

Were early Tertiary monotremes really all aquatic? Inferring paleobiology and phylogeny from a depauperate fossil record

The recent study of monotreme paleobiology and phylogeny by Phillips et al. (1) emphasized that the crown group Monotremata may have diverged relatively recently. However, they failed to discuss several aspects of the monotreme fossil record and functional morphology that may have a significant bearing on their conclusions.

It is important to note that the paucity of tachyglossid like monotremes in the Tertiary fossil record of Australia is not necessarily evidence of absence. It has been noted (ref. 2; ref. 11 in ref. 1) that the Late Oligocene-Early Miocene *Obdurodon* is only known from “aquatic” fossil deposits. Clearly, a preservational bias will exist in the fossil record when comparing the abundance of a terrestrial, fossorial taxon (e.g., *Tachyglossus*) with an aquatic one (e.g., *Ornithorhynchus*), particularly when (with the exception of cave assemblages) Australian fossils are usually derived from aquatic (i.e., fluvial, swamp, or lacustrine) deposits. Monotremes are neither abundant nor common in any Tertiary or Quaternary Australian fossil deposits (2) and, given the small size and fossorial habit of modern terrestrial tachyglossids, their rarity, or even absence, in the fossil record might be expected.

Phillips et al. (1) failed to discuss a publication (3) reporting a fossil humerus from the Cretaceous Flat Rocks site in Victoria, southeastern Australia: interpreted to represent a tachyglossid-like monotreme, with the gross morphology indicating a “considerable capacity for rotation-thrust digging” (3). This discovery calls into question the assertion that “echidnas had aquatically foraging ancestors that reinvaded terrestrial ecosystems” (1) and raises the possibility that tachyglossid-like and ornithorhynchid-like monotremes have coexisted as separate lineages for longer than is indicated by the molecular divergence dates (19–48 Ma) calculated by these and previous authors (refs. 15–22 in ref. 1; as

suggested by Rowe et al. in ref. 25 in ref. 1). Alternatively, multiple invasions of aquatic ecosystems may have occurred throughout the evolutionary history of monotremes.

The morphological characters of echidnas cited by Phillips et al. (1) as evidence of their aquatic ancestry are dorso-ventral compression (of the body), “front-wheel drive” locomotion, and reversed hind-foot posture.

The first two of these adaptations can also be interpreted as derived characters relating to a fossorial lifestyle (4), particularly because *Ornithorhynchus* is also semifossorial (4). Given that *Ornithorhynchus* does not display a “reversed hind-foot posture” when walking on land (5), the presence of this feature in *Tachyglossus* is unlikely to reflect adaptation to an aquatic lifestyle. The hypothesis that echidnas arose relatively recently from an aquatic ancestor is here rejected; the fossil record instead indicates that echidna-like (3) and platypus-like (refs. 9–12 in ref. 1) lineages may have existed throughout the Tertiary and possibly well back into the Cretaceous. In addition, the inference that the radiation of echidnas represents “a recent expansion of niche space despite potential competition from marsupials” (1) is ignorant of the fact that the Tertiary marsupial fossil record of Australia is completely devoid of myrmecophages (2). An alternative hypothesis is offered: that a myrmecophagic (i.e., echidna-like) monotreme has occupied this niche in Australia (to the exclusion of marsupial taxa) since the Cretaceous.

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