

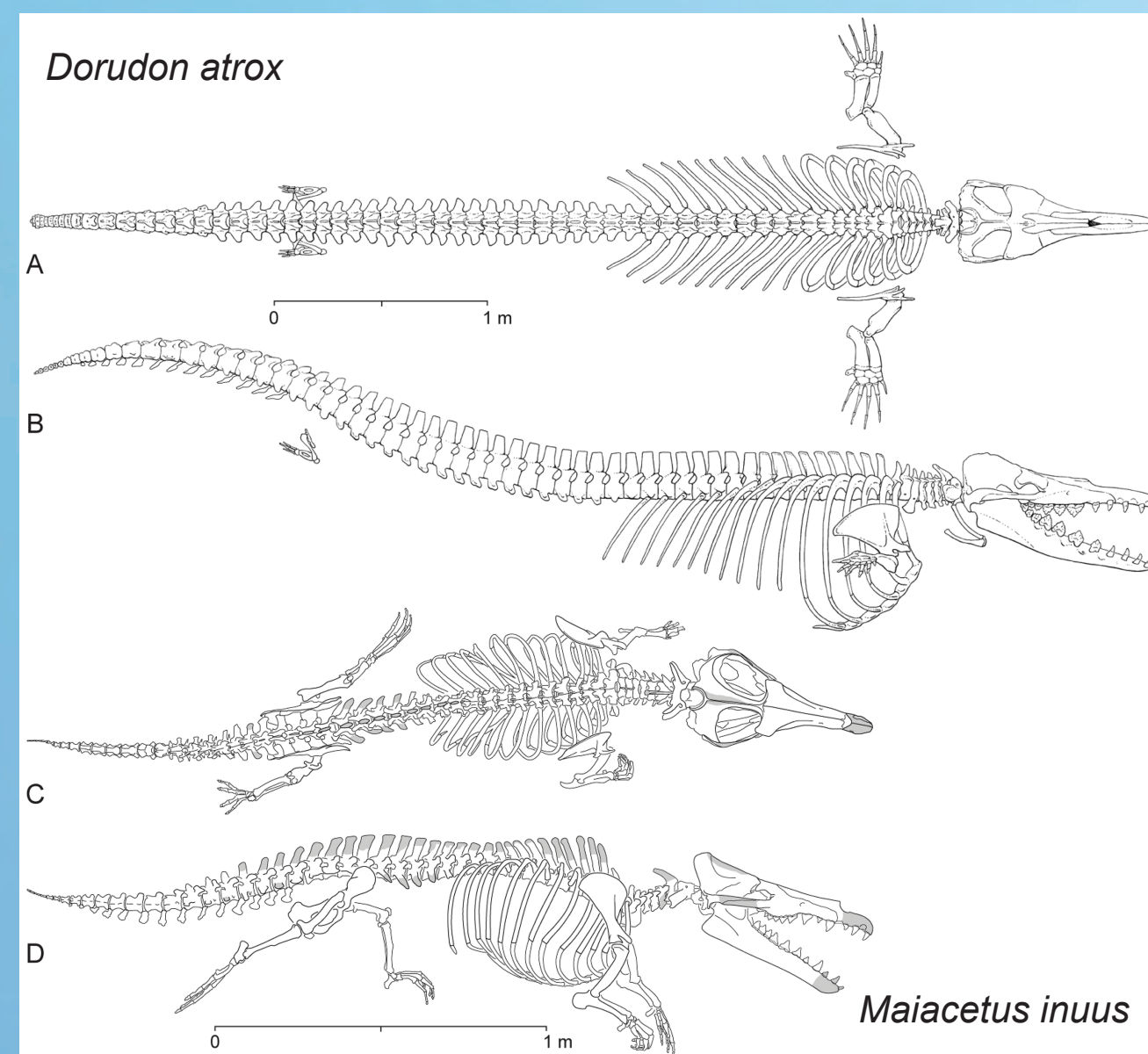
Hind Limb Form and Function in Terrestrial and Semi-Aquatic Mammals: Insights into Locomotor Evolution in Early Cetaceans

Alexandra N. Kuipers and Ryan M. Bebej, PhD

Introduction

Cetaceans (which include modern whales, dolphins, and porpoises) are descendants of terrestrial mammals. The earliest known cetaceans (about 52.5 million years old) had some adaptations for aquatic life, but remained quadrupedal with the ability to locomote on land. As cetaceans became increasingly adapted for life in water, their swimming became more efficient and resulted in adaptations such as flattened tail flukes, as seen in modern cetaceans. This also required an impressive amount of change in the hip and hind limb morphology of early cetaceans. While the earliest cetaceans had fully functional, stabilized hind limbs, those of modern cetaceans are significantly reduced or even lost. The purpose of this study was to understand the evolutionary pathway early cetaceans took as they transitioned from one type of aquatic locomotion (i.e., limb-dominated swimming) to another (i.e., tail-powered swimming) through quantitative comparisons of the hip and hind limb morphology of modern mammals.

Fig. 1 Skeletons of *Dorudon atrox* (A, B) and *Maiacetus inuus* (C, D) in swimming poses, both in dorsal view (A, C) and lateral view (B, D). Original source: PD Gingerich et al. (2009) PLoS ONE 4(2): e4366.



Materials and Methods

Skeletal specimens of modern mammals and fossil cetaceans were assessed at the University of Michigan Museums of Zoology and Paleontology (Ann Arbor, MI), the National Museum of Natural History (Washington, DC), and Northeast Ohio Medical University (Rootstown, OH). Linear measurements of major morphological landmarks on the innominate and femora were taken using digital calipers. Femoral head angles were quantified through digital photographs using Image J. The data were divided into subsets and analyzed using Principle Components Analyses (PCAs) in the program R.

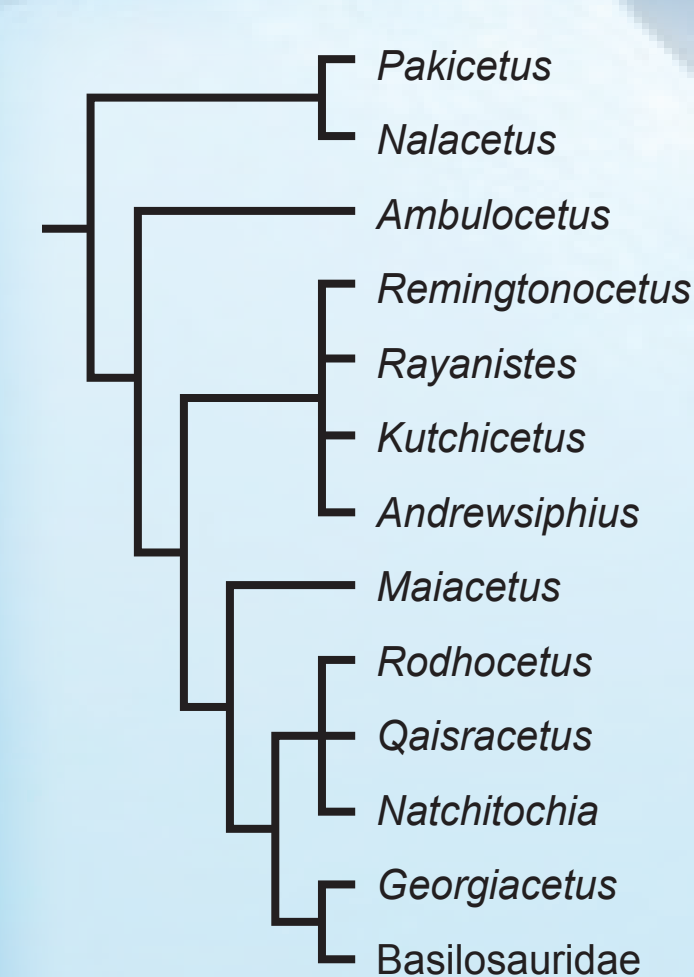


Fig. 2 (above) Phylogenetic relationships of cetaceans included in this study. Modified from Uhen (2014) Marine Mammal Science 30(3): 1029-1066.

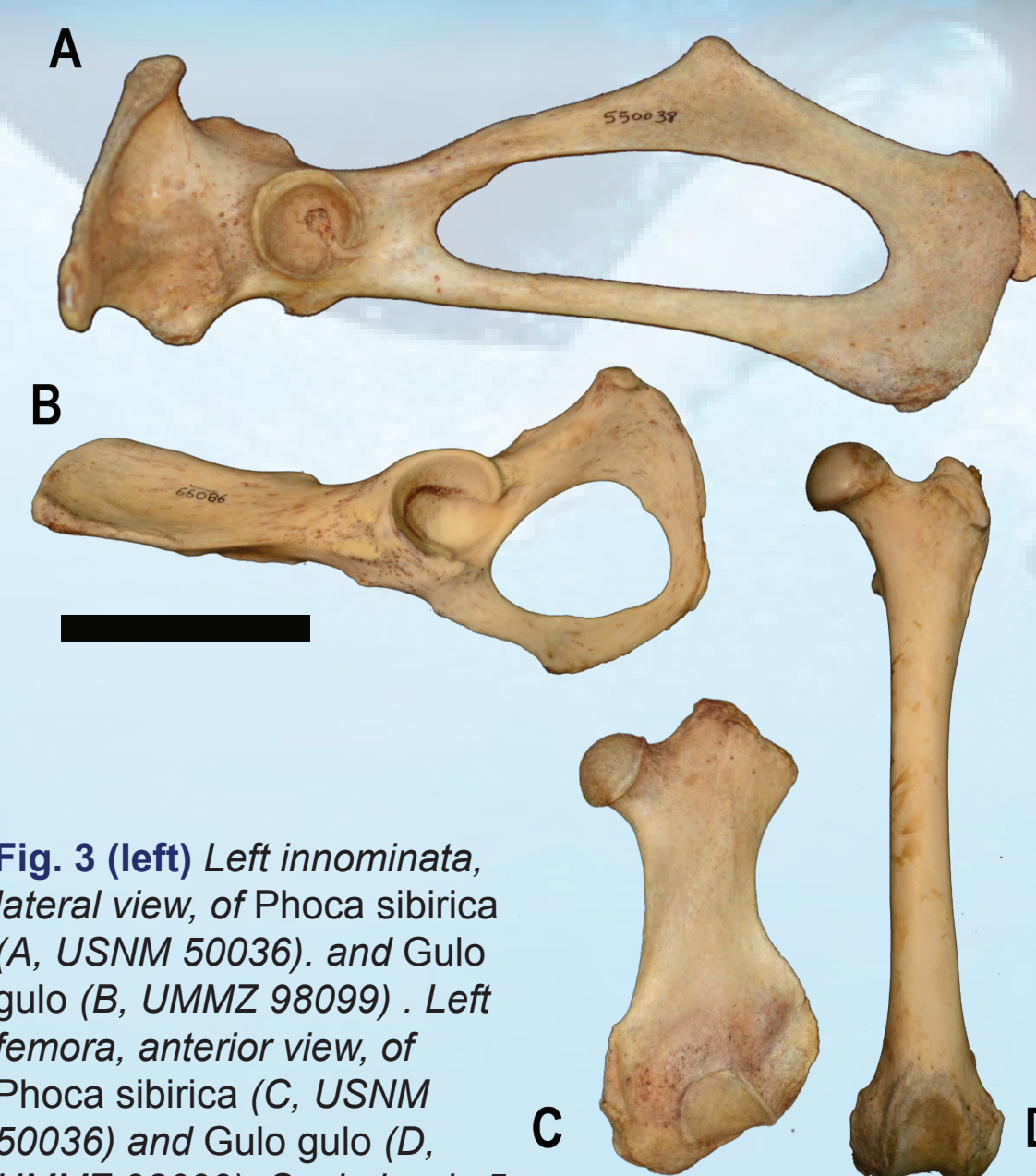


Fig. 3 (left) Left innominate, lateral view, of *Phoca sibirica* (A, USNM 50036), and *Gulo gulo* (B, UMMZ 98099). Left femora, anterior view, of *Phoca sibirica* (C, USNM 50036) and *Gulo gulo* (D, UMMZ 98099). Scale bar is 5 cm in length.

Conclusions

The results of the PCAs demonstrate:

- Derived protocetids, like *Qaisracetus*, *Natchitochia*, and *Georgiacetus*, actually have relatively longer ilia compared to more basal archaeocetes like *Pakicetus* and *Maiacetus*.
 - This is unlike the trend seen in other semi-aquatic mammals, in which the ilium shortens.
 - The ilium is an attachment site for muscles such as the gluteal muscles, which aid in the extension of the hind limb. A change in the morphology of the ilium could signify a subsequent change in function of those muscles.
- Derived protocetids generally exhibit a relatively open acetabular fossa, which may have implications for their hip mobility or weight-bearing capabilities.
 - Closed acetabular fossae are commonly found in stabilized hip joints (e.g., hippopotamus).
 - Open acetabular fossae are found in very mobile hip joints (e.g., most pinnipeds).
- The femora of remingtonocetids appear more specialized than other archaeocetes. Most remingtonocetids have small femoral head angles, but *Remingtonocetus domanensis* has the widest femoral head angle of the fossil cetaceans.
 - Femoral heads that are more vertically oriented result in limbs that are more splayed, which increases mobility and can thus assist in more lateral movements of the limb.
 - Femoral heads that are more horizontally oriented result in limbs that are brought in the parasagittal plane. This ultimately can increase propulsion force and reduce drag during swimming.

Results

Innominate

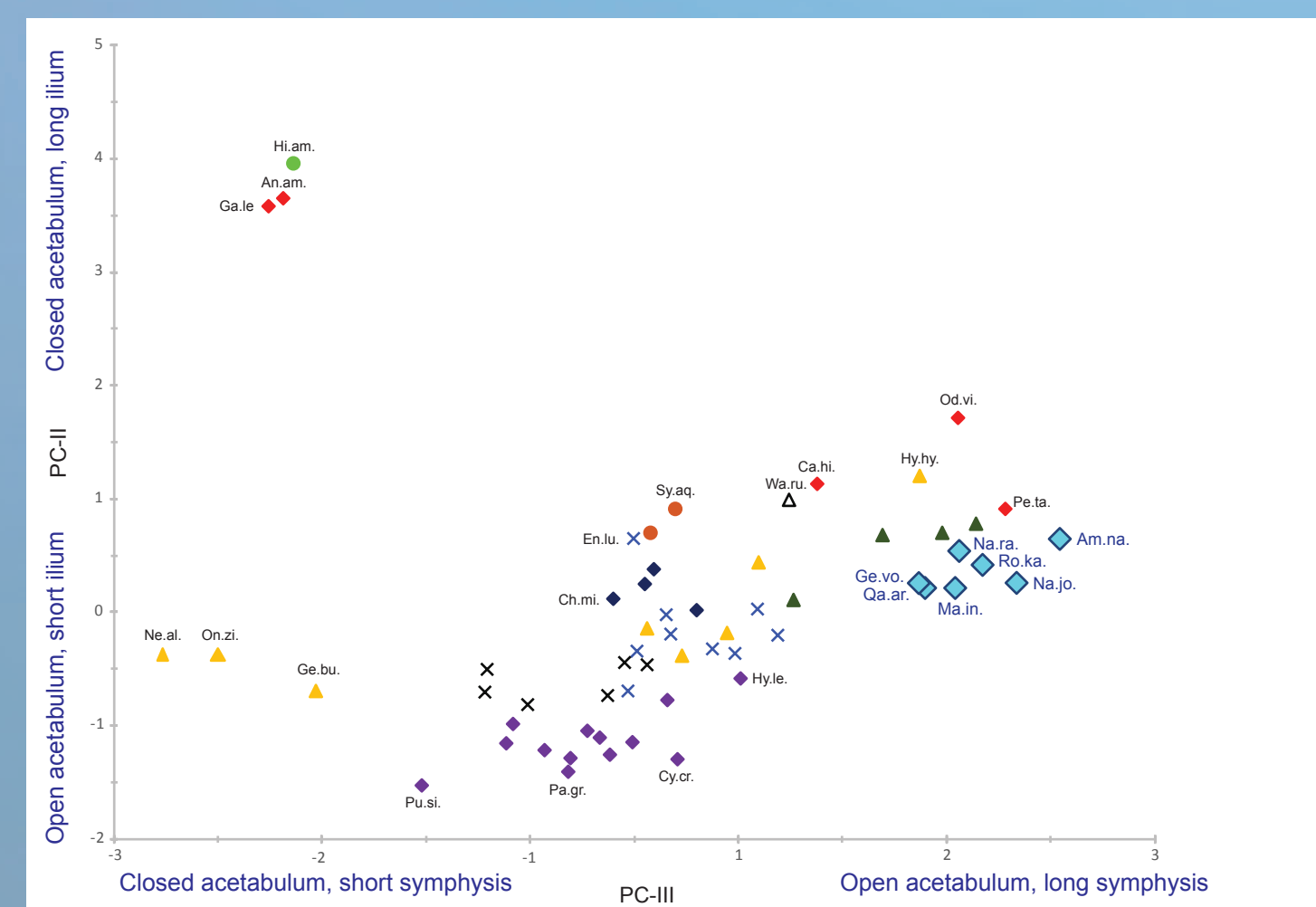


Fig. 4 PC-II and PC-III of all innominate measurements.

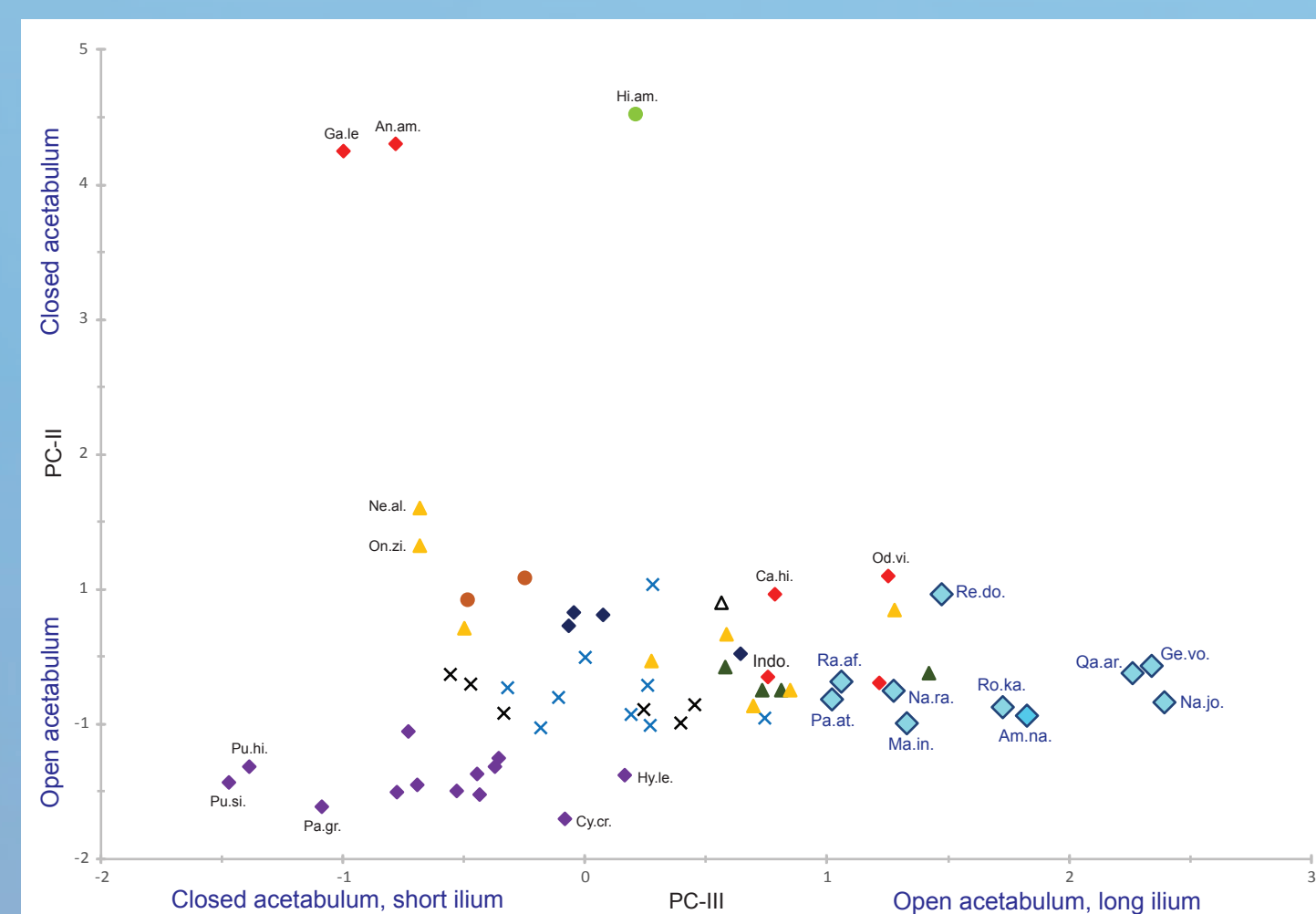


Fig. 6 PC-II and PC-III of innominate measurements, excluding the pubic measurements.

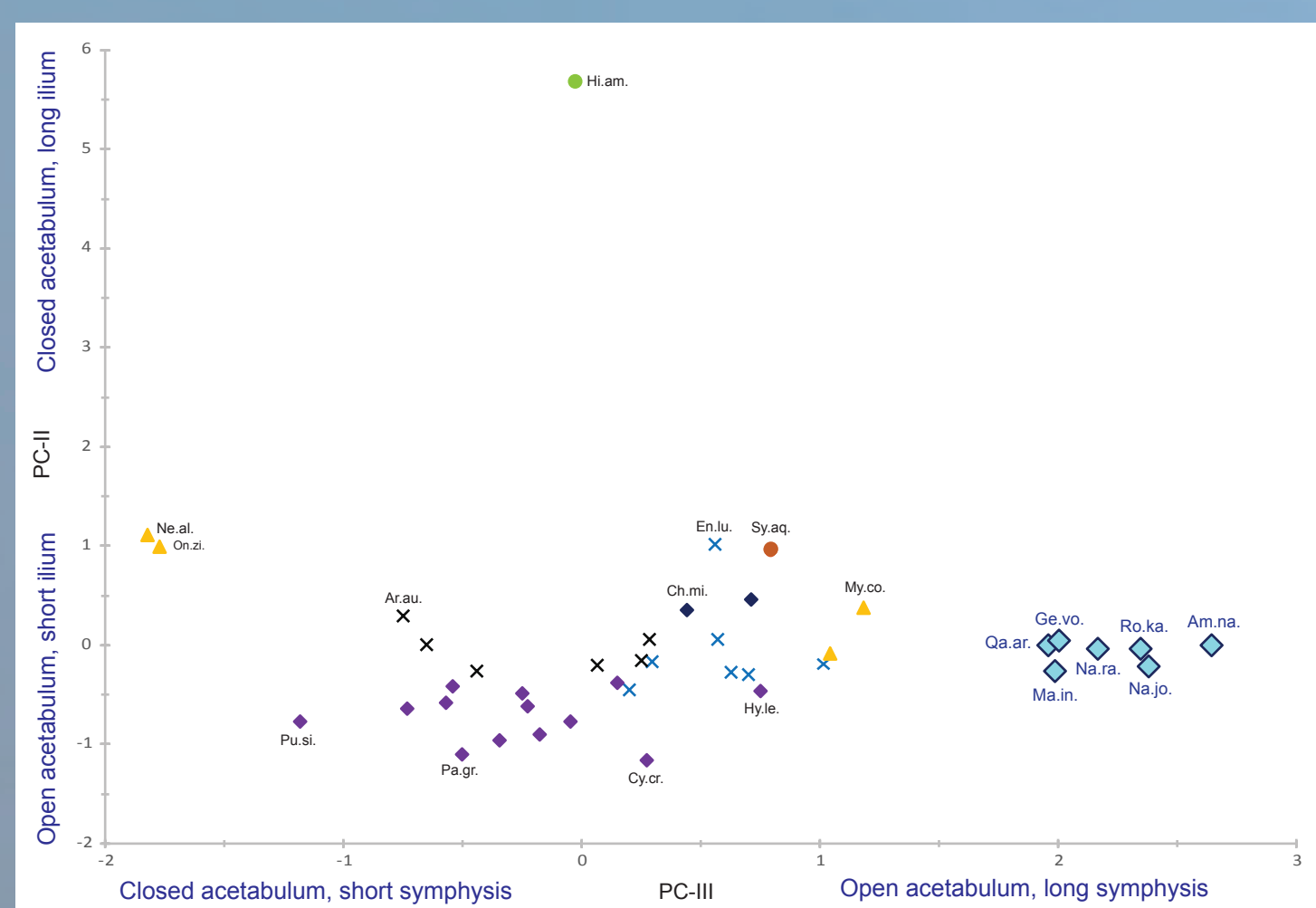


Fig. 5 PC-II and PC-III of all innominate measurements, including only semi-aquatic species.

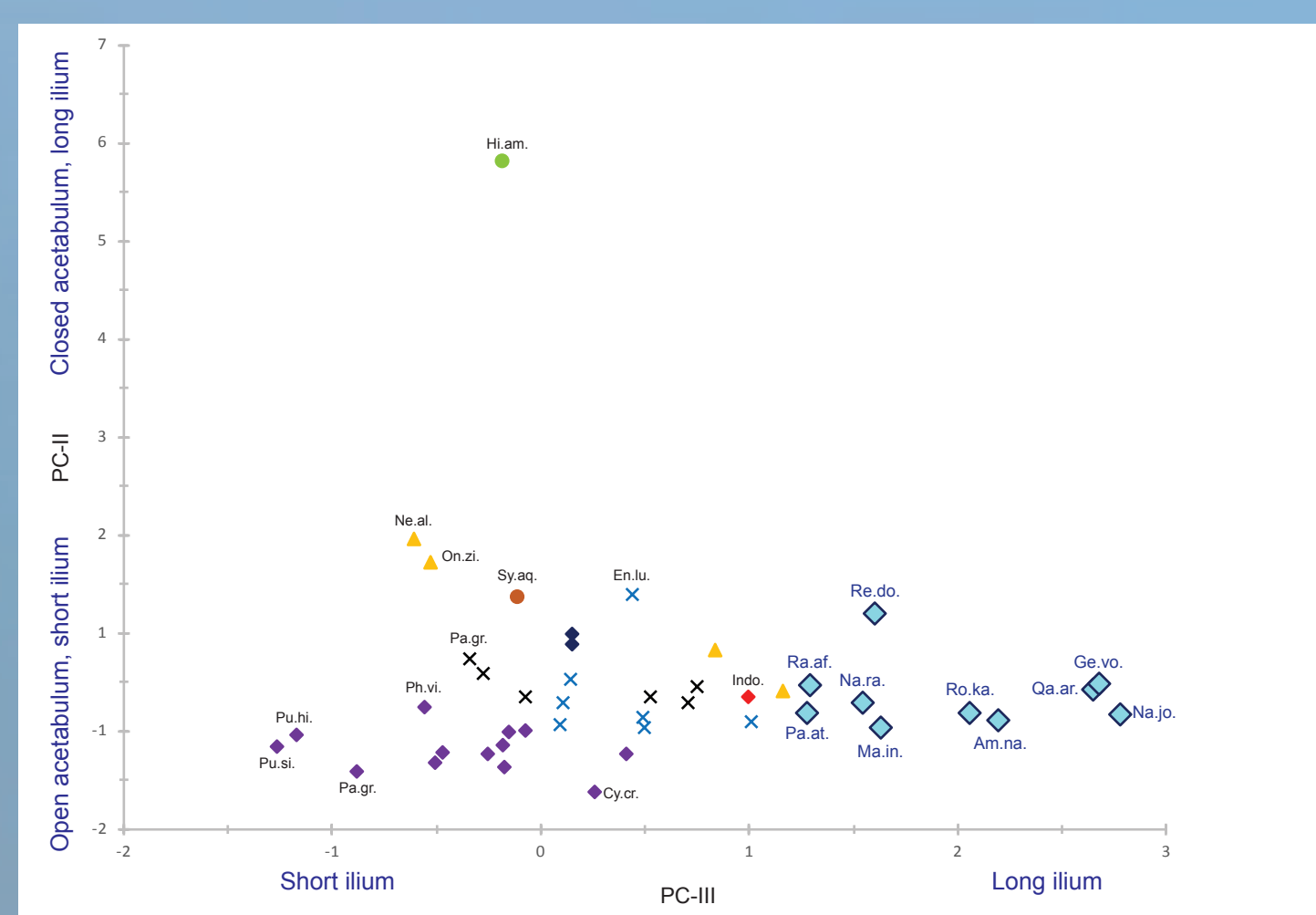


Fig. 7 PC-II and PC-III of innominate measurements, excluding the pubic measurements and including only semi-aquatic species.

Femur

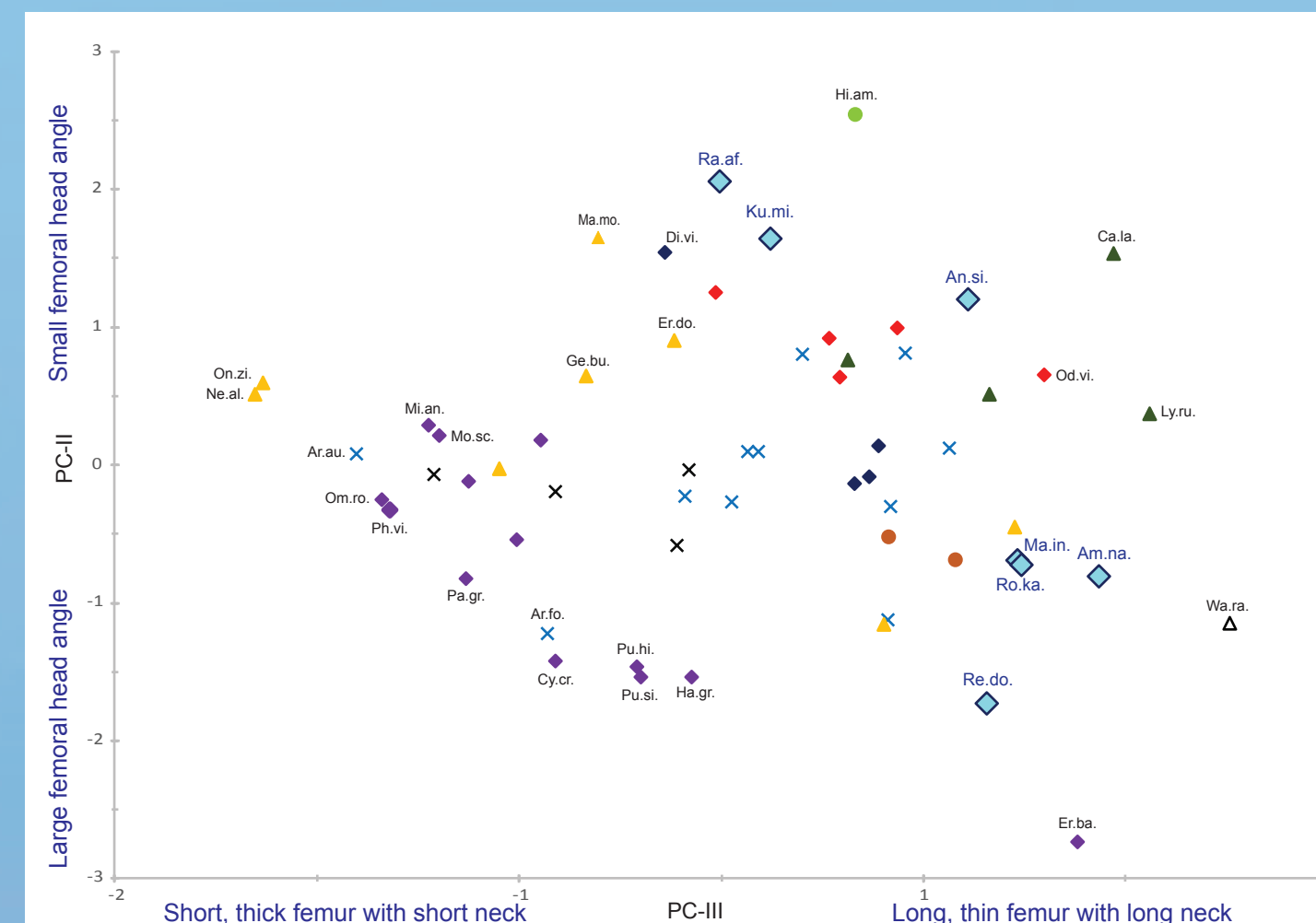
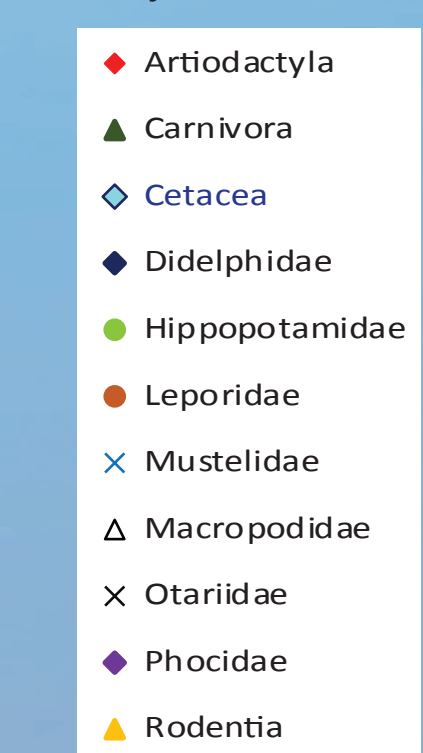


Fig. 8 PC-II and PC-III of proximal femur measurements plus the total length (estimates used for fossil specimens where the distal end was not preserved).



Fig. 9 PC-II and PC-III of proximal femur measurements plus the total length (estimates used for fossil specimens where the distal end was not preserved).

Fig. 10 (below) Taxonomic groups of specimens included in this study.



Note: PC-I generally distributed specimens on the basis of overall size, i.e., larger bodied specimens (like *Hippopotamus amphibius*) loaded towards the positive end of PC-I, while smaller specimens (like *Neofiber alleni*) loaded towards the negative end. This remained consistent for each analysis.

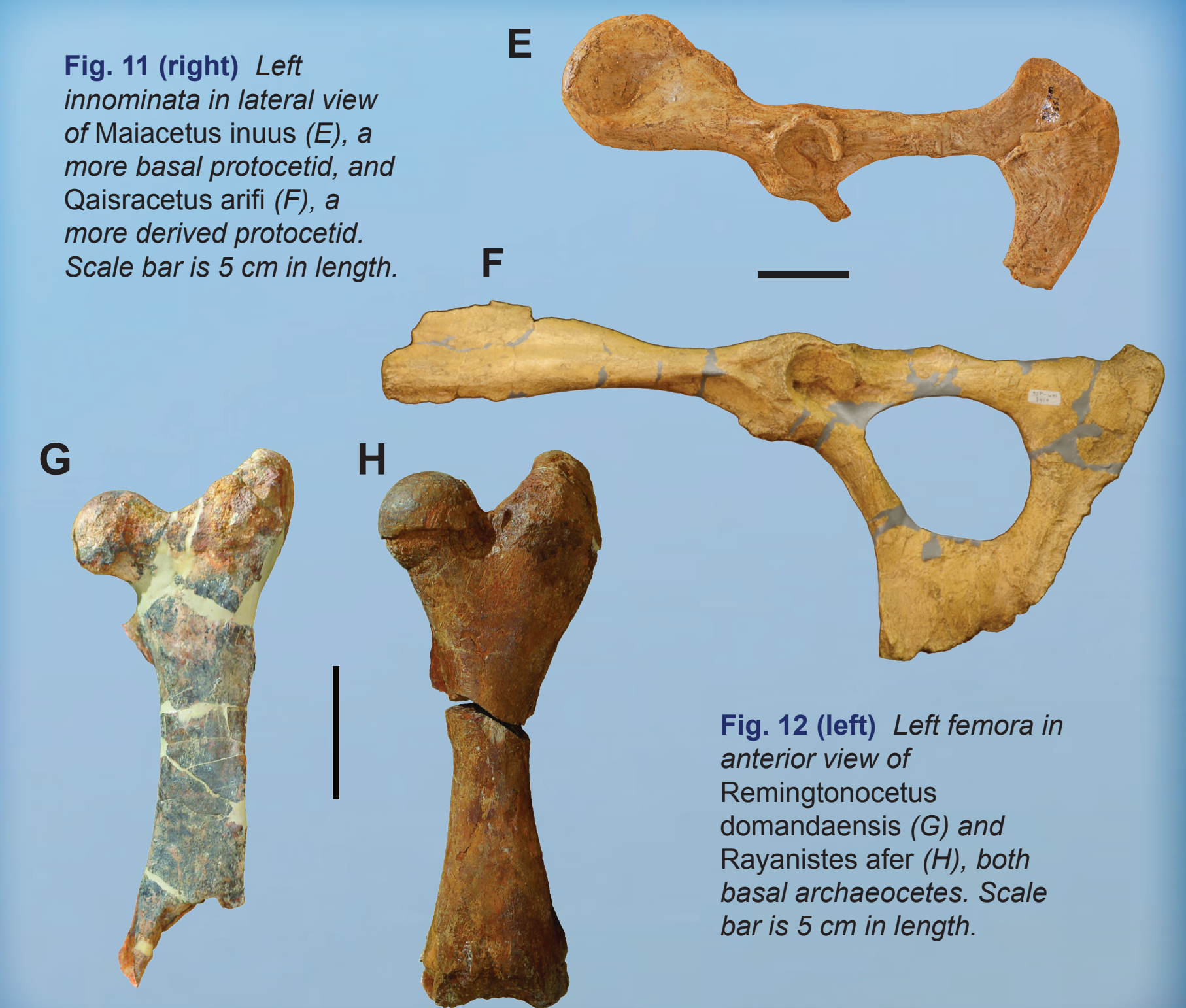


Fig. 11 (right) Left innominate in lateral view of *Maiacetus inuus* (E), a more basal protocetid, and *Qaisracetus arifi* (F), a more derived protocetid. Scale bar is 5 cm in length.

Fig. 12 (left) Left femora in anterior view of *Remingtonocetus domanensis* (G) and *Rayanistes afer* (H), both basal archaeocetes. Scale bar is 5 cm in length.

Acknowledgments

Cody Thompson (UMMZ), Philip Gingerich (UMMP), Adam Rountrey (UMMP), Hans Thewissen (NEOMED), Denise McBurney (NEOMED), and John Ososky (USMN) provided access to specimens under study. Mark Uhen (GMU) provided measurements for the innominate of *Natchitochia jonesi* (MMNS VP-4849).

This research has been funded by the Calvin College Science Division, the Jansma Family Research Fellowship in the Sciences, and the Calvin College Alumni Association.