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New discovery of rhyncholites and conchorhynchs (cephalopod jaw elements) from the Upper Cretaceous Mount Laurel Formation of Delaware

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ABSTRACT

Rhyncholites and Conchorhynchs are the calcitic elements of upper and lower jaws of cephalopods, respectively. Rhyncholites and conchorhynchs occur in relatively high abundance and are widely distributed, with a long geological range, extending from the Triassic to the Miocene. While rhyncholites and conchorhynchs are relatively common in Europe, there are only a few reports from North America. Here, we document 24 specimens of rhyncholites and 12 specimens of conchorhynchs from the Upper Cretaceous Mount Laurel Formation in Delaware. The specimens were found in isolation and, thus, identifying the taxon to which the rhyncholites and conchorhynchs belong is difficult. However, the Cretaceous nautilid *Eutrephoceras* occurs in the same formation, suggesting that the rhyncholites and conchorhynchs may belong to this taxon. We performed a morphometric analysis of these structures based on linear measurements. Our results reveal that some morphological parameters in rhyncholites are correlated with size. Additionally, our specimens exhibit high intraspecific variation, which may have been overlooked in previous studies.

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INTRODUCTION

Rhyncholites and conchorhynchs are the calcitic elements of the upper and lower jaws of cephalopods, respectively. Nautilids (*Nautilus* and *Allonautilus*) are the only modern cephalopod taxa that possess such calcitic jaw elements because the jaw apparatus of modern coleoids (octopuses and squids) are composed of only chitin (Saunders, 1978). Rhyncholites and conchorhynchs have been reported in various geological time periods worldwide, ranging without doubt from the Triassic (MacFarlan and Campbell, 1991; Klug, 2001) to the Miocene (Sacco, 1904). While some specimens are preserved within the body chamber (Klug, 2001), such specimens are relatively rare—most are found in isolation.

Fossil rhyncholites and conchorhynchs are usually attributed to nautiloids based on their morphological similarity to those of modern nautilus. However, some researchers have found similar structures inside the body chambers of Cretaceous ammonites (Tanabe et al., 1980; Riegraf and Schmitt-Riegraf, 1995). Thus, identifying the exact taxon that isolated rhyncholite/conchorhynch specimens belong to is often difficult. Therefore, the concept of parataxonomy is usually applied when describing and classifying rhyncholites and conchorhynchs (Mironenko et al., 2022). Rhyncholite and conchorhynch fossils are relatively common, in particular in the Cretaceous of Europe (Riegraf and Schmitt-Riegraf, 1995). In contrast, there are only a few reports of rhyncholites and conchorhynchs from North America (Teichert and Spinosa, 1971; Riegraf and Luterbacher, 1989). In this paper, we document newly discovered rhyncholite and conchorhynch fossils from the Upper Cretaceous Mount Laurel Formation in Delaware. We also discuss the intra- and interspecific variation of rhyncholite morphology using our rhyncholite specimens as well as previously documented rhyncholites from the Cretaceous and Paleogene of Europe and North America, based on linear measurements.

MATERIAL AND METHODS

All examined specimens were collected from the Mount Laurel Formation near the Chesapeake and Delaware Canal in Delaware (approximately 2 km southwest of Delaware City; fig. 1A). The Mount Laurel Formation is characterized by gray to greenish red-brown, glauconitic, fine to medium quartz sand with some silt (Pickett, 1970). Discrete burrows are common throughout the formation (Houlik et al., 1983). A large number of invertebrate fossils including bivalves, gastropods, scaphopods, worm tubes, decapods, and echinoids have been reported (Groot et al., 1954; Owens et al., 1970; Pickett, 1972; Sohl, 1977; Kennedy and Cobban, 1997). Although ammonites are relatively uncommon in the Mount Laurel Formation (Lauginiger, 1988), an increasing number of ammonites have been recently documented (Lauginiger, 1988; Kennedy and Cobban, 1994; Kennedy and Cobban, 1997). Belemnites are also common in the Mount Laurel Formation (Lauginiger, 1988). Biostratigraphy using dinoflagellates and foraminifera from the lower part of the formation appears to indicate a Maastrichtian age (Houlik et al., 1983) whereas ammonites indicate a late Campanian age (Kennedy and Cobban, 1994; Kennedy and Cobban, 1997; for details see Kennedy and Cobban, 1994). The upper part of the formation lacks microfossils according to Houlik et al. (1983). To our knowledge, nautilid fossils have never been documented from the Mount Laurel Formation.

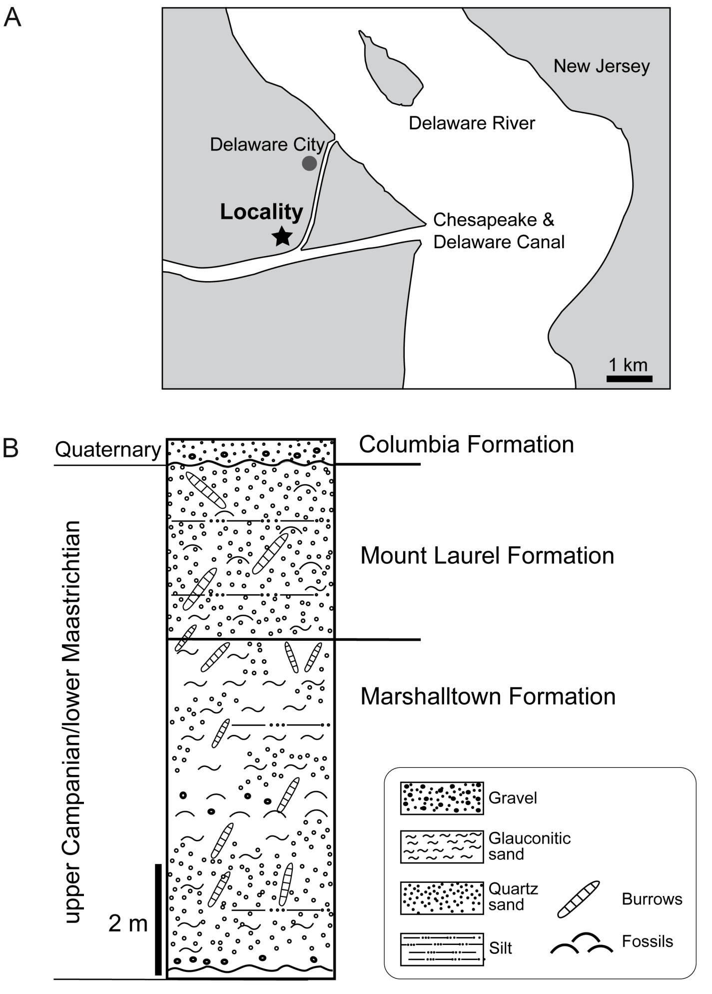


FIGURE 1. Locality and stratigraphy. **A,** collection locality of rhyncholites and conchorhyncs. **B,** stratigraphic column of an adjacent locality including the Mount Laurel Formation from which our specimens were collected (modified after Kennedy and Cobban, 1994).

In total, 24 rhyncholites and 12 conchorhynchs were collected. All the fossils were isolated, and thus the exact taxonomic assignment is difficult. Therefore, we apply a parataxonomic approach, following previous studies. In addition to jaw elements, three internal molds of nautilid conchs were collected, which we also document herein. All studied specimens are housed in the American Museum of Natural History (AMNH).

We CT-scanned most of our specimens at the Industrial Research Institute of the Hokkaido Research Organization using a Microfocus X-ray CT scanner (inspeXio SMX-225CT, Shimadzu Co.) to carry out morphometrics (linear measurements) for both the rhyncholites and conchorhynchs. Some specimens were CT-scanned using a General Electric Phoenix V|tome|X-S nanotube high-resolution CT scanner at the Microscopy and Imaging Facility of the American Museum of Natural History. We used the terminology and morphological parameters introduced by Teichert et al. (1964) and Teichert and Spinosa (1971) for rhyncholites and by Mironenko et al. (2022) for conchorhynchs (fig. 2). We measured the following parameters: height of rhyncholite (H), length of rhyncholite (L), length of hood (Lh), length of shaft (Ls), width of rhyncholite (W), width of shaft (Ws), angle formed by the median keel and the ventral plane (α), angle formed by the left and right anterior hood margins (β), and the angle formed between the left and right shaft edges which circumscribe the median shaft area (δ). To compare our data to previously published data on Cretaceous and Paleogene rhyncholites, we took measurements of previously documented specimens using the figures of Fritsch and Schlönbach (1872) and Riegraf and Schmitt-Riegraf (1995). We also compiled data from Till (1909), Van Der Tuuk (1985), Komarov (2005a, 2005b), Košťák et al. (2010), and Weaver et al. (2012). Using the six parameters H, L, Lh, Ls, W, Ws, and β, we performed a principal component analysis to identify the species of our specimens. Our specimens of conchorhynchs are generally poorly preserved, and thus we measured only the maximum preserved length, width, and shaft angle (fig. 2). We also documented some nautilid conchs that cooccurred with the rhyncholites and conchorhynchs from the same locality. We measured the classical conch parameters: conch diameter (dm), whorl width (ww), whorl height (wh), and the number of septa per half whorl (for details see Tajika et al., 2020).

RESULTS

The 24 rhyncholites and 12 conchorhynchs documented in this paper are illustrated in figures 3–7. The cephalopod conchs are illustrated in figure 8. The measurements of the morphological parameters are plotted in figures 9–10. The raw data are available in the online supplement (https://doi.org/10.5531/sd.sp.57).

SYSTEMATIC PALEONTOLOGY

Class Cephalopoda Cuvier, 1797

Order Nautilida Agassiz, 1847

Genus *Rhyncolites* Faure-Biguet, 1819

Discussion: The validity of the generic name *Rhyncolites* has been discussed for decades. Riegraf and Schmitt-Riegraf (1998) argued that *Rhyncolites* Faure-Biguet, 1819, was invalid according to Article 20 of the International Code of Zoological Nomenclature based on the assumption that *Rhyncolites* was derived from the name for the genus *Rhyncolus* Germar, 1817, which is a beetle. This suggestion was accepted by some authors (e.g., Klug, 2001; Košťák et al., 2010). However, there is no clear evidence that Faure-Biguet (1819) named the genus after the generic name of the beetle *Rhyncolus*. Thus, Article 20 is not applicable to this case in our opinion. Accordingly, we retain *Rhyncolites* Faure-Biguet, 1819 (see also Ward and Cooper, 1972).

Rhyncolites cf. *simplex* Fritsch, 1872

Figures 3–5

Rhyncholithus simplex Fritsch inFritsch and Schlönbach, 1872: 25, pl. 111, figs. 4, 5.
Rhyncolites simplex (Fritsch and Scholenbach, 1872), Riegraf and Schmitt-Riegraf, 1995; 82.
Nautilorhynchus simplex (Fritsch, 1872), Košťák et al. 2010; 421, pl. 1, figs. 1–5, 8–13, text-fig. 4 (with additional synonymy).

Type: *Rhyncholithus simplex* Fritsch in Fritsch and Schlönbach (1872: 25, pl. 111, figs. 4, 5) from the Turonian of the Czech Republic.

Material: Twenty-four specimens (AMNH 137104–137122, AMNH 137124–137128) from the Mount Laurel Formation, Delaware.

Description: All specimens are arrow-shaped. The rhomb-shaped hood possesses a vertical ventral ridge in the middle. The bottom part of the hood is often eroded. The shaft is much narrower than the hood. The bottom part of the shaft is often eroded. The dorsal part is generally flat with a vertical ridge in the middle (dorsal ridge) that is either eroded or covered with sediments and thus not apparent in some specimens. Length (L) ranges from 6.7 to 9.8 mm, width (W) 4.4 to 7.4 mm, height (H) 3.2 to 5.2 mm, length of shaft (Ls) 3.0 to 5.5, width of shaft (Ws) 1.9 to 3.5 mm, length of hood 4.0 to 7.5 mm. The angle formed by the median keel and the ventral plane (α) ranges from 42° to 60°. The angle formed by the left and right anterior hood margins (β) ranges from 59° to 90°. The angle formed between the left and right shaft edges, which delineates the median shaft area (δ), ranges from 88° to 153°. Most specimens probably underwent a certain degree of erosion/abrasion/corrosion. We did not measure some morphological characters in certain specimens when they were too poorly preserved. The measurements of all specimens are available in the online supplement (https://doi.org/10.5531/sd.sp.57).

Discussion: Our specimens are smaller than the holotype of *Ryncholithus simplex* described by Fritsch (in Fritsch and Schlönbach, 1872; 6.7–9.8 mm vs. 15 mm in length). The ratio W/L is similar (0.61–0.91 vs. 0.67). However, the ratio H/L seems slightly higher in our specimens (0.39–0.63 vs. 0.40). Our specimens are also similar to those from the same region as the holotype documented by Košťák et al. (2010; figs. 9, 10). Some of the specimens documented by Košťák et al. (2010) are similar to our specimens in size. However, those specimens tend to have lower ratios of H/L and W/L. The other ratios (Ws, Ls, and Lh vs. L) of Košťák et al. (2010) and the holotype are more similar to those of our specimens (fig. 9). It is worth noting that the ontogeny of rhyncholites is poorly known. However, in the plot of species from different geological time periods shown in figure 9, there seems to be a positive linear correlation between size and some morphological parameters. The angle formed by the median keel and the ventral plane (α) is much higher in our specimens than that in the holotype of *R. simplex* (42°–60° vs. 38°). The angle formed by the left and right anterior hood margins (β) of the holotype is within the range of our specimens (59°–90° vs. 78°). The

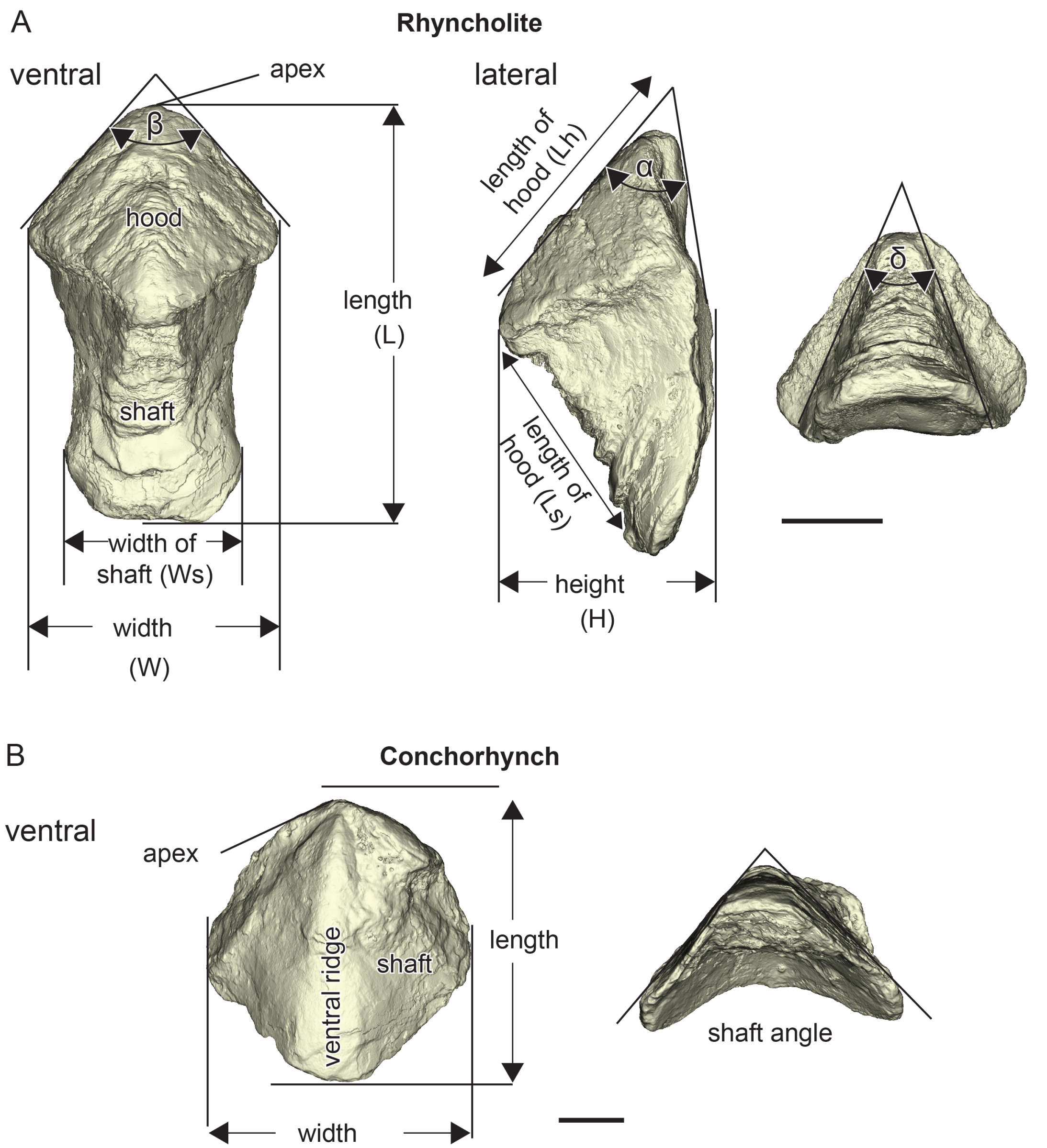
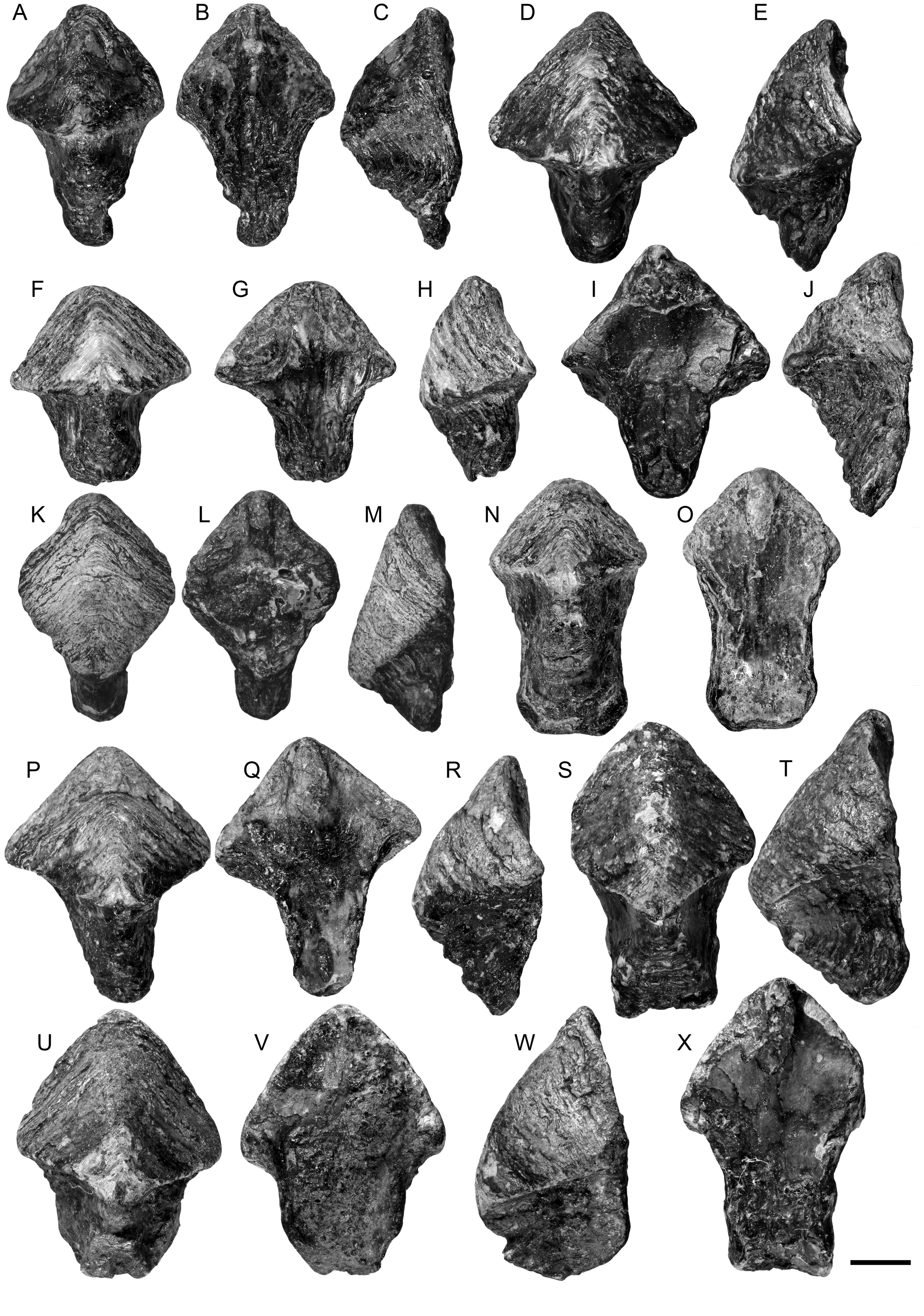


FIGURE 2. Measured morphological characters in rhyncholites and conchorhynchs. Scale bars = 2 mm.

FIGURE 3. *Rhyncolites* cf. *simplex* from the Mount Laurel Formation, Delaware. **A–C,** AMNH 137125. **D, E, I,** AMNH 137105. **F–H,** AMNH 137124. **J, N, O**, AMNH 137106. **K–M,** AMNH 137104, **P–R,** AMNH 137126, **S, T, X,** AMNH 137127, **U, V, W,** AMNH 137128. Scale bar = 2 mm.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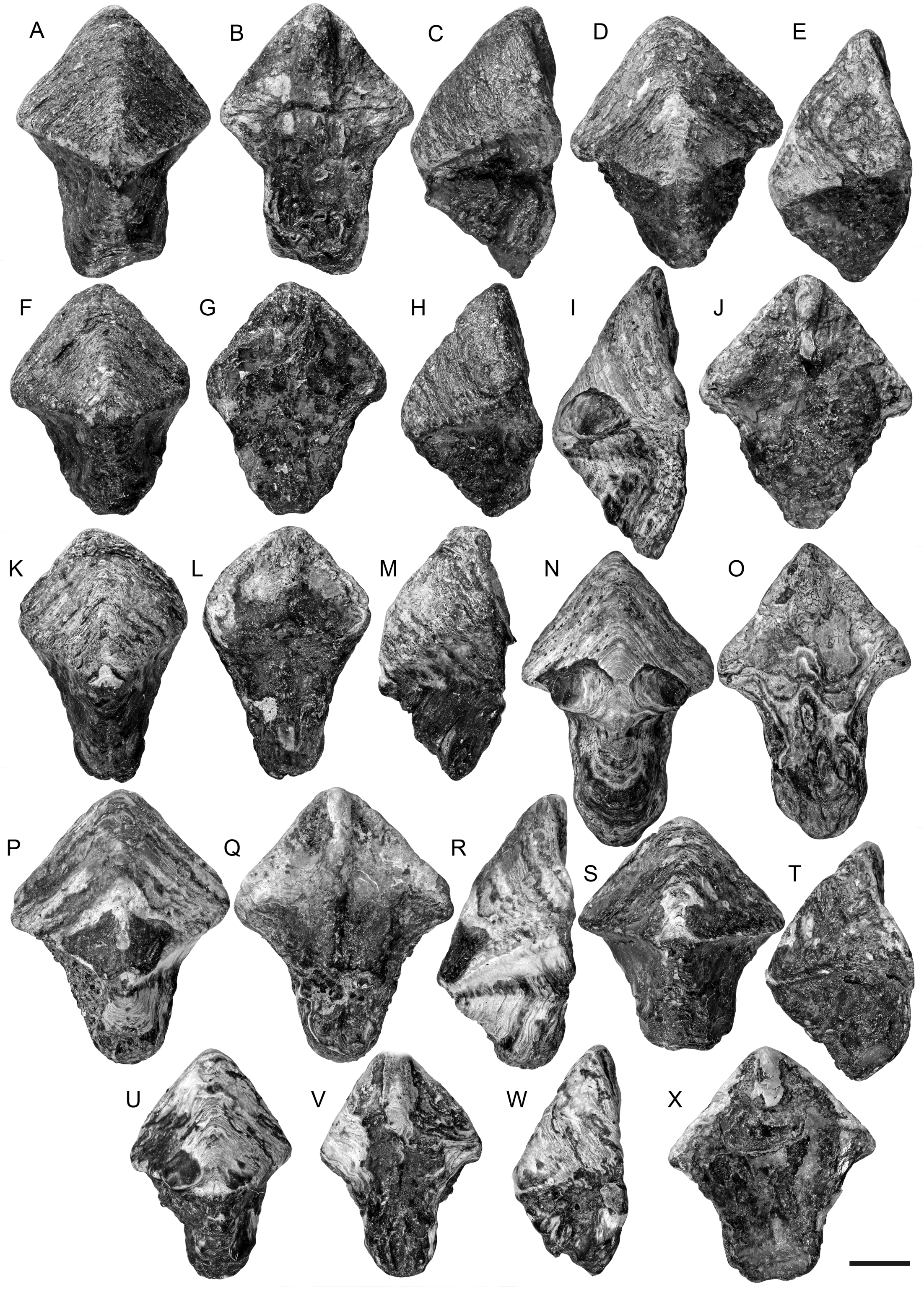
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principal component analysis using six parameters (H, L, Lh, Ls, W, Ws, and β) reveals that our specimens are comparable to *R. debeyi* illustrated by Riegraf and Schmitt-Riegraf (1995), *R.simplex* documented by Košťák et al. (2010), *R. lhommei,*and *R. sagittarius*, documented by Pacaud (2010), and *R. aethioparion* documented by Ward and Cooper (1972). The locality and age of the reported specimens of these species include the Cretaceous and Eocene of Europe and possibly North America.

Assuming that our specimens from the Mount Laurel Formation belong to a single species of *Eutrephoceras* (see *Eutrephoceras* sp. below), the intraspecific variation within them is high. Yet, it is likely that the intraspecific variation of our specimens may have slightly increased due to somewhat poor preservation. The similarity of the abovementioned rhyncholite species may be explained by high morphological variation within a single parataxon. Our morphometric analysis using the linear measurements, however, is not sensitive enough to detect subtle morphological differences and, thus, methods such as geometric morphometric analysis should be applied in future studies to better understand the evolution of rhyncholites.

Occurrence: *R. simplex* has been widely reported from the Cenomanian–Turonian of the Czech Republic, Germany, and Poland. Košťák et al. (2010) synonymized *R. curvatus* reported by Till (1907) into *R. simplex*, which extends the record to the Albian of the United Kingdom. If our specimens belong to *R. simplex*, this is the first record from the Upper Cretaceous of North America.

Genus *Conchorhynchus* de Blainville, 1827

Conchorhynchus sp.

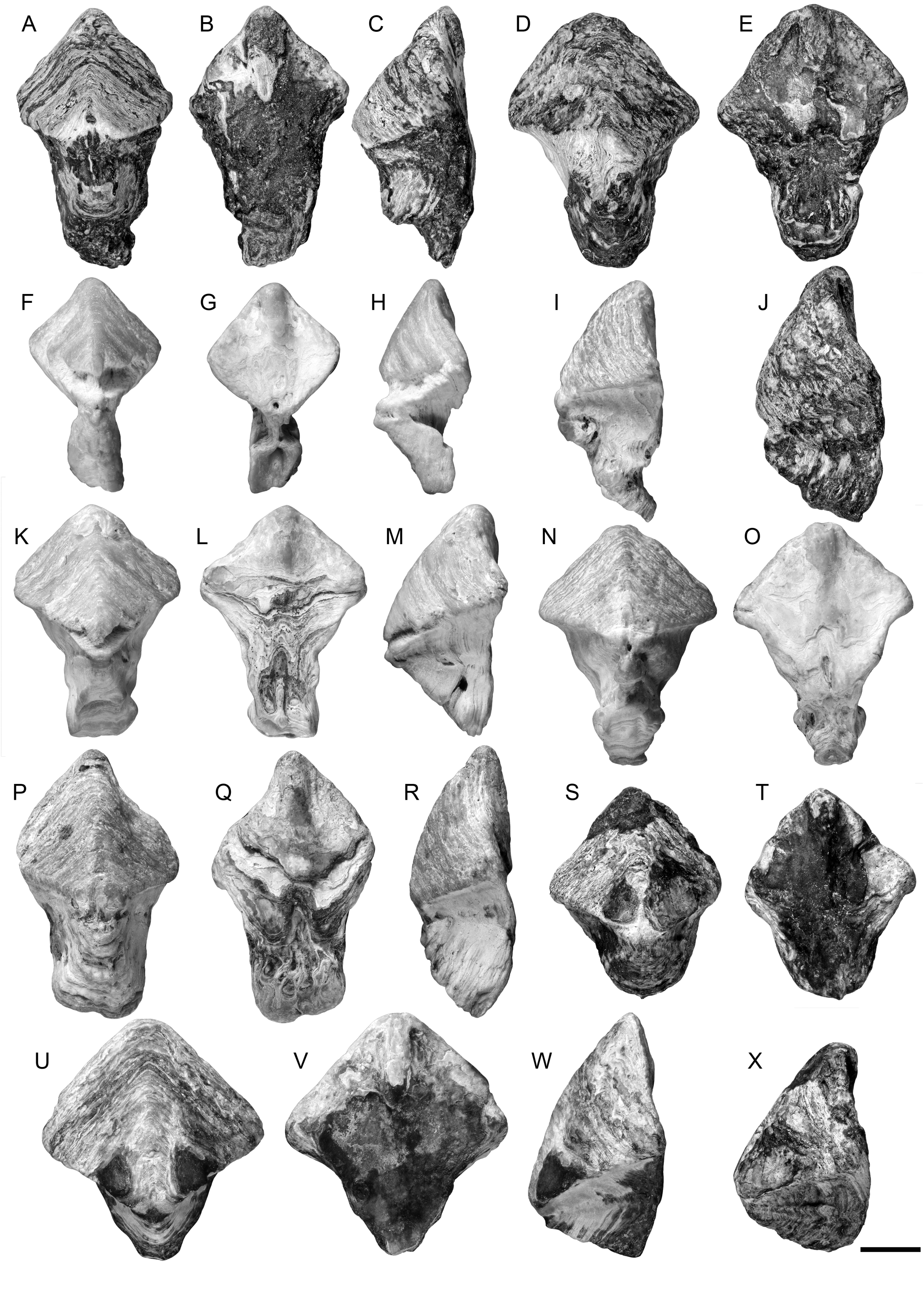
Figures 6, 7

Material: Twelve specimens (AMNH 137086, AMNH 137087, AMNH 137095–137103, AMNH 137123 from the Mount Laurel Formation of Delaware. All specimens are somewhat poorly preserved.

Description: The overall shape is unclear due to the poor preservation. The maximum preserved length and width range from 4.2 to 8.7 mm and 4.0 to 8.2 mm, respectively. The shaft angle ranges from 68° to 90°. The hood is not visible, but the anterior edge seems slightly folded (anterior fold). There are broad and shallow grooves between the anterior edge and shaft on the ventral side. The ventral ridge is present, which widens posteriorly. The ventral ridge is often smooth, but some specimens such as AMNH 137101 and AMNH 137102 exhibit lateral grooves. The dorsal side is sometimes covered by sediments or eroded, which masks the denticle/rib pattern.

Discussion: According to Košťák et al. (2010), Mesozoic and Cenozoic conchorhynchs are morphologically conservative. They also mention that *Rhyncolites simplex* and *Conchorhynchus*

FIGURE 4. *Rhyncolites* cf. *simplex* from the Mount Laurel Formation, Delaware. **A–C,** AMNH 137107. **D, E, J,** AMNH 137108. **F–H,** AMNH 137109. **I, N, O**, AMNH 137111. **K–M,** AMNH 137110, **P–R,** AMNH 137112. **S, T, X,** AMNH 137113, **U, V, W,** AMNH 137114. Scale bar = 2 mm.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cretaceous represent the upper and lower jaws of a single nautilid species. Our specimens resemble the overall morphology of specimens of *C. cretaceous* illustrated by Fritsch (1910) and Košťák et al. (2010). However, our specimens do not possess the V-shaped groove on the ventral edge that is visible in their specimens. Some other conchorhynchs reported from the Cretaceous such as *C. limburgicus* and *C. similis* also resemble our specimens. Nevertheless, the preservation (erosion and sediment covering the dorsal side) masks fine morphological details and, therefore, hampers the precise assignment of our species.

Superfamily Nautilaceae de Blainville, 1825

Family *Nautilidae* de Blainville, 1825

Genus *Eutrephoceras* Hyatt, 1894

Eutrephoceras sp.

Figure 8

Material: Three broken phragmocones from the Mount Laurel Formation of Delaware (AMNH 137092–137094).

Description: Our specimens are subspheroconic with a rounded flank, nearly closed umbilicus, and slightly sinuous suture. No trace of ribs is visible. These features characterize *Eutrephoceras*. The specimens range from 14.6 to 20.7 mm in maximum preserved conch diameter, but are broken phragmocones. Therefore, the actual diameter/ontogenetic stage of these individuals is not determinable. The whorl section is slightly depressed (ww/wh = 1.3–1.4; ww/dm = 0.82–0.84). The number of septa per half whorl is nine (AMNH 137092). The siphuncle is not preserved. Measurements of all specimens are available in the online supplement.

Discussion: *Eutrephoceras dekayi* (Morton, 1834) is an Upper Cretaceous nautilid that has been widely reported from the Atlantic Coastal Plain including Delaware (Landman et al., 2004). The conch parameters of our specimens are similar to those of *E. dekayi* reported by Landman et al. (2018) and Tajika et al. (2020). However, a recent study on modern nautilus suggests that the juvenile specimens of closely related nautilid species may not be morphologically distinct (Tajika et al., 2021). Indeed, Landman et al. (2018) showed that the juveniles of *E. dekayi* and *E. montanaensis* exhibit a similar whorl section (ww/wh). Considering the small size (i.e., presumably representing the ontogenetic stage slightly after hatching; dm = 14.6–20.7 mm), we refrain from assigning the specimens to a species.

FIGURE 5. *Rhyncolites* cf. *simplex* from the Mount Laurel Formation, Delaware. **A–C,** AMNH 137115. **D, E, J,** AMNH 137116. **F–H,** AMNH 137117. **I, N, O**, AMNH 137118. **K–M,** AMNH 137119, **P–R,** AMNH 137120. **S, T, X,** AMNH 137121, **U, V, W,** AMNH 137122. Scale bar = 2 mm.

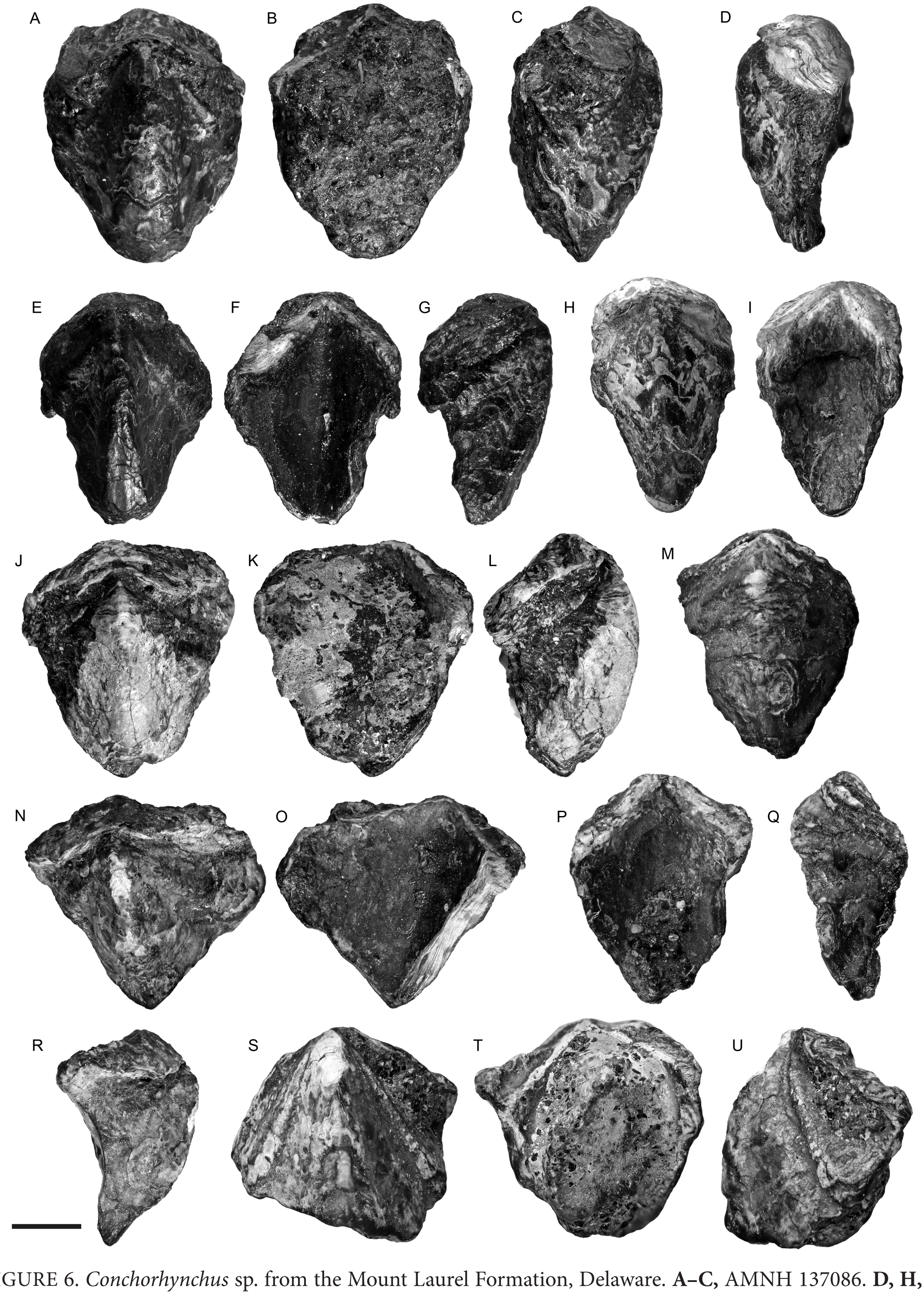


FIGURE 6. *Conchorhynchus* sp. from the Mount Laurel Formation, Delaware. **A–C,** AMNH 137086. **D, H, I,** AMNH 137095. **E–G,** AMNH 137123. **J, K, L**, AMNH 137087. **M, P, Q,** AMNH 137096, **N, O, R,** AMNH 137099. **S, T, U,** AMNH 137098. Scale bar = 2 mm.

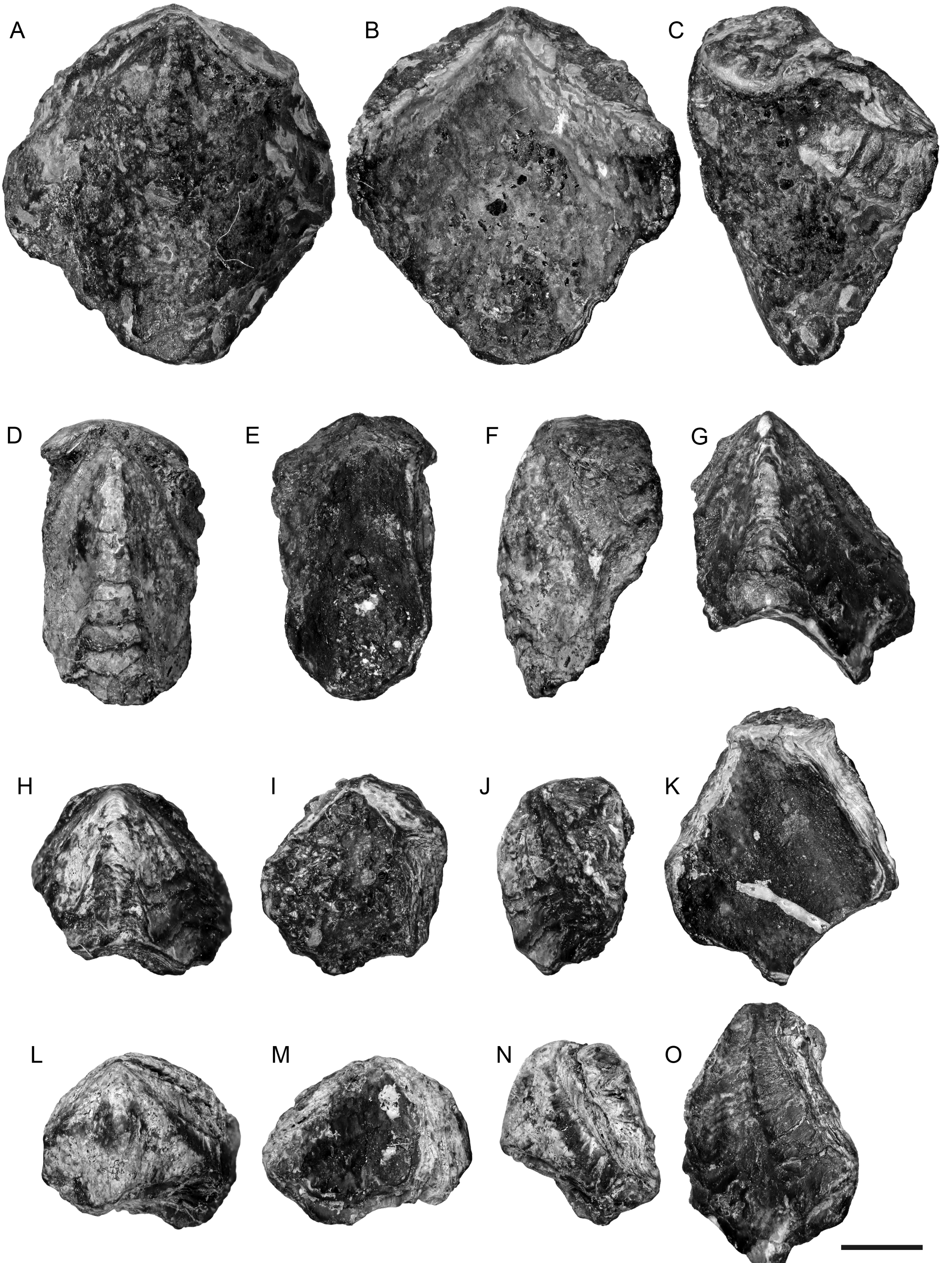


FIGURE 7. *Conchorhynchus* sp. from the Mount Laurel Formation, Delaware. **A–C,** AMNH 137097. **D–F,** AMNH 137101. **G, K, O,** AMNH 137102. **H, I, J,** AMNH 13710. **L, M, N,** AMNH 137103. Scale bar = 2 mm.

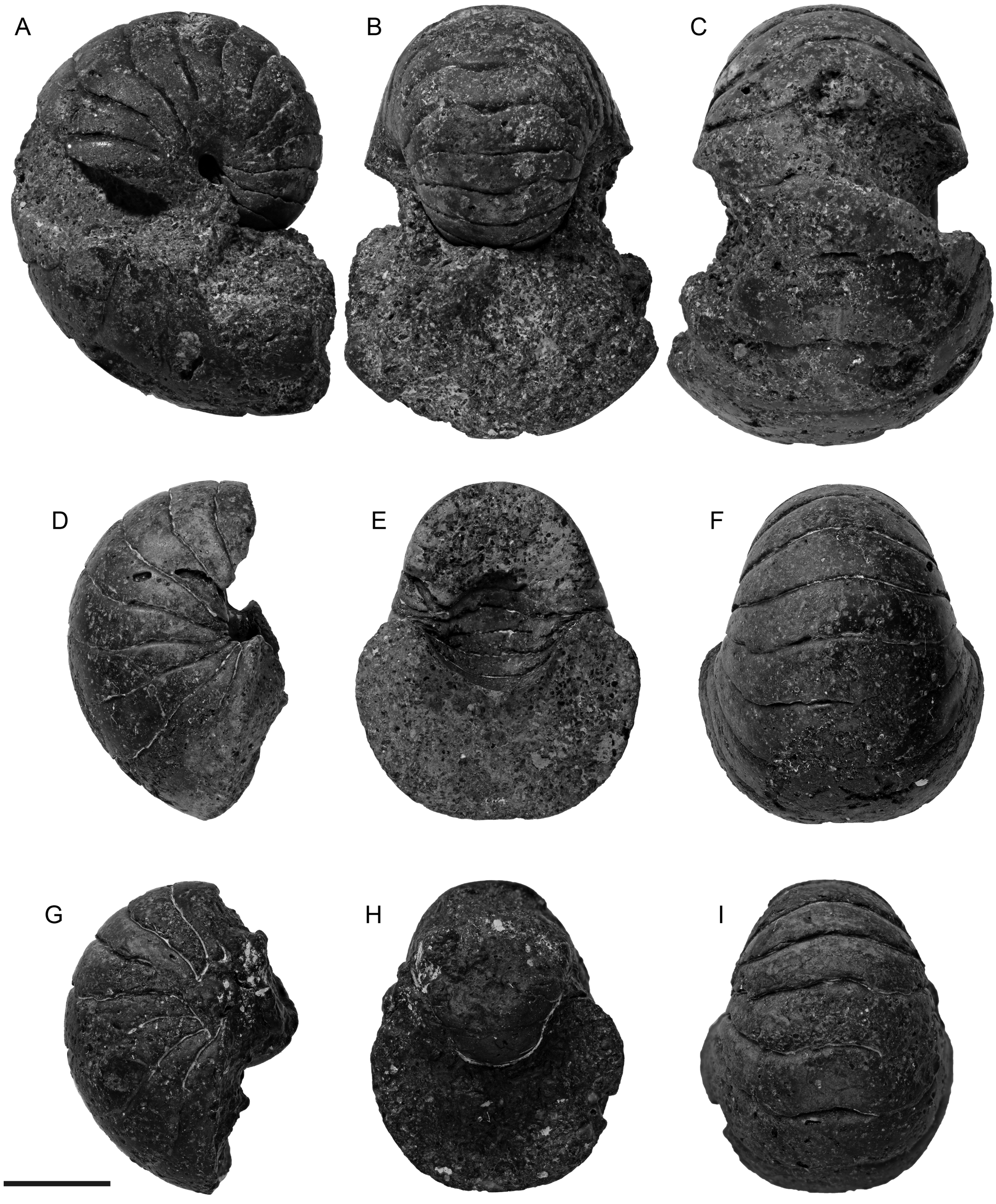


FIGURE 8. *Eutrephoceras* sp. from the Mount Laurel Formation, Delaware. **A–C,** AMNH 137092. **D–F,** AMNH 137093. **G–I,** AMNH 137094. Scale bar = 5 mm.

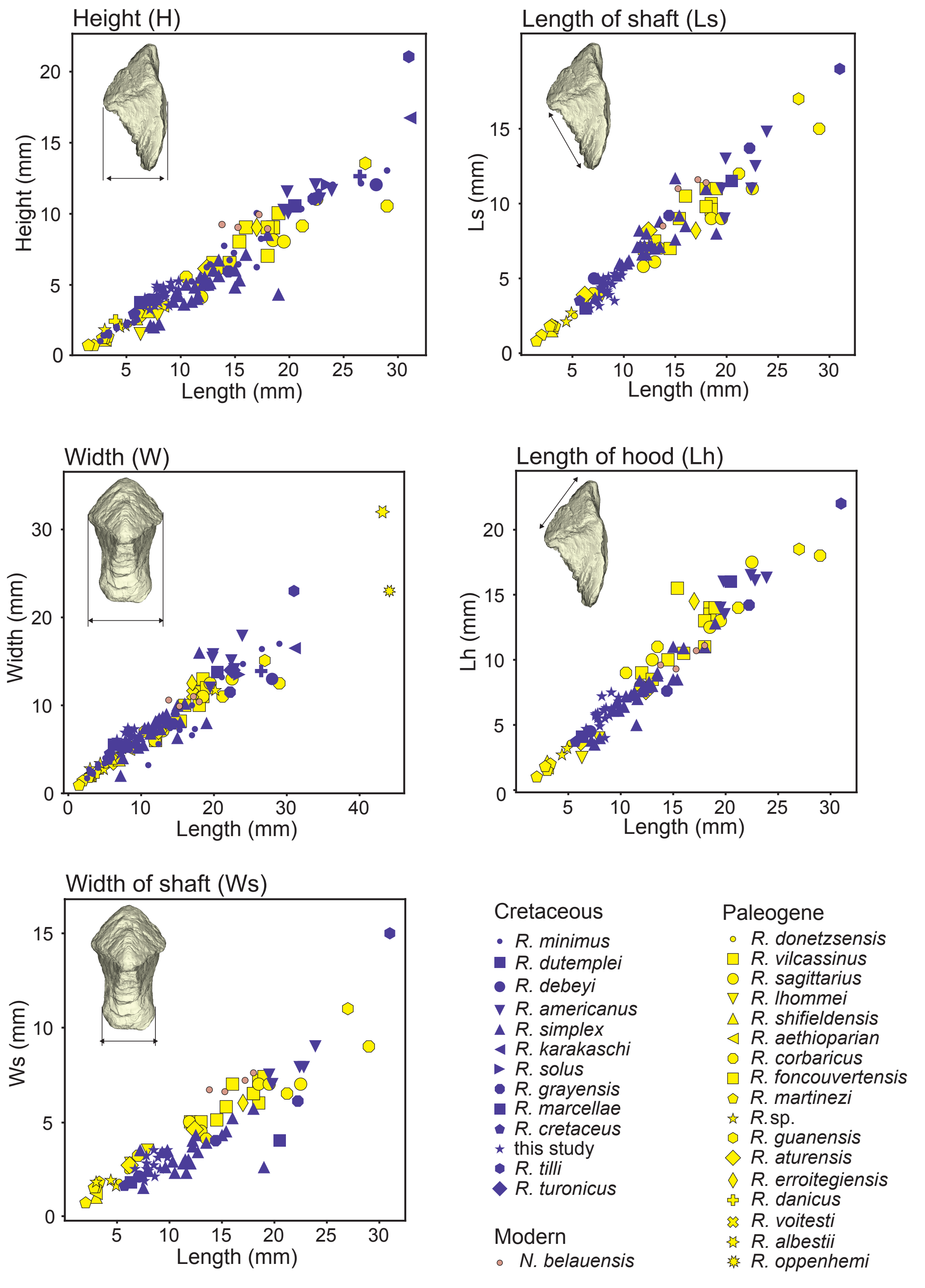
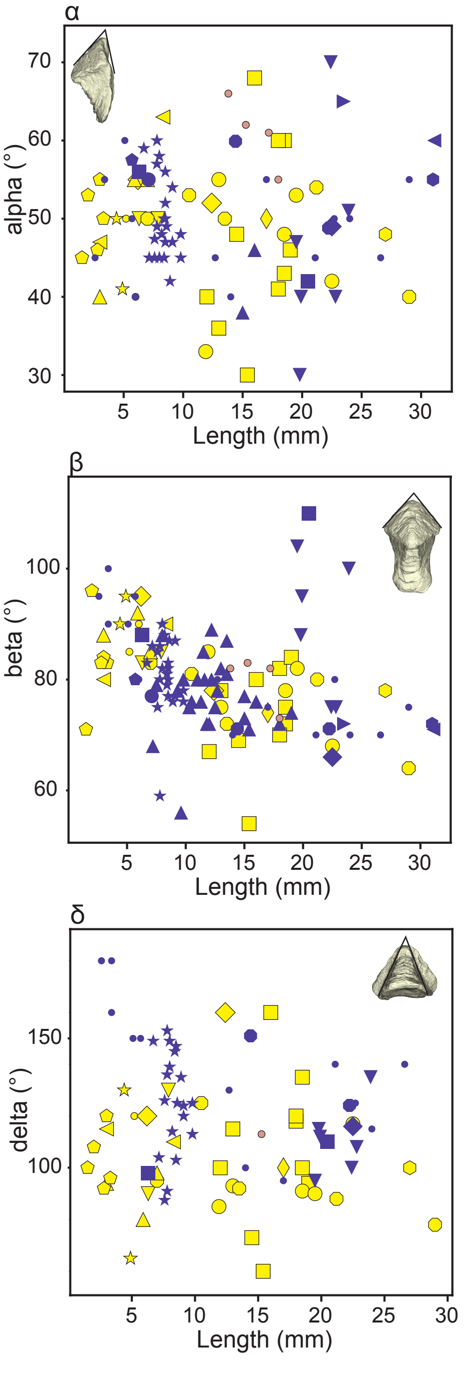


FIGURE 9. Linear measurements of our specimens from the Mount Laurel Formation plotted together with those from the Cretaceous and Paleogene published in previous studies (Till, 1909; Van Der Tuuk, 1985;



Riegraf and Schmitt-Riegraf, 1995; Komarov, 2005a, 2005b; Košťák et al., 2010; Weaver et al., 2012). Height, width, Ws, Ls, Lh, α, β, and δ are plotted against length, respectively.

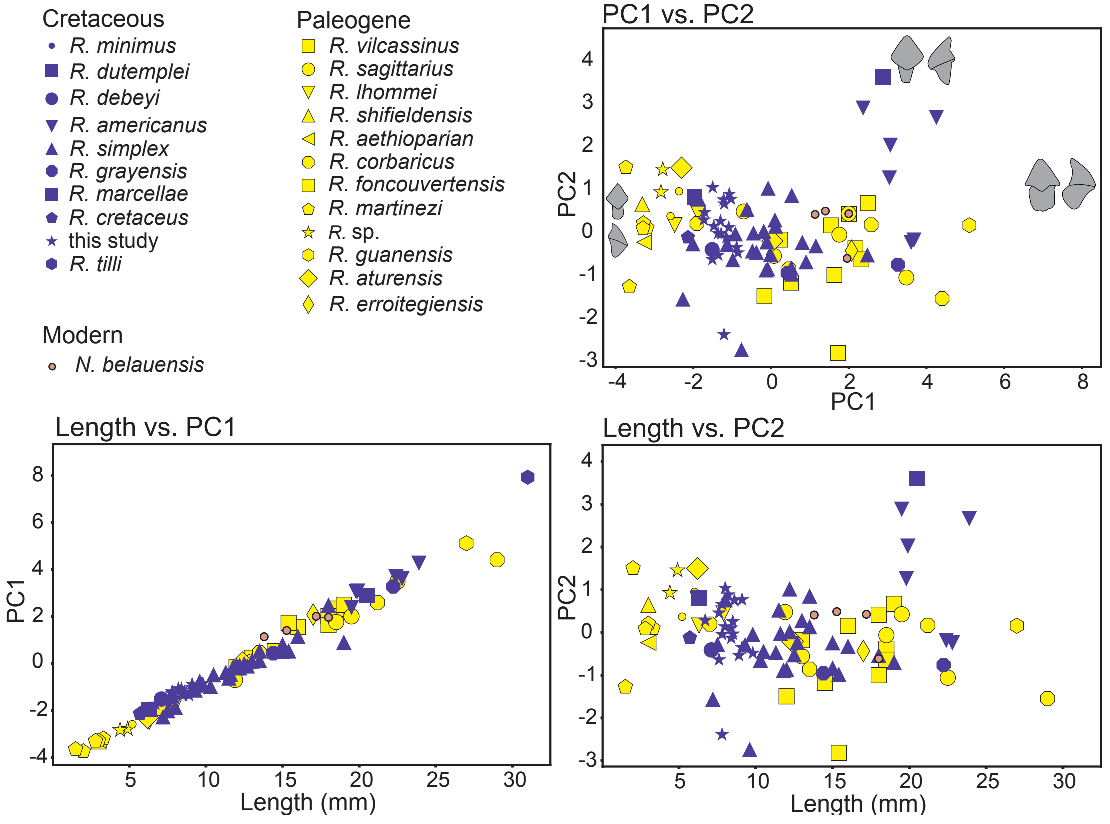


FIGURE 10. Results of principal component analysis using the six parameters L, W, H, Ls, Ws, Lh, and β. The original data are from preciously published papers (Till, 1909; Van Der Tuuk, 1985; Riegraf and Schmitt-Riegraf, 1995; Komarov, 2005a, 2005b; Košťák et al., 2010; Weaver et al., 2012)

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