

A Review of the Fossil Record of Gondwanan Turtles of the Clade *Meiolaniformes*

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ABSTRACT

Gondwanan turtles of the clade *Meiolaniformes* have a fossil record that reaches back to the Early Cretaceous of Patagonia (South America) and Australia. From the Late Cretaceous to the Middle Eocene the group is restricted to Patagonia, but appears to be extirpated afterwards. However, the fossil record of the clade commences once again in the Late Oligocene in Australia and surrounding islands and continues until the Holocene. Current phylogenies recognize *Meiolaniidae* as a subclade within *Meiolaniformes*. Early meiolaniforms show terrestrial adaptations, but their dietary preferences remain unclear. Meiolaniids, in contrast, show strong terrestrial adaptations, were herbivorous and appear to have been preadapted to floating across short to intermediate oceanic distances. A taxonomic review of the group concludes that of the 15 named taxa, 11 are nomina valida, 3 are nomina invalida and 1 is not recognized as a meiolaniid.

KEYWORDS

Anatomy, phylogeny, biogeography, paleoecology, *Meiolaniformes*, *Meiolaniidae*, Mesozoic, Cenozoic

Introduction

The name *Meiolaniformes* Sterli and de la Fuente, 2013 is defined as belonging to the branch-based clade including all taxa more closely related to *Meiolania platyceps* Owen, 1886 than to *Pleurodira* Cope, 1865 or *Cryptodira* Cope, 1868 (Sterli and de la Fuente 2013). The large exposure of the prefrontal on the skull roof, the absence of the frontal in the orbit, a well-developed processus pterygoideus externus and a well-developed crista supraoccipitalis, among others, diagnose various fossil turtles as belonging to this group (Sterli and de la Fuente 2013). The clade *Meiolaniformes* is primarily (perhaps entirely, see below) a Gondwanan clade and its known fossil record spans more than 125 million yr from the Early Cretaceous to the Holocene (Gaffney et al. 1984; Gaffney et al. 2007). The oldest known members are *Chubutemys copelloi* Gaffney et al., 2007 and *Otwayemys cunicularius* Gaffney et al., 1998 from the Aptian/Albian of Patagonia and the Albian of Australia, respectively (Gaffney et al. 1998; Gaffney et al. 2007). The youngest members are

Pleistocene and Holocene forms from Australasia (Gaffney et al. 1984; Gaffney 1996). White et al. (2010) reported the presence of meiolaniforms from the Holocene of Vanuatu (southern Pacific), but the assignment of these turtle remains to this clade is questioned herein (see Systematic Paleontology below).

The taxonomic and biogeographic extent of the clade *Meiolaniformes* is still under debate. In addition to an uncontroversial assemblage of taxa from the southern continents (e.g., Hirayama et al. 2000; Gaffney et al. 2007; Joyce 2007; Sterli and de la Fuente 2011a, 2013; Anquetin 2012; Sterli, Pol et al. 2013; Sterli et al. 2015), an eclectic mix of fossil turtles from the northern continents have occasionally been assigned to this clade as well, including *Mongolochelys efremovi* Khosatzky, 1997 from the Late Cretaceous of Asia (e.g., Hirayama et al. 2000, but see Gaffney et al. 2007), *Naomichelys speciosa* Hay, 1908 from the Early Cretaceous of North America (Anquetin 2012, but see Joyce et al. 2011), *Kallokibotion bajazidi* Nopcsa, 1923 from the Late Cretaceous of Europe (e.g., Sterli, Pol et al. 2013, but see Joyce 2007 or Anquetin 2012) and the enigmatic

taxon Sinochelyidae Čkhikvadzé, 1973 from the Late Cretaceous of Asia (Hirayama et al. 2000, not included in other studies). Future studies will perhaps confirm that most, if not all of these taxa indeed belong to Meiolaniformes and that this clade once possessed a global distribution. However, future analyses may also show that these taxa form a paraphyletic or polyphyletic assemblage of basal turtles. I herein take a more conservative approach and summarize only the unambiguous Gondwanan “core group” of this taxon. All northern taxa will be discussed elsewhere.

Meiolaniidae Boulenger, 1887, herein defined as the clade originating from the most recent common ancestor of *Niolamia argentina* Ameghino, 1899 and *Meiolania platyceps*, is deeply nested within *Meiolaniformes* (e.g., Gaffney et al. 2007; Sterli, Pol et al. 2013; Sterli et al. 2015). This group of extinct turtles with bizarre cranial horns, frills and a tail club was geographically and temporally restricted to the Cenozoic of Patagonia and Australasia (Gaffney 1996). The origin of meiolaniids and their relationships with other turtles have been controversial since their discovery (Gaffney 1983). In the first descriptions of meiolaniid remains, Owen (1880, 1886) thought them to be large-bodied terrestrial lizards and referred the available material from Queensland, Australia, to the gigantic varanid taxon *Megalia prisca* Owen, 1858 and the remains from Lord Howe Island, Australia, to the new taxon *Meiolania platyceps*. Owen (1887) later proposed the name *Ceratosauria* to group *Megalia prisca* and *Me. platyceps*. Huxley (1887:233) in parallel studied the specimens housed at the Natural History Museum in London and concluded that all of the remains identified by Owen as *Meiolania platyceps* and some of those recognized as *Megalia prisca* “are unmistakably [c]helonian.” Huxley (1887) furthermore proposed the name *Ceratochelys sthenurus* for the material from Lord Howe Island, but according to the rules of the International Commission on Zoological Nomenclature (ICZN 1999) this name is a junior objective synonym of *Me. platyceps*. The conclusion that *Me. platyceps* is a turtle has not been doubted ever since.

Using cranial and vertebral characters, Huxley (1887) proposed that *Me. platyceps* was allied with living cryptodiran turtles such as *Chelydra serpentina* Schweigger, 1812 and *Platysternon mega-*

cephalum Gray, 1831, but Boulenger (1887, 1889) felt instead that the same anatomical regions affiliate *Me. platyceps* with Pleurodira. Baur (1889a, 1889b) concurred with Huxley (1877) that *Me. platyceps* was allied with Cryptodira, particularly with the land tortoises (Testudinidae). Following the discovery of the Patagonian meiolaniid *Niolamia argentina* Ameghino, 1899, Woodward (1901) agreed with Boulenger’s statements about the pleurodiran affiliations of meiolaniids, but biogeographic concerns seem to have played a role, considering that Woodward (1901) does not explicitly discuss characters and their taxonomic distribution. Years later, Anderson (1925) described *Me. platyceps* and the new species *Me. mackayi* in detail and suggested that *Meiolania* spp. show several features characteristic of Amphichelydia Lydekker, 1889a, a wastebasket taxon of basal turtles that lack pleurodiran or cryptodiran characters (Gaffney 1975). This classification was later supported by Simpson (1938), who further suggested that meiolaniids may have originated from the “amphichelydian ancestors of the Cheloniodea” (Simpson 1938:252) and by Romer (1956), who alternatively classified Meiolaniidae as belonging to amphichelydian group Baenoidea.

Following the cladistic revolution, Gaffney (1983, 1985) and Gaffney and Meylan (1988) hypothesized *Meiolaniidae* to be the immediate sister group of crown Cryptodira (Eucryptodira Gaffney, 1975 sensu Gaffney 1983) within Pan-Cryptodira (Cryptodira sensu Gaffney 1983), but the later addition of characters and taxa pushed Meiolaniidae slightly farther down the cryptodiran stem basal to Sinemydidae (Gaffney 1996; Gaffney et al. 1998; Gaffney et al. 2007). An even more basal position for Meiolaniidae within Pan-Cryptodira was retrieved by Hirayama et al. (2000), who recovered *Meiolaniidae* basal to Paracryptodira as part of the then unnamed clade *Meiolaniformes*. Joyce (2007) finally recovered *Meiolaniidae*, again within the expanded clade *Meiolaniformes*, outside crown Testudines, and the vast majority of subsequent analysis has since recovered this result as well (e.g., Sterli and de la Fuente 2011a, 2013; Anquetin 2012; Sterli, Pol et al. 2013; Sterli et al. 2015). This shift towards the stem was likely caused by the use of expanded character/taxon matrices, but also by the discovery of numerous Mesozoic forms (e.g., Gaffney et al. 2007; Sterli and de la Fuente 2011a, 2013;

Sterli, de la Fuente et al. 2013) that firmly link derived meiolaniids with the stem lineage of turtles.

For institutional abbreviations see Appendix 1. Named meiolaniform genera are listed in Appendix 2.

Skeletal Morphology

Although the fossil record of Gondwanan meiolaniforms ranges from the Early Cretaceous to Pleistocene, few species are known from substantial cranial, shell and/or postcranial remains. I herein therefore concentrate on the morphology of the basal meiolaniforms *Chubutemys copelloi* and *Otwayemys cunicularius* and the derived meiolaniid *Meiolania platyceps*. However, I only provide figures for the shell morphology of *Otwayemys cunicularius* and the cranial morphology of *Meiolania platyceps*, as these anatomical systems are too poorly preserved in all other taxa and demand too much reconstruction.

Cranium

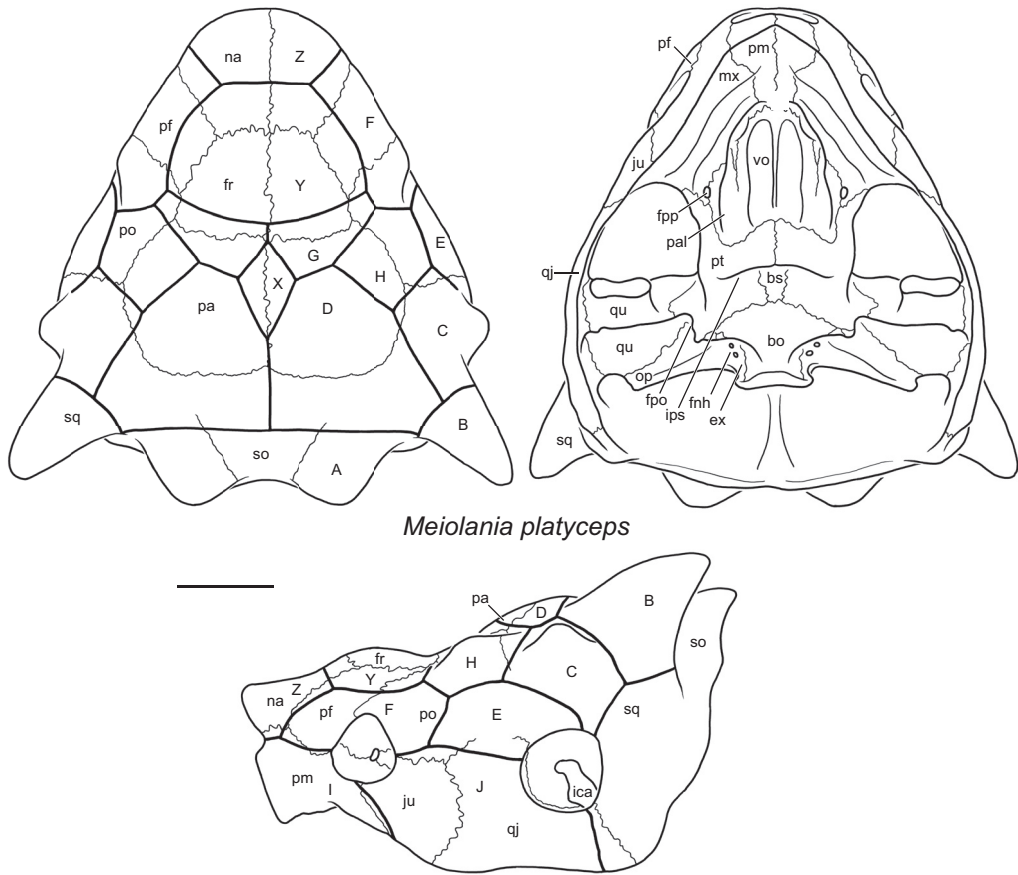
The detailed cranial anatomy is available for *Chubutemys copelloi* (Gaffney et al. 2007; Sterli et al. 2015) and *Me. platyceps* (Anderson 1925; Gaffney 1983, 1996), both of which are known from relatively well-preserved cranial material. Fragmentary or poorly preserved remains are otherwise known for *Me. brevicollis* (Megirian 1992; Gaffney 1996), *Me. mackayi* (Anderson 1925; Gaffney 1996), *Ninjemys oweni* (Gaffney 1992, 1996), *Niolamia argentina* (Simpson 1938; Gaffney 1996; Sterli and de la Fuente 2011b), *Patagoniaemys gasparinae* (Sterli and de la Fuente 2011a), *Peligrochelys walshae* (Sterli and de la Fuente 2013) and *Warkalania carinaminor* (Gaffney et al. 1992; Gaffney 1996). I here follow the general anatomical terminology of the skull of Gaffney (1979), as expanded and/or modified by Gaffney (1983, 1996), Sterli et al. (2010) and Rabi et al. (2013).

In general, the skull of meiolaniforms is well ossified, and, in some cases (e.g., *Meiolaniidae*), it is strongly ankylosed, preventing observation of sutures in adult specimens. The skull shows no upper or lower temporal emarginations (Figure 1). The dermal bones are covered by scutes, which provide valuable taxonomic information for the clade (Gaffney 1996; Sterli and de la Fuente 2013). The dermal bones furthermore bear a character-

istic ornamentation consisting of small, randomly distributed pits (Sterli, de la Fuente et al. 2013).

The nasal is generally present in meiolaniforms. It is relatively small in nonmeiolaniid meiolaniforms, but notably large in members of *Meiolaniidae*. The prefrontal is a conspicuous element, universally contacts the postorbital, and hinders the large frontal from entering the rim of the orbit (see Figure 1). The parietal is one of the biggest bones of the skull roof. It forms the well-developed temporal roofing of meiolaniforms, whereas the frill of meiolaniids is formed by the parietal together with the squamosal and a horizontal process of the supraoccipital. The jugal is included in the orbit in all known meiolaniforms. A peculiarity of the clade *Meiolaniidae* is the contact between the quadratojugal and squamosal below the cavum tympani, which superficially encloses the Eustachian tube and the stapes (see Figure 1). The squamosals of meiolaniids are characterized by the formation of horns. Each species of meiolaniid has its own horn shape (e.g., recurved/straight, triangular/round in cross section) and horn size (e.g., short in *Me. mackayi* and very large in *Meiolania* sp. from Walpole Island), and these differences have been used to differentiate species (Megirian 1992; Gaffney 1981, 1996). In nonmeiolaniid meiolaniforms (e.g., *Pe. walshae*) incipient protuberances are apparent on the squamosal in similar locations to the horns of meiolaniids.

The premaxilla and maxilla of meiolaniforms, as in other turtles, form the anterior and anterolateral part of the skull. In ventral view both bones are involved in the triturating surface. In all known meiolaniforms where the triturating surface is preserved, this surface is broad, structured by labial and lingual ridges and, in some cases (e.g., *Me. platyceps*, *Nin. oweni*), a third ridge is present (see Figure 1). In general aspects, the triturating surface of meiolaniforms is reminiscent of extant testudinids (Joyce and Bell 2004), which are mainly herbivorous (Ernst and Barbour 1989). The vomer is single and a conspicuous element in the palate. In meiolaniids, the vomer is laterally expanded and has a vaulted shape in lateral view. The vomer has a short ventral keel in basal meiolaniforms, but this keel is very thin, tall and developed along the entire length of the vomer in meiolaniids. The palatine of meiolaniforms exhibits no special structures and, as in most tur-



Meiolania platyceps

FIGURE 1. Cranial morphology of meiolaniforms as exemplified by *Meiolania platyceps* (redrawn from Gaffney 1983 and Sterli and de la Fuente 2013). *Abbreviations*: bo, basioccipital; bs, basisphenoid; ex, exoccipital; fnh, foramen nervi hypoglossi; fpo, fenestra postoticum; fpp, foramen palatinum posterius; fr, frontal; ica, incisura columella auris; ips, intrapterygoid slit; ju, jugal; mx, maxilla; na, nasal; op, opisthotic; pa, parietal; pal, palatine; pf, prefrontal; pm, premaxilla; po, postorbital; pt, pterygoid; qj, quadratojugal; qu, quadrate; so, supraoccipital; sq, squamosal; vo, vomer. Capital letters connote cranial scutes. Scale bar approximates 5 cm.

tles, contacts the pterygoid posteriorly. The foramen palatinum posterior is present and small (e.g., *Me. platyceps*) to medium sized (e.g., *Ch. copelloi*). The quadrate and the prootic universally form the processus trochlearis oticum. Meiolaniforms have a well-developed cavum tympani, but the antrum postoticum is absent in meiolaniids. The epipterygoid is present in meiolaniforms and, contrary to pancryptodires, it is short and columnar (e.g., Gaffney 1983, 1996; Sterli and Joyce 2007). Although the morphology of the pterygoid varies among meiolaniforms, it universally is located below the level of the basisphenoid, thereby leaving a horizontal space between both bones through which the palatine artery enters

the skull. In meiolaniids this space is well defined by bone as a slit that was termed the intrapterygoid slit by Gaffney (1983). In nonmeiolaniid meiolaniforms this step is filled by bone, which is pierced by the foramen posterior canalis carotici palatinum. In basal meiolaniforms the pterygoid generally resembles that of *Proganochelys quenstedti* Baur, 1887 by exhibiting a well-developed lateral process. In contrast, the pterygoid of meiolaniids is broader, the lateral process is reduced, and it is posteriorly pierced by the foramen posterior canalis carotici interni, which is absent in nonmeiolaniid meiolaniforms. The basisphenoid and basioccipital are very thick bones in meiolaniforms, notably thicker than

those of most other turtles (e.g., Gaffney 1979, 1990). The basisphenoid is pierced ventrally by the foramen posterius canalis caroticus cerebralis in all nonmeiolaniid meiolaniforms (see Figure 1). In meiolaniids the internal carotid artery enters the skull through the foramen posterior canalis carotici interni, which is located along the posterior part of the pterygoid. The internal carotid artery is anteromedially covered by the pterygoid but splits within the basisphenoid, close to the suture with the pterygoid, into the cerebral and palatine branches. This split occurs within a sinus that is not floored by bone and is therefore referred to as the fenestra caroticus (Rabi et al. 2013). In the fenestra caroticus, the cerebral branch penetrates the basisphenoid through the foramen posterius canalis caroticus cerebralis, while the palatine branch leaves and enters the skull through the intrapterygoid slit.

The lower jaws of meiolaniforms usually have the same external bone ornamentation as the skull consisting of small pits, but ridges may accompany these. The margin of the horny beak is revealed by the presence of a sulcus that laterally crosses the dentaries (Sterli and de la Fuente 2011b). The dentaries are fused at the symphysis in meiolaniforms and a medial hook is present along the symphysis of some taxa (e.g., *Nio. argentina*). The trituration surfaces usually correspond to the trituration surfaces of the premaxilla and maxilla. The foramen intermandibularis caudalis, located between the angular, splenial and prearticular, is expansive in meiolaniforms. The splenial is present, is well developed anteriorly and ends close to the symphysis. The coronoid process is generally low.

Shell

The shell anatomy is mainly known for *Chubutemys copelloi* (Gaffney et al. 2007; Sterli et al. 2015), *Otwayemys cunicularius* (Gaffney et al. 1998), *Patagoniaemys gasparinae* (Sterli and de la Fuente 2011a), *Trapalcochelys sulcata* Sterli, de la Fuente et al., 2013 (Sterli, de la Fuente et al., 2013), *Niolamia argentina* (Sterli and de la Fuente 2011b) and *Meiolania platyceps* (Gaffney 1996). Anatomical nomenclature follows Zangerl (1969).

The general shape of the shell in meiolaniforms is variable. The carapace is usually oval (longer than wide) but sometimes nearly circular (e.g., *Me. platyceps*). Some species show a deep nuchal notch (e.g.,

Ch. copelloi, *Pa. gasparinae*), whereas others seem to have a convex anterior margin (e.g., *Me. platyceps*). The bones of the shell have a peculiar fine-scaled ornamentation, which is also present in the dermal bones of the skull and lower jaw. This ornamentation consists of small, randomly arranged pits. Some species have very thin shell bones (e.g., *Ch. copelloi*, *Me. platyceps*), whereas others have thick shell bones (e.g., *T. sulcata*, *Nio. argentina*). In general, the carapace and the plastron are loosely attached to one another through pegs and sockets made of bone. The adults of some species (e.g., *Me. platyceps*) have small fontanelles between the costals and the peripherals.

The carapace consists of 1 nuchal, 22 peripherals, 16 or 18 costals, 8 or more neurals, 1 or 2 suprapygals and 1 pygal. A continuous neural series is present, but the neurals usually have an irregular shape. A cervical scute is generally present and vertebrals II to IV are wider than the pleurals in all meiolaniforms (Figure 2). The sulci between marginal scutes have a strong anterior inflection along the rim of the carapace. Supramarginal scutes are absent.

The plastron consists of the full set of bones and scutes typical of basal turtles. A dorsal epiplastral process is documented for *Me. platyceps*. A central plastral fontanelle in adult specimens is present in some meiolaniforms such as *O. cunicularius* and *Me. platyceps* (see Figure 2). An anal notch is absent.

Postcranium

Fragmentary postcranial remains are known for *Chubutemys copelloi* (Gaffney et al. 2007; Sterli et al. 2015), *Otwayemys cunicularius* (Gaffney et al. 1998), *Patagoniaemys gasparinae* (Sterli and de la Fuente 2011a), *Nio. argentina* (Sterli and de la Fuente 2011b), *Nin. oweni* (Gaffney 1992) and *Me. platyceps* Gaffney (1985, 1996). The most complete and, consequently, best described species of Gondwanan meiolaniforms is *Me. platyceps*, and I therefore mostly refer to this taxon in this section.

All meiolaniforms have formed central joints in the cervical and caudal vertebrae. In the neck of meiolaniforms there is usually one biconvex vertebra in the middle and, in some species, there is one biconcave one as well (e.g., *Pa. gasparinae*). In *Pa. gasparinae* and *Me. platyceps* the biconvex vertebra is cervical IV. In non-

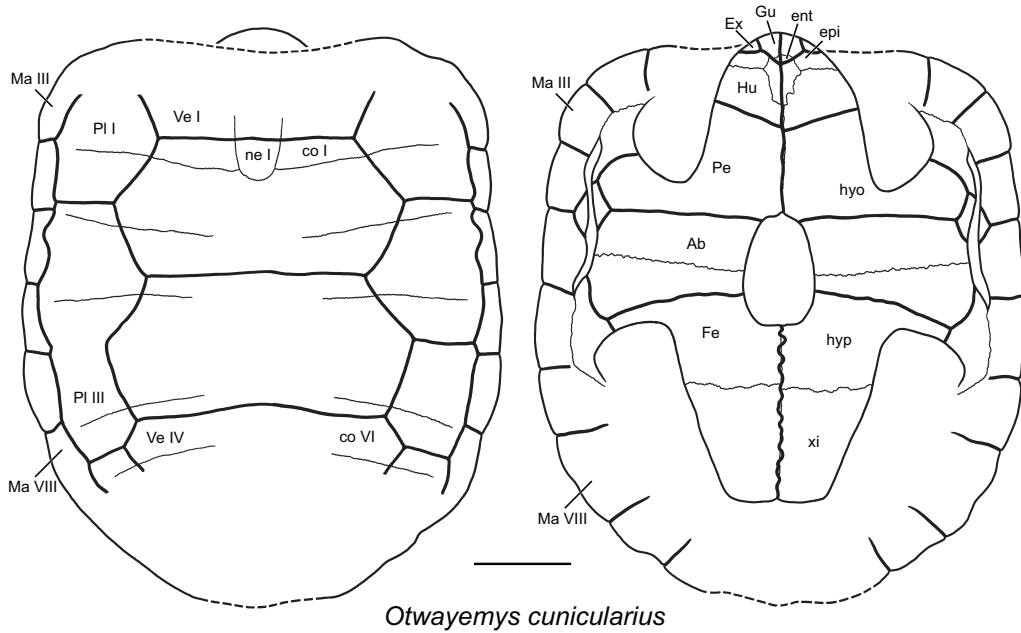


FIGURE 2. Shell morphology of meiolaniforms as exemplified by *Otwayemys cunicularius* (redrawn from Gaffney et al. 1998). Abbreviations: Ab, abdominal scute; co, costal; ent, entoplastron; epi, epiplastron; Ex, extragular scute; Fe, femoral scute; Gu, gular scute; Hu, humeral scute; hyo, hyoplastron; hyp, hypoplastron; Ma, marginal scute; ne, neural; Pe, pectoral scute; Pl, pleural scute; Ve, vertebral scute; xi, xiphiplastron. Scale bar approximates 5 cm.

meiolaniid meiolaniforms in which the cervical VIII is known (e.g., *Ch. copelloi*, *Pa. gasparini*, *O. cunicularius*), this vertebra is biconvex. In contrast, in meiolaniids, cervical VIII is procoelous. The cervical centra are usually as long as high or slightly longer than high, with tall and well-developed neural arches. The first thoracic centrum faces mostly anteriorly and thoracic rib I is more than half as long as thoracic rib II. The caudal series is only known from *Pa. gasparinae* and *Me. platyceps*, and some isolated vertebrae of *O. cunicularius*. Caudal vertebrae are predominantly opisthocelous, but in *Pa. gasparinae* some portions of the tail are procoelous. Almost all caudal vertebrae of meiolaniforms have chevrons. In the clade *Meiolaniidae*, tail rings cover at least part of the tail. At the tip of the tail, these tail rings fuse and form, together with the vertebrae, the tail club. Tail rings are known for *Nio. argentina* and *Nin. oweni*, whereas *Me. platyceps* also has a tail club. The tail rings are ventrally closed in *Nio. argentina* and in *Nin. oweni*, but ventrally open in *Me. platyceps*.

The pectoral girdle is triradiate as in all turtles. The scapula in meiolaniforms has a web of bone that connects the dorsal process of the scapula with the acromion, a feature not present in more derived turtles with a triradiate pectoral girdle. The pelvic girdle of *Me. platyceps* is robust, has separated thyroid fenestrae, and a short, ossified epipubic process. The stylopodium of *Me. platyceps* shows highly expanded ends and short shafts, giving a robust aspect, whereas the zeugopodium is formed by short and robust elements. As in extant testudinids, all digits in the hands and the feet of *Me. platyceps* consist of two short phalanges. Osteoderms are known for *Me. platyceps*, but likely occurred in other meiolaniforms as well (e.g., *Pa. gasparinae*). These range in shape from symmetric and asymmetric and from rounded to elongate. By comparison to extant and extinct testudinids (Vlachos et al. 2014) and the solemydid *Naomichelys speciosa* (Joyce et al. 2014), it is highly probable that each morphotype corresponds to a particular position of the osteoderm within the skin.

Phylogenetic Relationships

The first known meiolaniid turtles, *Meiolania platyceps* and *Niolamia argentina*, are highly apomorphic and it has therefore been difficult to place them with confidence in the traditional classification system of turtles. The precladistic history of research for the group is summarized in the Introduction above.

Gaffney (1983, 1996) and Gaffney and Meylan (1988) placed *Meiolaniidae* in the clade Eucryptodira, within crown Testudines, just outside of crown Cryptodira, using a series of characters that were thought to be unique to that clade. These characters include the contact of the descending process of the prefrontal with the vomer, presence of a processus trochlearis oticum, the complete flooring of the cranio-quadrate space by the pterygoid, the posterior position of the foramen posterior canalis carotici interni and the absence of mesoplastra. A similar result was also obtained by the global analysis of Hirayama et al. (2000), although *Me. platyceps* was retrieved in a more basal position within the cryptodiran stem lineage, which implied that many of the characters listed above were acquired homoplastically. Joyce (2007) soon after generated a larger morphological data set that only utilized species as terminal taxa, and that placed *Me. platyceps* outside of crown Testudines. The analysis of Joyce (2007) has served as the basis for numerous subsequent global phylogenies, which sought to further resolve the relationships among basal turtles by adding characters and taxa (e.g., Sterli 2010; Anquetin 2011; Joyce et al. 2011; Sterli and de la Fuente 2011a, 2013; Rabi et al. 2013; Sterli, Pol et al. 2013; Rabi et al. 2014; Sterli et al. 2015), but these universally recover a placement of *Me. platyceps*, or *Meiolaniidae*, along the phylogenetic stem of crown turtles as well, while implying that almost all characters once thought to unite *Meiolania platyceps* with crown cryptodires are actually symplesiomorphies or homoplasies. This novel insight is primarily a result from the discovery of numerous new taxa (e.g., *Chubutemys copelloi*, *Patagoniaemys gasparinae*, etc.) that bridge the morphological gap between *Meiolania platyceps* and the stem turtle lineage.

The second, novel insights from the last two decades of research have been that the stem lineage leading to *Meiolaniidae* is populated by a

diverse assemblage of turtles, although the exact composition of this assemblage is still being investigated. The “total clade” of *Meiolaniidae* was recently named *Meiolaniformes* by Sterli and de la Fuente, 2013 to facilitate communication.

Čkhikvadzé (1987) was the first to propose possible, close relationship of an eclectic sample of basal turtles with meiolaniids, including “Desmemydinae” from the Late Jurassic of Europe (i.e., *Desmemys bertelsmanni* Wegner, 1911, now thought to be a paracryptodire, Brinkman et al. 2000), “Helochelydridae” from the Early Cretaceous of Europe (i.e., *Helochelydra nopcsai* Lapparent de Broin and Murelaga, 1999, a solemydid), “Neurankylidae” from the Late Cretaceous of North America (i.e., *Neurankylus eximius* Lambe, 1902, now thought to be a paracryptodire, Joyce 2007), *Mongolochelys efremovi* from the Late Cretaceous of Asia (*Yumenemys inflatus* Bohlin, 1953 sensu Čkhikvadzé 1987) and *Kallokibotion bajazidi* from the Late Cretaceous of Europe. However, these ideas were not supported by reference to particular characters. Several phylogenetic analyses have since retrieved various taxa as meiolaniforms, but results have been inconsistent. *Mongolochelys efremovi* was retrieved as a meiolaniform, among others, by Hirayama et al. (2000), Joyce (2007), Anquetin (2012) and Sterli and de la Fuente (2013), but not by Gaffney et al. (2007). *Naomichelys speciosa* was similarly retrieved as a meiolaniform by Anquetin (2012), but not by Joyce et al. (2011), and *Kallokibotion bajazidi* by Sterli, Pol et al. (2013) but not by Anquetin (2012). Hirayama et al. (2000) also retrieved Sinochelyiidae Čkhikvadzé 1973 (= Peishanemydidae of Nessov 1981) as a meiolaniform, but representatives of this taxon are extremely poorly known and no other analysis has therefore been able to test this hypothesis. Most of the turtles listed above are highly apomorphic, much as *Me. platyceps*, and ancestral taxa are still missing that firmly link them with other taxa. It therefore remains unclear for the moment if these taxa are united by synapomorphies or homoplasies.

A number of specimens were collected from southern continents in the last decades that show unambiguous ties to *Meiolaniidae* (Gaffney et al. 1998; Gaffney et al. 2007; Sterli and de la Fuente 2011a, 2013; Sterli, de la Fuente et al. 2013; Sterli et al. 2015). The primary purpose of this contribution is to summarize this assemblage of turtles.

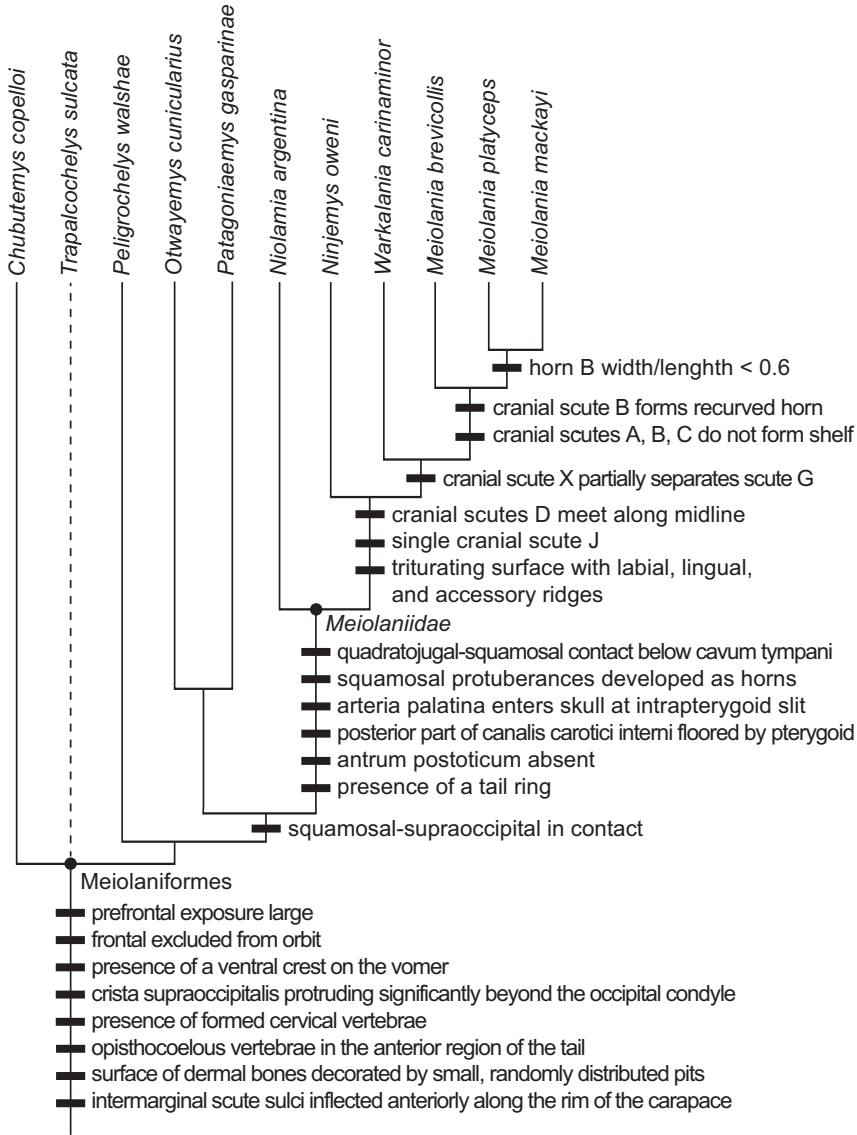


FIGURE 3. Phylogenetic hypothesis of valid meiolaniform taxa, with diagnostic characters for the most important clades (Sterli et al. 2015). *Trapalcochelys sulcata* has not yet been integrated into a phylogeny at this point and is therefore placed in a basal polytomy.

The turtle *Spoochelys ormondea* Smith and Kear, 2013 from the Lower Cretaceous of Australia was extensively compared to meiolaniids in the type description, but was eventually retrieved as a stem turtle. This taxon is therefore not included herein.

The phylogenetic relationships within *Meiolaniidae* have remained stable since the analysis of Gaffney (1996), in which the Patagonian *Nio. argentina* is recovered as the sister taxon of all

Australasian taxa (Gaffney 1996; Sterli and de la Fuente 2011a, 2013; Sterli, Pol et al. 2013; Sterli et al. 2015; Figure 3). This phylogenetic hypothesis is compatible with the stratigraphic record of the meiolaniids (Figure 4), because *Nio. argentina* is the oldest known species of the clade. Within the clade of Australasian meiolaniids, *Warkalania carinaminor* and *Ninjemys oweni* are recovered as the successive outgroups of *Meiolania*. Within *Meiolania*, *Me. platyceps* is the sister group of *Me.*

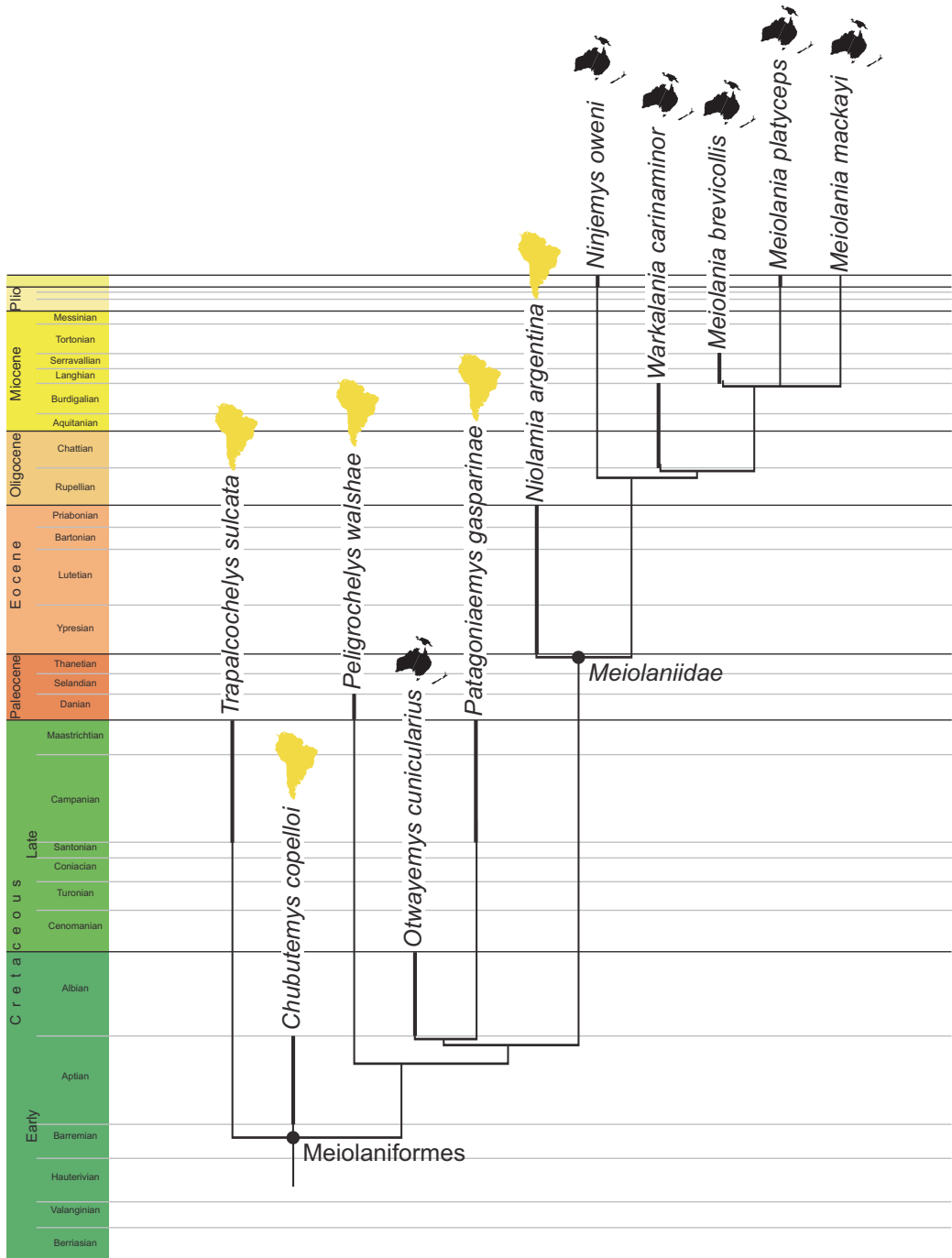


FIGURE 4. The stratigraphic and biogeographic distribution of valid meiolaniform taxa. Bold lines indicate temporal distribution based on type material.

mackayi + *Me. brevicollis* (see Figure 3). The remaining species of *Meiolania* are highly fragmentary, and their phylogenetic relationships therefore remain uncertain.

Paleoecology

Ever since the first remains of *Meiolania platyceps* were found in the 19th century, this taxon was pri-

marily regarded as a terrestrial turtle (Owen 1886; Boulenger 1887, 1889; Baur 1889a) because of the shape of the humerus, the shape of the ungual phalanges and the presence of tail rings and tail clubs. Anderson (1925:241) initially differed from this opinion and wrote “[...] I am rather inclined to the view that *M[e]. platyceps* and *M[e]. mackayi* were partly land, partly estuarine or shore-living forms, which could, however, make short sea trips.” He also stated “*Meiolania oweni* of the Darling Downs doubtless belongs to another branch of the same family, which crossed to Australia, probably from New Guinea, and remained more purely terrestrial in habit.” In his later contribution, however, Anderson (1930: 310–311) wrote, “It is evident that the fresh evidence now obtained confirms the view that *Meiolania* was essentially a terrestrial reptile. [...] In gait and posture *Meiolania* must have been very similar to *Testudo*. [...] In my previous paper I pointed out that, as Walpole Island is of coral origin; and has apparently never been connected with any larger land mass, the occurrence there of *Meiolania mackayi*, a form very similar to *Me. platyceps*, indicates that the animal was able to cross a considerable stretch of ocean. This possibility is not excluded by its adaptation for a terrestrial existence, for *Testudo* is a good swimmer, as Beebe has pointed out. But, on the whole, the skeleton of *Meiolania*, the proportions of its limb bone, the structure of its phalanges, and its heavily armoured condition, strongly indicate that it was built for life on land.” Later, Simpson (1938:252) mentioned, “It is almost certain that some or all members of the family [*Meiolaniidae*] could swim well; given some fifty or sixty million years they might have reached almost any place, under no necessity of getting there without wetting their feet.”

In his detailed contribution about the postcranial anatomy, Gaffney (1996) compared *Me. platyceps* with testudinids and suggested that both taxa have many similar postcranial structures, probably because meiolaniids were adapted to terrestrial habitats. Among others, both taxa have short coracoids, a large angle between the dorsal process of the scapula and acromion, similarly shaped olecranon and sigmoid notches, spherical femoral heads, limb osteoderms, a reduced digital formula in the manus of 2-2-2-2-2, short phalanges and vaulted carapaces (Gaffney 1996). Other charac-

teristics cited as evidence for terrestrial habits are the presence of tail rings and tail clubs (Joyce and Gauthier 2004) and the histology of the shell (Scheyer 2007). However, given that several meiolaniids are known from isolated oceanic islands, it is apparent that they occasionally dispersed across water, likely by analogy to extant giant tortoises. The likely presence of osteoderms in other meiolaniforms makes it likely that the entire clade was terrestrial.

The paleoecology of nonmeiolaniid meiolaniforms has not been explored in detail, in part because all known specimens lack postcranial remains that could be used to infer the habits of those meiolaniforms. However, recent fieldwork in the La Colonia Formation in Chubut Province, Argentina, resulted in the discovery of several new remains of *Patagoniaemys gasparinae*, including many osteoderms, suggesting terrestrial habits for *Pa. gasparinae*. In contrast, paleohistological studies on fragmentary shell remains of *Trapalcochelys sulcata* (Sterli, de la Fuente et al. 2013) suggest this turtle exhibits a mixture of terrestrial (category I) to semiaquatic (category II) features as defined by Scheyer (2007).

The palate of *Me. platyceps* is decorated by several rows of serrated ridges, which is indicative of herbivorous dietary preferences by analogy to numerous extant testudinoids (Ernst and Barbour 1989; Joyce and Bell 2004). In contrast, the palates of all other Gondwanan meiolaniforms are much less distinctive and their dietary preferences are therefore obscure.

Paleobiogeography

The record of Gondwanan meiolaniforms starts with *Chubutemys copelloi* from the Early Cretaceous (Aptian/Albian) of Chubut Province, Argentina (Gaffney et al. 2007; Sterli et al. 2015), and *Otwayemys cunicularius* from the Early Cretaceous (Albian) of Victoria, Australia (Gaffney et al. 1998; Figure 5). Late Cretaceous meiolaniforms are only known from Patagonia, Argentina, including *Patagoniaemys gasparinae* and *Trapalcochelys sulcata* from the Campanian/Maastrichtian of Chubut and Río Negro Province, respectively (Sterli and de la Fuente 2011a; Sterli, de la Fuente et al. 2013; see Figure 5). The record continues in Patagonia (Argentina) after the K-P boundary with *Peligrochelys walshae* and *Nio-*



FIGURE 5. The geographic distribution of figured Gondwanan meiolaniform turtles in South America. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations*: CH, Chubut Province; MZ, Mendoza Province; RN, Río Negro Province.

lamia argentina, both from the Paleogene of Chubut, Argentina (see Figure 5). The meiolaniform record ends in South America with fragmentary meiolaniid remains from the middle Eocene of Chubut, Argentina (de la Fuente and Fernández 1992), but restarts soon after in Australasia, with indeterminate meiolaniid fragments from the Late Oligocene of South Australia (Gaffney 1996; Figure 6). The oldest named meiolaniid from this continent is *Warkalania carinaminor* from the Oligocene/Early Miocene of Queensland (Gaffney et al. 1992). Miocene remains identified as *Meiolaniidae* indet. originate from New South Wales, South Australia, and Queensland, Australia (Gaffney 1992, 1996; see Figure 6), whereas *Me. brevicollis* is known from the middle Miocene of the Northern Territory (Megirian 1992; Gaffney 1996). Only a single find identified as *Meiolaniidae* indet. is recorded from the Pliocene of Queensland, Australia (Gaffney 1996). The highest known diversity of *Meiolaniidae* is recorded from the Pleistocene–Holocene of Australasia, with at least three valid species:

Ninjemys oweni from Queensland, Australia, *Meiolania platyceps* from Lord Howe Island, Australia, and *Me. mackayi* from New Caledonia (Owen 1886; Woodward 1888; Anderson 1925; Gaffney 1992; see Figure 6). Fragmentary Pleistocene–Holocene material referable to *Meiolania* cf. *Me. platyceps* and *Meiolaniidae* indet. have otherwise been documented from Queensland, Australia (Gaffney and McNamara 1990), and New Caledonia (Gaffney et al. 1984), respectively (see Figure 6). White et al. (2010) recently reported the putative presence of meiolaniids in Holocene deposits of Vanuatu and furthermore presumed that other large terrestrial turtles found in the Quaternary of Fiji (Worthy et al. 1999) and in the early Miocene of the South Island of New Zealand (Worthy et al. 2011) belong to *Meiolaniidae*, but these conclusions were apparently based on paleobiogeographic evidence. I demonstrate here that at least the specimens from Vanuatu do not exhibit meiolaniform characters and that they should therefore be dismissed (see Systematic Paleontology below).

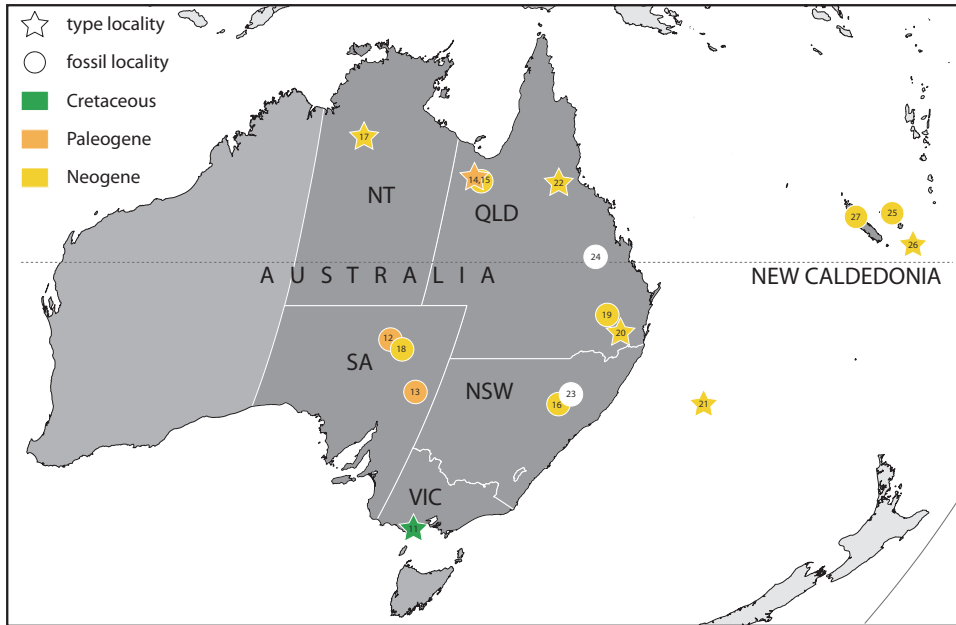


FIGURE 6. The geographic distribution of figured Gondwanan meiolaniform turtles in Australasia. Stars mark the type localities of valid taxa. Locality numbers are cross-listed in Appendix 3. *Abbreviations:* NSW, New South Wales; NT, Northern Territory; QLD, Queensland; SA, South Australia; VIC, Victoria.

The conspicuous presence of meiolaniids in Australasia and Patagonia has long piqued the interest of researchers. Moreno and Smith Woodward (1899:783) stated: “the discovery [of *Nio-lamia argentina*] was of great interest, as apparently favouring the hypothesis of a former great Antarctic continent, of which Australia and Patagonia are now mere remnants.” Woodward (1901:182) similarly noted that the occurrence of meiolaniids in Australasia and South America “seems to confirm the much-discussed theory of an old Antarctic continent and a former connection between South America and Australia,” an opinion with which Dollo (1904) agreed. To the contrary, Regan (1914) concluded that neither freshwater nor marine fishes support the idea that South America and Australia were connected via Antarctica during the Tertiary. And Huxley (1887) and Anderson (1925) entertained the possibility that meiolaniids arrived in Australia from Asia, passing through New Guinea and other islands. Simpson (1938), finally, did not support the idea of land bridges either.

Following the establishment of plate tectonics, Gaffney (1996) suggested that the distribution of meiolaniids is a combination of vicariant

processes during the Mesozoic and the “escalator hopscotch” processes (McKenna 1983) during the Paleogene. In particular, Gaffney (1996) noted that the basal position of *Nio. argentina* related to the Australasian species is consistent with the breakup of South America, Antarctica and Australasia sometime during the Cretaceous. Although recent hypotheses about the breakup of Southern Gondwana suggest that the separation of these three continents occurred around the end of the Eocene and not in the Cretaceous (Lawver et al. 2011), it is nevertheless possible that the habitat of meiolaniids was separated earlier.

The “escalator hopscotch” hypothesis states that organism may reach relatively distant oceanic islands, especially along island chains, by successively hopping from one emerging island to the next (McKenna 1983), but this model has only limited explanatory power for various Australasian island forms, as most island chains run parallel to the continental margin in this region. However, given that large-bodied extant testudinids readily disperse across short to intermediate ocean distances (e.g., Simpson 1943; Pritchard 1989; Meylan and Sterrer 2000) and given the

morphological similarities between testudinids and meiolaniids, it appears plausible that meiolaniids were able to conquer remote islands by passively drifting with ocean currents.

Sterli and de la Fuente (2013) recently applied the dispersal–extinction–cladogenesis (DEC) model of Ree and Smith (2008) to *Meiolaniformes*. The DEC model suggests that meiolaniforms were originally distributed in present-day South America during the Early Cretaceous. The model further suggests that the clade *Meiolaniidae* originated sometime during the Early Cretaceous to Paleocene and they were distributed in present-day Antarctica (Sterli and de la Fuente 2013) and only later expanded its range to Patagonia and Australasia. Although the DEC model suggests that meiolaniids were present in Antarctica, it is worth mentioning that no remains of meiolaniid turtles have been discovered in Antarctica up to now and, moreover, the fossil record of turtles during the Cretaceous and Paleogene in Australasia is very scarce.

Systematic Paleontology

Valid Taxa

See Appendix 4 for the hierarchical taxonomy of Gondwana meiolaniforms as described in this work.

Meiolaniformes Sterli and de la Fuente, 2013

Phylogenetic definition. As per Sterli and de la Fuente (2013), *Meiolaniformes* is referred to the branch-based clade that includes all taxa more closely related to *Meiolania platyceps* than to *Cryptodira* and *Pleurodira*.

Diagnosis. Representatives of *Meiolaniformes* are currently diagnosed relative to other turtles by the presence of a large prefrontal exposure, a lack of a frontal contribution to the orbit, the presence of a ventral crest on the vomer, a crista supraoccipitalis that extends posteriorly well beyond the foramen magnum, formed cervical vertebrae, opisthocelous vertebrae in the anterior part of the tail, randomly distributed small pits on the surface of the dermal bones of the skull and shell and anteriorly inflected marginal scute sulci along the carapacial margin (see Figure 3).

Chubutemys copelloi Gaffney et al., 2007

Taxonomic history. *Chubutemys copelloi* Gaffney et al., 2007 (new species).

Type material. MPEF PV1236 (holotype), almost complete skull (Gaffney et al. 2007, figs. 4–10; Sterli et al. 2015, figs. 2–4, 8).

Type locality. Turtle Town locality, Chubut Province, Argentina (see Figure 5); Puesto La Paloma Member, Cerro Barcino Formation, Chubut Group, Aptian/Albian, Early Cretaceous (Gaffney et al. 2007; Sterli et al. 2015).

Referred material and range. Early Cretaceous (Aptian/Albian) of Turtle Town locality, Chubut Province, Argentina (hypodigm of Gaffney et al. 2007; Sterli et al. 2015).

Diagnosis. *Chubutemys copelloi* can be diagnosed as a meiolaniform by the presence of all characters listed above for that clade. *Chubutemys copelloi* is differentiated from other meiolaniforms by the unique combination of following characters: skull emarginations absent, contact between supraoccipital and squamosal short, jugal reaches orbit, long contact between postorbital and squamosal, thick medial crest along full length of vomer, parasagittal choanal grooves absent, foramen palatinum posterius large and elongated, foramina posterior canalis carotici cerebri located on basisphenoid, foramina posterior canalis carotici palatinum located between basisphenoid and pterygoid, triturating surface consisting only of a tall labial ridge, basiptyergoid (= basitrabecular) process present, pterygoid does not enter the foramen palatinum posterius, basisphenoid pentagonal in ventral view, basioccipital does not contact pterygoid, prootic partially seen in ventral view, processus interfenestralis reduced and visible in ventral view, shell thin, carapace lacks nuchal notch, cervical scute reduced or absent, vertebral I almost reaches anterior border of carapace, small costo-peripheral fontanelles present, ligamentous carapace–plastron attachment and long posterior entoplastral process.

Comments. Gaffney et al. (2007) described *Chubutemys copelloi* based on a skull and some postcranial remains from the “Turtle Town” locality (near Chubut Province, Argentina) and placed this taxon as the sister to *Meiolaniidae* based on the presence of a prefrontal–postorbital contact. Fieldwork at the same locality in 2008 yielded more remains of the holotype (skull) and some of the referred specimens, which allowed Sterli et al. (2015) to describe the skull and postcranium of this taxon in more detail. The cladistic analysis of Sterli et al. (2015) also retrieved *Ch. copelloi* as the most basal representative of the clade *Meiolaniformes*. This basal position is in accordance with the stratigraphic record of the clade, because *Ch. copelloi* is also one of the oldest representatives of the clade.

Otwayemys cunicularius Gaffney et al., 1998

Taxonomic history. *Otwayemys cunicularius* Gaffney et al., 1998 (new species).

Type material. NMV P186116 (holotype), almost complete shell (Gaffney et al. 1998, figs. 1–4, 10–11).

Type locality. Slippery Rock site, Dinosaur Cove, Cape Otway, Victoria, Australia (see Figure 6); Eumeralla Formation, Otway Group, Albian, Early Cretaceous (Rich and Rich 1989).

Referred material and range. Early Cretaceous (Albian) of Slippery Rock site, Dinosaur Cove, Cape Otway, Victoria, Australia (hypodigm of Gaffney et al. 1998).

Diagnosis. *Otwayemys cucicularius* can be diagnosed as a meiolaniform by the presence of strongly anteriorly curved sulci between marginal scutes, the presence of small pits that decorate the surface of all dermal bones and the presence of formed vertebrae. *Otwayemys cucicularius* is differentiated from other meiolaniforms by the combination of the following characters: shell elements thick, costal II not anteriorly bent, lack of mesoplastra, bridge peripherals guttered, gular scutes extending onto entoplastron, large hyoplastron–hypoplastron fontanelle and inframarginals present (see Figure 2).

Comments. When describing *Otwayemys cucicularius*, Gaffney et al. (1998) were concerned whether *O. cucicularius* is conspecific with the coeval taxon *Chelycarapookus arcuatus* Warren, 1969 from the Lower Cretaceous, Merino Group, of Carapook, Victoria. *Chelycarapookus arcuatus* is preserved as a Steinkern, and few characters are directly comparable with *O. cucicularius*. Gaffney et al. (1998) nevertheless noticed some differences, including size, development of a central plastral fontanelle and surface texture. The strict consensus topology of Gaffney et al. (1998) finds *O. cucicularius* in a polytomy with *Meiolaniidae* and *Sinemydidae* + crown Cryptodira, but these authors nevertheless favored a placement of this taxon within *Sinemydidae* (sensu Rabi et al. 2014). Hirayama et al. (2000) later recovered *O. cucicularius* as the sister of *Sinochelyidae* within *Meiolaniformes*, but this Lower Cretaceous group from Asia is poorly known. In subsequent cladistic analyses (e.g., Sterli and de la Fuente 2011a, 2013; Sterli, Pol et al. 2013; Sterli et al. 2015), *O. cucicularius* has consistently been recovered inside *Meiolaniformes*, although its phylogenetic position has changed inside the group. This might be the result of missing scorings, especially for the skull, shell, vertebrae and appendicular skeleton. It is highly probable that the discovery and description of more remains will help to stabilize the phylogenetic relationships of this taxon.

Patagoniaemys gasparinae Sterli and de la Fuente, 2011a

Taxonomic history. *Patagoniaemys gasparinae* Sterli and de la Fuente, 2011a (new species).

Type material. MPEF PV3283 (holotype), left postorbital, carapace remains, plastron fragments, almost complete vertebral column, pelvic girdle and fibula (Sterli and de la Fuente 2011a, figs. 3–10).

Type locality. Buitre Chico locality, Chubut Province, Argentina (see Figure 5); La Colonia Formation, Campanian/Maastrichtian (Pesce 1979; Pascual et al. 2000).

Referred material and range. Late Cretaceous (Campanian/Maastrichtian), La Colonia Formation, Chubut Province, Argentina (at least 15 new, unpublished specimens, MPEF PV10541–10555).

Diagnosis. *Patagoniaemys gasparinae* can be diagnosed as a meiolaniform by the presence of strongly anteriorly curved sulci among marginal scutes, small foramina ornamenting the dermal bones and opisthocoelous vertebrae at least in the anterior

region of the tail. *Patagoniaemys gasparinae* is differentiated from other meiolaniforms by the unique combination of the following characters (autapomorphies marked with an asterisk): presence of a large nuchal bone, absence of guttered bridge peripherals, absence of a preneural, costal I small*, costal II large and strongly bent anteriorly*, absence of contact between neural I and costal II, thoracic rib I well developed and almost reaching axillary buttress, thoracic rib II fused with costal I and underlapping costal II*, pleural scute I reaching peripherals, marginal scute V curved anteriorly, sulcus between vertebral scutes III and IV located on costal V and probably VI, presence of costo-peripheral fontanelles, carapace-plastron connected by ligaments, cervical vertebrae formed with parapophyses and diapophyses, the latter located in the anterior half of the cervical centra, cervical centra ventrally keeled, presumed cervical formula $(2,(3,(4),5?,?6),)7,(8)$, first thoracic vertebrae facing mainly anteriorly, articular surface of sacral vertebra 1 faces strongly ventrally, first caudal rib also in contact with sacral vertebra II, caudal vertebrae with articulation facets for chevron bones, biconvex caudal vertebra between the anterior opisthocoelous centra and the procoelous posterior centra (Sterli and de la Fuente 2011a).

Comments. Sterli and de la Fuente (2011a) named *Patagoniaemys gasparinae* based on the holotype specimen only, which is mainly represented by postcranial remains. Fieldwork conducted in the La Colonia Formation in 2011 and 2012 resulted in the discovery of more than 15 additional specimens, which remain unpublished to date. These specimens include previously unknown cranial and appendicular elements and are therefore expected to provide new insights into the anatomy and phylogenetic relationships of *Pa. gasparinae*.

Peligrochelys walshae Sterli and de la Fuente, 2013

Taxonomic history. *Peligrochelys walshae* Sterli and de la Fuente, 2013 (new species).

Type material. MACN PV-Ch 2017 (holotype), skull remains (Sterli and de la Fuente 2013, figs. 4–9).

Type locality. Punta Peligro locality, Chubut Province, Argentina (see Figure 5); Banco Negro Inferior, Salamanca Formation, Danian, early Paleocene (Marshall et al. 1981; Marshall et al. 1997; Sterli and de la Fuente 2013).

Referred material and range. Early Paleocene (Danien) of Punta Peligro locality, Chubut Province, Argentina (Sterli and de la Fuente 2013).

Diagnosis. *Peligrochelys walshae* can be diagnosed as a meiolaniform by the presence of large exposure of the prefrontal and the exclusion of the frontal in the orbital rim. *Peligrochelys walshae* is differentiated from other meiolaniforms by the unique combination of the following features (autapomorphies marked with asterisks): scutes cover the skull roof, presence of several F scutes surrounding the orbit, posterior wall separating the fossa orbitalis from the fenestra temporalis inferior, small knobs in the squamosal, processus trochlearis oticum present, cavum

tympani well developed, only one opening for the exit of the nervi hypoglossi (XII) in the exoccipital*, thick basicranium, roughened area in the basisphenoid, two concavities in the basioccipital delimited by the well-developed tubera basioccipitalis*, foramina carotici cerebri posterior located close together, foramen posterior canalis carotici interni absent and union of foramen carotici cerebri anterior forming a slit*.

Comments. *Peligrochelys walshae* is the only known non-meiolaniid meiolaniform from the Cenozoic. All known specimens of this taxon were collected from the locality of Punta Peligro in outcrops of the Salamanca Formation in Chubut Province, Argentina, but it is notable that the most complete described specimen, which also serves as the holotype, had already been collected by Dr. J. Bonaparte between 1989 and 1991 during joint expeditions of the Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” and the Universidad de la Patagonia “San Juan Bosco.” Several new, uncatalogued specimens have been found since the description of this taxon, including cranial and postcranial remains, which are expected to provide valuable information about the anatomy of this meiolaniform. The identification of cranial scutes in *Pe. walshae*, and its similarities with the pattern found in *Mongolochelys efre-movi*, led Sterli and de la Fuente (2013) to propose a system of primary homology for the cranial scutes of basal turtles for use in phylogenetic reconstruction.

Trapalcochelys sulcata Sterli, de la Fuente et al., 2013

Taxonomic history. *Trapalcochelys sulcata* Sterli, de la Fuente et al., 2013 (new species).

Type material. MLP 86-IV-5-2 (holotype), fragment of nuchal bone, left peripherals 1, 2, 6–9, right peripherals 2, 3, 6–9, right costal 4 and several costal fragments, neurals? 3–5, several indeterminate carapace fragments, a fragment of the left hypoplastron, several indeterminate plastral fragments, thoracic vertebra 9, two neural arches of caudal vertebrae, a right opisthotic (Sterli, de la Fuente et al., 2013, figs. 2, 5–6).

Type locality. Salinas de Trapal-Co, Río Negro Province, Argentina (see Figure 5); Allen Formation, Late Campanian/Early Maastrichtian (Hugo and Leanza 2001; Leanza 1999; Leanza et al. 2004; Sterli, de la Fuente et al., 2013).

Referred material and range. Late Cretaceous (Late Campanian/Early Maastrichtian), Allen Formation, Salinas de Trapal-Co, Río Negro Province, Argentina (Sterli, de la Fuente et al., 2013).

Diagnosis. *Trapalcochelys sulcata* can be diagnosed as a meiolaniform by the presence of strongly anteriorly curved sulci among marginal scutes, small foramina ornamenting the dermal bones, the absence of pleural III on peripheral IX and opisthocelous vertebrae in the anterior region of the tail (Sterli, de la Fuente et al., 2013).

Comments. *Trapalcochelys sulcata* is the second species of non-meiolaniid meiolaniform from the Upper Cretaceous of

Argentina. The preserved remains (fragments of carapace and caudal vertebrae) are different from the other Upper Cretaceous taxon from Argentina, *Pa. gasparinae*, in the size and shape of the caudal vertebrae.

Scheyer (2007) has been a pioneer exploring the microanatomy of the turtle shell. He suggested a correlation between the aquatic adaptations of turtles and the degree of development of the compact and cancellous bone and vascularization. In this sense, he suggested that turtles could be divided in different categories: I for terrestrial turtles, II for semiaquatic to mainly aquatic, III for fully aquatic and IV for extreme aquatic/marine adaptation. The shell-bone histology of *T. sulcata* exhibits features of categories I and II, suggesting a terrestrial to semiaquatic habits.

Meiolaniidae Boulenger, 1887

Phylogenetic definition. The name *Meiolaniidae* is here defined as the node-based clade arising from the most recent common ancestor of *Niolamia argentina* Ameghino, 1899 and *Meiolania platyceps* Owen, 1886.

Diagnosis. Representatives of *Meiolaniidae* are diagnosed relative to more basal meiolaniforms by the presence of a contact between the quadratojugal and the squamosal below cavum tympani, presence of squamosal horns, absence of an antrum postoticum, presence of an intrapterygoid slit through which the arteria palatina enters the skull, presence of a bony flooring for the canalis carotici interni posterior to the bifurcation of the cerebral and palatine branches, formation of the foramen posterior canalis carotici interni by the pterygoid and the presence of a tail club and tail rings.

Niolamia argentina Ameghino, 1899 (= *Crossochelys corniger* Simpson, 1937)

Taxonomic history. *Niolamia argentina* Ameghino, 1899 (new species); *Meiolania argentina* Woodward, 1901 (new combination); *Niolamia argentina* = *Crossochelys corniger* Gaffney, 1996 (senior synonym).

Type material. MLP 26-40 (holotype, see comments below), an almost complete skull and lower jaw (Moreno 1899, fig. 2; Woodward 1901, pl. 15–18.1–2; Ameghino 1906, figs. 14–15; Simpson 1938, fig. 10; Gaffney 1996, figs. 63–64; Sterli and de la Fuente 2011b, figs. 1–6, 9–10).

Type locality. “Cañadón Blanco” locality, Chubut Province, Argentina (see Figure 5); Paleogene (Sterli and de la Fuente 2011b, see comments below).

Referred material and range. Paleogene of “Cañadón Blanco” locality, Chubut Province, Argentina (hypodigm of Woodward 1901); Middle Eocene of Cañadón Hondo locality (Pol et al. 2012), Chubut Province, Argentina (holotype of *Crossochelys corniger*).

Diagnosis. *Niolamia argentina* can be diagnosed as a meiolaniid by the full list of characters provided above, with the exception of the presence of a tail club. *Niolamia argentina* is differentiated

from other meiolaniids by the significantly large cranial scute A, contact of scute A with scute X, separation of the raised D scutes by a large, rectangular scute X, scute X does not separate G scutes in adults, the absence of scute H, contact between scutes D and F, straight, posterolaterally projecting scute B, presence of a broad shelf at the back of the skull formed by scutes A–C, protruding nasal bones, absence of pterygoid covering the foramen caroticum basisphenoidale, participation of the quadrate in the foramen stapedio-temporale, presence of a triturating surface with only two ridges (labial and lingual ridges), an undivided apertura narium externa, absence of a nasomaxillary sinus, presence of spines on the posterolateral border of the carapace, the presence of supracaudal scute and a broad pygal embayment and the presence of ventrally closed tail rings.

Comments. *Niolamia argentina* has a long and complex taxonomic history filled with ambiguities and speculations. Florentino Ameghino (1899) was the first to coin the name “*Niolamia argentina*” in a short note regarding a new turtle supposedly collected by his brother Carlos, but he did not designate a holotype, define a new species or provide a true description. According to the rules of the International Commission on Zoological Nomenclature (ICZN 1999), it is therefore questionable whether he established a valid taxon name. It is furthermore unclear if Ameghino (1899) intentionally spelt the word *Niolamia*, or simply mistyped the name *Miolania*, a justified speculation given that Ameghino (1906) later uses the name *Miolania*. Woodward (1901) soon after provided the description of well-preserved turtle material under the name *Miolania argentina*, which had been collected by staff of the Museo de La Plata, and it appears that he implicitly gave Ameghino (1899) credit for the name, as did all following authors explicitly (e.g., Simpson 1938; Gaffney 1996). The short note of Ameghino (1899) mostly focuses on finding similarities with the Australian *Meiolania platyceps*, which cannot serve as a diagnosis, but he also provides a short clause highlighting the presence of multiple cranial processes. Although this barely serves as the description of distinguishing characteristics, I here am inclined to accept this as a valid description (ICZN 1999) for the sake of nomenclatural stability. The alternative is to grant the species epithet to Woodward (1901) and the genus name to Simpson (1938).

In addition to barely providing an available taxon name, Ameghino (1899) did not explicitly list or describe specimens. Further confusion comes from the circumstance of the discovery. Ameghino (1899) stated that his specimens were collected by his brother Carlos, whereas the material figured by Moreno (1899), Woodward (1901) and even Ameghino (1906) himself had been collected by S. Roth. However, it seems suspicious that two identical turtle skulls with unambiguous meiolaniid characteristics were found within the same years in the same region of Argentina. It is furthermore known that the “bone wars” of Argentina were no less fierce at the end of the 19th century as they had been just a few decades earlier in the United States. And finally, if the skull of Ameghino (1899) were distinct from the skull of Moreno (1899) or Woodward (1901), would not Ameghino (1906) have highlighted this interesting fact in his later publication? It appears more likely that all three authors were referring to the same material, at least the same skull, and that Ameghino (1899) misrepresented the collector of his type material. I therefore accept the skull, the

only specimen certainly seen by Ameghino (1899), as the holotype of this taxon, in contrast to Simpson (1938), who declares this specimen to be the neotype. The only true alternative is to hypothesize that the type material of Ameghino (1899) is indeed lost (Simpson 1938), in which case *Nio. argentina* would have to be declared a nomen dubium. This would serve no nomenclatural stability, as the name *Nio. argentina* would be lost for future use.

Simpson (1938) described a new specimen of meiolaniid named *Crossochelys corniger* from the Middle Eocene of Cañadón Hondo (Chubut Province, Argentina). Gaffney (1996) later proposed that *Cr. corniger* is a juvenile of *Nio. argentina*, making the former a junior synonym of the latter. Sterli and de la Fuente (2011b) agreed with this synonymy while providing a comprehensive description of the newly prepared type skull. This preparation allowed the reaffirmation of some characteristics of this taxon, but also the discovery of others, particularly pertaining to the internal carotid circulation, anatomy of the palate and basicranium and the carapace remains. For detailed information about the history and anatomy of *Nio. argentina*, see Sterli and de la Fuente (2011b).

Ninjemys oweni (Woodward, 1888)

Taxonomic history. *Meiolania oweni* Woodward, 1888 (new species); *Ninjemys oweni* Gaffney, 1992 (new combination).

Type material. BMNH R391 (holotype), dermal bones of the skull, braincase missing (Owen 1880, pls. 37.1, 38.1–3; Moreno 1899, fig. 1; Gaffney 1992, fig. 1; Gaffney 1996, figs. 66–69).

Type locality. King’s Creek, Darling Downs, Queensland (see Figure 6); Pleistocene (Owen 1880; Bartholomai 1976; Gaffney 1992).

Referred material and range. Pleistocene of Darling Downs, Queensland (referred material of Owen 1880).

Diagnosis. *Ninjemys oweni* can be diagnosed as a meiolaniid by the presence of a contact between quadratojugal and squamosal below cavum tympani, presence of accessory ridge on the triturating surface of the palate, presence of horns in the squamosal and the presence of a tail club and tail rings (Sterli and de la Fuente 2013). *Ninjemys oweni* is differentiated from other meiolaniids by the unique possession of partially divided apertura narium externa, laterally projected horns, presence of scute A not much bigger than scute B, nasals that extend anteriorly beyond the premaxilla and ventrally closed tail rings.

Comments. Owen (1858) provided the name *Megalanias prisca* for a new species of gigantic land lizard based on three vertebrae from Queensland, Australia. According to Owen (1858), the procoelous vertebrae of *Me. prisca* resemble that of monitor lizards (*Varanus*) and this identification is recognized until now (e.g., Head et al. 2009). In a later contribution, Owen (1880) referred dorsal, sacral and caudal vertebrae and a skull from the same region to this taxon as well, also presuming them all to be of saurian origin. Owen (1886) furthermore described a new genus and species of land lizard from the Pleistocene of Lord Howe Island, Australia, under the name *Meiolania platyceps*. Soon after, Huxley (1887) and Woodward (1888) recognized

that both *Meiolania platyceps* and some of the remains from Queensland assigned to *Megalania prisca* by Owen (1880) actually belong to turtles, not to lizards. Woodward (1888) therefore proposed to name *Meiolania oweni* for the turtle skull from Queensland, a taxon referred to *Ninjemys* by Gaffney (1992). *Ninjemys oweni* is the largest known meiolaniid. In all cladistic analyses performed to date (e.g., Gaffney 1996; Sterli and de la Fuente 2013; Sterli, Pol et al. 2013; Sterli et al. 2015), *Nin. oweni* is recovered as the most basal Australasian taxon inside *Meiolaniidae* and as sister to the clade formed by *Warkalania carinaminor* and *Meiolania* spp.

Warkalania carinaminor Gaffney et al., 1992

Taxonomic history. *Warkalania carinaminor* Gaffney et al., 1992 (new species).

Type material. QM F22649 (holotype), right squamosal (Gaffney et al. 1992, fig. 2; Gaffney 1996, fig. 74).

Type locality. Pancake locality, Riversleigh Station, Queensland, Australia (see Figure 6); ?Late Oligocene to Early Miocene (Archer et al. 1989).

Referred material and range. Oligocene/Early Miocene of Riversleigh Station, Queensland, Australia (hypodigm of Gaffney et al. 1992).

Diagnosis. *Warkalania carinaminor* can be diagnosed as a meiolaniid by the presence of a contact between quadratojugal and squamosal below cavum tympani and the presence of squamosal horns (Sterli and de la Fuente 2013). *Warkalania carinaminor* is differentiated from other meiolaniids by the presence of processes in the squamosal and the scutes covering them forming low and horizontal ridges rather having prominent extensions away from the skull, scutes A, B and C of similar size and scute X small (Gaffney et al. 1992).

Comments. Gaffney et al. (1992) based the description of *Warkalania carinaminor* on a small sample of specimens found at the Pancake Site at Riversleigh Station, Queensland, Australia, while listing additional cranial and postcranial remains from other Riversleigh sites. However, a lack of better comparative material that would allow evaluating variability within meiolaniid species precluded them from referring these isolated remains to any known species of meiolaniid. In addition to *Meiolania brevicollis*, *W. carinaminor* is the oldest known species of meiolaniid in Australasia. In all the cladistic analyses presented so far (Gaffney 1996; Sterli and de la Fuente 2013; Sterli, Pol et al. 2013; Sterli et al. 2015), *W. carinaminor* is recovered as the sister clade to *Meiolania*.

Meiolania Owen, 1886

Type species. *Meiolania platyceps* Owen, 1886.

Diagnosis. *Meiolania* can be diagnosed as a meiolaniid by the complete list of characters listed above for that clade. *Meiolania* is differentiated from other meiolaniids by the presence of recurved B horns, the absence of a continuous shelf formed

by scutes A, B and C and the presence of ventrally open tail rings.

Meiolania platyceps Owen, 1886

Taxonomic history. *Meiolania platyceps* Owen, 1886 (new species); *Miolania platyceps* = *Miolania minor* = *Ceratochelys sthenurus* Lydekker, 1889b (senior synonym, objective senior synonymy and incorrect spelling of genus name).

Type material. BMNH R.675 (holotype), crushed skull, mainly skull roof preserved (Owen 1886, pls. 30.1, 31.1; Huxley 1887, fig. 3; Gaffney 1983, fig. 9).

Type locality. Lord Howe Island, Australia (see Figure 6); Pleistocene (Owen 1886; Gaffney 1983).

Referred material and range. Pleistocene of Lord Howe Island, Australia (hypodigm of Gaffney 1983).

Diagnosis. *Meiolania platyceps* shares with other members of the clade *Meiolania* the presence of recurved B horns and the absence of a continuous shelf formed by scutes A, B and C. *Meiolania platyceps* is differentiated from *Me. brevicollis* and *Me. mackayi* by the presence of a relatively wider horn core B, the presence of a parasagittal ridge on the premaxillary triturating surface and the absence of ventral keels in cervical vertebrae 5 and 6. *Meiolania platyceps* is differentiated from *Me. brevicollis* by the higher angle of the posterior projection of the horn core B, the larger horn core A, the relatively longer, lower and wider cervical vertebrae and the relatively low and flat neural spine of the axis. *Meiolania platyceps* is differentiated from *Me. mackayi* by the presence of relatively more robust limb bones. *Meiolania platyceps* is about 30% larger than *Me. mackayi* and about 10% to 20% smaller than *Me. brevicollis*.

Comments. *Meiolania platyceps* is the most emblematic taxon of the clade *Meiolaniidae* because its bizarre morphology has captured the attention of scientists since its discovery in the mid-19th century. Furthermore, with hundreds of known specimens representing nearly all parts of the skeleton, *Me. platyceps* is also the most completely known species of *Meiolaniidae*. Several papers have been devoted to the anatomy of this species (Anderson 1925, 1930; Gaffney 1983, 1985, 1996), finally rendering this taxon the best-described meiolaniid, or even meiolaniform.

Owen (1886) originally named two species of meiolaniid turtles from Lord Howe Island, *Me. minor* with *Me. platyceps* (based on specimen BMNH R.675) while presuming that they are saurian in nature. Huxley (1887) soon after recognized that the Lord Howe Island material is testudinate in nature and suggested a replacement name, *Ceratochelys sthenurus*, to highlight this conclusion. However, *Ce. sthenurus* is the objective junior synonym of *Me. platyceps*, given that they are typified by the same specimen, a conclusion alluded to by Boulenger (1887), but not formally acknowledged until Lydekker (1889b). In the catalog of the BMNH, Lydekker (1889b) mentioned the genus as *Miolania* and furthermore synonymized *Me. minor* with *Me. platyceps*, a conclusion accepted by all following authors (e.g., Anderson 1925; Gaffney 1996). This validity of this taxon is uncontroversial.

Meiolania brevicollis Megirian, 1992

Taxonomic history. *Meiolania brevicollis* Megirian, 1992 (new species).

Type material. NTM P87103-2 (holotype), right squamosal (Megirian 1992, fig. 1).

Type locality. Blast Site, Camfield Station, Northern Territory, Australia (see Figure 6); mid Miocene (Megirian 1992; Archer et al. 1997; Murray et al. 2000).

Referred material and range. Mid Miocene of Camfield Station, Northern Territory, Australia (Megirian 1992).

Diagnosis. *Meiolania brevicollis* is diagnosed as a meiolaniid by the presence of horns in the squamosal. *Meiolania brevicollis* is differentiated from *Me. platyceps* by having a flatter skull, posteriorly projecting horn core B and a vestigial scute A, presence of a small postorbital crest in the posterodorsal margin of the flat orbit, presence of relatively longer, lower and wider cervical vertebrae, presence of a relatively short, narrow and high neural spine of the axis and a distinct ventral keel on cervical centra 5 and 6 (Megirian 1992). *Meiolania brevicollis* is much bigger than *Me. mackayi* and it has a slender horn core B (Megirian 1992).

Comments. Although Megirian (1992) suggested that *Me. brevicollis* and *Me. mackayi* share a more slender horn core B relative to that of *Me. platyceps*, he also expressed his concerns about whether the relative width of this horn core is useful to differentiate *Me. brevicollis* from *Me. mackayi*. He states that the relative size is not a diagnostic character and the only differential character would be the width of the horn core B. Later, in the cladistic analysis of Gaffney (1996), *Me. brevicollis* was recovered as the sister clade of the meiolaniid from Wyandotte Creek, Queensland, based on the ratio between width and length of horn core B less than 0.48, while *Meiolania mackayi* has been recovered as their sister clade.

Meiolania mackayi Anderson, 1925

Taxonomic history. *Meiolania mackayi* Anderson, 1925 (new species).

Type material. AM F17720* (holotype), left B horn core (Anderson 1925, pl. 32.5–6; Gaffney 1996, fig. 77c).

Type locality. Walpole Island, New Caledonia (see Figure 6); ?Pleistocene.

Referred material and range. ?Pleistocene of Walpole Island, New Caledonia (referred material of Anderson [1925] and Gaffney [1996]).

Diagnosis. *Meiolania mackayi* is diagnosed as a meiolaniid by the presence of horns in the squamosal and as a member of the clade *Meiolania* by the presence of recurved B horn cores. *Meiolania mackayi* is differentiated from *Me. platyceps* by the presence of a narrower horn core B, more gracile limb bones and a 30% smaller relative size.

Comments. Gaffney (1996) stated that the fragmentary nature of the remains identified by Anderson (1925) as *Meiolania mackayi* does not provide enough data to allow distinguishing it from *Me. platyceps*. However, as the taxon has been already named and it is useful to recognize the Walpole Island material, Gaffney (1996) kept this a valid species. I concur with this assessment, in part also because Walpole (New Caledonia) is a small island located more than 1,500 km from mainland Australia and more than 1,300 km from Lord Howe Island (where *Me. platyceps* has been found) and because it is unlikely that meiolaniids could maintain active gene flow across such enormous distances.

Invalid and Problematic Taxa

Ceratochelys sthenurus Huxley, 1887
nomen invalidum
(objective junior synonym of *Meiolania platyceps* Owen, 1886)

Taxonomic history. *Ceratochelys sthenurus* Huxley, 1887 (new species); *Miolania platyceps* = *Miolania minor* = *Ceratochelys sthenurus* Lydekker, 1889b (junior synonym).

Type material. BMNH R.675 (holotype), crushed skull, mainly skull roof preserved (Owen 1886, pls. 30.1, 31.1; Huxley 1887, fig. 3; Gaffney 1983, fig. 9).

Type locality. Lord Howe Island, Australia (Owen 1886; Gaffney 1983; see Figure 6); Pleistocene (Gaffney 1983).

Comments. Huxley (1887) named *Ceratochelys sthenurus* based on the holotype of *Me. platyceps*. Consequently, *Ce. sthenurus* is an objective junior synonym of *Me. platyceps*, as briefly noted by Lydekker (1889b).

Crossochelys corniger Simpson, 1937
nomen invalidum
(junior synonym of *Niolamia argentina* Ameghino, 1899)

Taxonomic history. *Crossochelys corniger* Simpson, 1937 (new species); *Niolamia argentina* = *Crossochelys corniger* Gaffney, 1996 (junior synonym).

Type material. AMNH 3161 (holotype), disarticulated skull remains (Simpson 1938, figs. 1–9; Sterli and de la Fuente 2011b, figs. 7–8).

Type locality. Cañadón Hondo locality, Chubut Province, Argentina (see Figure 5); Sarmiento Formation, Middle Eocene (Simpson 1938; Pol et al. 2012).

Comments. In 1931, Coleman S. Williams and George G. Simpson collected a disarticulated skull of a meiolaniid from Eocene outcrops in Chubut, Argentina, which Simpson (1937) named *Crossochelys corniger*. Gaffney (1996) later proposed that *Cr. corniger* is a young individual of *Nio. argentina*, an interpretation suggested but rejected by Simpson (1938). The sutures in the type specimen of *Cr. corniger* are all open, which is indicative of

skeletal immaturity in turtles. Simpson (1938) noticed several other differences between *Cr. corniger* and *Nio. argentina*, and he interpreted them as specific differences. However, Gaffney (1996) noticed that those differences are mainly a consequence of using reconstructed casts of *Nio. argentina* and *Me. platyceps*, not actual specimens. As many of the characters mentioned by Simpson (1938) as differences between *Cr. corniger* and *Nio. argentina* are actually the same in the original material or cannot be determined in the latter, Gaffney (1996) proposed the synonymy between both species. A further cleaning of the holotype of *Nio. argentina* and the restudy of *Cr. corniger* allowed Sterli and de la Fuente (2011b) to corroborate Gaffney's (1996) synonymy.

Meiolania minor Owen, 1886
nomen invalidum

(junior synonym of *Meiolania platyceps* Owen,
1886)

Taxonomic history. *Meiolania minor* Owen, 1886 (new species); *Meiolania platyceps* = *Miolania minor* Lydekker, 1889b (junior synonym).

Type material. BMNH uncat. (holotype), occipital and anterior part of a skull (Owen 1886, pl. 29.1–6).

Type locality. Lord Howe Island, Australia (see Figure 6); Pleistocene (Owen 1886; Gaffney 1996).

Comments. Owen (1886) described anterior and posterior skull remains from Lord Howe Island as a new species of land lizard, *Meiolania minor*, but the chelonion nature of the material was soon after established by Huxley (1887). According to Owen (1886), *Me. minor* differs from *Me. platyceps* in the absence of a third ridge in the upper triturating surface and by its smaller size. Woodward (1888) suggested in the taxonomic list that *Me. minor* could be a synonym of *Me. platyceps*, but this suggestion was only formalized by Lydekker (1889b). Anderson (1925) later synonymized *Me. minor* with *Me. platyceps*.

?*Meiolania damelipi* White et al., 2010
(not meiolaniid)

Taxonomic history. ?*Meiolania damelipi* White et al., 2010 (new species).

Type material. AM F136641, right humerus (White et al. 2010, fig. 3a).

Type locality. Area 3B, Teouma Lapita site, Efate, Vanuatu; layer 2, Unit 3.3–3.4, Holocene, 2890–2760 cal BP at 94.3% probability (White et al. 2010).

Referred material and range. Holocene of Vanuatu (hypodigm of White et al. 2010).

Comments. White et al. (2010:15512) identified these remains as belonging to *Meiolaniidae* by the following synapomorphies: "(i) humerus with ectepicondylar foramen beginning as a groove dorsally, but distally penetrating the condyle to open ven-

trally; (ii) ulna with a distinct ridge dorsoproximally, extending distally from articular facet, forming a flat radioulnar articulation medially; (iii) digits with two phalanges and a robust ungual; (iv) shell fragments that are relatively thin and bear pits and grooves without a regular pattern on their outer surface; and (v) presence of dermal armor on shell margin." White et al. (2010:15513) then diagnosed the species as: "meiolaniid differing from other Pleistocene species with more gracile longbones; shoulder girdle with coracoid unfused, well developed dorsal and acromion processes diverge at approximately 105°; minor and major femoral trochanters ventrally enclose a deep intertrochanteric fossa; much smaller than *Ninjemyx oweni*."

Comparisons of the descriptions and photographs published by White et al. (2010) and meiolaniid remains highlight many differences, of which most were already noted by the authors. The humerus of ?*Me. damelipi* is slender, more than twice as long than wide, their ends are not expanded, the lateral process is not developed and the ectepicondylar foramen is open. The dorsal process of the scapula and the acromion forms an angle of 90–100° in ?*Me. damelipi*, and there is no web of bone at their base connecting both processes. The ulna is slender, with the distal end expanded and the proximal end not expanded. The femur is also slender, with the trochanter major well separated from the head by a depression; both trochanters are united in ventral view, forming a continuous process. The tibia is a slender element more than twice as long than wide and with a slender diaphysis. Meiolaniids, by contrast, possess very robust limb bones, the humerus is less than twice as long than wide, the ends of the humerus are expanded, the lateral process is well developed, the ectepicondylar foramen is closed, a web of bone connects the dorsal process of the scapula and the acromion, the ulna is robust and its distal end is not expanded, whereas the proximal end is, the head of the femur is continuous with the trochanter major, the trochanter major and minor are not united in ventral view, the tibia is robust and the proximal end of the tibia is very wide. In all regards, the material of ?*Me. damelipi* agrees with the anatomy of terrestrial turtles of the clade *Testudinidae*, which is doubly surprising, as this group has not yet been reported from the South Pacific. In light of this conclusion, I urge the careful revision of this taxon.

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Appendix 1 Institutional Abbreviations

AM	Australian Museum, Sydney, Australia
AMNH	American Museum of Natural History, New York, New York, USA
BMNH	Natural History Museum, London, United Kingdom

MACN	Museo Argentino de Ciencias Naturales “Bernardino Rivadavia,” Buenos Aires, Argentina, Pv-Ch, Vertebrate Paleontology collection, Chubut Province
MLP	Museo de La Plata, La Plata, Argentina
MMF	Geological Survey of New South Wales (ex Mining Museum Fossil), Sydney, Australia
MPEF	Museo Paleontológico Egidio Feruglio, Trelew, Argentina
NMV	National Museum of Victoria, Melbourne, Australia
NTM	Museum and Art Gallery of the Northern Territory, Darwin, Australia
QM	Queensland Museum, Brisbane, Australia

Appendix 2 Named Gondwanan Meiolaniform Genera

<i>Ceratochelys</i> Huxley, 1887 (type species: <i>Ceratochelys sthenurus</i> Huxley, 1887)
<i>Chubutemys</i> Gaffney et al., 2007 (type species: <i>Chubutemys copelloi</i> Gaffney et al., 2007)
<i>Crossochelys</i> Simpson, 1938 (type species: <i>Crossochelys corniger</i> Simpson, 1938)
<i>Meiolania</i> Owen, 1886 (type species: <i>Meiolania platyceps</i> Owen, 1886)
<i>Ninjemyx</i> Gaffney, 1992 (type species: <i>Meiolania oweni</i> Woodward, 1888)
<i>Niolamia</i> Ameghino, 1899 (type species: <i>Niolamia argentina</i> Ameghino, 1899)
<i>Otwayemys</i> Gaffney et al., 1998 (type species: <i>Otwayemys cunicularius</i> Gaffney et al., 1998)
<i>Patagoniaemys</i> Sterli and de la Fuente, 2011a (type species: <i>Patagoniaemys gasparinae</i> Sterli and de la Fuente, 2011a)
<i>Peligrochelys</i> Sterli and de la Fuente, 2013 (type species: <i>Peligrochelys walshae</i> Sterli and de la Fuente, 2013)
<i>Trapalcochelys</i> Sterli, de la Fuente et al., 2013 (type species: <i>Trapalcochelys sulcata</i> Sterli, de la Fuente et al., 2013)
<i>Warkalania</i> Gaffney et al., 1992 (type species: <i>Warkalania carinaminor</i> Gaffney et al., 1992)

Appendix 3 Biogeographical Summary of Gondwanan Meiolaniform Turtles

Numbers in brackets reference Figures 5 and 6. *Abbreviation*: TL = type locality.

Argentina

- [1] Lower Cretaceous, Aptian/Albian; Turtle Town Locality, Chubut Province; *Chubutemys copelloi* (TL) (Gaffney et al. 2007; Sterli et al. 2015)
- [2] Upper Cretaceous, Campanian/Maastrichtian; Ranquil-Co Locality, Mendoza Province; *Meiolaniformes* indet. (González Riga 1999; Sterli, de la Fuente et al. 2013)
- [3] Upper Cretaceous, Late Campanian/Early Maastrichtian; El Abra and Salitral de Santa Rosa Localities, Río Negro Province; *Meiolaniformes* indet. (Broin and de la Fuente 1993; Sterli, de la Fuente et al. 2013).
- [4] Upper Cretaceous, Late Campanian/Early Maastrichtian; Los Alamitos Locality, Río Negro Province; *Meiolaniformes* indet. (Broin 1987; Sterli, de la Fuente et al. 2013)
- [5] Upper Cretaceous, Campanian/Maastrichtian; Cerro Bayo Locality, Chubut Province; *Meiolaniformes* indet. (Gasparini and de la Fuente 2000; Sterli, de la Fuente et al. 2013)
- [6] Upper Cretaceous, Campanian/Maastrichtian; Buitre Chico Locality, Chubut Province; *Patagoniaemys gasparinae* (TL) (Sterli and de la Fuente 2011a)
- [7] Upper Cretaceous, Late Campanian/Early Maastrichtian; Salinas de Trapal-Co, Río Negro Province; *Trapalcochelys sulcata* (TL) (Sterli, de la Fuente et al. 2013)
- [8] Paleocene, Danian; Punta Peligro Locality, Chubut Province; *Peligrochelys walshae* (TL) (Sterli and de la Fuente 2013)
- [9] Middle Eocene; Campo de Acosta, Chubut Province; *Meiolaniidae* gen. et sp. indet. (de la Fuente and Fernández 1992)
- [10] Paleogene; Cañadón Blanco and Cañadón Hondo Localities, Chubut Province; *Niolamia argentina* (TL) (Ameghino 1899; Woodward 1901; Gaffney 1983, 1996; Sterli and de la Fuente 2011b)

Australia

- [11] Lower Cretaceous; Dinosaur Cove, Cape Otway, Victoria; *Otwayemys cucularius* (TL) (Gaffney et al. 1998)
- [12] Late Oligocene; Lake Pitikanta, South Australia; *Meiolaniidae* indet. (Gaffney 1996)
- [13] Late Oligocene; Lake Pinpa, South Australia; *Meiolaniidae* indet. (Gaffney 1996)
- [14] Late Oligocene/Early Miocene; Pancake locality, Riversleigh Station, Queensland; *Warkalania carinaminor* (TL) (Gaffney et al. 1992)
- [15] Probably Early Miocene; Gulgong, New South Wales; *Meiolaniidae* indet. (Gaffney 1996)
- [16] Early Miocene?; Riversleigh Station, Queensland; *Meiolaniidae* indet. (Gaffney 1992, 1996)
- [17] Middle Miocene; Blast Site, Camfield Station, Northern Territory; *Meiolania brevicollis* (TL) (Megirian 1992, Gaffney 1996)
- [18] Middle Miocene; Lake Ngapakaldi, South Australia; *Meiolaniidae* indet. (Gaffney 1996)
- [19] Pliocene; Armour Station, Queensland; *Meiolaniidae* indet. (Gaffney 1981)

- [20] Pleistocene; King's Creek, Darling Downs, Queensland; *Ninjemys oweni* (TL) (Owen 1886; Gaffney 1992, 1996)
- [21] Pleistocene; Lord Howe Island; *Meiolania platyceps* (TL) (Owen 1886; Gaffney 1983, 1985, 1996)
- [22] Late Pleistocene; Wyandotte Creek, Queensland; *Meiolania* cf. *Me. platyceps* (Gaffney and McNamara 1990)
- [23] Age indeterminate, probably Pleistocene; Oaky Creek, northwest of Coolah, New South Wales; cf. *Ninjemys oweni* (Etheridge 1893; Gaffney 1996)
- [24] Age indeterminate; Sandhurst Creek, Queensland; *Meiolaniidae* indeterminate (Gaffney 1996)

Fiji

- Quaternary; Voli Voli site, Viti Levu; ?*Meiolaniidae* indet. (Worthy et al. 1999; White et al. 2010)

New Caledonia

- [25] Pleistocene; Tiga Island, Loyalty group; *Meiolaniidae* indet. (Gaffney et al. 1984)
- [26] ?Pleistocene; Walpole Island; *Meiolania mackayi* (TL) (Anderson 1925; Gaffney 1996)
- [27] Holocene; Main Pindai Cave, Nepoui Peninsula; *Meiolaniidae* indet. (Gaffney et al. 1984)

New Zealand

- Early Miocene; Home Hills Station, Manuherikia River, Central Otago, South Island; ?*Meiolaniidae* indet. (Worthy et al. 2011)

Republic of Vanuatu

- Holocene; Teouma Lapita site, Efate; *Testudines* indet. (non-*Meiolaniidae*, holotype of ?*Meiolania damelipi* sensu White et al. 2010)

Appendix 4 Hierarchical Taxonomy of Gondwanan Meiolaniforms

- Meiolaniformes* Sterli and de la Fuente, 2013
Chubutemys copelloi Gaffney et al., 2007
Otwayemys cucularius Gaffney et al., 1998
Patagoniaemys gasparinae Sterli and de la Fuente, 2011a
Trapalcochelys sulcata Sterli, de la Fuente et al., 2013
Peligrochelys walshae Sterli and de la Fuente, 2013
Meiolaniidae Simpson, 1937
Niolamia argentina Ameghino, 1899
Ninjemys oweni (Woodward, 1888)
Warkalania carinaminor Gaffney et al., 1992
Meiolania Owen, 1886
Meiolania platyceps Owen, 1886
Meiolania brevicollis Megirian, 1992
Meiolania mackayi Anderson, 1925

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Editor's note: This article is intended to be included with others in a forthcoming book being coordinated by Walter G. Joyce to elucidate the fossil record of turtles. The individual articles that will form the components of this book are being published separately in the next several volumes of the *Bulletin of the Peabody Museum of Natural History*.