



The enigmatic palaeoecology and palaeobiogeography of the giant, horned, fossil turtles of Australasia: a review and reanalysis of the data

Lauren E. Brown¹ & Don Moll²

¹School of Biological Sciences, Illinois State University, Campus Box 4120, Normal, Illinois 61790-4120, USA

²Department of Biology, Missouri State University, Springfield, Missouri 65897, USA

The distribution pattern of the bizarre Australasian giant, horned, fossil turtles of the clade Meiolaniidae has puzzled biogeographers since their discovery late in the nineteenth century. While their distribution suggests a Gondwanan origin, the lack of fossil evidence from key times and places has inhibited a better understanding of their dispersal pathways to Australia and the south-west Pacific islands in which their fossils have been found. Much palaeoecological speculation related to their dispersal capabilities, ranging from purely terrestrial to freshwater, estuarine, and saltwater lifestyles, has been proposed to explain their enigmatic presence across a wide swath of Oceania. Various lines of fossil, anatomical and ecological evidence now strongly suggest a highly terrestrial lifestyle, and we believe these traits, reinforced by an abundance of marine predators and ever-widening saltwater gaps between land areas during the Late Mesozoic and Tertiary, minimise the importance of saltwater dispersal as an explanation for the observed meiolaniid distribution pattern. Here we propose that the fragmentation of Gondwana provided the main dispersal vehicle for the meiolaniids and that land connections were also used to access suitable habitats and expand their range. The recently recognised continent of Zealandia, along with Australia, South America, and probably Antarctica, transported all known meiolaniid turtles to their present locations. However, ice cover on Antarctica, and the nearly total submergence of Zealandia in essence preclude the current likelihood of fossil discovery in these critical locations. The islands of New Caledonia, Tige (in the Loyalty Islands), Walpole, and Lord Howe served as refugia for Zealandia meiolaniids as the continent submerged.

Keywords: Meiolaniidae, horned turtles, fossils, Australasia, Gondwana, Zealandia, palaeoecology, palaeobiogeography

INTRODUCTION

The giant, horned, fossil turtles (Fig. 1) are among the most bizarre and largest terrestrial chelonians in the world. The Australasian forms (Meiolaniidae) have been found in eastern Australia and on islands in the south-west Pacific Ocean east of Australia. Fossils date from Mid to Late Eocene into the Holocene. The closest taxonomic relatives are often considered to be the frilled turtles (Cretaceous and Paleocene) of Argentina.

The meiolaniids are quite large. In *Meiolania platyceps* the maximum length was probably greater than 3 metres (Gaffney, 1996). However, the carapace and plastron are quite thin except in the marginal areas such as the peripherals (Gaffney, 1996). The carapace is only moderately domed, unlike the higher domes of the terrestrial, testudinid, giant tortoises (Ritchie, 1978). The most unusual anatomical character is the presence of enlarged cow-like horns on the skull which project posteriorly or laterally. The distance between the horn tips for *Ninjemys* is almost 70 cm (Orenstein, 2012). However, in *Warkalanian carinaminor*, horns are lacking, instead having a low horizontal ridge (Gaffney

et al., 1992). The skull is too massive to be withdrawn into the shell in all meiolaniids. The cervical vertebrae have long transverse processes (Boulenger, 1887) to attach or support muscles and ligaments to elevate, depress, and laterally move the huge head. Cervical ribs are absent in almost all other turtles (Gaffney, 1985). The tail is quite long with a club at the terminal end (Gaffney, 1985; Gaffney et al., 1992). A protective osseous sheath encases the caudal vertebrae. The tail is segmented and each ring bears a pair of stout spikes.

It is probable that the meiolaniids were potentially aggressive and very dangerous animals. Gaffney (1991:710) wrote "It is likely that the Pleistocene of Queensland had two, contemporary species of giant horned turtle wandering about, wreaking havoc". The horns and armoured tail may have been used for defence against predators (e.g. the large reptiles *Megalania* and *Quinkana*) or for pre-mating combat among males (as favoured by Jannel, 2015, based upon *M. platyceps* insularity and skull configuration), or both. The horns also may have been used to knock down vegetation for consumption.

Correspondence: Don Moll (donmoll@missouristate.edu)

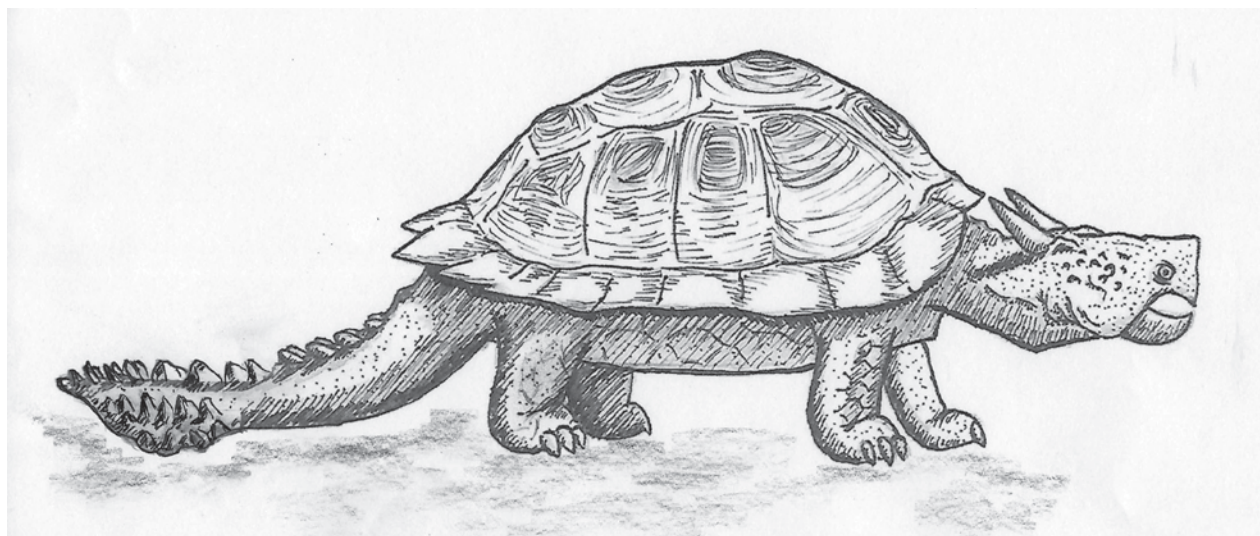


Figure 1. Reconstructed image of the giant, horned, fossil turtle (*Meiolania*). Drawing by Allyson Belcher, after Orenstein (2012) and by Janice Moll who portrayed the terminal tail club.

Many meiolaniid researchers have given their interpretation of the palaeoecology and palaeobiogeography of this group, particularly the mode of dispersal in relation to their geographical origin. However, there has been only one notable paper devoted to the palaeobiogeography of this fascinating group, in Mittermeier (1972) and in a slightly revised version in 1984. In the last 47 years, there has been considerable research on horned turtles. Herein, we review all research we found (to date) concerning their palaeoecology, dispersal, and biogeographical origin. Many possible explanations for the meiolaniid distribution patterns were provided with their merits and problems discussed.

The topics covered include taxonomy and distribution, convergent evolution, introduction by early humans, a brief history of perceptions concerning meiolaniid palaeoecology and dispersal modes, dispersal via water or land, requirements for successful colonisation, dispersal across land bridges, breakup of Gondwana, and the distributional significance of Zealandia for meiolaniid turtles.

METHODS

A comprehensive literature search was carried out following the methodologies of Brown et al. (2008); Moll & Brown (2017); and Brown et al. (2018). The search topics pertained to (1) the palaeontology of horned turtles, and (2) the geology of the breakup of Gondwana as well as the geological formation of islands in the south-west Pacific Ocean on which horned turtles have been found. We used a variety of search engines with numerous combinations of search words. Traditional searching for paper publications was carried out at Milner Library at Illinois State University. Some of these were on microfilm and many were from deep storage. In addition, the authors' extensive palaeontological and zoological libraries were searched. Interlibrary loan and I-Share were used frequently to obtain copies of publications

not available in the libraries heretofore mentioned. LEB translated from French to English the pages covering *Meiolania* in the Reptiles section of Dollo (1904). Everhart (2017) presented a translation of part of Dollo (1887).

RESULTS & DISCUSSION

Taxonomy and distribution

Gaffney (1996) and Sterli (2015) reviewed the species of meiolaniid turtles that have been described from Australasia. These include, with the known distributions, the following taxa:

- *Meiolania platyceps* Owen. Lord Howe Island, New South Wales, Australia (Gaffney, 1996).
- *Meiolania brevicollis* Megirian. Camfield Station, Northern Territory, Australia (Gaffney, 1996).
- *Meiolania mackayi* Anderson. New Caledonia, including Pindaï Caves on the main island, Tiga Island in the Loyalty Islands, and Walpole Island (Bauer & Sadlier, 2000).
- *Meiolania damelipi* White, et al. Teouma on Efate Island, Vao and Uripiv islands, Vanuatu; Naigani and Viti Levu islands, Fiji (White et al., 2010; Hawkins et al., 2016).
- *Ninjemys oweni* Woodward. Eastern Darling Downs, southern Queensland, and New South Wales, Australia (Gaffney, 1996).
- *Warkalania carinaminor* Gaffney, et al. Riversleigh Station, north-west Queensland, Australia (Gaffney, 1996).
- Gaffney (1996) reported localities of additional meiolaniid records of indeterminate identification from Queensland, New South Wales, and South Australia.
- Validity of the species names *mackayi* and *damelipi* was questioned by several workers (e.g. Gaffney, 1996; White et al., 2010; Sterli, 2015; Hawkins et al., 2016). Sterli (2015) indicated that *damelipi* was "not meiolaniid". Future research may further demonstrate these names to be erroneous.

In summary, there are three genera and 4-6 species of meiolaniids known from Australasia. The species have been reported from eastern Australia, Lord Howe Island, Tiga Island, Walpole Island, New Caledonia, Vanuatu, and Fiji.

Convergent evolution

Convergent evolution (or parallelism) has been frequently cited as an option for similarities of two biogeographically separated groups, but it was in most cases an explanation of last resort when nothing else seemed convincing. Simpson (1938) and Mittermeier (1972, 1984) were the only authors we found that suggested convergent evolution to explain similarities of the Australasian horned turtles and the frilled turtles of Argentina, but they presented no evidence. Basically, one needs to demonstrate the two groups do not have a common ancestor, which is very difficult because of lack of fossils. We found no evidence for or against convergent evolution in these turtles. The South American and Australasian forms have been treated as relatives within the clade Meiolaniformes (Sterli, 2015; Sterli et al., 2015).

Introduction by early humans

Bauer & Vindum (1990) suggested that meiolaniids may have been introduced into New Caledonia by humans, but we found no evidence that this occurred. However, this possibility should not be dismissed, even though there are several reasons described below why this activity seems unlikely. Presumably the reason for the human introduction would have been as a source of food. The capture and transport by boat of the 3 m long heavily armoured meiolaniids would have been particularly dangerous for humans. Young individuals of both sexes would have been the easiest and safest way to introduce the turtles, but due to typical turtle life history characteristics, including high juvenile mortality, slow growth, and slow generation times (~30 years in extant, testudinid, giant tortoises), it is unlikely that simple translocation and domestication would have been possible (Swingland & Coe, 1979; Cheke et al., 2017). In addition, larger reproductive adults probably could not have been harvested in turtle populations if the population was to remain viable (Congdon et al., 1993, 1994) and repeated introductions of new individuals from established populations would have been necessary to shore up population numbers. Another consideration is that translocated adult turtles may often quickly move out of the release area as observed by Sosa & Perry (2015) with ornate box turtles (*Terrapene ornata ornata*). They found that juveniles were more likely to remain closer to the release area than adults. Other studies have also shown similarly low release site fidelities for adult box turtles translocated into natural habitats (e.g. *T. ornata*: Doroff & Keith, 1990; and *T. carolina*: Cook, 2004; Hester et al., 2008).

However, a higher percentage of captive-bred juvenile ploughshare tortoises (*Astrochelys yniphora*) remained near their release site in studies conducted in Madagascar (Mandimbihasina & Woolaver, 2014). Although most

extant terrestrial turtles establish relatively small home ranges and usually return to them if displaced, some adult box turtles are considered transients and seem to wander over relatively long distances without ever establishing home ranges (see Dodd, 2001 for a review). We can only speculate upon the behaviour of meiolaniids which may have been transported long distances and translocated from a distant home to which they could never return. Perhaps we can gain some insight from “rewilding” projects in progress in some of the western Indian Ocean islands that involved the translocation of giant Aldabra tortoises (*Aldabrachelys gigantea*) and radiated tortoises (*Astrochelys radiata*) to other islands, hopefully to provide ecosystem characteristics once available to the now extinct native species (Cheke & Bour, 2014; Griffiths, 2014). The translocated species seem to be adapting successfully to their new homes in several of these locations (Griffiths, 2014), so it is possible that the meiolaniids adapted similarly to their translocation sites.

During the Holocene, the people of the Lapita culture became the first humans to colonise New Caledonia, Fiji, and Vanuatu (White et al., 2010). They were avid hunters of Meiolania and bones (some burnt) have been found in archaeological middens, possibly from turtles killed and transported from other locations (White et al., 2010; Orenstein, 2012; Hawkins et al., 2016). The Lapita seemed to prefer Meiolania over sea turtles (Orenstein, 2012). Hogs were introduced and raised for food by them (Orenstein, 2012), but we found no evidence of any attempt to keep meiolaniids in captivity or to domesticate them. Although people of archaic and extant cultures are known to keep freshwater turtles, sea turtles, and tortoises in captivity for food and other purposes (e.g. Parsons, 1962; Moll & Moll, 2004; Bell et al., 2005; Cheke & Bour, 2014) it is difficult to imagine the challenges that would have confronted the Lapita in domesticating or merely keeping in captivity adult, horned turtles as a source of food. The potential dangers of maintaining these formidable animals as well as the difficulties and time required to raise a “crop” to maturity due to the life history characteristics of most known turtles (see above) would have likely precluded domestication. Moreover, the questionable species identification of the turtles (*M. damelipi*) on Vanuatu and Fiji suggest the possibility that it could have been a more docile form (perhaps similar to extant, giant testudinids) that could have been more easily kept in captivity. Nevertheless, we found no evidence that the Lapita ever tried to keep in captivity or domesticate the turtles of questionable identity (*M. damelipi*) in Vanuatu and Fiji, although they hunted them avidly and travelled widely in search of better hunting grounds as more local stocks were depleted (White et al., 2010; Kinaston et al., 2014; Hawkins et al., 2016). It is reasonable to suggest that human hunting played an important role in the extinction of meiolaniids and other turtles elsewhere throughout the world during the Holocene.

History of perceptions concerning meiolaniid palaeoecology and dispersal modes

There has long been controversy as to whether this

group could have dispersed in water or if they were strictly terrestrial. Early researchers suggested they were terrestrial (Boulenger, 1887; Baur, 1889; Dollo, 1904) with Woodward (1901) indicating they were “truly” terrestrial or marsh dwelling. Anderson (1925) followed, suggesting they were probably strong swimmers, but also indicated terrestrialism. In 1926 Anderson again vacillated between marine, river, marsh, estuarine, shore-living, and land dwelling habitat, but by 1930 he indicated *Meiolania* was terrestrial.

Starting in 1925 and lasting nearly to the present there has been a series of papers all proposing that these turtles were capable of swimming, floating, walking, wading or drifting in water (e.g. McCulloch [in Anderson, 1925]; Anderson, 1925; Simpson, 1938, 1940; Paramonov, 1958; Fletcher, 1960; White et al., 2010; Orenstein, 2012; Sterli, 2015; Hawkins et al., 2016; Cheke et al., 2017; Lichtig & Lucas, 2018a, b). Many other publications suggested that the horned turtles were adapted for terrestrial life (e.g., Sutherland & Ritchie, 1974; Ritchie, 1978; Pritchard, 1979; Molnar, 1984; Gaffney, 1991; Molnar, 1991; White et al., 2010; Kinaston et al., 2014; Heinsvig, 2015; Jannel, 2015; Paulina-Carabajal et al., 2017).

Lichtig & Lucas (2018a, b) contradicted the most recent majority viewpoint supporting terrestrialism which is based upon evidence cited herein, and summarised in their own papers. They primarily employed an analysis based upon shell dimension ratios purported to identify whether extant and extinct chelonians were aquatic or terrestrial (Lichtig & Lucas, 2018a, b). They also examined the morphology of the forelimbs and femurs of *M. platyceps* for comparison with other chelonians. According to their analyses, *M. platyceps* was aquatic and was probably a bottom-walker similar to extant common snapping turtles (*Chelydra*) and alligator snapping turtles (*Macrochelys*).

We found no other information concerning aquatic habitat preferences for Australasian meiolaniids. We reject the conclusions of the Lichtig & Lucas (2018a, b) based upon the following considerations: 1) The use of ratios in statistical analyses is problematic in numerous respects that can lead to the misinterpretation of data and Allison et al. (1995), advocate that investigators should use regression-based approaches as alternatives; 2) The single meiolaniid specimen included in the Lichtig & Lucas (2018a, b) studies is itself a reconstructed composite specimen derived from skeletal elements obtained from multiple *M. platyceps* from Lord Howe Island (Burke et al., 1983). The main specimen used in the model had been found in an incomplete state (~60 % complete, including only three fragments of carapace), was damaged in initial recovery efforts, and again in the reconstruction effort itself (Burke et al., 1983). Lichtig & Lucas (2018a, b) relied upon the reconstruction by Gaffney (1996) of the limb proportions described in Joyce & Gauthier (2004), and on images provided by Juliana Sterli (Lichtig & Lucas 2018a, b) to guide the development of their model. Lichtig & Lucas (2018a) admit that “working from reconstructions is not ideal, and an inherent result of this is the dependence of our results on the accuracy of the used reconstructions”. We

conclude that the use of a single composite specimen with shell damage and reconstruction from multiple sources, and with the inherent problems associated with the use of images and reconstructions is very problematic. The shell proportions used in the development of the critical ratios employed in habitat prediction are potentially unreliable, and therefore, suspect as a result. Even if the ratios obtained are considered valid only one (of two) meiolaniid shell ratios calculated by Lichtig & Lucas (2018a, b) suggests an aquatic lifestyle (i.e., the carapace width to plastron width ratio). The small sample size for *M. platyceps* greatly exaggerates the problems with their analysis (Matt Dugas, pers. comm.). In addition, the model specimen used for the analyses was relatively small, probably juvenile (Burke et al., 1983), and possibly with different shell proportions than adults, as is the case with many extant turtles and tortoises (Ernst & Lovich, 2009). Thus, its comparison with the adult chelonians used in the (Lichtig & Lucas, 2018a, b) analysis is not valid. An even more serious problem related to comparing shell proportion/ratios between meiolaniids and other chelonians is that the meiolaniids are evolutionarily and structurally archaic and unique among chelonians. They are arguably neither cryptodires nor pleurodires, and could represent a stem group more basal than any extant turtle suborder (we even question their inclusion in the Testudinata as currently defined); 3) The morphology of the forelimbs and femora of *Meiolania* are, of course, subject to individual and ontogenetic variation also, and a larger series than those that can be contributed by one composite specimen is necessary for valid, meaningful conclusions concerning their functional significance.

Under the circumstances, we reject the Lichtig & Lucas (2018a, b) reinterpretation of the habitat and lifestyle of *M. platyceps* as it does not rise to the level of the aphorism that “extraordinary claims require extraordinary evidence” (Deming, 2016). The evidence they provided is inadequate to support the radical changes in viewpoint they promote. These problems and uncertainties dictate caution in reinterpreting the habitat and lifestyle of *M. platyceps* in particular, and meiolaniids in general.

Very little information is available to precisely define preferred terrestrial habitats for Australasian meiolaniids either, although *M. platyceps* of Lord Howe Island has been proposed to be a beach dweller based on discovery of some fossils in aeolian calcarenite strata (i.e. indurated coral-sand rock common in coastal areas of the south-west Pacific and elsewhere initially deposited by aeolian processes [Etheridge, 1889a in Jannel, 2015]). Beaches are often difficult environments thermally and in terms of resource availability, however, and if they lived there they must have been well adapted for life in arid conditions as suggested by Paulina-Carabajal et al. (2017). The unusual elongation of the vestibulum of the nasal cavity in *M. platyceps* was also observed in iguanid lizards specialised for desert life as it limits the possibility of sand grains entering the nose (Parsons, 1959). A windy beach habitat would seem to be conducive to the evolution of such an adaptation. Alternatively, it is possible that meiolaniids used beaches for nesting, but lived elsewhere during

other stages of their life history. Meiolaniid egg clutches have also been found in calcarenite on Lord Howe Island, and many other extant reptiles are known to inhabit other, sometimes distant, habitats in non-reproductive periods before returning to beaches to nest (e.g. green iguanas, *Iguana iguana*, [Hirth, 1963]; painted terrapin, *Batagur borneoensis*, [Dunson & Moll, 1980]; all sea turtles, [Ernst & Barbour, 1989]; Central American slider turtle, *Trachemys venusta*, [Moll, 1994]).

Studies of neck vertebrae flexibility, the heavy, horn-bearing head, the suspected mass of soft tissue in the dorsal region of the neck, and the projecting anterior margin of the carapace of *M. platyceps* suggest that it was probably, primarily a terrestrial grazer, bending its neck downward to feed on fallen palm fruits, ferns and other herbaceous vegetation rather than raising it to browse (Heinsvig, 2015; Jannel, 2015). Jannel (2015) suggested it could have browsed occasionally however (perhaps on low hanging vegetation). Due to the stable, mild climate of Lord Howe Island during *M. platyceps*' tenure there an abundant and predictable food supply would have been present (Jannel, 2015). *Meiolania platyceps* probably wandered across the island searching for new food supplies which became seasonally available in different locations. Paulina-Carabajal et al. (2017) suggested the possibility that *M. platyceps* could have had acute olfactory capabilities, based upon analysis of its endocranial morphology. If so, this could have been important in identifying and locating new food sources as they appeared (Heinsvig, 2015; Jannel, 2015).

Isotopic evidence from Vanuatu (*M. damelipi*, which may not be meiolaniid; Sterli, 2015) supports the view that ?*M. damelipi* was terrestrial, herbivorous to omnivorous, may have utilised foods under a forest canopy, and possibly also used mangrove habitats as foraging sites (Kinaston et al., 2014).

Dispersal via water or land

Based upon the totality of the evidence presented above, and because all meiolaniid fossils have been found in terrestrial strata and locations, we strongly support the terrestrial niche concept for the Australasian meiolaniid turtles. In particular, we conclude that several specialised adaptations of meiolaniids could have made sea travel, and therefore continent and island colonisation by saltwater dispersal, nearly impossible for them. Most importantly, the skulls of meiolaniids are huge, well ossified, strongly ankylosed (Sterli, 2015), and adorned with horns or ridges, all of which would have made them extremely heavy and non-retractable into the shell (Heinsvig, 2015; Jannel, 2015). The neck of meiolaniids is quite rigid and is probably linked to the need to support the massive, heavy skull (Heinsvig, 2015; Jannel, 2015). It has somewhat greater flexibility in a downward plane than in an upward plane, probably related to its grazing, feeding style (Heinsvig, 2015; Jannel, 2015). All of these skull and neck characteristics would have driven the head end of the floating animal into and under the water as the neck muscles tired and extension of the neck upward to allow the turtle to see and breathe would have quickly become more difficult. The limbs and feet

were more similar in structure to those of the extant, terrestrial, testudinid tortoises, although the feet have been described as “ridiculously dainty” (Burke et al., 1983). Others have also noted the small size of the limbs (Sutherland & Ritchie, 1974; Sterli, 2015). They were not similar to the large, paddle-like forelimbs of extant sea turtles or the extant, estuarine pig-nosed turtle (*Carettochelys insculpta*). Therefore, efficient forward or upward propulsion would not have been possible for any extended period of time in water for meiolaniids. The extremities were probably covered with heavy osteoderms (Sterli, 2015). The shell is relatively thin and the carapace of meiolaniids is more oblong and lower domed than in the extant, testudinid tortoises (Ritchie, 1978). Therefore, the meiolaniid shell would have trapped less air and would not have increased buoyancy. Posteriorly, the long, osseous, sheathed tail with a heavy terminal club would have acted as a sea anchor. We conclude that these adaptations, undoubtedly useful in their terrestrial life, would have caused them to sink and drown after a short period of immersion in deep water. Lichtig & Lucas (2018a) considered *M. platyceps* to be negatively buoyant and would have sunk if immersed in water. The influence of turbulent seas, strong currents and winds, and thermal stress from sun exposure would have exacerbated the problems of flotation and movement in saltwater for these terrestrially adapted species. It seems unlikely that an overturned meiolaniid turtle could have righted itself, especially under the kinds of suboptimal conditions described above, and it would have surely drowned. A turtle fortunate enough to survive and stay upright long enough would soon have been afflicted by the debilitating physical and physiological impairments related to prolonged saltwater immersion (e.g. destruction of the nasal and alimentary canal epithelia, damage to the cornea of the eye). Furthermore, if the turtle drank the sea water it would have developed blood plasma ionic stress which requires a huge amount of energy to rectify, if even possible (Craig Gatto, pers. comm.).

Natural rafting, a saltwater dispersal mechanism suggested for meiolaniids by Mittermeier (1972, 1984), and by many other biogeographers for other species (see Darlington, 1963; Udvardy, 1969) would have theoretically allowed them to avoid many of the problems associated with immersion and movement through saltwater, but their great size and weight would have required a very large and unusually sturdy raft to transport them over long distances. Juvenile meiolaniids might have been more likely to successfully raft to suitable locations because of their smaller size, but their non-reproductive condition, vulnerability to predation, and the long generation times with delayed maturation typical of many turtles and tortoises (Congdon et al., 1993, 1994) would probably have reduced their chances for successful colonisation compared to adults.

Stepping stone dispersal was proposed by Anderson (1926) as another means of dispersal of meiolaniids. A variant of this, the escalator hopscotch model (McKenna, 1983), was also proposed for meiolaniids by Gaffney (1996). These would have required eliminating water

gaps between the mainland and islands by lowering sea levels and dispersal would have presumably been quite slow across the archipelago.

Ironically, extant, giant, testudinid tortoises are known to drift in saltwater and successfully cope with the harsh environmental conditions long enough to occasionally reach land and potentially colonise suitable habitats (e.g. Galapagos Islands, Mascarene Islands, and Seychelles Islands). Townsend (1936) reported two extant, giant tortoises (*Chelonoidis nigra* species complex) adrift 20 miles (~32.2 km) from land in the Gulf of Florida that had escaped from a captive colony. The presumption was that they were swept out to sea by a hurricane. Subsequently, Gerlach et al. (2006) reviewed a number of cases of Aldabra giant tortoises (*Aldabrachelys gigantea*) floating around Aldabra Atoll and in the open sea of the western Indian Ocean. Gerlach et al. (2006) also reported the first substantiated evidence of trans-oceanic dispersal by *A. gigantea*. In 2004 a female tortoise was found walking out of the Indian Ocean at Kimbiji, Tanzania. The animal was emaciated and had an excessive number of goose-necked barnacles, particularly on the lower limbs and carapace suggesting a long period of time spent at sea. Close examination of the tortoise indicated it was probably from Grande Terre, Aldabra Atoll. This tortoise had travelled a remarkable 740 km across the western Indian Ocean.

Testudinid tortoises and meiolaniids share a number of structural characteristics that are probably similar due to terrestrial lifestyles (e.g. walking and herbivory). However, there are several important differences between testudinid tortoises and meiolaniids that affect their seaworthiness. The testudinids have smaller, lighter retractable heads and tails than meiolaniids. Furthermore, testudinids have an elongated flexible neck which allows them to easily raise their head above water. The higher and thicker domed carapace of testudinids probably protected them from predators and contained more of an air pocket which enhanced their buoyancy. The shell shape in association with these other factors gives the testudinids a centre of gravity that enhances stability in water. Also, their ability to survive without food or freshwater for long time periods (Moll & Brown, 2017) adapts them for greater survivorship at sea than would otherwise be the case.

Mittermeier (1972, 1984) suggested that meiolaniid turtles might have had marine ancestors which have not yet been identified in the fossil record. If correct, they could have dispersed to their known locations via sea travel and subsequent terrestrial travel. This has also been proposed in other turtle groups (e.g., podocnemidid turtles). Until relevant, marine-adapted fossil forms should appear, it seems prudent to remain cautious concerning marine dispersal explanations for meiolaniid distribution patterns, and favour terrestrial dispersal pathways.

Immediately upon entering saltwater, meiolaniids would have also been exposed to the onslaught of a variety of turtle predators of the marine environment (see below). In order to move the head sideways during attack or defence, the feet of meiolaniids had to have

been firmly stabilised on the ground (Jannel, 2015). If swimming or drifting in water, such stability would have been non-existent. Moreover, movements of the non-retractable head and tail would have been slower because of the density of the water. These factors plus the thinness of the shell (e.g., Gaffney, 1996, *M. platyceps*) suggest that Meiolania would have been nearly defenceless if attacked by predators in water.

There were numerous carnivorous species of ancient oceanic animals that could have preyed on turtles, including horned turtles (if present). However, we found only one reference (Orenstein, 2012) that mentioned possible oceanic predation on meiolaniids (by Pacific, marine crocodilians). There are three groups, mosasaurs, sharks, and crocodilians that stand out as threats because of abundant evidence that they aggressively preyed on turtles (e.g. Dollo, 1887; Carr, 1940; Loveridge, 1946 [1974]; Neill, 1971; Cogger, 1975; Carpenter & Lindsey, 1980; McCoy, 1980; Erickson, 1984; Mazzotti & Dunson, 1989; Ellis, 2003; Karl & Tichy, 2004; Gandola et al., 2006; Fernández & Gasparini, 2008a, b; Ernst & Lovich, 2009; Schwimmer, 2010; Milàn et al., 2011; Erickson et al., 2012; Main et al., 2012; Amalfitano et al., 2017; Everhart, 2017; Scheyer et al., 2018).

The problem of successful colonisation

All successfully dispersing organisms must cope with the difficult and diverse problems posed by a newly entered habitat if successful colonisation is to be realised. Carlquist (1974) stated that “island elements are present in proportion to not only dissemination ability, but also to establishment ability”, and that the “difficulties of establishment seem much greater than those of transport”. MacArthur (1972) summarised many of the problems of island colonisation. These statements are scarcely different for the colonisation of continental habitats, except that dispersers arriving via terrestrial routes may often arrive in less weakened and emaciated condition than those drifters, swimmers, or rafters that have endured prolonged exposure to saltwater en route. Nevertheless, probably only a fraction of arrivals in either category manage to establish a successful colony in any case (Carlquist, 1974). Carlquist (1974) provided examples of some of the traits that influence success (or not). Australasian meiolaniids, present on both islands and the Australian continent, would seem to have had a colonisation advantage over many other dispersers since they could slowly adapt to changing climatic conditions and habitats, and forage as they rode their Gondwanan continental fragments to their final destinations without ever having to get their feet wet. The mechanisms that we presume allowed this to occur are explained in more detail below.

As a result of the factors described above we reject long distance dispersal via water as an explanation for Australasian meiolaniid distributions in all its forms that have been proposed. We support the view that the Australasian meiolaniid distribution pattern resulted solely from terrestrial movements of meiolaniids and/or their ancestors passively via the fragmentation of Gondwana and drifting of derivative continents, as well

as actively via the use of land connections when and where available.

Unlike other non-tortoise, giant, armoured species, such as ankylosaurid dinosaurs and the glyptodont mammals which were restricted to continents and perhaps a few continental islands (Olivero et al., 1991; Palmer, 1999; Arbour & Currie, 2016; Dixon, 2016), the meiolaniids were able to become established on a few remote Pacific islands. Their presence there has been one of the great enigmas of Pacific palaeobiogeography, and the need for an explanation of their presence has undoubtedly influenced the judgment of many meiolaniid researchers to envision aquatic capabilities for a group that is clearly highly specialised and ill-equipped for anything other than terrestrial life and dispersal. We propose a more likely explanation for meiolaniid presence on these islands below.

Dispersal across land bridges and breakup of Gondwana

During the 19th and 20th centuries, a plethora of biogeographers indiscriminately suggested the presence of land bridges in attempting to resolve the evolutionary history of organisms with puzzling geographical distributions. Many of these “bridges” were transoceanic, and the authors did not take into consideration the geology of the regions. Thus, they often should not be considered as viable hypotheses.

Over 100 years ago, (Moreno & Woodward, 1899) suggested that the discovery of *Miolania* (sic) on Lord Howe Island, Queensland, and Patagonia favoured the hypothesis of a former great Antarctic continent of which Australia and Patagonia were a part. Woodward (1901) was apparently the first to suggest an ancient land bridge connecting Australia, Antarctica, and South America across which *Meiolania* could have dispersed. Other researchers (e.g. Dollo, 1904; Anderson, 1926; Fletcher, 1960; Mittermeier, 1972, 1984; Molnar, 1991) agreed with this concept. Mittermeier (1972, 1984) stressed that the turtles could have passed in either direction. This 100+ year old concept became the precursor of the most recent research on the geographic origin of this turtle group.

There is a huge literature on the breakup of Gondwana that is beyond the scope of this paper to review. However, an excellent detailed description by Lomolino et al. (2017) is readily available. In this section, we summarise (after Lomolino et al., 2017) the breakup of this vast supercontinent and address problematic issues of palaeobiogeographic significance to the evolution of meiolaniids.

The landmass Gondwana separated from the much larger Pangea during the Jurassic (Lomolino et al., 2017). The original Gondwana consisted of the present day continents Africa, South America, Australia, Antarctica, Zealandia (including New Zealand), and India, as well as Madagascar. The breakup began with splitting off of South America and Africa from the rest of Gondwana. This was followed by the rifting of India and Madagascar from Gondwana. Lastly Australia and Zealandia rifted from Antarctica. The entire process probably lasted for a time span from ca. 160 mya to 80 mya years ago. The

speed of rifting varied. India's northward migration was particularly fast (Lomolino et al., 2017). The direction of continental movement could have also been reversed. For example, Africa reunited with remnants of Gondwana and then rifted away a second time (Lawver et al., 1992).

The regions that were to become the future continents Australia, Antarctica, and South America were aligned in a row (with Antarctica in the middle) early in the history of Gondwana. Zealandia was connected to and adjacent to west Antarctica at this time (Mortimer et al., 2017).

Several researchers (e.g. Mittermeier, 1972, 1984; Gaffney, 1996; Sterli, 2015; Sterli et al., 2015) suggested that the breakup of Gondwana might have been involved in the distribution and evolution of horned and frilled turtles in Australasia and South America. We propose that Zealandia played a similar role for Australasian meiolaniids.

Mittermeier (1972, 1984) suggested the possibility that Antarctica (in the middle position) was the region of origin of meiolaniids. The dispersal-extinction-cladogenesis model (DEC) used by Sterli & de la Fuente (2013); Sterli (2015); and Sterli et al. (2015) also suggested Antarctica as an area of origin. However, they were reluctant to designate Antarctica as such because no fossil meiolaniids have been found there, and because of the scarcity of fossil turtles in the Cretaceous and Paleocene of Australia. Instead they considered South America as the more likely place of origin. Meiolaniid ancestors could have moved through and into the other, future continents from South America while all were connected, or in either direction if Antarctica turns out to be the centre of origin. Then they could ride with these land areas to their future locations as the continents continued to fragment and drift. The opportunities for vicariance in the populations inhabiting the separating fragments would be enhanced as they rifted further apart over time. The problems of determining the true place of origin might be resolved if the melting of considerable ice on Antarctica, resulting from extensive climate warming, allows more exploration for fossils there in the future.

Another problem concerns the dating of the rifting of South America from the remainder of Gondwana. Lawver et al. (1992) and Lomolino et al. (2017) indicated it occurred during the Mid to Late Jurassic (160 mya) which made it the first continent to break away from Gondwana. However, Sterli et al. (2015) followed Woodburne & Case (1996) and Lawver et al. (2011) indicating the separation occurred in the Early Eocene along the Eocene-Oligocene boundary (this was after the Cretaceous when the oldest fossil frilled turtles were found). This timing would have made the separation the final stage of the breakup of Gondwana. Other researchers (e.g., Royer & Sandwell, 1989; Blakey, 2008) indicated the separation occurred during the Mid Cretaceous. These extreme differences may reflect disparity in methodologies used. In effect, they represent the use of different proxies. Moll & Brown (2017) discussed the problem of inappropriate use of proxies. For instance, at a Quaternary site in southern Illinois, USA, no consensus was reached after nine methods were used over 25+ years to date the site (Curry et al., 2011; Blackwell et al., 2016).

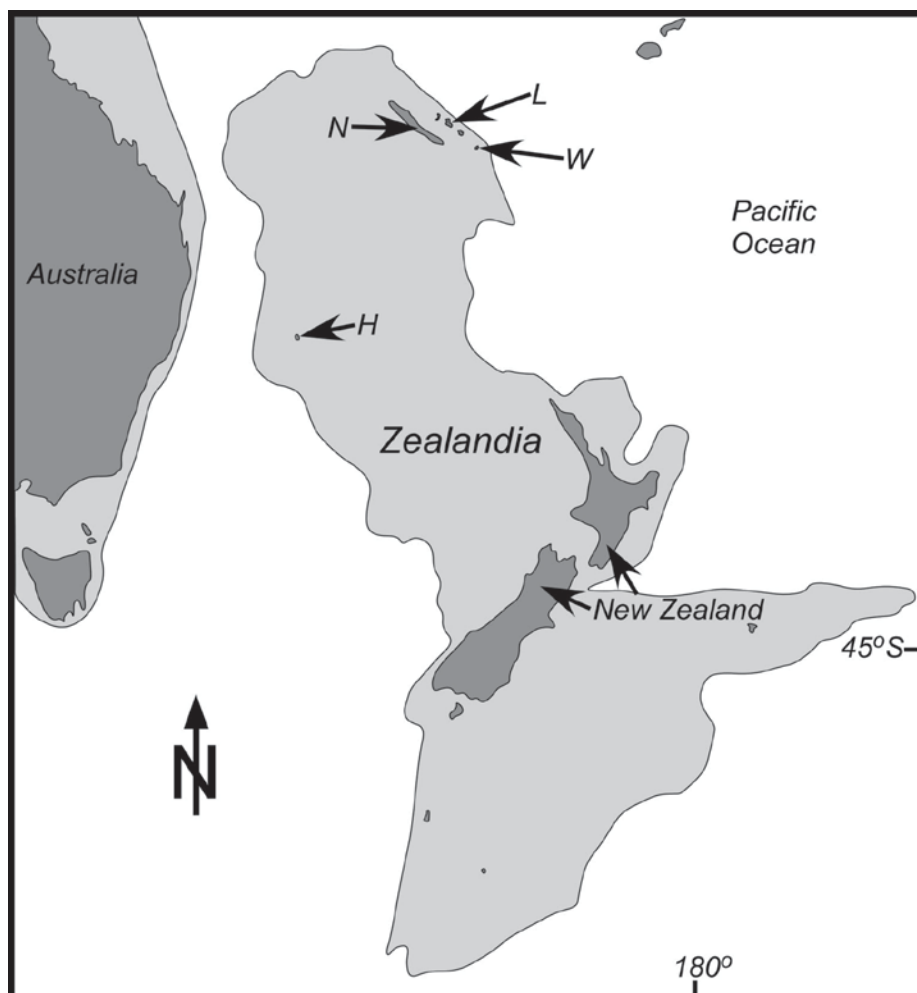


Figure 2. Map of the position of the mostly submerged continent of Zealandia showing emergent localities where fossil *Meiolania* were found. “N” designates New Caledonia; “H” designates Lord Howe Island; “L” designates the Loyalty Islands (arrow points to Tiga Island); “W” designates Walpole Island. Cartography by Dave Malone.

The timing of separation of continents has important implications for interpretation of the palaeobiogeography of horned turtles. Forty-seven years ago Mittermeier (1972) succinctly pointed out: “If common ancestors were not present in the continents in question before they split (and fossil evidence available at this time suggests that they were not) then it becomes most difficult to explain the distribution patterns of these turtles solely by continental drift”.

Distributional significance of Zealandia for meiolaniid turtles

Zealandia is a large mostly submerged continent (Fig. 2) east of Australia that has been recently recognised as such. Mortimer et al. (2017) presented a convincing argument that Zealandia is indeed a continent. Zealandia’s defining characteristics include elevation, geology, and crustal structure, as well as limits and area. Among the more important attributes are the presence of igneous, metamorphic, and sedimentary continental rocks, whereas oceanic crustal rocks are basalt and gabbro. In size, Zealandia is 4,500,000 km² of continental crust (Bache et al., 2014). At present it is 94 % submerged (Mortimer et al., 2017). It was part of Gondwana that was originally adjacent to present day West Antarctica.

The separation of Zealandia from Gondwana occurred between the Late Cretaceous to the Eocene (Bache et al., 2014; Mortimer et al., 2017). Isostatic balance and thermal relaxation led to Zealandia’s eventual submergence (Mortimer et al., 2017). New Caledonia, the Loyalty Islands, Walpole Island, and Lord Howe Island as well as New Zealand now occur as projections of Zealandia above the ocean surface (Fig. 2). The distribution of meiolaniids on these islands may reflect a past wider distribution on Zealandia, and the islands’ use as refugia when Zealandia submerged. There are many other archaic species resident in New Caledonia and Lord Howe Island (especially plants) that are also not recognised as good saltwater dispersers (Carlquist, 1965). Many probably were stranded there in similar fashion to the meiolaniid turtles. Fossil remains of a large, terrestrial turtle of early Miocene age were discovered on the South Island of New Zealand (a Zealandia remnant) also (Worthy et al., 2011), but its taxonomic designation remains uncertain (Sterli, 2015).

The islands of Vanuatu and Fiji occur north and north-east of Zealandia. The fossil turtles of these islands were thought to be ?*M. damelipi*, White et al. (2010). However, the identification of these fossils has been seriously questioned by White et al. (2010); Sterli (2015),

and Hawkins et al. (2016). It is very unlikely that they are even meiolaniids (Sterli, 2015). Thus, the locality records of this “species” of *Meiolania* from Vanuatu and Fiji may likewise be invalid.

CONCLUSIONS

Mittermeier (1972, 1984) argued that the lack of fossils at the right times and places casts doubt upon the importance of Gondwana fragmentation and drift as an explanation for the meiolaniid distribution pattern in Gondwana-derivative continents and islands. We submit that the absence of fossils from critical times and locations is frustrating, but it does not disqualify the fragmentation/drift-land connection scenario as the principal driving force resulting in the meiolaniiform distribution pattern as we see it today. A major problem is that it is often difficult to identify the critical times and places that relate to meiolaniid dispersal because there is still very imprecise understanding of the fine timing of fragmentation and rift (due to different methodologies and proxies employed [see above discussion under Dispersal across land bridges and Breakup of Gondwana]), and, also an inadequate knowledge of movement and interaction of rifting land masses and connections over shorter time frames. A better grasp of these issues would help to narrow down the best locations and time periods to search for critical meiolaniid fossils. We also stress that the critical locations from which relevant fossils have not been found, ice-covered Antarctica and submerged Zealandia, are among the most difficult places on earth in which fossiliferous strata could be investigated. Where critical locations and strata are accessible for exploration (e.g. South America and Australasia) meiolaniid fossils have been found.

Since sea travel is not a viable option to explain the meiolaniid distribution pattern then what explanation remains? The simplest explanation, with what we know now, is the Gondwana fragmentation/rift hypothesis, and terrestrial movement when and where possible. The recognition of the continent of Zealandia, its submergence, and its geographic location encompassing the south-west Pacific islands where meiolaniid fossils have been found provides a simple resolution to the formerly insoluble enigma of explaining their presence in these remote, insular locations.

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