

PARALBULA IN NORTH AMERICA: REVISITING AN ENIGMATIC CAMPANIAN – LATE PALEOCENE TELEOST WITH HOPE FOR NEW INSIGHTS

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ABSTRACT

Paralbula is a common genus of teleost fish in Campanian to Thanetian units nearly throughout North America, though it is also found in Europe and Africa where it survived into the Eocene. The genus, and the entire family Phyllodontidae, is known almost solely from uncommon basibranchial and parasphenoid tooth plates and common, isolated teeth. As a result, important paleoecological interpretations and phylogenetic relationships are inferred entirely from tooth characteristics, tooth plate form, and stratigraphic distribution. Most gross generic anatomical characteristics are completely unknown.

Paralbula is most common in North America, where its isolated teeth are often very abundant within marine vertebrate fossil assemblages. The genus is found almost exclusively in deposits representing near-shore and/or marginal marine environments, where the rounded, phyllodont dentition characteristic of the family is thought to represent an adaptation for crushing invertebrate shells or exoskeletons. *Paralbula* appears to occur rarely in fluvial sediments, suggesting either that these fish were diadromous, or that those remains are allochthonous.

Within North America, only two species of *Paralbula* are recognized. *P. casei* is far more common, with remains collected from middle Campanian through Paleocene (Thanetian) sediments across the continent. Until recently, *P. marylandica* was known only from two basibranchial tooth plates from the Thanetian Aquia Formation of Maryland. However, a recent discovery of autochthonous *P. marylandica* remains from the Maastrichtian – Danian basal Homerstown Formation in New Jersey (NJSN 21877) requires a revision of this species' geographic and stratigraphic range. More importantly, these remains consist of multiple skull elements, including several toothed elements, and scales; thus constituting by far the most complete set of remains known from any specimen within the genus, and highly unusual for the Phyllodontidae as a whole.

REVISITING PARALBULA

Phylogeny & Taxonomy

All taxonomic relationships presented herein will follow Estes (1969a).

Infraclass Teleostei
Superorder Elopomorpha
Order Elopiformes
Suborder Albuloidi
Family Phyllodontidae Darteville and Casier, 1943

The Phyllodontidae earned this moniker from their phyllodont dentition - defined as the presence of multiple superimposed sets of replacement teeth. The family is known only from relatively uncommon basibranchial and parasphenoid tooth plates and from abundant, isolated phyllodont teeth. As a result, the family is poorly known.

Subfamily Paralbulinae Estes, 1969a

The Paralbulinae is diagnosed by convex basibranchial and concave parasphenoid tooth plates lacking sigmoidal curvature, irregularly stacked phyllodont teeth that are hemispherical or bulbous and that are set in a profuse or moderate matrix, and a well-defined basilar foramen with striated edges.

Paleogeography (Fig. 1)

To date, *Paralbula* has been recovered in England, Spain, Egypt, and Morocco. However, *Paralbula* is most common in North America, with remains recovered from Alberta, Canada, Montana, North Dakota, Wyoming, New Mexico, Mississippi, Georgia, North Carolina, Virginia, Maryland, Delaware, and New Jersey (Fig. 1; see references). Throughout this range, isolated teeth are a common component of many marine vertebrate faunal assemblages (e.g., Manning and Dockery, 1992; Beavan and Russell, 1999; Hartstein et al. 1999; Brinkman et al., 2004). Locally, *Paralbula* teeth are even more abundant than those of the ubiquitous aulopiform teleost *Enchodus* (Poyato-Ariza et al., 1999). Basibranchial and parasphenoid tooth plates are extremely rare, with only a few complete specimens known to date (e.g., Blake, 1940; Estes, 1969a; Case and Schwimmer, 1988; Robb, 1989).

Paleoecology

Very little is known about the paleoecology of *Paralbula* and the Phyllodontidae, primarily a result of the highly fragmentary nature of the group's fossil record (e.g., Estes, 1969a; Fiorillo, 1989; Eberth and Brinkman, 1997). Phyllodont dentition is believed to provide a more solid, inflexible oral frame, which is interpreted as an adaptation for crushing invertebrate shells or exoskeletons (Estes, 1969a; Estes and Hiatt, 1978). Indeed, the stratigraphic distribution of phyllodontids supports this interpretation: all phyllodont species, with the exception of *Phyllodus*, are predominantly recovered from near-shore marine facies (Estes, 1969a). *Paralbula* remains, in particular, exhibit a strong association with near-shore marine sediments (e.g., Estes, 1969a; Estes and Berberian, 1970; Williamson and Lucas, 1992), estuarine (e.g., Estes, 1969a; Case and Schwimmer, 1988), and/or coastal facies (Estes, 1969a; Robb, 1989).



Figure 1. Paleogeographic distribution of *Paralbula* species during the Late Cretaceous Period in North America. Red areas indicate the reported occurrences of *P. casei*. The yellow area indicates the reported range of *P. marylandica*. Map from GoogleEarth.

Paralbula casei Estes, 1969

Paralbula casei is the oldest and longest-ranging phyllodontid known, with a stratigraphic range extending from the middle Campanian into the Eocene (Fig. 9). It is also the most common and widely-distributed species (Fig. 1).

Paralbula casei is distinguished from other *Paralbula* species on the basis of thin tooth enamel and very well developed tooth surface sculpturing, often in a radiating pattern (Fig. 2, 3; Blake, 1940; Estes, 1969).

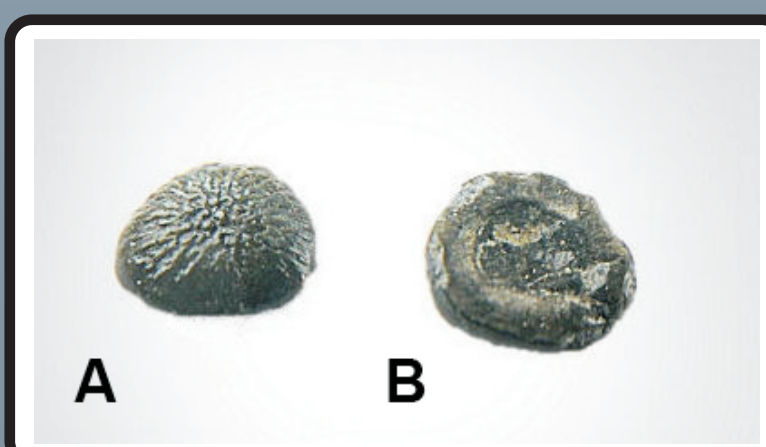


Figure 2. *Paralbula casei* teeth (from fossilsn.com). A, occlusal view; B, ventral view. Each tooth is approximately 2.5mm in diameter.

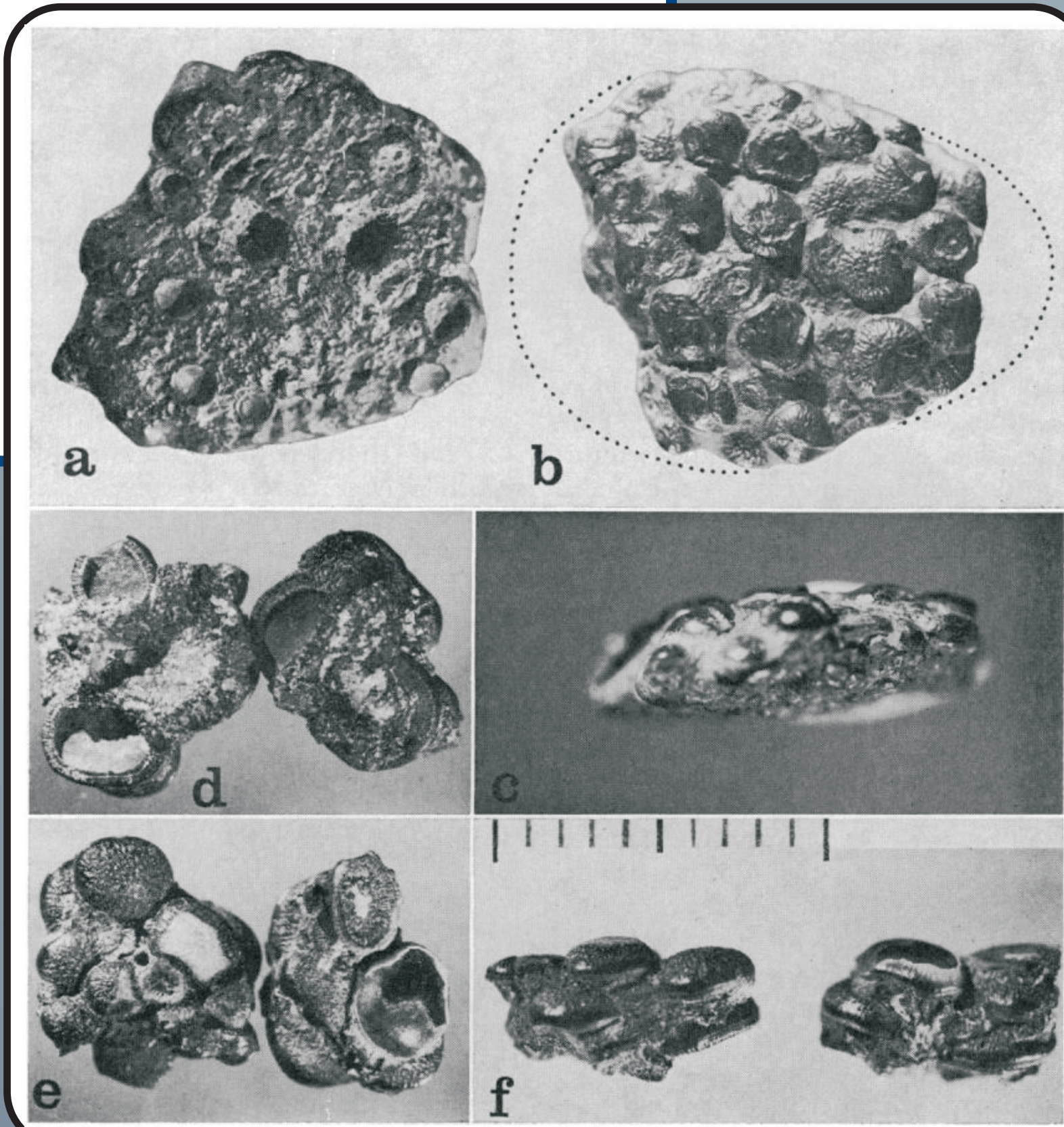


Figure 3. *Paralbula casei* type specimen (Museum of Comparative Zoology MCZ 9285): fragmentary basibranchial tooth plate a, basal view, b, occlusal view, c, lateral view; Maastrichtian Navesink Formation of New Jersey; d – f, (MCZ 9272, 9273) tooth plate fragments, d, basal, e, occlusal, f, lateral view, Campanian of Alberta, Canada, anterior to right; scale in mm (from Estes, 1969a).

Paralbula marylandica Blake, 1940

Paralbula marylandica was previously known only from two basibranchial tooth plates (USNM 13855; 16134) from the late Paleocene Aquia Formation of Maryland (Blake, 1940; Estes, 1969a). Here we report this species in the latest Cretaceous - earliest Paleocene (Fig. 9) of New Jersey as well (Fig. 1).

Paralbula marylandica is distinguished from other *Paralbula* species by smooth, generally unornamented teeth and a convex occlusal surface of the basibranchial tooth plate (Fig. 4; Myers, 1936; Blake, 1940; Estes, 1969a).

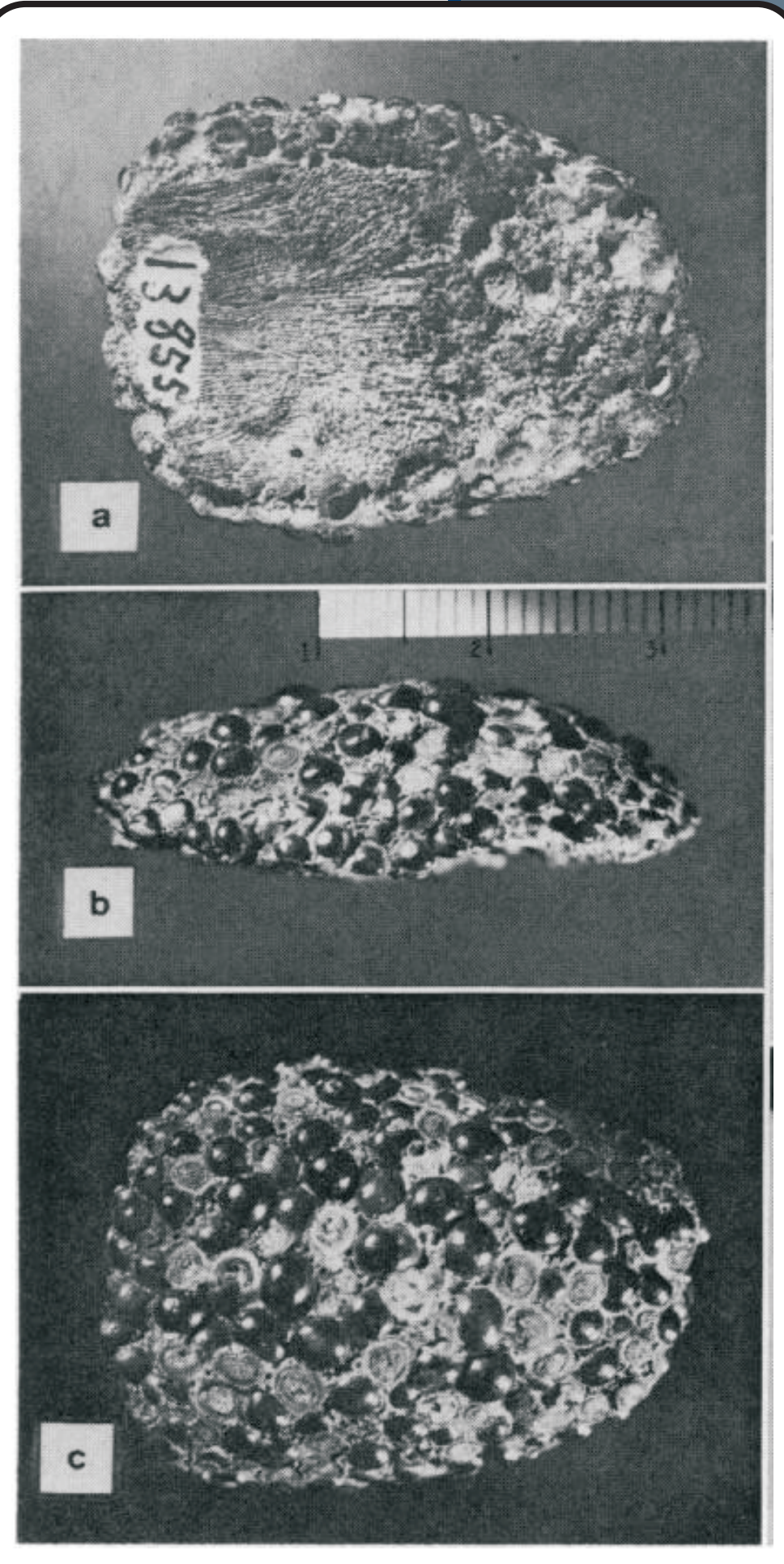


Figure 4. *Paralbula marylandica* type specimen (USNM 13855). a, basal, b, lateral, c, occlusal views of basibranchial tooth plate, anterior to right; scale in mm (from Estes, 1969a).

NEW INSIGHTS

In May 2007, members of the Drexel University *Field Methods in Paleocology* course discovered and excavated the remains of a teleost fish (NJSN 21877) from the Main Fossiliferous Layer (MFL) of the latest Cretaceous – earliest Paleocene basal Homerstown Formation. Elements recovered include the prootic and basioccipital (braincase), left quadrate, atlas, anterior portions of both left (Fig. 5) and right dentaries (Fig. 6), the ethmoid (Fig. 7), palatine (Fig. 8), and numerous yet-to-be-identified skull elements. Several highly ornamented scales are also present and remarkably well preserved, either as a mass of multiple articulated scales in a concretionary matrix, or as complete, isolated, individual elements. Tooth-bearing elements display both empty tooth sockets and in-place teeth. The sockets are circular and concave. Each tooth is less than 1mm in diameter, hemispherical in profile and circular in occlusal view with a smooth surface. Teeth are undistorted by growth pressures, irregularly stacked, densely packed, and randomly arranged on the toothed elements. These characteristics are identical to those ascribed to *Paralbula marylandica* by Blake (1940), and later described in more detail by Estes (1969a).

This discovery has already resulted in a number of significant results:

A) Paleogeography:

This is the first report of *P. marylandica* outside of Maryland (Blake, 1940).

B) Stratigraphic Range:

This is the first report of *P. marylandica* in latest Cretaceous earliest Paleocene age sediments, which is significantly earlier than the latest Paleocene date of origination for the species (Fig. 9) as predicted by Estes (1969a).

C) Taphonomy:

These remains are taphonomically significant because they demonstrate a high degree of preservational quality rarely seen in the MFL, which supports the hypothesis that the MFL represents a time-averaged condensed section (e.g., Egerton et al., 2008; Schein et al., 2008) rather than a transgressive lag, and highly unusual for the Phyllodontidae as a whole.

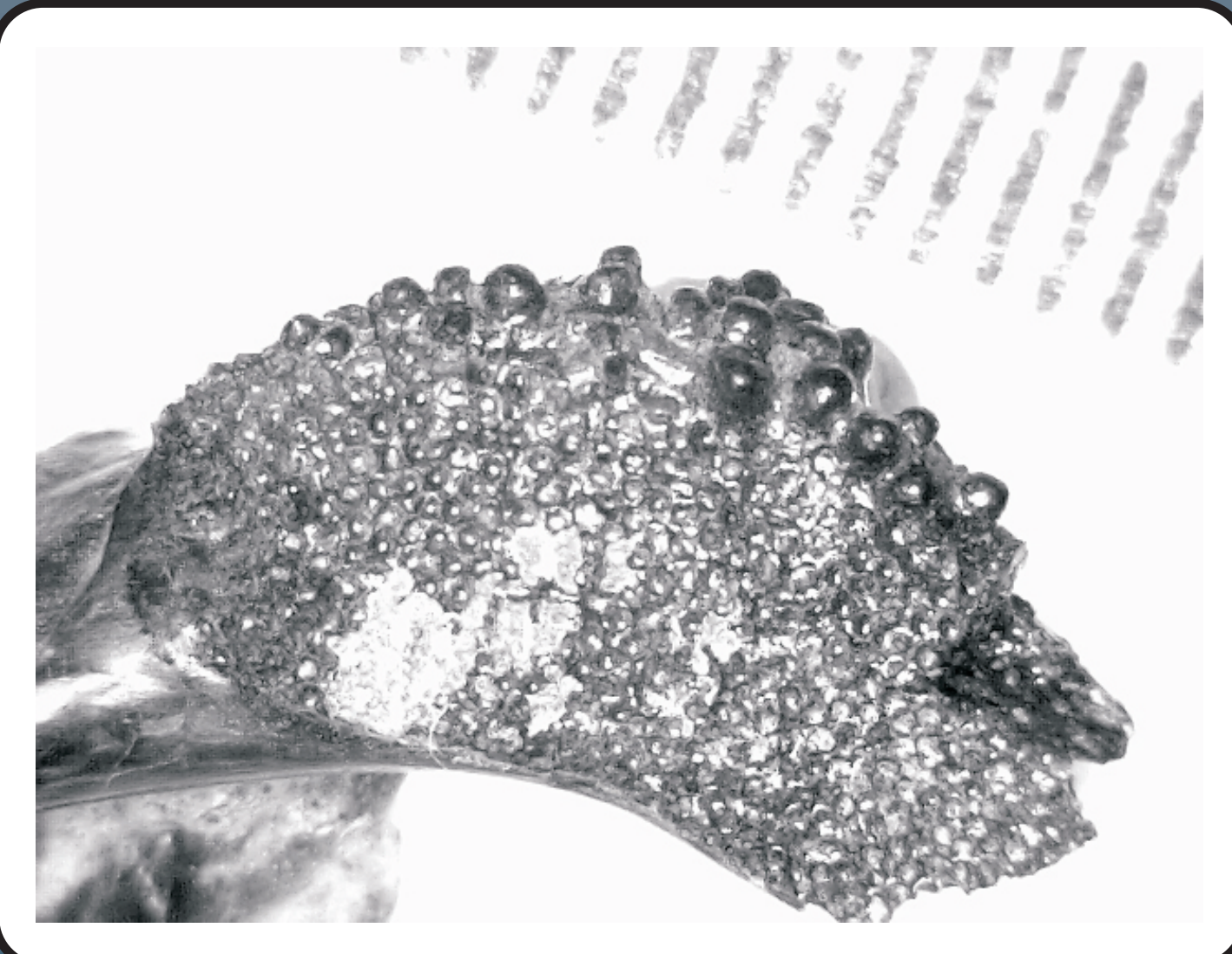


Figure 8. *Paralbula marylandica* palatine (NJSN 21877), occlusal view. Scale in mm.



Figure 5. *Paralbula marylandica* left dentary (NJSN 21877), lateral view, anterior toward the left. Scale in mm.



Figure 6. *Paralbula marylandica* right dentary (NJSN 21877), lateral view, anterior to the right. Scale in mm.

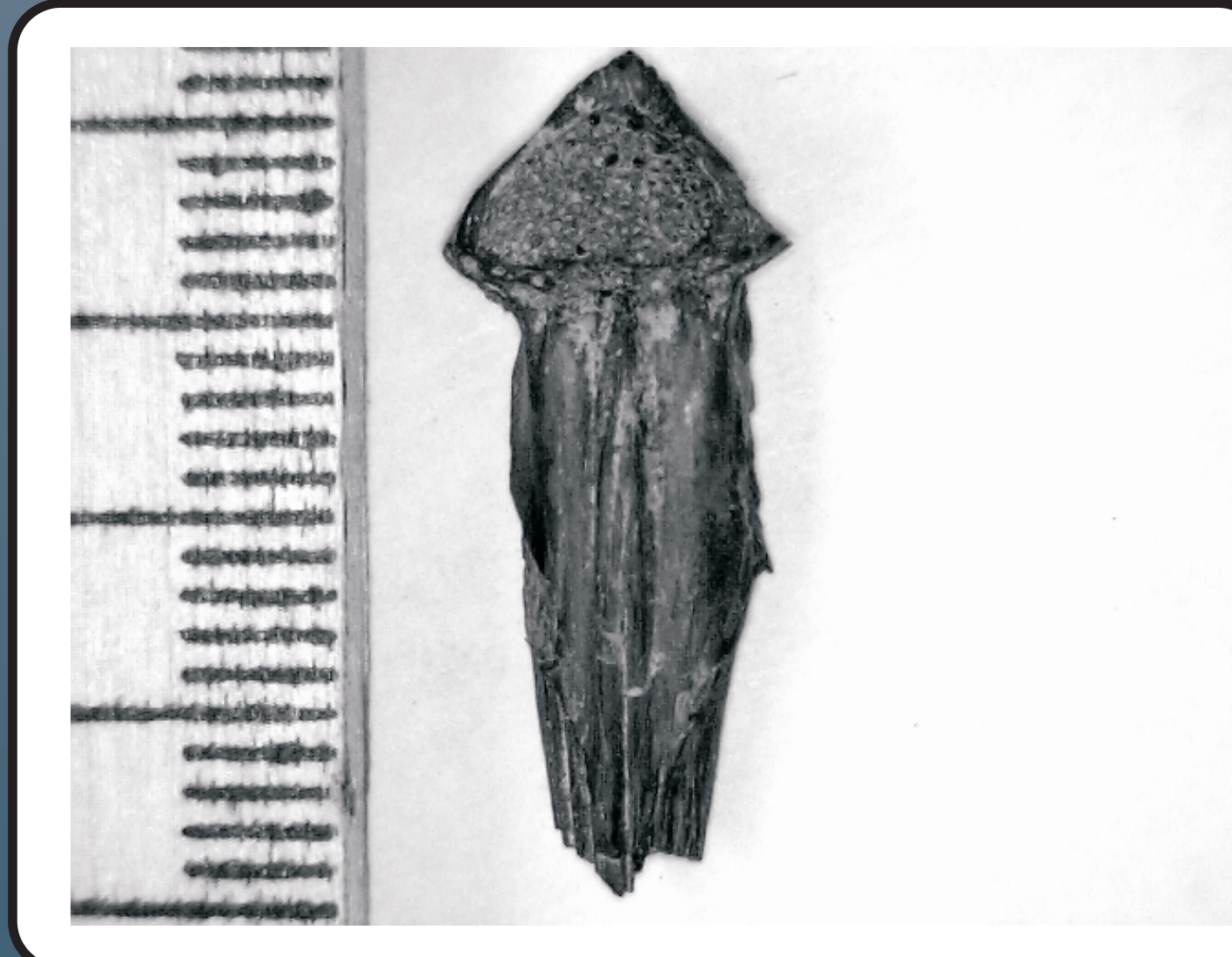


Figure 7. *Paralbula marylandica* ethmoid (NJSN 21877), occlusal view, anterior toward the top. Scale in mm.

FUTURE RESEARCH

Future research projects will involve a complete redescription of *P. marylandica* based on the new material described herein (NJSN 21877) in order to address the following questions:

A) Phylogeny:

- What are the true phylogenetic relationships among *Paralbula* spp. and within the Paralbulinae?
- Are *P. salvani* and *P. stromeri* in fact distinct species?

Additional research projects already underway include a survey of *Paralbula* remains in numerous museum collections, with the intention of answering the following questions:

Paleogeography:

- Is *P. marylandica* truly endemic only to the mid-Atlantic Coastal Plain as has been reported to date?

Biostratigraphy:

- Is *P. marylandica* limited to latest Cretaceous – late Paleocene sediments in North America?

Paleoecology:

- Are *Paralbula* remains in fact only found in near-shore marine sediments?

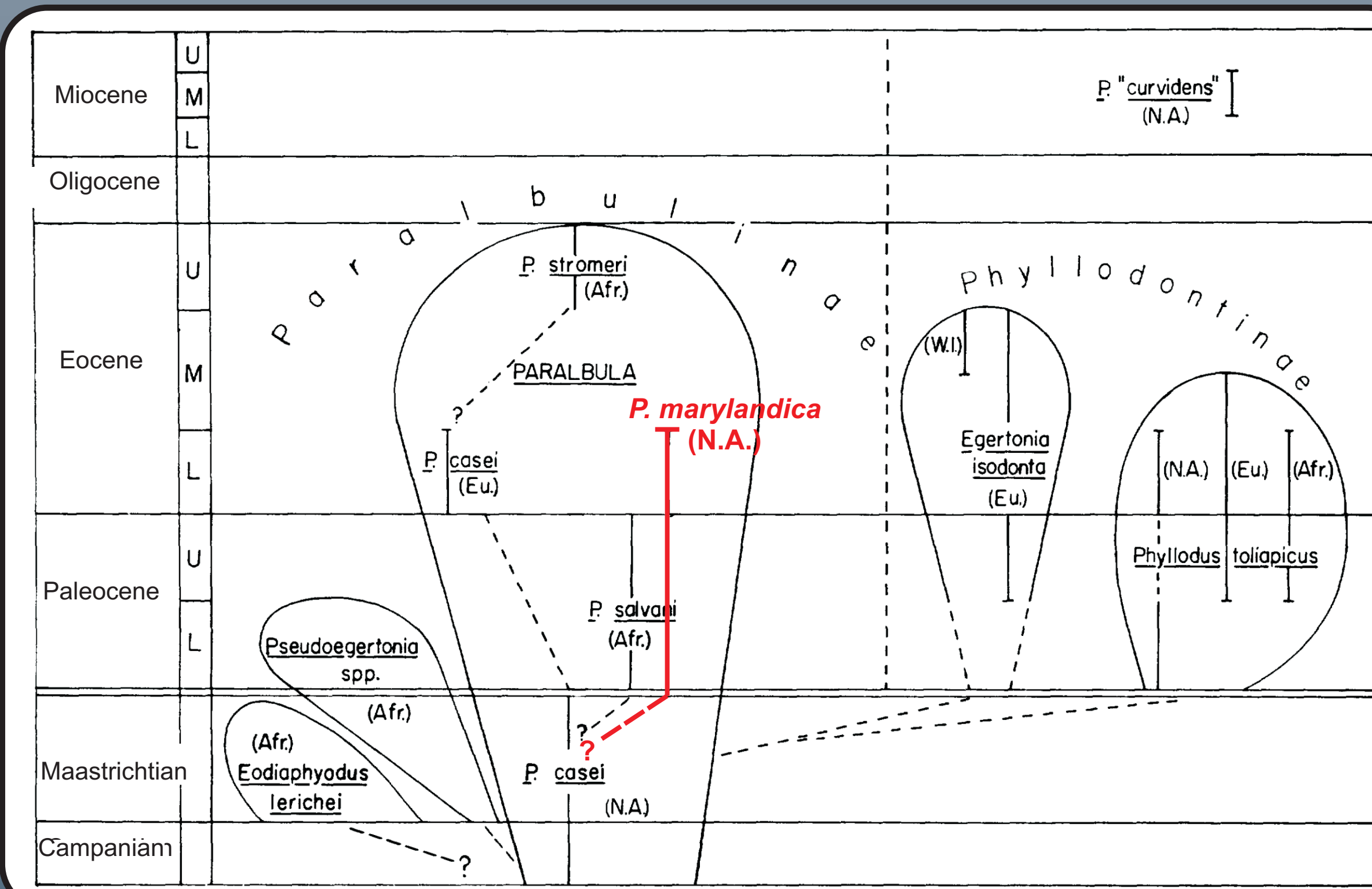


Figure 9. Revised stratigraphic and presumed phylogenetic relationships of Paralbulinae in light of the discovery of NJSN 21877 (after Estes, 1969a).

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Contact Information