, Sidor et al. 2023; *Arctops*, Kammerer 2017 etc). The subtemporal portion of the jugal deflects ventrally on the posterior-most portion of the bone.

The orbital rim (Fig. 1A, B) and its surrounding area are slightly pachyostosed forming low bosses and a slightly raised orbital rim, similar to some specimens of *Aelurognathus tigriceps* (Kammerer 2016: figs. 5–7). The frontal contribution to the dorsal margin of the orbit is present and relatively small (9–11 mm) similar to *Lycaenops ornatus*, *Arctops umulunshi* and *Smilesaurus ferox* (Colbert 1948: fig. 1; Kammerer 2016: fig. 55A; Mann and Sidor in press: fig. 2A). The frontals (Fig. 2A, B) are anteriorly elongated, subtriangular in shape, widest in the middle, and narrow anteriorly. Posteriorly, the contact between frontals is interrupted by a small, diamond-shaped preparietal. The frontal-parietal suture occurs just anterior to the pineal boss and is strongly interdigitated. The dorsal surface of the frontals is slightly concave in between the orbital margin and the slight median interorbital ridge.

The postfrontals (Fig. 2A, B) are subtriangular in shape and contribute to the posterodorsal portion of the orbit. The elongate form is unique in comparison to the postfrontals of other gorgonopsians. Some, like *Gorgonops* sp. (NHCC LB120; Sidor et al. 2023: fig. 3) and *Arctops umulunshi* (Mann and Sidor in press: fig. 4A), share an elongate morphology compared to the shorter morphology present in *Lycaenops ornatus* (Colbert 1948: fig. 2). Laterally they border the postorbitals (Fig. 1A, B), with which they share a crescent-shaped suture. Their medial margin is well-rounded, sharing a large suture with the frontal, and a smaller suture with the parietal. Posteriorly they extend to the posterior level of the pineal foramen.

The moderately thickened postorbital bar (Fig. 1A, B) is raised laterally from the rest of the skull, displaying a distinct "brow" ridge running posteroventrally from the posterodorsal corner of the orbit to the anterior margin of the temporal fenestra. In the lateral aspect, the postorbital bar appears obliquely oriented and ventrally expanded, not quite as expanded as the condition seen in *Aelurognathus* (Kammerer 2016), but more expanded than the condition seen in *Cyonosaurus* (Olson 1937). The ventral ramus of the postorbital constricts abruptly at about the mid-height of the temporal fenestra, causing the temporal fenestra to appear oblong in this area. In dorsal view, the postorbital constricts further as it braces the postfrontal forming the outer wall of the temporal fenestra, and runs adjacent to the parietal, terminating at the level of the dorsal occiput. Strongly interdigitated sutures with the squamosal are visible in lateral view at the posterodorsal edge of the temporal fenestra.

The interfrontal suture is interrupted by the preparietal (Fig. 2A, B) which is a relatively small, longer than wide, and vaguely diamond-shaped element. This condition is narrower than both the spade-like shape found in NHCC LB178 and the rectangular condition in *L. ornatus* (Colbert 1948: fig. 1; Levy 2023: fig. 6), but is similar to that of AMNH FARB 5537. Additionally, it is wider than what is seen in *Arctops umulunshi*, which possesses a narrow slit-like preparietal morphology (Mann and Sidor: fig. 4A).

The parietal (Fig. 2A, B) is centrally concave, and the posterior processes are convex and curved ventrally to be slightly visible in the occipital view (Fig. 3). The parietal contacts the squamosal posteroventrally, the tabular posteromedially, and the postorbital laterally, wedging between the three bones. A medial process of the parietal appears to cut into the shape of the tabular, making the parietal appear butterfly-shaped in the occipital view. The pineal foramen is present (Fig. 2A, B), though the pineal boss is overprepared, with a ring of relatively flat bone likely representing the remnants of the boss.

Overall, the subtemporal bar is significantly ventrally deflected, displaying an angle greater than 45 degrees from the long axis of the skull. This is similar to what is observed in NHCC LB178 (Levy 2023: fig. 6), but cannot be compared to AMNH FARB 2240 due to deformation. The squamosal is both ventrally and laterally deflected (Fig. 1A, B). The ventral portion of the squamosal is well-rounded and the squamosal sulcus is visible in lateral view and is a smooth, concave groove at the posterior margin of the squamosal. These both closely resemble what is seen in *Arctops umulunshi* (Mann and Sidor in press: fig. 2A). Similar to *Lycaenops ornatus* (Colbert 1948: fig. 1), the anteriorly directed, rounded zygomatic process of the squamosal wedges into the posterior margin of the jugal, where it forms a double-scarf joint with the latter. The suture between the squamosal and paroccipital process forms a raised ridge with a recessed portion of the squamosal abutting it laterally. Adjacent to the suture with the paroccipital process is a deep inset groove, oriented dorsoventrally. The right squamosal has been highly compressed and the lateral flange of the squamosal has been flattened medially towards the temporal fenestra. This form of taphonomic distortion of the squamosal and temporal fenestra region is common amongst gorgonopsian fossils that have been laterally compressed during preservation.

The tabular is visible in the occipital view (Fig. 3) and well-preserved on the right side, while the left-side is covered in matrix. It is irregularly-shaped compared to what is found in other species of *Lycaenops* (e.g., *L. ornatus*, Colbert 1948: fig. 3; NHCC LB178, Levy 2023: fig. 6), with its dorsal edge tapering to a tip that extends onto the

parietal. It is less broad than the squamosal and it borders the postparietal medially and the parietal dorsally.

The occiput is nearly as tall as it is wide (Fig. 3). The postparietal is partially covered in matrix, though the suture with the tabular is visible in occipital and dorsal views. The postparietal is inferred as quite wide and box-like in shape. This configuration of a nearly square occiput and wide postparietal is similarly seen in *Lycaenops ornatus* (Colbert 1948: fig. 3)

The braincase is narrow and elongated in ventral view (Fig. 2C, D) similar to the condition seen in other *Lycaenops* species (e.g., *L. ornatus*, Colbert 1948: fig. 1). In posterior view, the paroccipital processes of the opisthotic (Fig. 3) are large and subtriangular, the lateral aspect points ventrally more drastically than *Aelurognathus tigriceps*, but has a higher dorsal point than *Lycaenops ornatus* (Colbert 1948: fig. 3; Kammerer 2016: fig. 2). Along the lateral aspects, the paroccipital process sutures with the squamosal. Dorsal to the paroccipital process is the post-temporal foramen. The paroccipital processes contacts the parabasisphenoid ventrally. The parasphenoid region possesses an elongate parasphenoid rostrum, whose lateral edges are mostly covered in matrix. The ventral surface of the parabasisphenoid displays two massive and elongated basal tubera with a strong medial depression between the two. The parabasisphenoid looks similar to what is observed in the majority of non-rubidgine gorgonopsians (Sigogneau-Russell 1989). The basioccipital condyle is a large, round, strongly-pronounced protuberance. Towards the left side the basioccipital is dorsally bordered by a thickened bone that may represent part of the supraoccipital and a compressed element that may be the left exoccipital (Fig. 3). Aside from the aforementioned, the majority of the supraoccipital is covered by matrix, but based on the presence of surrounding bones, the supraoccipital appears to be narrow. On the right side, the exoccipital is mostly covered in matrix, however, it is visible bordering the basioccipital condyle as tubular protrusions.

The foramen magnum is visible; however, it is slightly obscured by matrix. The ventral portion below the dentary of this specimen remains largely unprepared obscuring the pterygoid and the palate. However, the relatively long and narrow morphology of the snout and dentary of FMNH UC 1513, similar to what is seen in other *Lycaenops* species (e.g., *L. ornatus*, Colbert 1948), is suggestive of a similarly elongate and narrow palatal morphology.

Mandible: Both left and right mandibles (Fig. 1) are well-preserved and visible on both sides; however, the left mandible is much better preserved, showing a well-preserved dentary. Overall, the mandible of FMNH UC 1513 is deep, elongate, and robust compared to other *Lycaenops* species (Colbert 1948; Sigogneau-Russell 1989). It is complementary to the snout. Similar to virtually all gorgonopsians, the dentary is roughly sigmoidal in shape when viewed laterally and bears a posteriorly directed mandibular protuberance at the symphysis (Sigogneau-Russell 1989; Kammerer, 2016). The dentary is thick and tall with an expanded symphysis that is equivalent in height to the snout. Neither side preserves any visible mandibular dentition, however, the left anterior end of the dentary, at the diastema between the maxillary canine and I5, there is a distinctive lateral expansion that partially serves to accommodate the large dentary canine tooth root. Posterior to the lateral expansion there is a rounded groove to accommodate the enlarged maxillary canine that smoothly attenuates into the rest of the posterior position of the dentary.

Lycaenops sp. indet.

Material: AMNH FARB 5537, a laterally compressed skull with mandible.

Horizon and Locality: upper Permian, *Cistecephalus* AZ, Wilgersbosch, New Bethesda, Graaff-Reinet, Eastern Cape, South Africa. Collected by Robert Broom.

Potentially Referrable Material: A skull with limited postcranial fragments, AMNH FARB 5535 (type specimen of *Scymnognathus minor*, Broom 1915), *Cistecephalus* AZ, New Bethesda, South Africa. Note this skull is also highly over-prepared and its utility as a voucher specimen is limited.

Comments: At present we are unable to provide an adequate diagnosis to support the identity of AMNH FARB 5537. Due to a lack of diagnostic features, we recognize '*Lycaenops angusticeps*' as a nomen dubium (see Discussion). Extreme preparation has damaged the surface of the skull beyond the level of recognition for much of the original anatomy. Though it is overprepared, it retains some of the defining characters for *Lycaenops* including a jugal that is short below the postorbital bar, postfrontal invades the parietal border, 4 postcanines, and a long snout.

Description

Preservation: The skull is mostly complete and the left side of the skull (Fig. 4A, B) is far better preserved than the right side (Fig. 4C, D), where the matrix obstructs most of the temporal fenestra. In addition, distortion to the skull is far more evident on the left side where the jaw has been compressed towards the zygomatic region of the cranium. Both sides suffer from lateral compression making the skull appear very narrow when viewed dorsally and ventrally (Fig. 5). In addition, the skull has been severely over-prepared in certain areas, leaving large gashes, surfaces that have been ground flat and smaller scars, indicating many areas around the cranial opening and margins have been shaved down from their original morphology. The over-preparation is

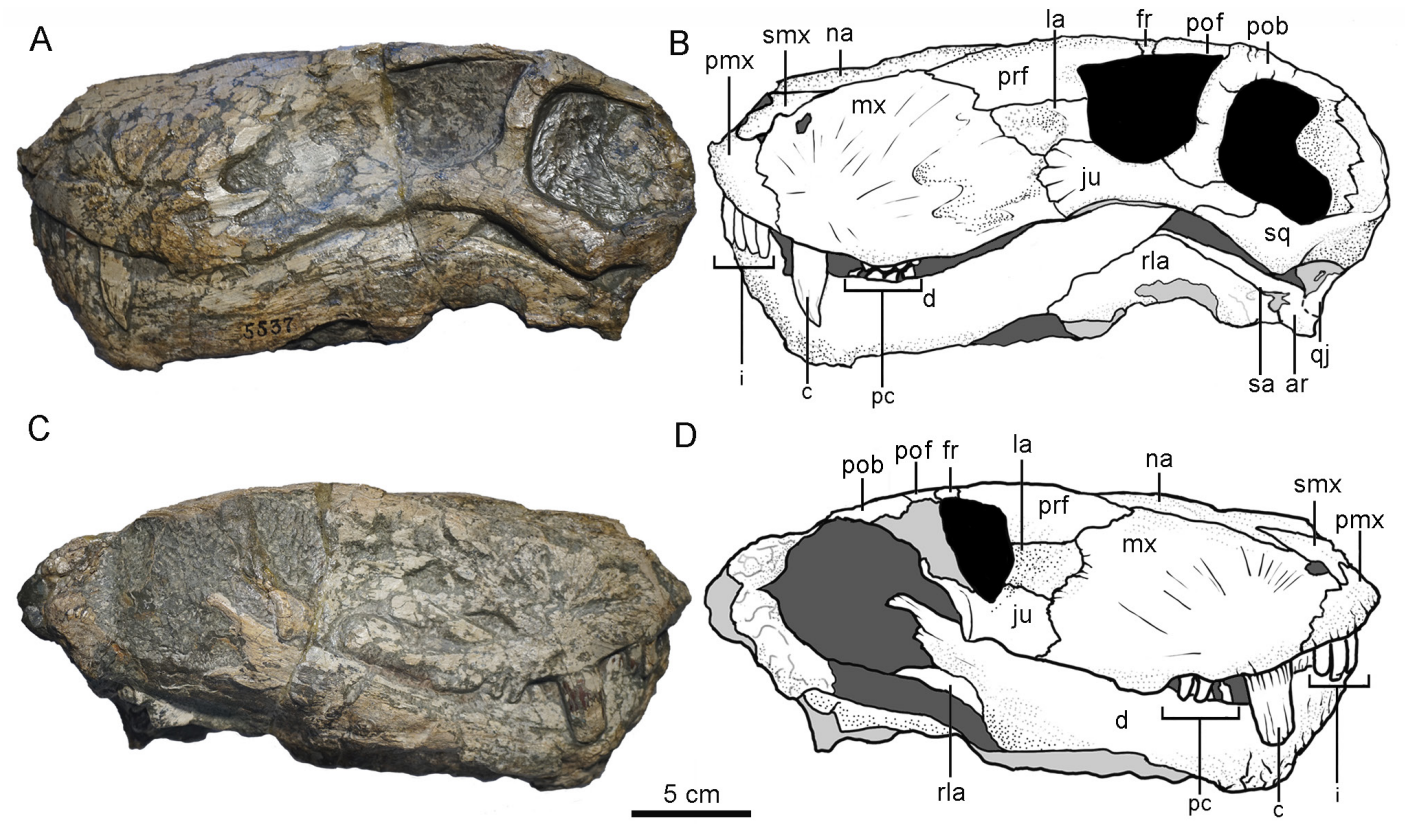

Figure 4. Cranium of *Lycaenops angusticeps*, AMNH FARB 5537. A, photograph of right side of skull in lateral view; B, line drawing of right side of skull in lateral view; C, photograph of left side of skull in lateral view; D, line drawing of left side of skull in lateral view. In the illustrations, black indicates natural skull openings, dark grey indicates matrix, and light grey indicates out of view sections of the skull. Abbreviations: ar, articular; c, upper canine; d, dentary; fr, frontal; i, incisor; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pc, postcanine; pmx, premaxilla; pob, postorbital; pof, postfrontal; prf, prefrontral; qj, quadratojugal; rla, reflected lamina; sa, surangular; smx, septomaxilla; sq, squamosal.

most conspicuous on the dorsal surface of the skull where the dorsal surfaces, including all cranial ornamentation of the postorbital, frontals, prefrontals, and nasals have been shaved off, leaving smooth surfaces with shallow grooves left from preparation equipment. The temporal fenestrae appear to be weathered posteriorly, and the anterior end of the snout also appears to be highly worn, not preserving the ascending process of the premaxilla. Ventrally, the specimen reveals a mostly complete braincase, though the parasphenoid rostrum and most of the palate anterior to the braincase are unprepared, being covered by a thick layer of matrix.

Cranium: The snout of AMNH FARB 5537 is elongate and anteroventrally sloping. Under the left orbit the ventral margin of the snout curves anteroventrally until the postcanines where it curves dorsally towards the incisors (Fig. 4A). This is the condition that appears in all gorgonopsians (Sigogneau-Russell 1989) but more closely resembles the gradual slope present in *Lycaenops* species (e.g., *L. ornatus*, Colbert 1948). The anterior end of the snout is poorly preserved, with most of the premaxilla and part of the septomaxilla missing. Preparation of the snout has severely altered the appearance of the specimen, where the tooth-bearing portions of the premaxilla, and the dorsolateral portions of the nasal have been sheared off. Despite this, the morphology of the snout is mostly complete on both sides including the anterior orbital bones, maxillae, nasals, premaxillae, and septomaxillae. All the elements are far better preserved on the left side. Thus, paired elements will be described primarily using the left side.

The prefrontals have been sheared flat on the lateral (Fig. 4) and dorsal (Fig. 5) surfaces by over-preparation. They are significantly raised compared to the surrounding bone and show evidence of some pachyostosis. The prefrontal is highly elongate, and sub-rectangular in shape, with an anterior pointed projection that meets the maxilla-nasal suture. This anterior projection of the prefrontal is slightly lower than that of FMNH UC 1513, in which the process is located above the nasal-maxillary suture. A second, much smaller anterior projection lies directly anterodorsal to the prefrontal-lacrimal contact and extends onto the maxilla. The prefrontal is also quite narrow dorsally, even accounting for the alteration and taphonomic distortion.

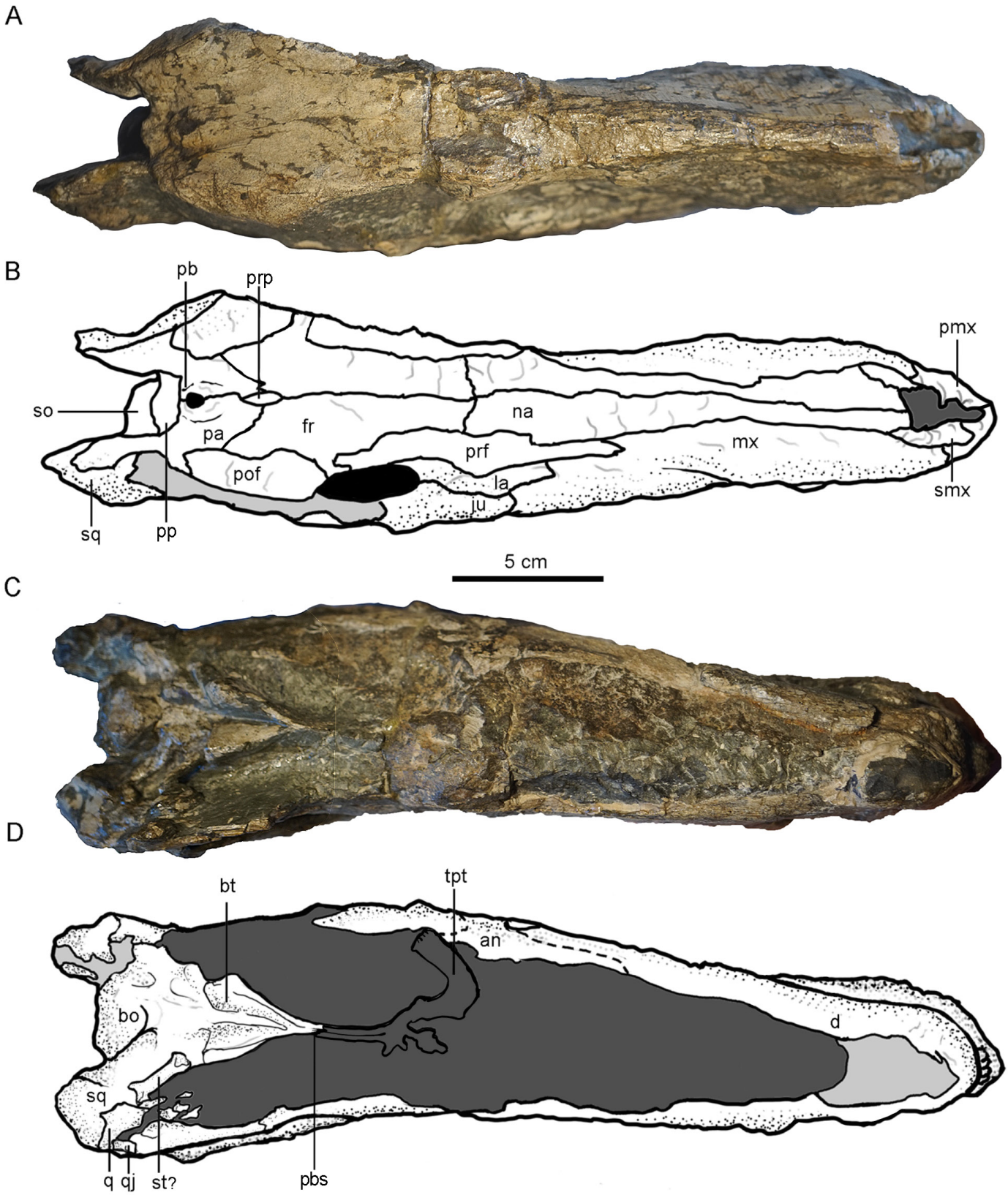

Figure 5. Cranium of *Lycaenops angusticeps*, AMNH FARB 5537. A, photograph in dorsal view; B, line drawing in dorsal view; C, photograph in ventral view; D, line drawing in ventral view. In the illustrations, black indicates natural skull openings, dark grey indicates matrix, and light grey indicates out of view sections of the skull. Abbreviations: an, angular; bo, basioccipital; bt, basal tuber; d, dentary; fr, frontal; ju, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pbs, parabasisphenoid; pmx, premaxilla; pof, postfrontal; pp, postparietal; prf, prefrontral; prp, preparietal; q, quadrate; qj, quadratojugal; smx, septo-maxilla; so, supraoccipital; sq, squamosal; st, stapes; tpt, transverse process of pterygoid.

The lacrimal is a sub-rectangular bone located ventral to the prefrontal (Fig. 4). It is poorly preserved on both sides. Its concave lateral surface represents the deepest portion of the antorbital depression as with most gorgonopsians (Sigogneau-Russell 1989; Kammerer 2016) though the degree of depression on this skull is likely exaggerated due to overpreparation. The posterior portion of this bone contributes to the anterior margin of the orbit and is slightly raised forming part of a small pachyostosed ring around the orbit that continues through the jugal.

The anterior portion of the jugal lies just below the lacrimal, and flares laterally outward towards the ventral margin of the cranium (Fig. 4). The antorbital depression smoothly attenuates within this region; thus the jugal is slightly concave dorsomedially as in most gorgonopsians (Sigogneau-Russell 1989). The anterior aspect of the jugal contact the maxilla slightly posterior to the lacrimal-maxilla contact. Similar to the other *Lycaenops* species (e.g., *L. ornatus*, Colbert 1948), the jugal under the postorbital bar is rather gracile and, in the case of AMNH FARB 5537, it is particularly dorsoventrally compressed. The posterior border of the jugal forms a scarf joint with the squamosal.

The maxilla is a large bone that bears the canine and the four postcanines and often laterally overlaps the premaxilla dorsal to the root of the posterior most incisor (Fig. 4A, B). The bone is relatively deep, and elongate. The lateral face of the maxilla is poorly preserved. It appears to be swollen around the root of the canine, making the surface convex. The four postcanines are separated from the canine by a distinct diastema, and are located at the peak of the convex ventral margin of the maxilla. Although obscured by preparations, the posterior process of the maxilla, which usually wedges under the jugal to at least the middle of the orbit in *Lycaenops* (e.g., *L. ornatus*, Colbert 1948), appears to terminate at the middle of the postorbital bar. Similarly, the anterior margin of the maxilla is also obscured, particularly on the left side. The maxilla is ornamented with a shallow radial groove pattern and the weathered remnants of small pits, which may represent the exposed maxillary nerve canals.

The septomaxilla is a narrow, elongated, irregular bone that is surrounded by the premaxilla, nasal and the maxilla (Fig. 4). The bone is roughly cleaver shaped with the long axis of the facial process extending to a point that wedges between the nasal and maxilla at an angle similar to other non-rubidgine gorgonopsians (Colbert 1948; Sigogneau-Russell 1989). The anterior margin of the septomaxilla forms the posterior portion of the external naris. Ventrally along the suture with the maxilla there is the roughly oval septomaxillary foramen. In addition, the transverse lamina of the septomaxilla is not preserved on either side, though the base of this process can still be distinguished on the left side.

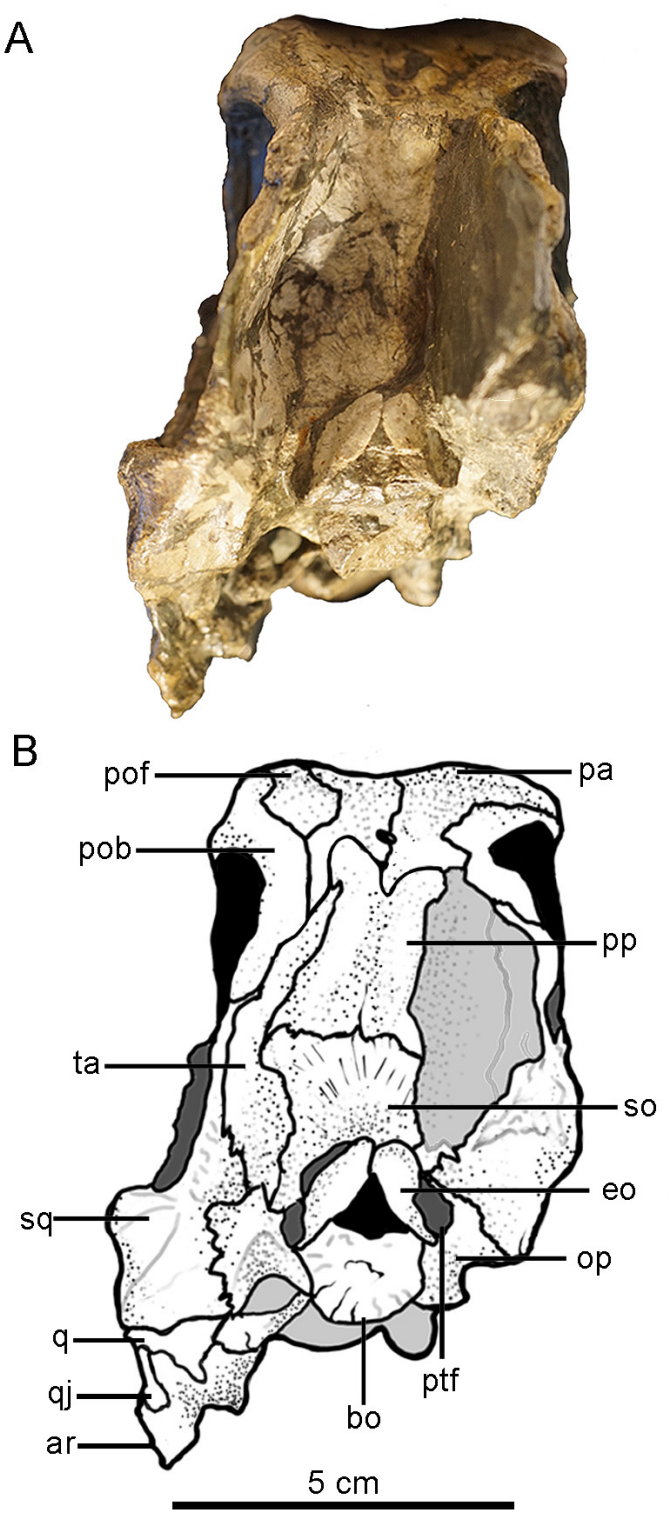

Figure 6. Occiput of *Lycaenops angusticeps*, AMNH FARB 5537. A, photograph in occipital view; B, line drawing in occipital view. In the illustrations, black indicates natural skull openings, dark grey indicates matrix, and light grey indicates out of view sections of the skull. Abbreviations: ar, articular; bo, basioccipital; eo, exoccipital; op, opisthotic; pa, parietal; pob, postorbital; pof, postfrontal; pp, postparietal; ptf, post-temporal foramen; q, quadrate; qj, quadratojugal; so, supraoccipital; sq, squamosal; ta, tabular.

Both premaxillae are present on either side of the specimen (Fig. 4) and are highly taphonomically distorted or crushed. The tooth-bearing surface appears to have been sheared off, leaving only a flat surface. A posteroventrally sloping premaxilla-maxillary suture is visible to various degrees on both sides of the skull. Both ascending processes of the premaxilla that divide the nares into lateral compartments are mostly not preserved.

Both flat, plate-like nasals are preserved (Figs. 4, 5). The nasals are narrow posteriorly and widen anteriorly towards the nares. The shape is generally similar to that of *L. ornatus* despite being highly elongated (Colbert 1948). The anterior process of the prefrontal of FMNH UC 1513 angles medially and bifurcates the nasal, whereas in AMNH FARB 5537 it is leaned laterally into the maxilla (Figs. 2, 5). The dorsal surface of the nasal is not well preserved, particularly the contact with the frontals. Although highly worn, it is likely that dorsally the snout narrowed similar to other specimens of *Lycaenops* (e.g., *L. ornatus*, Colbert 1948).

The dentition of AMNH FARB 5537 has been largely ground away, leaving only the tooth roots. The upper dentition of AMNH FARB 5537 is (I5-C1-PC4) with only four incisors present on the left and three on the right, the canine on each side present, and four postcanines roots present on the left, and only two teeth in place on the right. The dentition of '*L. angusticeps*' has previously been described as possessing four postcanine teeth, however, while four large postcanine roots are visible, the last tooth position appears to have two roots in place on the same level and posteriorly angled. This is best interpreted as a replacement tooth as it occupies the same tooth position. We note that this area is severely over-prepared which makes diagnosing the condition in this specimen, the holotype, unreliable. Until further specimens attributable to '*L. angusticeps*' are re-examined, the exact postcanine tooth count of this species will remain uncertain.

The canine has been damaged by mechanical preparation where it appears to have been shaved flat and had the serration worn away. The canine on the right, although fragmentary, is much better preserved, showing a more robust morphology compared to *L. ornatus* (Colbert 1948: fig. 1), and similar to FMNH UC 1513. The canine is separated from the incisors and post canines by a diastema on each side of the canine.

The paired, subrectangular frontals of AMNH FARB 5537 were ground down during preparation (Fig. 5A, B). The frontals are relatively flat and plate-like, aside from small bumps that may be the remnants of an interorbital ridge. The frontals have long anterior projections and short lateral projections that contribute slightly to the dorsal portion of the orbit. The overall shape is similar to what is seen in other non-rubidgine gorgonopsians, but the more posterior placement of the lateral projection is most akin to *Lycaenops ornatus* (Colbert 1948: fig. 2). The interfrontal suture appears relatively straight and not interdigitated, though this may be caused by over-preparation. Posteriorly, the frontals are separated by a median anterior projection of the preparietal. The frontal-parietal suture is strongly interdigitated.

The preparietal of AMNH FARB 5537 is a small unpaired element that is ovular to somewhat diamond-shaped in outline (Fig. 5A, B). It is located at the center of the dorsal surface of the cranium between the frontal and the parietal, and is significantly smaller than that of *L. ornatus*, and even slightly smaller than FMNH UC 1513 (Colbert 1948: fig. 1). It does not reach the pineal boss unlike the condition present in *L. ornatus* and NHCC LB178. In the closely related (see phylogenetic results) *Arctops* and *Smilesaurus*, the preparietal appears to be reduced or absent respectively; it is possible this is related to the larger size of these individuals (Kammerer 2016; Mann and Sidor in press).

The parietals are paired irregular shaped bones (Fig. 5A, B). They are highly distorted by lateral compression and weathered posteriorly, leaving the bone incomplete. Both parietals are long and the anterolateral border of each is invaded by the postfrontal similar to other species of *Lycaenops* (Colbert 1948: fig. 2; Sigogneau-Russell 1989). The parietals are interrupted by the remnants of what would have been the pineal boss, which appears to have been ground down during preparation. Posterior to this pineal boss there is the remnant of a slight nuchal ridge. The posterior processes of the parietals are poorly preserved but appear to elongate and wedge between the postorbital and tabular posteroventrally.

The postfrontals are elongate and reniform or subtriangular similar to FMNH UC 1513. They are widest anteriorly where they form the posterodorsal border of the orbit. They curve medially away from the orbit and reduce in size to a rounded point at their posterior extent, which invades the anterolateral border of the parietal.

The postorbital is best preserved on the left side (Fig. 4A, B); it remains largely unprepared and broken on the right side (Fig. 4C, D). The left side has also been slightly over-prepared, most notably on the posterodorsal corner of the orbit and slightly around the edges of the postorbital bar. The posterior process of the postorbital is present and well-preserved, contributing to the dorsal wall of the temporal fenestra and terminating at the contact with the squamosal and tabular. The postorbital bar is quite gracile, even accounting for the over-preparation. It closely resembles the condition found in *L. ornatus*, and contrasts the robust postorbital bar found in FMNH UC 1513, which is significantly expanded along its ventral contact with the jugal (Colbert 1948: fig. 1).

Similarly, the jugal of AMNH FARB 5537 is weakly ex-

panded dorsoventrally under the orbit and postorbital bar (Fig. 4). The specimen has been over-prepared in this area on the left side and likely under-prepared on the right side, though this is not enough to account for the weak dorsoventral expansion compared to FMNH UC 1513. The condition in AMNH FARB 5537 more closely resembles the species *L. ornatus* in this regard. The jugal and zygomatic process of the squamosal comprise the subtemporal bar, which appears to be moderately deflected similar to that of *L. ornatus* (Colbert 1948: fig. 2).

The squamosal is much better preserved on the left side (Fig 4C, D) although again it is over-prepared (Fig. 4A, B). The zygomatic process is rounded and terminates under the temporal fenestra similar to what is seen in most gorgonopsians (Sigogneau-Russell 1989; Kammerer 2016). Although highly worn, there is a lateral squamosal ridge that extends anterolaterally from the posterior-most corner of the temporal fenestra on to the subtemporal bar. The squamosal portion of the subtemporal bar appears to be slightly dorsoventrally expanded compared to *L. ornatus* but not as broad as in FMNH UC 1513 (Colbert 1948: fig. 1); however, this may be a result of the poor state of preservation in this area. The temporal fenestra region is quite poorly preserved though the contact with the postorbitals appears to be well preserved near the postero-dorsal corner.

The lateral compression suffered by the skull is most noticeable in occipital view (Fig. 6). The bones of this region have been highly compressed making them appear very narrow. In addition, the right side of the occiput has been heavily abraded leaving, for the most part, only the negative impression of the original bone. In general, the occiput appears quite tall, similar to other *Lycaenops* species (e.g., *L. ornatus*, Colbert 1948), and was likely equally as wide in its undistorted form.

The tabulars are normally paired, irregularly-shaped bones; however, on this specimen, only the left tabular is present (Fig. 6). It is elongated, crescent-shaped, and bordered medially by the postparietal and the supraoccipital, laterally by the postorbital and the squamosal, and ventrally by the opisthotic. At its dorsal extent, the tabular tapers to a tip that encroaches on the lateral border of the postparietal. Compared to other gorgonopsians, the tabular is remarkably narrow, even lacking the wider base present in specimens like FMNH UC 1513 and *Aelurognathus tigriceps* (Kammerer 2016), though this may be due to the severe lateral compression of the skull.

The unpaired butterfly or dumbbell shaped postparietal is also distorted and partially worn on the right side (Fig. 6). Its shape is similar to that in all gorgonopsians (Sigogneau-Russell 1989; Kammerer 2016), though in this specimen the postparietal is taller than it is wide which may, again, be attributed to lateral compression. A small process of the parietal cuts into the dorsal margin. There also appears to be a slight nuchal ridge running dorsoventrally through the middle of the bone.

Ventral to the postparietal, the supraoccipital is compressed and worn on the right side. As in most non-rubidgine gorgonopsians (Sigogneau-Russell 1989; Mann and Sidor in press) the supraoccipital appears slightly wider than tall (Fig. 6). Ventral to the supraoccipital there are highly worn, paired elements that represent the exoccipitals, that have been displaced medially towards the foramen magnum due to lateral compression of the skull. Normally, the exoccipitals contribute to the lateral margins of the foramen magnum; however, this displacement creates the illusion that they make up the anterior margins as well. The basioccipital of AMNH FARB 5537 forms the ventral portion of the foramen magnum. While usually forming a large reniform occipital condyle it is highly worn posteriorly, and its morphology is obscured.

Adjacent to the basioccipital, both well-preserved paroccipital processes expand laterally and narrow medially, as in most gorgonopsians (Sigogneau-Russell 1989). The processes connect the central braincase area to the squamosal and part of the tabular. Its suture with the squamosal lies on a slightly raised ridge that forms the medial margin of a small crevasse. This is similar, but less extreme than that of FMNH UC 1513. The foramen post-temporalis, which usually lies above the main body of the processes, is not visible, likely due to poor preservation.

The parabasisphenoid complex is present ventrally although slightly worn (Fig. 5C, D). Two moderately enlarged basal tubera are present on the ventral surface of the parabasisphenoid. These are slightly smaller than those present in FMNH UC 1513. The parasphenoid rostrum is elongate and blade-like, unlike the condition observed in rubidgeines gorgonopsians (Kammerer 2016).

There is possibly a left stapes preserved; however we are not confident in this identification due to the poor preservation of this element. The main body of the proposed stapes of AMNH FARB 5537 is cylindrical with a bulbous expansion on the lateral end and a bulbous dorsal process. The medial portion of the main body appears to expand to form a footplate. A stapedial foramen is not visible.

On the left side, a poorly preserved complex composed of the quadratojugal and quadrate is present. In gorgonopsians, this complex is not strongly sutured to the skull and is thus often not preserved (Kemp 1969; Kammerer 2015). These elements, housed within the squamosal recess (Bendel 2018), are generally similar to those of *L. ornatus* (Colbert 1948: fig. 1). The complex appears to be somewhat isolated from the quadrate branch of the pterygoid, likely due to the element's overall

poor preservation.

Mandible: The mandible of AMNH FARB 5537 is preserved on both sides of the skull, with the left side being more complete (Fig. 4A, B). The right side only preserves the dentary and a small portion of the angular (Fig. 4C, D). The left side preserves the dentary, surangular, articular, and angular including a large portion of the reflected lamina. In general, the dentary is elongated compared to *L. ornatus*. The dentary is also considerably thickened anteriorly at the symphysis. Although partially covered in plaster, there appears to have been a prominent mandibular protuberance forming a distinct chin similar to FMNH UC 1513. The dentary is also transversely expanded at the anterior end and possesses a small bulge that accommodates the root for the dentary canine located anterior to the maxillary canine. Due to over-preparation of the ventral margin of the maxilla and dorsal margin of the dentary, the lower dentition of the dentary is partially visible despite the preservation of the specimen with its jaw closed. Visible on each side of the dentary are four post canines, and one dentary canine. Although there are likely four dentary incisors, this cannot be confirmed due to the presence of matrix and the upper incisors obscuring this region. The majority of the main body of the dentary (posterior to symphysis) is slender and gracile, similar to *L. ornatus* (Colbert 1948: fig. 1). However, on the better preserved left dentary, the posteroventral corner is broken, exaggerating the slenderness in this area. The height of the dentary under the zygomatic region was likely slightly more expanded than *L. ornatus*, but not to the degree of FMNH UC 1513, which appears to have been massive in this region and dorsoventrally expanded throughout (Colbert 1948: fig. 1).

The preserved postdentary elements are all on the left side and include the angular with a portion of the reflected lamina, the surangular, and the articular (Fig. 4A, B). The ventral portion of the angular is absent leaving a reniform shape. Anteriorly, the angular abuts the ventral aspect of the dentary and posteriorly it abuts the ventral aspect of the surangular. The lateral surface has been worn leaving a reduced reflected lamina. What remains of the lamina suggests cruciate ornamentation as is seen in nearly all gorgonopsians. The surangular is a thin element that sits posterodorsal to the angular and is oriented anterodorsally to posteroventrally. As in most gorgonopsians, the anterior aspect of the surangular reaches the apex of the dorsal aspect of the angular to abut with the dentary. The small articular sits ventral to the surangular and posterior to the angular. It has a concave posterior border like what is seen in *Arctops umulunshi* and *Lycaenops ornatus* (Colbert 1948; Mann and Sidor in press).

DISCUSSION

Phylogenetic Analysis of Gorgonopsia Including Historical Specimens of *Lycaenops*

As detailed in the Materials and Methods section, we entered data from AMNH FARB 5537 and FMNH UC 1513 into the matrix of Mann and Sidor (in press) and ran a branch and bound parsimony analysis. The resulting 5 most parsimonious trees (MPTs) each had 120 steps (CI = 0.608; HI = 0.467; RI = 0.821; RC = 0.500). Using the strict consensus of the MPTs (Fig. 7), we recovered the gorgonopsian *Nochnitsia* in the most basal position on the tree. The slightly more derived *Viatkogorgon* is established as the sister taxon to the 'Russian' and 'African' clades of gorgonopsians. Our topology for the 'Russian' clade matches that recovered by Mann and Sidor (in press). The sister taxon to the 'Russian' clade is the 'African' clade which includes the majority of the African gorgonopsians; the noted exception being *Inostrancevia africana*. The 'African' clade is established by a basal polytomy consisting of *Phorcys dubai, Eriphostoma microdon*, and *Gorgonops torvus* and *Cynariops robustus*. The sister taxon of *Cynariops robustus* consists of two clades. The first contains *Arctognathus curvimola* and the family Rubidgeinae. The topology of this group matches what has been previously recovered (Mann and Sidor in press). The remaining taxa are recovered in a clade consisting of two sister clades. One of these includes a sister taxon relationship between *Arctops willistoni* and *Arctops umulunshi*, to the exclusion of *Smilesaurus ferox*. Sister to this grouping is a clade consisting of a polytomy which includes all species of *Lycaenops* considered in this paper (*L. ornatus*, NHCC LB178, FMNH UC 1513, and AMNH FARB 5537).

The positions of FMNH UC 1513 and AMNH FARB 5537 within the polytomy of *Lycaenops* species concurs with the previous suggestion that these specimens do in fact represent members of this genus (Sigogneau 1970; Gebauer 2007; Mann and Sidor in press). The position is supported by the short height of the jugal below the post orbital bar (character 30, state 1) and the dorsal edge of the tabular being either very broad or tapering to a tip (character 44, states 0,1; see associated nexus file).

Mann and Sidor (in press) recovered a close relationship between *Arctops*, *Smilesaurus* and *Lycaenops*, which is supported by our analysis. In addition to previous features noted by Mann and Sidor (in press), recent direct observation of the holotype, *L. ornatus*, suggests there are 2 or 3 tooth roots limited to the medial portion of the transverse flange of the pterygoid–this condition is also found in *Arctops umulunshi* (Mann and Sidor in press). While we concur with Kammerer (2016) that the dentition on the

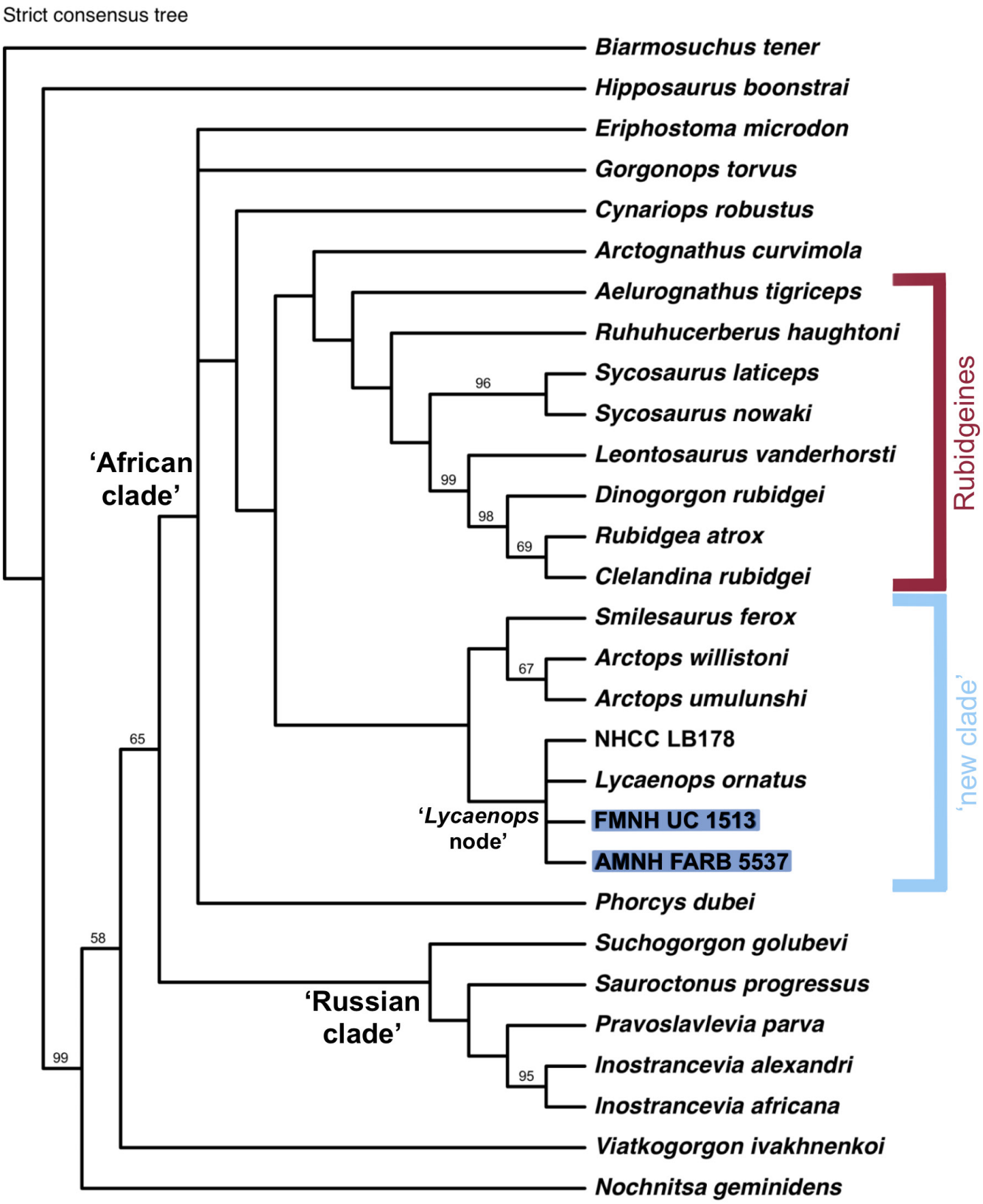

Figure 7. Strict consensus tree of the parsimony results. Bootstrap values over 50 are shown above nodes. Major clades are labelled with brackets and specimens this study have been highlighted in blue.

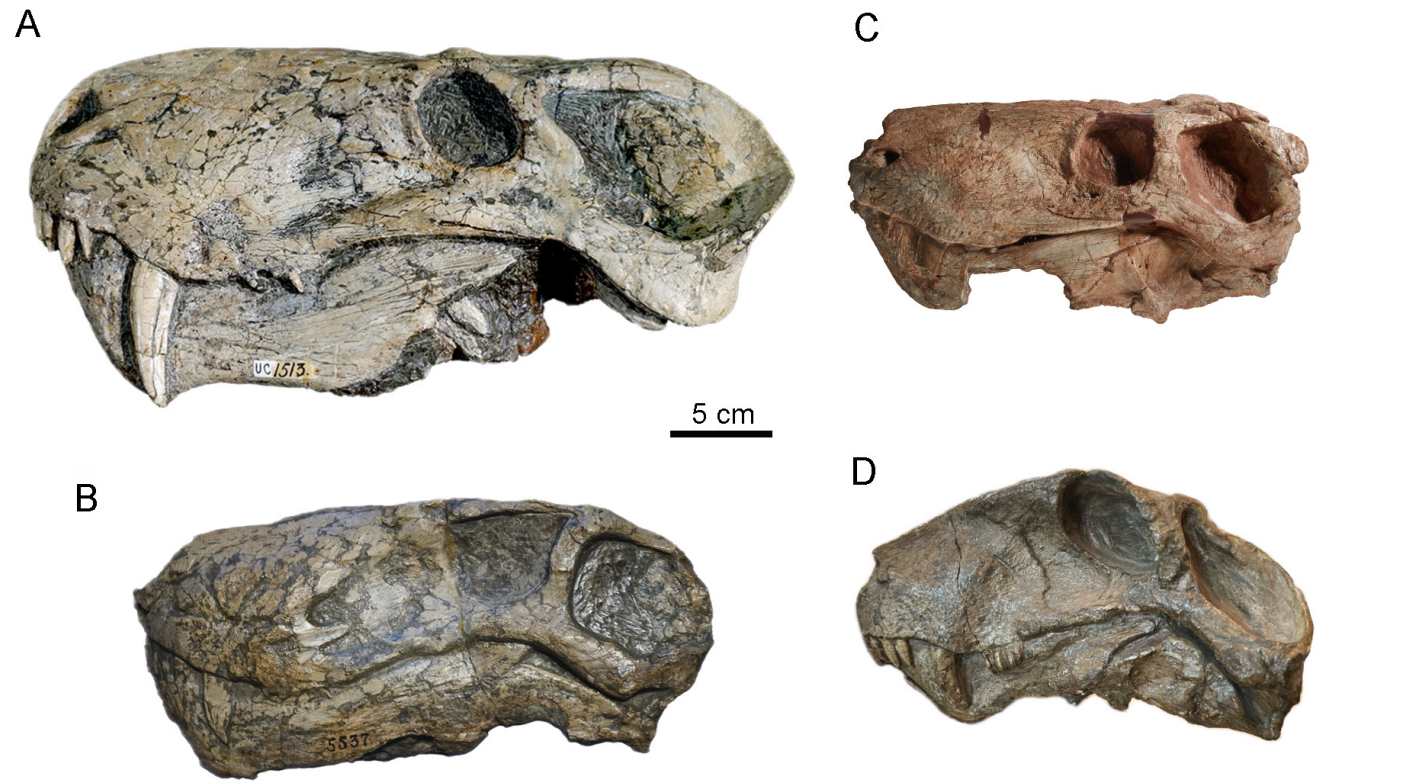

Figure 8. Lateral views of the *Lycaenops* species considered in this paper. A, FMNH UC 1513; B, AMNH FARB 5537; C, NHCC LB178; D, AMNH FARB 2240, *Lycaenops ornatus*.

transverse processes might be ontogenetically variable, ostensibly present only in immature specimens, it seems likely this could represent an intermediate condition between the extensive tooth rows that are found in earlier diverging gorgonopsians and the complete loss of dentition exhibited by more derived rubidgeines. If so, this could potentially represent an additional character shared by *Lycaenops*, *Arctops* and *Smilesaurus*.

The Status of FMNH UC 1513 and AMNH FARB 5537, and the *Lycaenops* Species Complex

The *Lycaenops* species complex was most recently reviewed more than 35 years ago by Sigogneau-Russell (1989). She recognized the genus as containing six species: *L. ornatus* (the type species), *L. angusticeps*, *L. kingwilli*, *L.* ? *microdon*, *L.* ? *minor*, and *L.* ? *tenuirostris*. Subsequently, Gebauer (2007) further revised the genus and concluded that five species were valid (*L. ornatus*, '*L. angusticeps*', *L. sollasi*, *L. attenuatus,* and *L. quadrata*). Since these revisions there have been significant advances in our understanding of gorgonopsian anatomy and phylogeny (e.g., Kammerer 2016; Kammerer 2017; Bendel et al. 2018; Kammerer and Masyutin 2018; Sidor and Mann 2023; Mann and Sidor in press), but the focus of new research has yet to be applied to *Lycaenops* beyond inclusion of the type species in phylogenetic analysis.

Many of the characters used to diagnose *Lycaenops* in these previous studies (e.g., Sigogneau-Russell 1989) are now recognized as widely distributed among non-rubidgiene gorgonopsians, and the genus can be viewed largely as a 'wastebasket taxon' including mid-sized gorgonopsians with slender skull arches and a reduced postcanine tooth count among other characters. At present, we are unable to provide a comprehensive revision to the *Lycaenops* species complex and recognize the need for further anatomical work. However, our updated descriptions and phylogenetic results provide significant clarifications on the status of the specimens evaluated in this paper.

The phylogenetic analysis we conducted resulted in an unresolved clade containing *L. ornatus*, NHCC LB178, FMNH UC 1513 and AMNH FARB 5537, supporting the placement of these specimens within the genus *Lycaenops*. Previously, Gebauer (2007) and Sigogneau (1970) reassessed AMNH FARB 5537 and FMNH UC 1513, recognizing a close relationship between these two specimens; however, since neither author was able to directly observe the latter, its assignment to '*L. angusticeps*' remained preliminary. Despite this, both specimens seemingly share a number of anatomical features including a narrow skull, elongated snout, four postcanines, and a small, diamond-shaped preparietal. While the small preparietal may seem diagnostic, this trait is highly variable in gorgonopsians, and may vary throughout ontogeny, as has been suggested in other non-mammalian therapsids, making its diagnostic value unclear (Kammerer et al. 2016).

Additionally, the snout of FMNH UC 1513 is proportionally shorter than what would be expected for a skull of its size when compared to *L. ornatus* and AMNH FARB 5537 (Fig. 8), and if it was a larger ontogimorph it does not follow the predicted longer snout proportions posited by Krone et al. (2019). Some further distinctions from the existing species of *Lycaenops* can be seen in FMNH UC 1513, including the increased height of the jugal under the orbit, a taller dentary, and a higher snout. While the overall combination of traits supports the referral of FMNH UC 1513 to *Lycaenops*, they do not support referral to the species '*L. angusticeps*' and suggest that it may be a new species under the new combination *L. major*, retaining the specific epithet from '*Scymnognathus major*' originally introduced by Olson and Broom (1937).

Furthermore, due to a combination of taphonomic deformation and severe overpreparation, AMNH FARB 5537 (the holotype of '*L. angusticeps*') is of little taxonomic utility and of little use in comparative anatomical analyses. It should therefore be considered a nomen dubium; however, until extensive taxonomic revisions to the *Lycaenops* species complex are conducted we abstain from formally assigning this designation. Many of the defining features that would be useful in diagnosing this taxon are severely damaged to a degree that make it difficult to even describe them with any certainty.

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