Ecophysiological steps of marine adaptation in extant and extinct non-avian tetrapods

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ABSTRACT

Marine reptiles and mammals are phylogenetically so distant from each other that their marine adaptations are rarely compared directly. We reviewed ecophysiological features in extant non-avian marine tetrapods representing 31 marine colonizations to test whether there is a common pattern across higher taxonomic groups, such as mammals and reptiles. Marine adaptations in tetrapods can be roughly divided into aquatic and haline adaptations, each of which seems to follow a sequence of three steps. In combination, these six categories exhibit five steps of marine adaptation that apply across all clades except snakes: Step M1, incipient use of marine resources; Step M2, direct feeding in the saline sea; Step M3, water balance maintenance without terrestrial fresh water; Step M4, minimized terrestrial travel and loss of terrestrial feeding; and Step M5, loss of terrestrial thermoregulation and fur/plumage. Acquisition of viviparity is not included because there is no known case where viviparity evolved after a tetrapod lineage colonized the sea. A similar sequence is found in snakes but with the haline adaptation step (Step M3) lagging behind aquatic adaptation (haline adaptation is Step S5 in snakes), most likely because their unique method of water balance maintenance requires a supply of fresh water. The same constraint may limit the maximum body size of fully marine snakes.

Steps M4 and M5 in all taxa except snakes are associated with skeletal adaptations that are mechanistically linked to relevant ecophysiological features, allowing assessment of marine adaptation steps in some fossil marine tetrapods. We identified four fossil clades containing members that reached Step M5 outside of stem whales, pinnipeds, sea cows and sea turtles, namely Eosauropterygia, Ichthyosauromorpha, Mosasauroidea, and Thalattosuchia, while five other clades reached Step M4: Saurosphargidae, Placodontia, *Dinocephalosaurus*, Desmostylia, and *Odontochelys*. Clades reaching Steps M4 and M5, both extant and extinct, appear to have higher species diversity than those only reaching Steps M1 to M3, while the total number of clades is higher for the earlier steps. This suggests that marine colonizers only diversified greatly after they minimized their use of terrestrial resources, with many lineages not reaching these advanced steps.

Historical patterns suggest that a clade does not advance to Steps M4 and M5 unless these steps are reached early in the evolution of the clade. Intermediate forms before a clade reached Steps M4 and M5 tend to become extinct without leaving extant descendants or fossil evidence. This makes it difficult to reconstruct the evolutionary history of marine adaptation in many clades. Clades that reached Steps M4 and M5 tend to last longer than other marine tetrapod clades, sometimes for more than 100 million years.

Key words: marine tetrapod, marine mammal, marine reptile, marine adaptation sequence, Mesozoic, Cenozoic.

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I. INTRODUCTION

Secondary aquatic adaptation by tetrapod vertebrates has intrigued and misled scientists and naturalists for centuries. Marine mammals were grouped with aquatic vertebrates since at least as early as Aristotle, until Linnaeus finally suggested that cetaceans and pinnipeds were mammals (Romero, 2012). It is now common knowledge that tetrapods have given rise to multiple clades of returners to the sea (Pyenson, Kelley & Parham, 2014; Kelley & Pyenson, 2015; Vermeij & Motani, 2018). Secondary marine invaders are known in all four major groups of tetrapod vertebrates, namely reptiles, birds, mammals, and probably some fossil amphibians.

Life in the sea requires many physiological, morphological, and behavioural characteristics that are acquired during the process of secondary marine colonization, through modification of existing features or acquisition of new ones (Houssaye & Fish, 2016). The order in which such features are acquired has been studied in selected groups, especially snakes and turtles (Dunson & Mazzotti, 1989). However, whether there is a specific sequence of marine adaptation common to all marine tetrapod groups is poorly understood, probably because a cross-taxonomic comparison is rarely made. One of the broader comparisons, across snakes, turtles, crocodilians, and lizards, revealed that many differences existed in the details of marine adaptions even among these reptilian taxa, although the net effects may be similar (Dunson, 1984). Another confusing factor is that marine invasions may occur directly from land to sea, or indirectly through fresh water and brackish water, and the choice of the route may be somewhat phylogenetically constrained (e.g. direct invasions may only be possible if the land ancestor already had the mechanism to excrete extra salt) (Dunson & Mazzotti, 1989).

Despite the differences in the details of mechanisms, there are ecophysiological characteristics that are found commonly across marine-adapted tetrapod clades, mostly concerning osmoregulation and aquatic locomotion. For example, for a clade to be marine adapted to a certain level, its constituent species must maintain water balance while at sea regardless of the differences in the details of the mechanisms to achieve it. It is then useful to list such common ecophysiological characteristics across extant marine reptiles, mammals, and birds to examine if there is a specific sequence in which these characteristics evolved across the clades.

Here we review the extensive literature on marine adaptations in extant tetrapods to test the hypothesis that such a sequence exists across marine tetrapod clades. Then we use the resulting sequence to infer the degree of marine adaptation in extinct clades of tetrapods. Marine tetrapods began to invade the open sea after the end-Permian mass extinction (~252 million years ago). A recent review listed 69 tetrapod clades that colonized the sea since that time (Vermeij & Motani, 2018) – skeletal reconstructions of some of these clades are given in Fig. 1 to provide an illustrative overview. Despite recent interest in fossil marine tetrapods (Pyenson *et al.*, 2014; Kelley & Pyenson, 2015; Vermeij & Motani, 2018), the degree of marine adaptation in fossil clades has not been compared based on explicit criteria. Finally, we will discuss some of the notable trends seen among marine tetrapods, especially in their diversity patterns and tempos of evolution.

We are not including birds in this review for two reasons. First, their marine colonization often represents air-to-water rather than land-to-water transitions and thus has unique sets of constraints and adaptations that make them not directly comparable to other tetrapods. For example, the anterior shift of the centre of mass is an apomorphy related to body trim control in derived marine mammals and reptiles (see Section V.1*a*), but is a plesiomorphy in marine birds because they have already adapted to body trim control in air. Second, their adaptations to haline environments are known based on some representative species, but many other species still remain unexamined in detail. For the same reasons, we will not be including pterosaurs, flying reptiles of the Mesozoic, in our review.

II. FIVE STEPS OF ECOPHYSIOLOGICAL MARINE ADAPTATION

(1) Haline and aquatic adaptations

We begin with an overview of the marine adaptations seen in non-avian tetrapods. Marine adaptation extends across several aspects of ecophysiology, of which two have attracted the most attention: osmoregulation in haline environments and occupation of aquatic environments. We refer to them as ‘haline’ and ‘aquatic adaptations’, respectively.

Aquatic adaptation includes adaptations in locomotor morphology, kinematics and kinetics, communication, mode of feeding, respiration and circulation. All of these need to be modified at least to some extent if a terrestrial animal becomes aquatic. As stated earlier, phylogenetic constraints often lead to different solutions and mechanisms, but the net effects of these mechanisms can be compared across taxa. Such effects, in this case, may be seen in the proportion of distance covered on land and in water through locomotion, defined herein as:

A0: completely terrestrial lifestyle (plesiomorphy);

A1: at least occasional locomotion in water;

A2: absence of terrestrial travel (may bask onshore regularly);

A3: fully aquatic lifestyle except for reproduction.

These stages can be followed by A4: fully aquatic across all aspects of life history. However, there is no known case where viviparity evolved from oviparity after marine invasion (Motani *et al.*, 2014). A1–A3 are called steps because A2 is conditional on A1, and A3 on A2. Also, when sorting extant marine tetrapod species with the presence/absence of these features, it can be seen that the features are acquired stepwise, i.e. A2 does not exist without A1, and A3 without A2 (Table 1).

Haline adaptation mainly concerns acquisition of water and removal of excess salt in haline environments. Different mechanisms are found in different clades of marine tetrapods, but the net effects of such haline adaptation can be seen in how animals acquire food and water. The following steps are seen among extant marine tetrapods:

H0: fully terrestrial diet (plesiomorphy);

H1: diet of at least some food originating in brackish or saline marine water, including beached food;

H2: diet of at least some food collected directly in sea water. This involves consumption of salty food and incidental ingestion of sea water through prey capture in water;

H3A: water balance maintenance without terrestrial fresh water;

H3B: completely marine diet without any terrestrial food.

H1–H3 are called steps for the same reasons as given above for A1–A3. H3A is somewhat separate from the rest in the series because it concerns water supply rather than food. H3A may be observed without H3B, and *vice versa*, depending on the lineage (compare snakes and others in Table 1).

(2) Combining haline and aquatic adaptations

These steps of aquatic and haline adaptations exist in combination in any given animal. A pattern emerges when sorting the list of extant marine tetrapods by the combination of both aquatic and haline adaptations (Table 1), suggesting there is a common pattern across marine tetrapods, except in snakes. The following sequence is seen during marine adaptation:

M1: incipient use of marine resources, i.e. A1, H1, or both

  (*a*) ocean swimmer without marine diet;

  (*b*) Intertidal feeders;

  (*c*) Brackish swimmers and feeders;

M2: direct feeding in the saline sea, i.e. H2 (and A1 if absent at first);

M3: water balance maintenance without terrestrial fresh water, i.e. H3A;

M4: minimized terrestrial locomotion and loss of terrestrial feeding, i.e. A2 and H3B;

M5: loss of terrestrial thermoregulation and fur/plumage, i.e. A3.

Whereas this is the most common sequence observed, snakes depart from it, most likely due to constraints related to water balance as discussed later. Marine adaptation in snakes seems take place in the following sequence:

S1: incipient use of marine resources, i.e. A1, H1, or both

  (*a*) ocean swimmer without marine diet;

  (*b*) Intertidal feeders;

  (*c*) Brackish swimmers and feeders;

S2: direct feeding in the saline sea, i.e. A1 and H2;

S3: minimized terrestrial locomotion and loss of terrestrial feeding, i.e. A2 and H3B;

S4: loss of terrestrial thermoregulation, i.e. A3;

S5: water balance maintenance without terrestrial fresh water, i.e. H3A.

Notably, features seen at Step S3 are equivalent to those at M4. This shift is caused by a delay in acquisition of H3A, i.e. water balance maintenance without terrestrial fresh water (which becomes Step S5). Thus, aquatic adaptation is more easily achieved than haline adaptation in snakes, in comparison with other marine tetrapods.

Theoretically speaking, sequences of aquatic and haline adaptations other than those presented above are possible. For instance, a clade may complete aquatic adaptation before engaging in haline adaptation, if it first inhabits fresh water. However, as Table 1 shows, there is no such case known in extant marine tetrapod clades. Possible exceptions to the sequences listed are provided by pinnipeds, which, as discussed in Section VI.15), may have achieved stage A2 before stage H1 but further fossil evidence will be necessary to scrutinize this point.

Detailed description of the marine adaptation steps and a review of the taxa that exhibit each are given in Sections III and IV and summarized in Table 1. A total of 31 marine colonizations, involving 249 living species, are included.

III. EXTANT MARINE MAMMALS AND REPTILES: OVERVIEW

Only marine mammals and reptiles with limbs are reviewed in this section. Snakes will be reviewed in Section IV. The review below is intentionally brief, and readers are referred to the online supporting Appendix S1 for a more detailed discussion.

(1) Step M1: incipient use of marine resources

The onset of marine adaptation may occur in three ways: (*a*) surface swimming in open saline water without feeding on marine food; (*b*) intertidal feeding on marine food without swimming in saline water; or (*c*) feeding while swimming in brackish water. Of these three possibilities, *c* is most common among extant non-avian tetrapods while *a* and *b* are rare, with only one and two examples, respectively. These numbers, however, may be underestimates because behaviours of extant species at the fringe of the sea are far from completely characterized.

(*a*) *Ocean swimmer without marine diet*

We could not find any species in this category outside of snakes (see Section IV). We do not include some large mammals that sometimes cross narrow straits, such as elephants in Singapore.

(*b*) *Intertidal feeders*

There are many intertidal feeders known, but most also feed directly in the sea or brackish water. When restricting the list to those animals that feed intertidally but not in these waters, we are left with only two species, the crabeating frog (*Fejervarya cancrivora*) and the Japanese macaque (*Macaca fuscata*). The crabeating frog has been found with a sea slug and marine flatworm in its stomach contents (Elliott & Karunakaran, 1974), presumably collected intertidally. Its tadpoles may live in brackish water. At least one island population of the Japanese macaque in Koshima (more commonly called Kōjima), Miyazaki, Japan, is known to eat marine foods, such as limpets (*Cellana toreuma*), octopods, and marine fish including beached Japanese seabass (*Lateolabrax japonicus*) (Watanabe, 1989; Leca *et al.*, 2007). Some livestock, such as North Ronaldsay sheep (*Ovis aries*), feed on seaweeds (Hansen, Hector & Feldmann, 2003), but they are not counted in this review because their habitats and diets cannot avoid human influences.

(*c*) *Brackish swimmers and feeders*

Brackish feeding has been documented for at least three species of crocodile, the freshwater crocodile (*Crocodylus johnstoni*) (Taplin *et al.*, 1999), the broad-snouted caiman (*Caiman latirostris*) (Grigg *et al.*, 1998), and the American alligator (*Alligator mississippiensis*) (Mazzotti & Dunson, 1984)], three species of turtles [the painted terrapin (*Batagur borneoensis*) (Davenport & Wong, 1986), the northern river terrapin (*B. baska*) (Dunson & Moll, 1980) and the pig-nosed turtle (*Carettochelys insculpta*) (Groombridge & Wright, 1982)], and a mammal, the long-tailed monkey (*Macaca fascicularis*) [Son, 2003; Malaivijitnond *et al.*, 2007; see also BBC *Planet Earth* documentary (http://www.bbc.co.uk/pressoffice/pressreleases/stories/2006/02_february/01/earth_firsts.shtml)].

There are additional species that may possibly be assigned to Step M1. These include the Dumeril's monitor (*Varanus dumerilii*) (Bennett, 2004), mangrove monitor (*V. indicus*) (Dryden & Ziegler, 2004), *Eleutherodactylus caribe* (a frog from Haiti that may be extinct) (Hedges & Thomas, 1992), the pygmy three-toed sloth (*Bradypus pygmaeus*) (Hayssen, 2008; Kaviar, Shockey & Sundberg, 2012) and the proboscis monkey (*Nasalis larvatus*) (Kern, 1964).

(2) Step M2: direct feeding in the saline sea

The next step is reached when the animal evolves to capture food in salt water (salinity of 30‰ or higher). Animals at this step still need to have access to terrestrial resources, such as brackish or fresh water for drinking, and air rather than water around the body during basking for thermoregulation. Many animals at this step still consume terrestrial food while also feeding in the sea. They lose body mass when kept in saline water due to their limited ability to excrete salt; the latter also prevents them from drinking saline water or eating too much marine food. They are usually amphibious because of their need for terrestrial resources. These animals may have some ability to remove extra salt, either through renal (Ortiz, 2001; Costa, 2018) or extrarenal mechanisms, such as salt glands (Cowan, 1974, 1990; Dunson, 1974; Taplin, 1988; Taplin & Grigg, 2006; Dantzler & Bradshaw, 2008).

We found at least five species of reptiles and three species of mammal belonging to this category. At least two species of *Varanus* forage in the saline sea, namely the Asian water monitor, *V. salvator* (Editorial, 2008) and the rusty monitor, *V. semiremex* (Jackson, 2005; James & Tremul, 2017), as do at least two species of crocodile, the American crocodile *Crocodylus acutus* (Platt *et al.*, 2013) and the saltwater crocodile, *C. porosus* (Allen, 1974). The diamondback terrapin (*Malaclemys terrapin*) feeds in the sea as well as brackish water (Cowan, 1974; Baldwin *et al.*, 2016). The marine otter (*Lontra felina*) (Mangel *et al.*, 2011), as well as some other mustelids, such as the Eurasian otter (*Lutra lutra*) and the North American river otter (*Lontra canadensis*) have coastal populations that feed in the sea (Kruuk & Moorhouse, 1990; Bowyer *et al.*, 2003).

Humans may be placed in this category. We are capable of diving in the sea to catch food but still need access to terrestrial resources. Another candidate is the fishing cat (*Prionailurus viverrinus*). It captures fish in tidal flats (Malla, 2016), although direct feeding in the sea has not been documented explicitly.

(3) Step M3: water balance maintenance without terrestrial fresh water

At the next step, animals evolve to feed primarily, although not necessarily exclusively, on marine resources without drinking land-derived fresh water. Tetrapods reaching this step must obtain fresh water by any of three mechanisms: (*a*) seawater drinking plus salt excretion, through kidneys and/or the salt gland; (*b*) use of by-product water from metabolism; and (*c*) collection of brackish or fresh water while at sea (e.g. from rainfall). They must also reduce water loss through cutaneous water efflux, although exceptions may occur when Step M5 is reached. Published data on extant marine reptiles suggest that salt glands found in Step M3–M5 marine colonizers have a greater ability to excrete salts than those of Step M1–M2 colonizers (Fig. 2).

We identified only two species in this category, one reptile and one mammal. The marine iguana (*Amblyrhynchus cristatus*) balances water influx and efflux while in saline water, sometimes drinking sea water (Dunson, 1969; Shoemaker & Nagy, 1984) The polar bear (*Ursus maritimus*) maintains water balance through metabolic water, part of which is derived from seafood (Barros & Clarke, 2009; Rode & Stirling, 2018).

(4) Step M4: minimized terrestrial travel and loss of terrestrial feeding

Species at this step have evolved to survive without access to terrestrial food or water, although many still spend time on land for grooming and basking. As a result, extensive locomotion on land no longer occurs. Only pinnipeds and sea otters belong to this category. The sea otter (*Enhydra lutris*) is a highly aquatic species that spends most of its time (including reproduction) at sea but occasionally rests on land, and energetically dries its fur after hauling out (Kenyon, 1969). Pinnipeds contain two of the major marine mammalian clades that exclusively feed in the sea: Otariidae and Odobenidae (Bowen, Beck & Austin, 2009). Most of the third group of Pinnipeds, Phocdae, are also marine. Some may remain at sea for prolonged durations but still need to spend considerable amounts of time on land or ice (Crocker & Costa, 2009).

(5) Step M5: loss of terrestrial thermoregulation and fur/plumage

Species at this step can thermoregulate in the sea without ever leaving the water. Some of the animals reaching this step may still use terrestrial environments for reproduction, probably because viviparity may be hard to acquire in water (Motani *et al.*, 2014). Water is more heat conductive than air, so species in this category need to be able to withstand elevated levels of potential heat loss to the surrounding medium, for which increased body insulation and reduction of blood flow near the body surface are often effective. Mammals generally use integumental structures, fur, to aid body heat insulation. However, these structures require maintenance in air, so it is unlikely that any species reaching Step M5 can retain fur or plumage. Notably, the only two mammal groups at this step have lost their fur, i.e. cetaceans and sirenians. The loss of fur may lead to increased cutaneous water efflux, as seen in some but not all cetaceans (Ortiz, 2001; Costa, 2018), requiring further physiological adjustment of water balance.

We recognize three clades that reached this step: cetaceans, some sirenians, and sea turtles. Extant cetaceans are an exclusively aquatic clade in which most species never use fresh water (Ballance, 2009). Of the sirenians, at least Dugongidae qualify for Step M5: dugongs are fully marine (Marsh, Heinsohn & Marsh, 1984; Marsh, 2009), although they have been sighted giving birth essentially aground on two occasions (Marsh *et al.*, 1984). However, birth usually takes place in the sea, and they usually do not utilize terrestrial environments. Manatees frequently drink fresh water and therefore may not qualify for Step M5. It is unknown if manatees evolved from fully marine ancestors (Domning, 2009) but, if so, the lineage should be considered to have reached Step M5. Sea turtles (Chelonioidea) can maintain their daily physiology without access to land (Limpus, 1993; Limpus & Miller, 1993; Babonis & Brischoux, 2012), and therefore need land access only for nesting by females. There are exceptions: some populations of the green sea turtle (*Chelonia mydas*) occasionally bask terrestrially (Van Houtan, Halley & Marks, 2015). However, given that this behaviour is limited to some members of only one species, it was likely acquired secondarily. Sea turtles therefore qualify as Step M5.

IV. EXTANT SNAKES WITH MARINE ADAPTATION

Snakes exhibit a sequence of marine adaptation that is slightly different from those of other marine tetrapods because of the delay in haline adaptation. Apart from this difference in sequence, however, they exhibit the same categories of aquatic and haline adaptations as the rest of the tetrapods.

(1) Step S1: incipient use of marine resources

Step S1 is the same as Step M1 (see Section III.1).

(*a*) *Ocean swimmer without marine diet*

We identified only one open marine swimmer without a marine diet, the reticulated python (*Python reticulatus*). This species has been observed surface-swimming far out in the sea (O'Shea, 2007) but there is no record of it feeding on marine food.

(*b*) *Intertidal feeders*

We are not aware of any snake representing a step equivalent to Step M1b.

(*c*) *Brackish swimmers and feeders*

We recognize at least one acrochordid and seven homalopsine species in this category. The Java file snake (*Acrochordus javanicus*) lives and feeds in estuaries and fresh water (Shine *et al.*, 1995), unlike congeners that are found only in fresh water (*A. arafurae*) or sea water (*A. granulatus*) (Lillywhite & Ellis, 1994). Snakes of Homalopsinae (Serpentes: Colubridae) are aquatic reptiles in Australia, Southeast Asia, and parts of South Asia. Murphy (2011) listed 16 species with brackish to marine habits. One of these, *Cerberus rynchops*, was later divided into two species (*C. rynchops* and *C. schneiderii*), making the total 17 (Murphy, Voris & Karns, 2012). We had difficulty confirming the habitats of many of these 17 species in the primary literature based on direct observations. Habitat information about this group has been recycled over the years, based on old literature (e.g. Smith, 1943), which relied on museum specimens without direct field observations. Of the 17 species, we removed *Homalopsis buccata*, *Cerberus micrilepis*, and *Erpeton tentaculatum* because they were classified as freshwater species in the IUCN *Red List* (Jayne, Ward & Voris, 1995). We also placed three species in Step S2, as discussed below. This left 12 of the 17 species in Step S1c. The 12 included *Gerarda prevostiana* and *Fordonia leucobalia* (Voris & Murphy, 2002; Vyas, Murphy & Voris, 2013), for which diets have been documented to some extent.

Other candidates for this step include some species of Natricinae (Colubridae) and Dipsadidae. Some snakes of Natricinae are known to tolerate salty water (Murphy, 2012), including *Nerodia fasciata* in which the degree of salt tolerance varies even within conspecific races depending on their habitats (Dunson, 1980), and the genus *Natrix* (Koleva *et al.*, 2017). Some species of Dipsadidae have been documented from salty water (Murphy, 2012). Although most of the primary literature comprises dated naturalist accounts, the presence of *Tretanorhinus* in brackish water is sufficiently documented (Grant, 1946).

(2) Step S2: direct feeding in the saline sea

Step S2 is the same as Step M2 (see Section III.2). Three species of amphibious homalopsine snakes are placed in Step S2: *Cerberus rynchops, C. schneiderii*, and *Bitia hydroides*. *C. schneiderii* from the Philippines and Malaysia was sighted while swimming in coastal sea water, capturing fish (Jayne, Voris & Heang, 1988), although it is also known from mud flats and brackish water (Voris, 2015; Dunson & Minton, 1978). A unique facultative salt gland was found in the premaxillary region of this species but it is most likely functional only during dehydration (June, Dunson & Dunson, 1973). *C. rynchops* occupies similar habitats (Vyas *et al.*, 2013). *Bitia hydroides* was also observed in the sea and brackish waters (Jayne *et al*., 1988), and it was suspected that they may be foraging in waters deeper than the intertidal zone (Jayne *et al.*, 1995).

(3) Step S3: minimized terrestrial travel and loss of terrestrial feeding

Step S3 shares the list of features with Step M4 (see Section III.4). Only one clade of snakes belongs to this category: sea kraits (*Laticauda* spp.). However, it is notable that the degree of terrestriality and impairment of terrestrial locomotion depends on the species complexes within a clade (Shine & Shetty, 2001; Shetty & Shine, 2002; Bonnet, Ineich & Shine, 2005; Heatwole, Busack & Cogger, 2005; Bonnet & Brischoux, 2008; Brischoux *et al.*, 2013). At least some species can search for fresh water in the sea and follow terrestrial freshwater sources, and may even drink from the thin hyposaline layer on the sea surface following rainfall (Lillywhite *et al.*, 2008; Kidera, Mori & Tu, 2013). Their distribution is limited to coastal regions, and their salt gland has salt-excretion capabilities comparable to that in Step S2 even in one of the most sea-going species, *L. semifasciata* (Fig. 2).

(4) Step S4: loss of terrestrial thermoregulation

The condition achieved in this step corresponds to that of Step M5 (see Section III.5). Only one species belongs to this category. The little file snake (*Acrochordus granulatus*) is a piscivorous species that inhabits a wide salinity range, from fully marine to fresh water (June *et al.*, 1973; Garcia *et al.*, 2014; Lillywhite, Heatwole & Sheehy, 2014). Marine populations routinely access fresh water derived from land (Lillywhite & Ellis, 1994). The species has a lingual salt gland and can remove salt to some extent (June *et al.*, 1973) but Fig. 2 shows that the ability of *A. granulatus* to excrete salt is more limited than in species in Steps M3–M5, being more similar to those in Step M2. For these reasons, we consider that this species has not reached Step S5, and tentatively place it in Step S4.

(5) Step S5: water balance maintenance without terrestrial fresh water

The condition of this step corresponds to that of Step M3 (see Section III.3). Only one clade belongs to this step: the true sea snakes (Elapidae: Hydrophiinae). These are a group of entirely aquatic snakes that never leave water voluntarily (Heatwole & Cogger, 1993). They comprise about 70 species, of which the yellow-bellied sea snake (*Hydrophis (Pelamis) platurus*) is the only species with a trans-Pacific distribution (Rasmussen *et al.*, 2011). They have a lingual salt gland that excretes salt (June *et al.*, 1973) but still need access to fresh water (Lillywhite, Heatwole & Sheehy, 2015; Lillywhite *et al.*, 2012).

V. MORPHOLOGICAL FEATURES ASSOCIATED WITH MARINE ADAPTATION STEPS

The marine adaptation steps M1–M5 and S1–S5 are not directly observable from the skeleton. Given that extinct species of tetrapods are known only from skeletons, it is useful to examine whether there are morphological correlates allowing us to infer marine adaptation steps based only on skeletal remains. Unfortunately, we did not identify any such correlates for M1–M3 or S1–S5. However, steps M4 and M5 can be associated with morphological features that are mechanistically linked to their respective ecophysiological features. These features cannot be assessed in limb-less forms (specifically snakes herein) because they are found in the limbs. These features and their presence in extant marine tetrapods are summarized in Table 2.

(1) Robust indicators of marine adaptation steps

(*a*) *Humerus longer than femur (Step M4)*

Dominance of the hind limb over the forelimb is a basic feature of tetrapod vertebrates. This is reflected in the relative lengths of the respective propodial bones: the femur of a given tetrapod vertebrate tends to be longer than the humerus, beginning with the late Devonian *Acanthostega* (Coates, 1996). The mechanical connection with the vertebral column differs between the fore- and hind limbs. The forelimb articulates with the shoulder, which is not directly connected to the vertebral column *via* hard tissue, i.e. none of the bones bearing the glenoid directly connects to the vertebral column. By contrast, the hind limb connects to the vertebral column *via* sacral ribs that are usually fused to the sacral vertebrae (Hoffstetter & Gasc, 1969). The hind limb, therefore, plays a major role in terrestrial body support, e.g. in *Alligator mississippiensis,* 51.3% of the body weight is estimated to be supported by the hind limb, as opposed to 36.8% by the forelimb and 11.8% by the tail (Willey, 2004). Exceptions are found among aerial, fossorial, and aquatic tetrapods, as well as some large terrestrial herbivores with raised shoulders (e.g. Brachiosauridae and Megatheriidae).

A reversal of the limb dominance pattern in marine tetrapods has been noted by previous authors. For example, cetaceans and sea cows usually lack the hind limb almost completely (Thewissen *et al.*, 2006; Adam, 2018), and it has been recognized that it is an apomorphy of sea turtles to have the humerus longer than the femur (Hirayama, 1998). A broader survey based on published bone measurements suggests that the humerus is indeed longer than the femur in all extant marine tetrapods of Steps M4 and M5 (Fig. 3, Table 2,

Table S1). These tables are based on published compilations of morphological data of tetrapods originally used for purposes other than the present one. We retained all species in the original tables except those that are noted as exceptions in the previous paragraph (e.g. aerial and fossorial species). Terrestrial species are allocated the marine adaptation step M0. This condition thus is a robust indicator of at least Step M4 and beyond. When including fossil forms, however, the dominance of the humerus over the femur may be absent in some clades (Table S2, see Sauropterygia and Thalattosuchia).

From a mechanical perspective, limb dominance reversal is likely a result of two factors. First, once an animal minimizes its travel on land, the importance of having a strong hind limb diminishes, unless the hind limb is the main propulsive organ in the water, or it is important in reproduction, e.g. in mating behaviours. Second, shrinkage of the hind limb leads to anterior displacement of the centre of mass relative to its position in terrestrial ancestors, i.e. closer to the centre of buoyancy, which is usually more anterior due to the location of the lungs (Domning & de Buffrénil, 1991; Domning, 2000). Positioning these two centres in close proximity makes it easier for animals to control their body trim in water.

(*b*) *Loss of forearm twisting through pronation/supination (Step M5)*

Forearm twisting through pronation and supination is absent in all extant marine tetrapod lineages that reached Step M5, including sea turtles and sea cows which use their limbs for propulsion, at least occasionally (Wyneken, 2001; Cooper, 2009). This feature therefore is an indicator of Step M5 (Table 2). The ability to twist the forearm likely was lost because it was no longer necessary in the absence of locomotion on land: pronation and supination of the forearm is necessary to adjust the angle of the manus on land. It is a basic feature shared by most land tetrapods (Hutson & Hutson, 2013). Loss of forearm twisting allowed the flippers to become more rigid, facilitating their use as rudders (DeBlois & Motani, 2019).

(2) Other indicators of marine adaptation

(*a*) *Flattened wrist joint (sufficient but not essential for Step M5)*

The flexibility of the wrist, both among wrist bones as well as between the wrist and forearm, is lost in some species at Step M5. In these species, the joints between relevant bones have been flattened, whereas these joints are three-dimensionally curved in species at Steps M1–M4 to facilitate bending. Wrist flexibility in these species was lost at Step M5, likely because it was no longer necessary to bend the wrist. It is known that wrist flexibility increases the efficiency of terrestrial locomotion using the forelimb; a robotic study of terrestrial locomotion involving flippers showed that flexible flippers were more efficient than rigid flippers during locomotion on land (Mazouchova, Umbanhowar & Goldman, 2013).

Confusingly, some fossil lineages have a reduced degree of ossification in the carpal region, which remained largely cartilaginous throughout life (Motani & You, 1998; Jiang *et al.*, 2008a; Motani *et al.*, 2015*c*,*d*). In these cases, the wrist must have retained at least some flexibility. Such a construction would not be sufficiently strong to facilitate rapid locomotion on land but may have enabled impaired locomotion, as seen in Step M4, given that flexible flippers are more efficient for locomotion on land.

(*b*) *Flattened elbow joint (sufficient but not essential for Step M5)*

Flexion and extension of the elbow joint is lost in some species at Step M5, through flattening of the joint surfaces of the elbow, as in modern cetaceans. The elbow joint is flexible in sirenians and sea turtles, but flexion and extension are limited compared with those in terrestrial limbs (Cooper, 2009; Rivera, Wyneken & Blob, 2011). For example, the elbow is not fully extended even when the flippers point anteriorly in sea turtles, due to twisting of the humerus, according to published videos (Fujii *et al.*, 2018). Elbow flexibility is retained in all marine tetrapods up to Step M4, which use terrestrial locomotion at least to some extent (English, 1976).

The loss of elbow flexibility is also reflected in the angle formed by the upper arm and forearm planes. In terrestrial forms, the distal end of the humerus is expanded along a plane that is at an angle to the plane formed by the proximal parts of the radius and ulna. This allows the ulna to rotate around the trochlea of the humerus, facilitating elbow flexibility. In Step M5 species without elbow flexion, the distal end of the humerus and the proximal ends of the radius and ulna all fit onto a single plane, thus disabling the plesiomorphic rotation of the ulna around the humerus.

It appears that the loss of elbow flexibility in modern cetaceans facilitated a rigid flipper that is useful as the rudder (DeBlois & Motani, 2019), forsaking terrestrial locomotion. As discussed above, the loss of wrist flexibility and forearm twisting lead to the same result.

(*c*) *Flattened and packed carpal bones (sufficient but not essential for Step M5)*

In sea turtles and cetaceans, carpal bones have flat dorsal and ventral surfaces while being densely packed to allow minimal flexion within the carpus (Wyneken, 2001; Cooper, 2018). This feature is not seen in other extant marine tetrapods and therefore considered a sufficient yet not essential feature of Step M5 marine adaptation.

(*d*) *Loss of nails (sufficient but not essential for Step M4)*

Nails of the forelimb have been lost in otariids, dugongs, and cetaceans, while phocids, odobenids, and most manatees retain them (Cooper, 2018). Otariids, however, still retain the claws of the hind limb (Adam, 2018). Therefore, the loss of nails may be a sufficient condition for Step M4. However, it is difficult to identify an osteological correlate. Claw-shaped terminal phalanges are an imperfect correlate: they are absent from odobenids despite the presence of nails, and present in dugongs despite the lack of nails. Some terrestrial mammals, such as humans, do not have claw-shaped terminal phalanges despite the presence of nails. Therefore, this feature has limited use in the fossil record unless the loss of nails can be established independently.

The loss of nails corresponds roughly with the loss of fur, although otariids are an exception. Nails are used for grooming the fur in marine mammals (Kenyon, 1969; Loughlin & Gelatt, 2018), so their loss in furless species may reflect the absence of grooming behaviour.

VI. MARINE ADAPTATION IN EXTINCT TETRAPODS

In this section we assess marine adaptation steps for selected clades of extinct tetrapods based on the morphological features discussed above. Table 3 provides a summary of our results, and detailed information for all taxa investigated is provided in Table S2.

The assessment of limb joint features in fossil marine tetrapods involves two notable difficulties. First, distortion of fossil specimens, especially flattening during fossilization, can obscure or alter the morphology of joint surfaces. For example, the humerus of basal sauropterygians often appears to have a flattened distal end, but it is three-dimensionally round in rare specimens that are preserved without compaction (e.g. in *Keichousaurus* and *Placodus*). When a limb bone is flattened during fossilization, there is a tendency for its margins to become elevated around bone extremities, i.e. the degree of compaction is greater in the inner part of the bone than along the bone margin, giving rise to a preserved topology where the margins of a bone are elevated relative to the inner parts. While such a pattern may help to clarify the presence of compactional shape modifications, it is not always present even in obviously flattened specimens. It is important to consider taphonomic modifications of the original morphology because they are likely to make the animals appear more adapted to marine life than they were in reality.

Second, the presence of cartilage may compromise interpretations. Cartilages are usually not preserved in fossils. Epiphyses remain cartilaginous in many reptiles until osteological maturity (Haines, 1969), but note that osteological maturity often lags behind reproductive maturity. Thus, the joint region often appears empty in fossils (e.g. the holotype of *Placodus inexpectatus*), obscuring the joint morphology and creating a false impression that the limb was not sufficiently strong to support the body. However, the cartilages that filled the gap in life would usually have been mechanically sufficient for body support, as is evident from many immature terrestrial reptiles as well as sea turtles where the humerus is usually widely separated from the radius and ulna by cartilage. Thus, a cartilaginous joint is most likely sufficient for terrestrial locomotion in Step M4, and possibly also in other steps.

In the following review, we primarily use two conditions to judge the degree of marine adaptation in fossil taxa. The first is the relative length of the humerus to the femur: if the humerus is longer (i.e. the ratio exceeds zero), the taxon is judged to belong to Step M4 or M5; where the ratio is less than zero the taxon belongs to Steps M1–M3 (Fig. 4). The second condition is the possibility for pronation and supination of the forearm. If fossil bone morphology suggests restricted pronation and supination, then the taxon is placed in Step M5. Otherwise, it belongs to one of Steps M1–M4. The two characters in combination allow us to place a given taxon in one of three categories, Step M1–M3, M4, or M5. These two are augmented by three additional characters, namely flattening and packing of wrist/ankle bones the flatness of joint surfaces of the elbow/knee and forearm-wrist/shin-ankle joints, which are sufficient but not essential for Step M5. We also use an accessory criterion to distinguish Step M1 from Steps M2–3: the depositional environment. If a given taxon only has a marine fossil record, then it is unlikely to belong to Step M1, so the taxon is identified as Step M2–3. By contrast, a taxon with a non-marine fossil record is most likely at Step M1 although the possibility of Step M2 cannot be completely denied. These cases are identified as Step M1–2. This accessory criterion based on geology is only valid if the skeletal adaptation indicates Steps M1–3, given that Step M5 tetrapods may inhabit freshwater, as for example in river dolphins. The results are summarized in Table 3, with the major groups discussed individually below in the approximate order of their marine colonization in geologic time.

(1) Trematosauria

This clade is the only non-amniote tetrapod lineage for which there are marine records. It belongs to Temnospondyli, which gave rise to extant amphibians (Lissamphibia). It was the first marine tetrapod clade to appear after the end-Permian Mass Extinction. Marine fossils belong to genera that also are found in terrestrial deposits, suggesting that the degree of marine adaptation was minimal. For example, *Aphaneramma* from Spitsbergen is found in multiple localities (Cox & Smith, 1973), whose palaeoenvironments vary from coastal plain to distal sea (Abdullah, 1999).

Marine fossils of this group are fragmentary, preventing assessment of the body plan in most cases. Our knowledge of this clade is largely based on a freshwater species, *Trematolestes hagdorni* (Schoch, 2006). The limbs are short for the body, but the femur is longer than the humerus, suggesting a level of aquatic adaptation in accordance with marine adaptation Steps M1–M3. However, the possibility remains that gills rather than lungs may have been used for breathing (Schoch, 2006), potentially allowing the centres of mass and buoyancy to be in close proximity without requiring shortening of the hind limb. Given the presence of terrestrial fossil records in species with marine occurrences, the marine adaptation step is interpreted as Step M1–2.

(2) Ichthyosauromorpha

This clade comprises Hupehsuchia and Ichthyosauriformes (Motani *et al.*, 2017). Hupehsuchians have rigid bodies with vertically elongated body cross sections and short and inflexible limbs (Carroll & Dong, 1991; Motani *et al.*, 2015*a*) (Fig. 1E). Their elbows, knees, wrists, and ankles all have very limited flexibility, the humerus is much longer than the femur, and pronation and supination of the forearm would not be permitted by the shape of the distal humerus. They therefore belong to Step M5.

Ichthyosauriformes is divided into the Nasorostra and Ichthyopterygia (Jiang *et al.*, 2016). *Cartorhynchus*, one of the two known nasorostrans (see Fig. 1F for *Sclerocormus*, the other example of a nasorostran, for which a complete skeleton is known), was a small animal with flexible flippers that are large compared to the body, so the possibility of some limited terrestrial locomotion, as in seals or sea turtles, cannot be eliminated (Motani *et al.*, 2015*d*). They therefore were likely at Step M4 or M5. Ichthyopterygia, which is the most diverse clade of Ichthyosauromorpha, comprises species that appear fully marine, with inflexible elbows, knees, wrists, and ankles (Motani, 1999; McGowan & Motani, 2003). Some species of the most basal genus, *Chaohusaurus*, retained a largely cartilaginous wrist and elbow joint but the limbs were short relative to the body in comparison with nasorostrans. Therefore, terrestrial locomotion is unlikely for this genus. Their humerus is longer than the femur except possibly in a heavily distorted specimen of *Utatsusaurus hataii* (Motani, Minoura & Ando, 1998), and the shape of the distal end of the humerus would have prevented pronation or supination. Therefore, we classify all ichthyopterygians as Step M5.

(3) Sauropterygia

This clade comprises Placodontia and Eosauropterygia, with the former comprising unarmoured Placodontoidea and armoured Cyamodontoidea, whereas the latter comprise the derived Pistosauroidea and successively more basal Nothosauroidea, Cymatosauridae, and Pachypleurosauridae (Rieppel, 2000; Ma *et al.*, 2015; Cheng *et al.*, 2016; Lin *et al.*, 2021). Pistosauroidea in turn comprises the derived Plesiosauria and a grade of more basal forms, with the most basal forms being *Wangosaurus*, Pistosauridae, and *Yunguisaurus* in that order (Lin *et al.*, 2021).

In Placodontia (Fig. 1D), the humerus is slightly longer than the femur based on the best preserved skeleton of Placodontoidea, of *Placodus inexpectatus* (Jiang *et al.*, 2008*a*). However, this specimen has the limb bones flattened through preservational compaction (Jiang *et al.*, 2008a), so it is difficult to infer flexibilities of the joints with confidence. There are isolated limb bones of the same genus from the Muschelkalk that are preserved in three dimensions (Rieppel, 1995), but it remains difficult to reconstruct the elbow based on bones from a single individual. However, there is no doubt that the elbow and knee were flexible because the three-dimensionality of the distal end of the humerus suggests the capacity for pronation and supination. In Cyamodontoidea the humerus is also longer than the femur, and flexibility of the elbow and knee joints is evident from the preserved postures of the limbs (Zhao *et al.*, 2008). Given these observations, placodonts likely reached at least Step M4 but there is no evidence that they reached Step M5.

Non-pistosauroid eosauropterygians (Fig. 1A) likely belong to Step M3 or M4. The length of the humerus relative to the femur varies among non-pistosauroid sauropterygians depending on the species (Fig. 5). For about half of the species, the femur is longer than the humerus: this assemblage includes Nothosauroidea and part of Pachypleurosauroidea. In the remaining non-pistosauroid eosauropterygians, the humerus is longer than the femur in large adults. This assemblage mostly comprises Pachypleurosauridae from the late Middle Triassic (Ladinian) but three others, namely the nothosauroid *Simosaurus*, the Middle Triassic (Anisian) pachypleurosaurid, *Panzhousaurus,* and the Olenekian (Early Triassic) pachypleurosaur *Keichousaurus*? *yuananensis*. However, in this assemblage, juveniles tend to have a longer femur than humerus, and these proportions reverse as they grow larger when growth series are known. Note that juveniles of Ladinian pachypleurosaurids (*Keichousaurus hui*, *Neusticosaurus,* and *Serpianosaurus*), tentatively identified as specimens that are less than half the size of the largest known individual, are not included in Fig. 5 (see Table S2). A second complication is that sexual shape dimorphism is known to be present in these species: presumed males have enlarged forelimbs relative to those of females (Rieppel, 1989; Sander, 1989; Cheng *et al.*, 2009), probably as a result of sexual selection at least in one of these species (Motani *et al.*, 2015*b*), which may affect the reliability of use of the humerus to femur ratio to infer aquatic adaptation. However, as seen in Fig. 5, large individuals have the humerus equal to or longer than the femur even when the sexes are separated, at least in *Keichousaurus hui* for which such data are available. It is therefore likely that these eosauropterygians showed increased aquatic adaptation as they grew, eventually reaching Step M4, i.e. perhaps they spent more time swimming in the water column where body trim control is important. An obvious outlier is *Neusticosaurus edwardsi,* in which the humerus is larger than the femur in even the smallest known individuals. The reasons why *Neusticosaurus* showed a more extreme elongation of the humerus relative to the femur (Fig. 5) await further investigation.

We cannot yet argue that non-pistosauroid eosauropterygians with a longer humerus than the femur, as identified above, reached Step M5: they most likely retained pronation/supination of the forearm, together with elbow and knee flexibility, with a possible exception being *Keichousaurus hui*. The distal end of the femur is not flattened, and in virtually all specimens the knees are preserved in flexion, with the femur and the tibia forming an angle of about 90° (±30°). The elbow joint, by contrast, is usually preserved almost fully extended, with some variations (±15°). However, in a single specimen of *Nothosaurus* the elbows are preserved flexed by more than 90° (Ji *et al.*, 2014), suggesting that this joint also was flexible unlike in sea turtles where the degree of flexion is limited. The same specimen also reveals that pronation was possible. While the distal end of the humerus does appear flattened in many specimens, this flattening most likely reflects taphonomic compaction during preservation. Rare three-dimensional specimens reveal an unflattened joint that would have facilitated elbow flexion. The wrist is usually poorly ossified, especially preaxially, with flattened elements, and the wrist region was likely filled by cartilage that would have allowed some flexibility. We therefore classify all non-pistosauroid eosauropterygians with humerus longer than femur as Step M4, whereas the rest are considered Step M2-3—the latter comprises Nothosauroidea except *Simosaurus*, as well as all Pachypleurosauridae except *Panzhousaurus* and those from the Ladinian.

The Pistosauroidea had inflexible elbows and knees except in the most basal form, *Wangosaurus* (Ma *et al.*, 2015). They also have flippers in which pronation and supination would be mechanically very difficult either due to extensive widening of the ulna or to flattening of the elbow joint surfaces, again except in *Wangosaurus*. Thus, most pistosauroids likely belong to Step M5, with *Wangosaurus* being an exception. The limbs of *Wangosaurus* are similar to those of non-pistosauroid eosauropterygians, although the exact length of the humerus is not known because the proximal ends are hidden under the clavicles. However, it appears unlikely that the humerus is longer than the femur based on the exposed material. Therefore, among pistosauroids, *Wangosaurus* alone may belong to Steps M2–3.

The humerus/femur ratio is poorly known in non-plesiosaurian Pistosauroidea, with *Yunguisaurus* from the last segment of the Middle Triassic being the only exception (Fig. 5).

The holotype of *Yunguisaurus* is a juvenile, with the femur slightly longer than the humerus (Sato *et al.*, 2010). However, the humerus is longer than the femur in an adult specimen (Sato *et al.*, 2014*b*). As discussed above, a similar age-related change is known in the non-pistosauroid eosauropterygian *Keichousaurus hui,* also from the late Middle Triassic (Ladinian). In some basal plesiosaurs from the Early Jurassic, such as Plesiosauridae and Microcleididae, the humerus is longer than the femur (O'Keefe, 2002). However, the reverse applies in other plesiosaurs (Fig. 5). Elasmosauridae, Pliosauridae, and Rhomaleosauridae all contain species in which the femur is longer than the humerus, in addition to species in which the reverse is true (O'Keefe, 2002; see Table S2). Therefore, some derived plesiosaurs, together with some thalattosuchians (see Section VI.9), are the only marine tetrapods that we classify as Step M5 despite having a femur longer than the humerus (see Table S2). Debate continues as to whether plesiosaurs used the hind limb for propulsion, and our observations might support a significant role of the hind limb in at least some derived plesiosaurs. Note also that a shortened hind limb most likely facilitates an anterior location of the centre of mass (see Section V.1*a*), but that some plesiosaurs with unusually large heads or very long necks (see Fig. 1B) may have had sufficient mass in the anterior body to allow the hind limbs to be slightly longer without affecting the position of the centre of mass relative to the centre of buoyancy. Most plesiosaur fossils are marine but non-marine fossils have also been reported worldwide [Gao *et al.* (2019) and papers cited therein].

(4) Saurosphargidae

This clade was poorly known until recent discoveries of well-articulated specimens from China (Li *et al.*, 2011, 2014). It is most likely the sister clade to Sauropterygia (Chen *et al.*, 2014*b*). In the best known genus, *Largocephalosaurus,* the humerus is longer than the femur, suggesting Step M4 adaptation (Li *et al.*, 2014). It is difficult to judge the possibility of pronation and supination because of compaction, but the shape of the distal end of the humerus suggests that twisting was probably not impossible. Most of the carpal bones are flattened and packed but the proximal wrist remains largely cartilaginous, thus the sufficient condition for Stage M5 is only partially fulfilled by the carpals. They are tentatively placed in Step M4.

(5) Thalattosauria

This clade is divided into durophagous Thalattosauridae and piscivorous Askeptosauridae (Fig. 1L) (Müller, 2005). In all thalattosaurs the femur is much longer than the humerus, suggesting marine adaptation no higher than Step M3 (Liu & Rieppel, 2005; Müller, 2005; Li *et al.*, 2016). In other respects, the limbs of these two groups were very different. In Thalattosauridae, the limbs are short relative to the body, with wrists and ankles poorly ossified (Rieppel, 1987; Liu *et al.*, 2013; Li *et al.*, 2016), whereas in Askeptosauridae the relative length of the limb propodials to the body is comparable with those of terrestrial lizards, with the wrist and ankle largely ossified although they have been flattened unlike in terrestrial equivalents (Liu & Rieppel, 2005; Müller, 2005). Askeptosauridae thus were probably more capable of terrestrial locomotion than Thalattosauridae. Terrestrial locomotion in Thalattosauridae may be doubtful given the small size of the limbs, but salamanders with even shorter legs relative to their body length (e.g. *Phaeognathus*) are capable of terrestrial locomotion (Bakkegard & Guyer, 2004), as are short-limbed lizards. Thalattosaurs have claw-shaped terminal phalanges that has been used to infer a habit similar to marine iguanas (Nicholls, 1999) but this feature remains inconclusive because keratinous nails are not preserved in any of the known fossils. However, the claw bone has grooves and ridges that would imply the presence of a keratinous covering. If true, the feature would lend support to the current interpretation of marine adaptation Step M2–3 by making more advanced steps less likely. A discovery of a fossil with nail preservation in the future would enable further scrutiny of marine adaptation in Thalattosauridae.

(6) Tanystropheidae and *Dinocephalosaurus*

Tanystropheus and *Macrocnemus* are known from Middle Triassic (Anisian: Illyrian to Ladinian) marine deposits of the Italy/Switzerland border and China (Nosotti, 2007; Rieppel *et al.*, 2010; Jiang *et al.*, 2011). They have terrestrial limbs but lack non-marine fossil records. They are therefore placed in Stages M2–3. Note: some other tanystropheids are non-marine.

Dinocephalosaurus is an archosauromorph from the Middle Triassic (Anisian: Pelsonian) that may or may not be related to Tanystropheidae (Rieppel, Li & Fraser, 2008; Liu *et al.*, 2017). It has a humerus that is longer than its femur, while its wrist bones are flattened disks (Rieppel, Li, & Fraser, 2008). These features place the monotypic genus in Stage M4. It is geologically older taxon than *Tanystropheus* and *Macrocnemus* despite its more advanced marine adaptation stage.

(7) Pseudosuchia

Qianosuchus is an archosaur from the Middle Triassic (Anisian; Pelsonian) that is only known from marine deposits (Li *et al.*, 2006). It is considered a poposauroid (Nesbitt, 2011). Its limbs show no modification from a terrestrial design, and there is no evidence to suggest that it reached an advanced stage. It is placed in Stages M2–3.

Ticinosuchus is another pseudosuchian exclusively known from marine sediments. It is from the Middle Triassic (Anisian/Ladinian boundary). Its limb skeleton does not reveal any particular marine adaptation, but it has been found with fish scales in the stomach (Nesbitt, 2011), suggesting that it was capturing fish at sea. It is placed in Stages M2–3.

Sikannisuchus, from the Late Triassic, is known exclusively from marine fossils and co-occurs with pelagic ichthyosaurs, such as *Shonisaurus* and *Macgowania* (Nicholls, Brinkman & Wu, 1998). Its fossils are fragmentary but the dental and skull morphologies warrant its placement in Pseudosuchia. Without evidence for an advanced marine adaptation stage, we remain conservative and tentatively place it in Stages M2–3.

(8) Phytosauria

Phytosaurs are usually non-marine but there are a few exceptions. *Diandongosuchus* from the Middle Triassic (Ladinian) was originally considered an enigmatic archosauriform but a more recent phylogenetic analysis placed it in Phytosauria (Stocker *et al.*, 2017). It is exclusively known from marine deposits but lacks a clear signature of marine adaptation in its limbs. It is therefore placed in Stages M2–3. *Mystriosuchus* from the Late Triassic (Norian) is usually non-marine but there are some fossils from marine deposits (Renesto & Paganonp, 1998). Its limbs show no evidence of marine adaptation. It is therefore placed in Stages M1–2. Note: Phytosauria is treated here as non-pseudosuchian following Stocker *et al*. (2017) but some other phylogenetic hypotheses place it as part of Pseudosuchia (e.g. Ezcurra, 2016).

(9) Thalattosuchia

There are two types of body plans in Thalattosuchia. Basal members share a body plan with typical crocodylians, although with some differences such as a relatively large skull for the body. These basal members, such as *Steneosaurus*, *Teleosaurus,* and *Pelagosaurus,* were most likely capable of terrestrial locomotion with flexible limb joints and are tentatively placed in Step M2–3. Derived members, in Metriorhynchidae, evolved one of the most bizarre body plans known in marine reptiles (Fig. 1J), with a combination of an extremely shortened forelimb with inflexible elbow and wrist joints, a normal hind limb with bendable knee, and a tailbend that turned the caudal vertebral column downwards near its end, to support the lower lobe of a caudal fin. The caudal fin was not as deep as in ichthyosaurs relative to body size but was sufficiently large to hamper terrestrial locomotion, in addition to the small and inflexible limbs. Therefore, Metriorhynchidae must have reached Step M5.

Confusingly, Metriorhynchidae lack the dominance of the humerus over the femur, a skeletal feature found in all extant marine tetrapods of Steps M4 and M5. Indeed, the femur is more than three times the length of the humerus (Fig. 4). This unusual proportion is only found in a limited number of terrestrial tetrapods with large legs and small forelimbs, such as Tyrannosauridae and Alvarezsauridae, and must have reflected a selective pressure unique to Thalattosuchia overriding selection for the dominance of the humerus in marine adaptation. It is possible that the unusually long femur of Metriorhynchidae may reflect terrestrial reproductive constraints. Viviparity has been suspected for this group based on the shape of the hip bones (Herrera, Fernández & Gasparini, 2013) but they were most likely oviparous given that viviparity never evolved in crown-group Archosauria (Liu *et al.*, 2017), and there is no known example of viviparity evolving after marine adaptation (Motani *et al.*, 2014). Metriorhynchids probably needed to come ashore to bury eggs, as in sea turtles, and the large hind limbs may have allowed some terrestrial locomotion and substrate digging.

(10) Fossil marine turtles

The Triassic marine turtles *Odontochelys* (Li *et al.*, 2008) and *Eorhynchochelys* (Li *et al.*, 2018) are likely secondarily marine. Limb measurements for these taxa are not available and it is currently difficult to access these specimens, but published photographs suggest that the femur is longer than the humerus in *Eorhynchochelys*, which is considered the more basal, but the humerus is longer than the femur in *Odontochelys*. Based on this character, we tentatively place *Eorhynchochelys* in Step M2–3, and *Odontochelys* in Step M4.

In the Jurassic, the eurysternid *Solnhofia* has a femur longer than the humerus, and the limb joints appear flexible (Joyce, 2000), making it a candidate for Step M2-3. In the Cretaceous, derived Pan-Chelonioidea, including Protostegidae (Fig. 1R) and Toxochelyidae, most likely reached Step M5 because skeletal adaptations found in extant Chelonioidea are already present: dominance of the humerus over the femur, and the nature of articulation of the flipper segments (Wieland, 1896; Nicholls, Tokaryk & Hills, 1990). The potential for pronation and supination cannot be assessed accurately because they are prevented by fibrous connective tissue in extant chelonioids (Wyneken, 2001), which is unlikely to be preserved in fossil material.

(11) Mosasauroidea and Dolichosauridae

Dolichosauridae belong to a clade that is sister to Mosasauroidea. In a recently discovered dolichosaurid, *Primitivus*, the femur is longer than the humerus (Paparella *et al.*, 2018), placing it in Step M2–3. Other forms such as *Adriosaurus* also have a femur longer than the humerus based on published photographs (Lee & Caldwell, 2000). Within Mosasauroidea, basal members outside of Mosasauridae, such as *Aigialosaurus*, were probably more similar to Dolichosauridae in the degree of aquatic adaptation, given similarities in general limb morphology (Dutchak *et al.*, 2009; Paparella *et al.*, 2018). However, no specimens have both a complete humerus and femur, making it impossible to judge if they reached Step M4. In Mosasauridae (e.g. Fig. 1I), the morphology of the humerus, radius, and ulna would not have allowed pronation or supination (Williston, 1898; Russell, 1967; Caldwell, 1996), allowing this clade to be place in Step M5. The humerus is longer than the femur in at least *Platecarpus*, *Plioplatecarpus*, and *Prognathodon* (Williston, 1898; Cuthbertson *et al.*, 2007), but the femur is longer than the humerus in *Clidastes* (Williston, 1898). Mosasauroids are usually marine but at least two freshwater occurrences are known (Makadi, Caldwell & Osi, 2012; Garcia *et al.*, 2015).

(12) Sphenodontia

At least two lineages of fossil sphenodontians are considered marine: Pleurosauridae from the late Jurassic–early Cretaceous (Carroll, 1985) and *Ankylosphenodon* from the Cretaceous (Reynoso, 2000). There is no specimen of *Ankylosphenodon* in which both the humerus and femur are completely preserved. However, the humerus of the holotype is clearly shorter than the only measurable femur, belonging to a referred specimen which is undoubtedly a smaller individual than the holotype (Reynoso, 2000). Thus, it is likely that *Ankylosphenodon* belongs to Step M2–3.

Three species, belonging to two genera, are recognized among Pleurosauridae (Carroll, 1985). Published measurements suggest that the femur is longer than the humerus in all three. Therefore, Pleurosauridae most likely belongs to Step M2–3. However, the most derived species, *Pleurosaurus ginsburgi* (see Fig. 1K), has a diminutive forelimb and a large hind limb, which suggests that this species reached a higher level of aquatic adaptation, as in Metriorhynchidae (see Section VI.9).

(13) Stem Cetacea

Stem cetaceans without fully formed hind limbs must have belonged to Step M5, as in extant cetaceans. Some of these fossil forms, such as the basilosaurid *Dorudon* (Fig. 1O), retained a flexible elbow joint but pronation and supination seem unlikely (Uhen, 2004), qualifying them for Step M5. *Dorudon* also has the humerus longer than the femur.

Clades which possessed large hind limbs, however, need to be examined carefully. Unfortunately, in most cases preservation is too incomplete to assess relative lengths of the humerus and femur. No single individual of Pakicetidae (Bajpai & Gingerich, 1998) or Ambulocetidae (Thewissen, Madar & Hussain, 1996) has both the humerus and femur completely preserved. The same is true for the raoellid *Indohyus* (Cooper *et al.*, 2012), a taxon closely related to Cetacea. However, published skeletal reconstructions suggest that femora were longer than humeri in *Indohyus* and Pakicetidae. Both are known from both marine and non-marine deposits, so they are classified as Step M1–2 (Gingerich *et al.*, 1983; Bajpai & Gingerich, 1998). Sufficiently well-preserved specimens are available for the remingtonocetid *Kutchicetus* (Thewissen & Bajpai, 2009) and protocetid *Maiacetus* (Fig. 1M) (Gingerich *et al.*, 2009), that reveal the humerus to be longer than the femur. Puzzlingly, published measurements suggest that the femur is longer than the humerus in another remingtonocetid, *Andrewsiphius* (Thewissen & Bajpai, 2009), although the femoral length was an estimate and the humerus is slightly longer than the femur in a published photograph. This leaves the status of Remingtonocetidae ambiguous. We tentatively place Remingtonocetidae and Protocetidae in Step M4.

(14) Stem Sirenia

Stem sirenians without fully formed hind limbs must have belonged to Step M5. Four-legged sirenians, namely Prorastomidae and Protosirenidae, however, need to be examined separately. Prorastomidae is considered more basal than Protosirenidae. There are no published measurements of the humerus and femur in one individual, but a published reconstruction of *Pezosiren* suggests that the femur was longer than the humerus (Domning, 2001). Thus, prorastomids had yet to reach Step M4. For Protosirenidae, there is at least one specimen with both bones preserved, in which the humerus was longer than the femur (Zalmout & Gingerich, 2012). Therefore, protosirenids most likely had reached Step M4.

(15) Pinnipedomorpha

In the fossil pinnipedomorphs *Enaliarctos* (Fig. 1P), *Allodesmus* and *Puijila*, the humerus was longer than the femur (Bebej, 2009; Rybczynski, Dawson & Tedford, 2009). Note, however, that *Puijila* is known only from freshwater deposits, so aquatic adaptation may have evolved in fresh water in this lineage. If that is the case, adaptation Step A2 would have preceeded Step H1, presenting the only exception to the marine adaptations sequence. However, this interpretation currently hinges on a single taxon, whereas additional taxa would enable scrutiny of this sequence in the future. It is most likely that *Enaliarctos* and *Allodesmus* had reached Step M4, as in extant pinnipeds.

(16) Desmostylia

In Desmostylia the humerus and femur are equal in length in the desmostylid *Desmostylus japonicus*, and very similar (456 *versus* 453 mm) in the paleoparadoxiid *Neoparadoxia* (Fig. 1N) (Barnes, 2013). It is therefore difficult to judge whether this clade reached Step M4, although they were at least very close to that step given that no Step M3 species are known to reach a neutral humerus:femur ratio. Desmostylians are tentatively ranked as Step M4.

(17) Pilosa: *Thalassocnus*

At least four specimens of the marine sloth *Thalassocnus* (Fig. 1Q), belonging to three species, have both the humerus and femur preserved (Amson *et al.*, 2015*a,b*), with the longer femur than humerus suggesting that this genus had yet to reach Step M4.

VII. DISCUSSION

(1) Absence of very large sea serpents

There is a tendency among tetrapods that reached Step M4 to have larger maximum body sizes than their terrestrial mammalian ancestors (Gearty, McClain & Payne, 2018), likely reflecting a balance among the effects of gravity, cost of thermoregulation and feeding efficiency. A phylogenetic analysis of variance (ANOVA) of published data on the body size of turtles (Regis & Meik, 2017), using a tree obtained from TimeTree (Kumar *et al.*, 2017), shows that the mean body mass of male sea turtles is significantly greater than males of other turtles ($N = 137$, $F = 22.9$, $P < 10^{-6}$; Fig. 6A); the same is true for females (results not shown). Plesiosaurs, ichthyosauromorphs, metriorhynchids and mosasaurs all gave rise to species exceeding 10 m in total length, far larger than typical terrestrial reptiles. However, extant marine snakes do not share this tendency: a similar analysis of body masses for snakes (Feldman & Meiri, 2013) shows no difference between the average body mass of male sea snakes and other male snakes ($N = 238$, $F = 0.399$, $P = 0.528$; Fig. 6B). The reason for this puzzling exception is likely to involve haline rather than aquatic adaptation *per se*: the largest extant snake, the green anaconda (*Eunectes murinus*), is highly aquatic but lives in fresh water.

The mechanisms for control of water balance are unique in marine snakes; although they have salt glands (Dunson & Taub, 1967; June *et al.*, 1973; Dunson & Dunson, 1979), they require a source of fresh water which they collect from sea surface layers following rainfall (Lillywhite *et al.*, 2008, 2012, 2014, 2015; Kidera *et al.*, 2013). The thickness and abundance of these layers is limited, thus constraining freshwater supply for marine snakes. This reliance on a limited supply of fresh water may mean that marine snakes cannot grow large. A potential way to circumvent this restriction would be enlargement of the salt gland, but the relatively small size of the skull will limit the maximum size of the salt glands. Skull size scales with negative allometry to the body size, so this lack of space will be exacerbated at larger body sizes. The limited ability to secure fresh water at sea may also explain the delay in achieving the haline adaptation stage H3A (water balance maintenance without terrestrial fresh water) in snakes relative to other marine tetrapods.

This hypothesis might be rejected if there was evidence for large marine palaeophiids. However, as discussed below, there is little evidence for marine adaptations in vertebrae from marine deposits. Palaeophiidae is a clade of snakes with various body sizes that spanned from the Late Cretaceous to Eocene. This clade contains many species, most of which are based on isolated vertebrae (Parmley & Reed, 2003) with a few exceptions where articulated partial vertebral columns are known (Houssaye *et al.*, 2013). Constituent species exhibit various degrees of aquatic adaptation, while their body size varies from less than a metre to over 9 m (Parmley & Reed, 2003; Rage *et al.*, 2003). Many of these fossils were found in estuarine deposits but at least some are from marine or freshwater deposits (Westgate, 2001; Rage *et al.*, 2003). It has been suggested that *Palaeophis casei*, which is the smallest species with tail vertebrae modified for aquatic locomotion through becoming laterally compressed and tall for efficient tail-based propulsion in water, shows similar features to the extant species *Acrochordus granulatus* (Rage *et al.*, 2003), which would place it in Step S4 or lower. The largest species for which there is fossil evidence, *Palaeophis colossaeus*, does not have laterally compressed vertebrae, although isolated and damaged vertebrae have been found in marine deposits (Rage *et al.*, 2003; Mccartney *et al.*, 2018). The occurrence of fossilized vertebrae of large palaeophiids in marine deposits may perhaps be explained if, like the extant *Python reticulatus*, they could swim significant distances without feeding on marine food. Alternatively, at least some of these bones may have been transported from their place of origin in the terrestrial realm.

(2) Marine adaptation steps and diversity

There is a tendency for marine tetrapod clades that reached marine adaptation steps M4 or M5 to have higher species diversity than those at earlier steps. In extant marine tetrapods excluding snakes, the highest species diversities per unique colonization event (Table 1) are found in steps M4 (17.0 species per event) and M5 (32.7), whereas species diversity for earlier steps is 1.13 or less. A similar tendency is present for snakes (note that Step M4 is equivalent to Step S3). Not all clades that reached Steps M4 and M5 (Steps S3–S5 for snakes) necessarily have high diversity. For example, *Enhydra lutris* (Step M4) and *Acrochordus granulatus* (Step S4) are both single species in their clades that show marine adaptation, and there are only three species of extant marine sirenians (Step M5). Inclusion of extinct sirenians, however, will give a much higher value (Table 4). Thus, opportunities for diversification clearly become available for taxa achieving Step M4, although not all lineages exploit this opportunity.

The same diversity pattern seems to hold for other fossil marine tetrapods. The minimum number of marine species in relevant clades is summarized in Table 4, based on numbers of species-level OTUs (operational taxonomic units) in recent cladistic analyses as well as systematic revisions (Carroll, 1985; Li *et al.*, 2008, 2014, 2018; Chen *et al.*, 2014*a*; Neenan *et al.*, 2015; Anquetin, Püntener & Joyce, 2017; Moon, 2017; Domning, Heal & Sorbi, 2017; Jiang *et al.*, 2019; Matsui & Tsuihiji, 2019; Peralta-Prato & Solórzano, 2019; Perini, Nascimento & Cozzuol, 2019; Evers, Barrett & Benson, 2019; Gentry, Ebersole & Kiernan, 2019; Jiménez-Huidobro & Caldwell, 2019; Huang *et al.*, 2019; Young *et al.*, 2020; Madzia & Cau, 2020; Druckenmiller *et al.*, 2020). Clades with more than 30 marine species, such as Sauropterygia, Saurosphargidae, Ichthyosauromorpha, Mosasauroidea, and Thalattosuchia, all contained members that had reached Step M4 or M5. By contrast, less marine-adapted clades, such as Pleurosauridae and *Thalassocnus*, had low diversity. Note that species diversities of fossil lineages will not be directly comparable to those of extant animals: our knowledge of the diversity of extinct forms is limited by the availability of sedimentary rocks of suitable ages and environments, so diversity estimates will be vast underestimates (Dodson, 1990). In addition, taxonomic biases exist for diversity estimates involving fossil taxa, which undergo cycles of 'lumping and splitting' by taxonomists, with some clades appearing less diverse when revision reduces the number of valid species. For example, the number of ichthyosaur species dropped from 235 to 80 in 2003 as a result of a rigorous revision (McGowan & Motani, 2003), although later discoveries increased this to 114.

Possible reasons for increased diversity of taxa reaching Steps M4 or M5 are worth discussing. The obvious boundary between steps M3 and M4 is changes in the relative proportions of the humerus and femur that result in an anterior shift of the centre of mass, enabling a horizontal body posture in the water at rest (see Section V.1*a*). This is useful in water because it enables trim control with less energy expenditure (Domning & de Buffrénil, 1991). This adaptation, however, reduces locomotory ability on land, so species reaching Steps M4 and M5 limit terrestrial excursions to grooming, basking, and sometimes to reproduction. We argue here that once Step M4 is achieved, new opportunities become available. Improved swimming abilities would both allow different styles of hunting involving higher speed or longer pursuit and broadening of habitat range, both horizontally and vertically. In addition, release from constraints imposed by terrestrial locomotion would allow body designs that are not possible on land, further enhancing the above benefits. Geographic spread, together with availability of new food resources, is likely to favour diversification of a lineage over time. It remains difficult to test these interpretations with currently available data.

(3) Marine adaptation through time

Fig. 7 depicts a time-calibrated phylogeny of major groups of marine tetrapods with different colours indicating different marine adaptation steps. Unfortunately, multiple constraints make the tree less informative than it might be. Most extant clades exhibit a uniform step of marine adaptation per clade, e.g. all true sea snakes (Hydrophiinae) are at Step S5 and all modern whales (Neoceti) are at Step M5. Usually, there are no extant species representing intermediate steps of marine adaptation, making it difficult to reconstruct the evolutionary history of marine adaptation through ancestral state reconstruction. Clades in which all representatives show the same marine adaptation step are represented by a single terminal branch in Fig. 7. However, in some cases fossil stem species at intermediate marine adaptation steps are known, for example in whales (Cetacea) and sea cows (Sirenia), and partial ancestral state reconstructions are possible. The discovery of intermediate fossil forms will be essential to the reconstruction of the evolutionary sequence and tempo of marine adaptation.

Despite these limitations, Fig. 7 still illuminates one prominent pattern: if Steps M4–M5 are reached by a lineage, that transition tends to take place early in its evolutionary history, i.e. no such lineage remained at Step M1–M3 for two chronostratigraphy stages or longer before advancing to Step M4–M5. For example, mosasaurs advanced to Step M5 rapidly within the first geological stage of their existence whereas their sister lineage, dolichosaurs, never reached Steps M4–M5 although they lasted almost as long as mosasaurs. If this pattern remains consistent, it is likely that current lineages that have existed at Steps M1–M3 for a long period, such as the marine iguana of Galápagos, may never advance to Steps M4–M5. However, the predictive value of this statement is limited because the underlying mechanism is unknown.

The rapid evolution of the final steps of marine adaptation suggested by the observed pattern also explains, at least in part, why extant clades with advanced marine adaptation rarely have a surviving sister clade exhibiting intermediate adaptation stages. The fossil record suggests that these sister clades would not survive for long time after branching from the clade that reached Steps M4 or M5. In some clades, such as Ichthyosauromorpha, any intermediate sister clades must have been extremely short-lived because they left no record despite the reasonably high resolution of the fossil record from the relevant geological time segment (Motani *et al.*, 2017).

Fig. 7 also suggests that clades that reached Steps M4 and M5 tend to last longer than other marine-adapted clades, although individual species may still be short lived. The three longest-lasting marine tetrapod lineages are the Eosauropterygia, Ichthyosauromorpha, and Chelonioidea, in that order, all of which survived for more than 100 million years and reached Step M5 early in their evolution. Other long-lasting marine lineages, also mostly at Step M4 or M5, include Cetacea, Sirenia, Thalattosuchia, Mosasauroidea, and Pinnipedomorpha, although some lineages at Steps M1–M3, such as Pleurosauridae, lasted almost as long. Note, however, that for most extant lineages at Steps M1–M3 (light blue in Fig. 7), a fossil record to suggest when their marine adaptation began is not available, and thus Fig. 7 indicates the maximum possible spans of marine adaptation.

So our review suggests both that clades at Steps M4–M5 survive longer, and that clades at Steps M4–M5 tend to have higher diversity. It would make sense for a long-lasting lineage to have more opportunities to speciate and thus have a high diversity. However, it is also true that Chelonioidea, which is one of the three longest-lasting lineages, is much less diverse than, for example, Mosasauroidea, and the same is true for a comparison between the Sirenia and Pinnipedomorpha. Also, the true sea snakes (Hydrophiinae) are highly diverse despite their relatively recent appearance compared with most other marine tetrapod lineages.

Obviously, many factors, such as body size, ecology, and environmental history, play large roles in determining the diversity of such clades.

VIII. CONCLUSIONS

(1) Extant marine reptiles and mammals exhibit adaptations that have similar ecophysiological effects that can be categorized as aquatic and haline adaptations.

(2) We identify five steps of haline and aquatic adaptation that are shared by most marine tetrapods except snakes. Thus, a hypothesis that there is a common sequence of events in marine adaptation across tetrapods is largely supported by our data. These five steps are: Step M1, incipient use of marine resources; Step M2, direct feeding in the saline sea; Step M3, water balance maintenance without terrestrial fresh water; Step M4, minimized terrestrial travel and loss of terrestrial feeding; and Step M5, loss of terrestrial thermoregulation and fur/plumage.

(3) The pattern observed in snakes differs from other marine tetrapods in that haline adaptation lags behind aquatic adaptation. This lag is likely due to the requirement for fresh water and limited ability to remove salt from sea water *via* salt glands. The same constraint may limit body size in marine snakes.

(4) Certain osteological features of the limb allow identification of marine adaptation steps in extinct marine tetrapods. These features suggest that at least four groups of Mesozoic marine tetrapods reached Step M5 of marine adaptation.

(5) While many tetrapod clades have colonized the sea, only a limited number reached Steps M4 and M5. Species diversity appears to remain low until a lineage reaches Step M4 or M5, after which high species diversity may result.

(6) Where they have evolved, the evolution of Steps M4 and M5 seems to take place early in the evolutionary history of a lineage.

(7) Lineages that reached Steps M4 and M5 tend to last longer than those that remain at Steps M1–M3.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting information section at the end of the article.

Appendix S1. Detailed accounts of observations on life habits of Recent secondarily marine tetrapods.

Table S1. Humoral and femoral lengths in extant marine and terrestrial tetrapods from previously published data.

Table S2. Humoral and femoral lengths in fossil marine and terrestrial tetrapods.

Figure legends

Fig. 1. Skeletal reconstructions of selected fossil marine tetrapods. (A) *Dactylosaurus* (Sauropterygia: Eosauropterygia); (B) *Hydrotherosaurus* (Sauropterygia: Plesiosauria); (C) *Peloneustes* (Sauropterygia: Plesiosauria); (D) *Placodus* (Sauropterygia: Placodontia); (E) *Eretmorhipis* (Ichthyosauromorpha: Hupehsuchia); (F) *Sclerocormus* (Ichthyosauromorpha: Nasorostra); (G) *Chaohusaurus* (Ichthyosauromorpha: Ichthyosauriformes); (H) *Stenopterygius* (Ichthyosauromorpha: Parvipelvia); (I) *Plotosaurus* (Squamata: Mosasauridae); (J) *Metriorhynchus* (Thalattosuchia: Metriorhynchidae); (K) *Pleurosaurus* (Rhynchocephalia: Pleurosauridae); (L) *Askeptosaurus* (Thalattosauria: Askeptosauridae); (M) *Maiacetus* (Cetacea: Protocetidae); (N) *Neoparadoxia* (Desmostylia: Paleoparadoxiidae); (O) *Dorudon* (Cetacea: Basilosauridae); (P) *Enaliarctos* (Pinnipedomorpha: Enaliarctidae); (Q) *Thalassocnus* (Pilosa: Megatheriidae); (R) *Archelon* (Pan-Chelonioidea: Protostegidae). Panels drawn based on: E, Cheng *et al.* (2019); F, new; G, Motani *et al.* (2018); H, Motani *et al.* (2014); M and O, Gingerich *et al.* (2009); N, Barnes (2013); P, Berta & Ray (1990); and all others, Motani (2009). Scale bars: black and white segments span 10 cm each (i.e. a pair of black and white segments, as in E, is 20 cm in total).

Fig. 2. Scaling of salt excretion in marine tetrapods of different marine colonization steps. Marine tetrapods of Steps M3–M5 have an elevated ability to excrete salt compared to Step M1–M2 tetrapods of the same body mass. Step S5 aligns with Step M5 but Step S4 snakes, namely *Acrochordus granulatus* (blue circles) and *Laticauda* spp. (blue squares), align with Step M3 tetrapods. Non-marine tetrapods are allocated to Step M0 based on all data that we could locate without screening. Data compiled from the literature (Dunson & Taub, 1967;

Dunson, 1968, 1969, 1970, 1974; June *et al.*, 1973; Dunson & Dunson, 1974, 1979; Taplin *et al.*, 1982; Nicolson & Lutz, 1989).

Fig. 3. Boxplot of humerus length/femur length in extant marine and terrestrial tetrapods, plotted according to marine adaptation steps M2–M5 (A) and taxonomic grouping (B). Non-marine tetrapods are allocated to Step M0. See Table S1 for the data and their sources. In the boxplot, boxes represent the middle two quartiles, whereas whiskers extend 1.5 times the quartile space beyond the boxes. Thick lines inside the box indicate the median value. Specimens outside of the whiskers are outliers, represented by circles. Groups along the *x*-axis are sorted according to the median values. Lutrinae (Other) indicates lutrines other than *Enhydra*.

Fig. 4. Boxplot of humerus length/femur length in fossil marine tetrapods except Sauropterygia (see Fig. 5), plotted according to (A) estimated marine adaptation steps (M2–M5) and (B) taxonomic grouping. Non-marine tetrapods are labelled M0. See Table S2 for the data and their sources. Specifications of the box plots are as described in the legend to Fig. 3, except that clade names in B are not according to the median values but to the relative positions within the current phylogenetic hypothesis, with more basal forms toward the left, to illuminate the reversal of the trend in most derived taxa. Panel A is provided to show that there are outliers to the ratios derived from extant groups, rather than to justify the use of these ratios.

Fig. 5. Boxplot of humerus length/femur length in Sauropterygia, plotted according to two levels of taxonomic grouping. See Table S2 for the data and their sources. For *Keichousaurus hui* data for males (M) and females (F) are plotted separately. Specifications of the box plots

are as described in the legend to Fig. 3. Juveniles of *K. hui*, as identified by Xue *et al*. (2015), have been excluded from this plot.

Fig. 6. Boxplots of body size ranges of marine and other turtles and snakes. (A) Extant male turtles, based on body mass data from Regis & Meik (2017). (B) Extant male snakes, based on body mass data from Feldman & Meiri (2013). Details of the box plots are as described in the legend to Fig. 3.

Fig. 7. A time-calibrated phylogenetic tree of major groups of marine tetrapods, with selected terrestrial sister taxa. The tree topology and branch lengths are largely based on TimeTree.org (Kumar *et al.*, 2017). augmented by the paleobiology database (http://paleodb.org), although some details were refined using Jiang *et al.* (2014). and Motani *et al.* (2017). Branch colours indicate marine adaptation steps. See Section III for definition of marine adaptation steps M1–5 (for marine tetrapods excluding snakes) and Section IV for definition of S1–S5 (for marine snakes). Steps M4 and M5 and Steps S3–S5 are considered here to represent the highest levels of marine adaptation.

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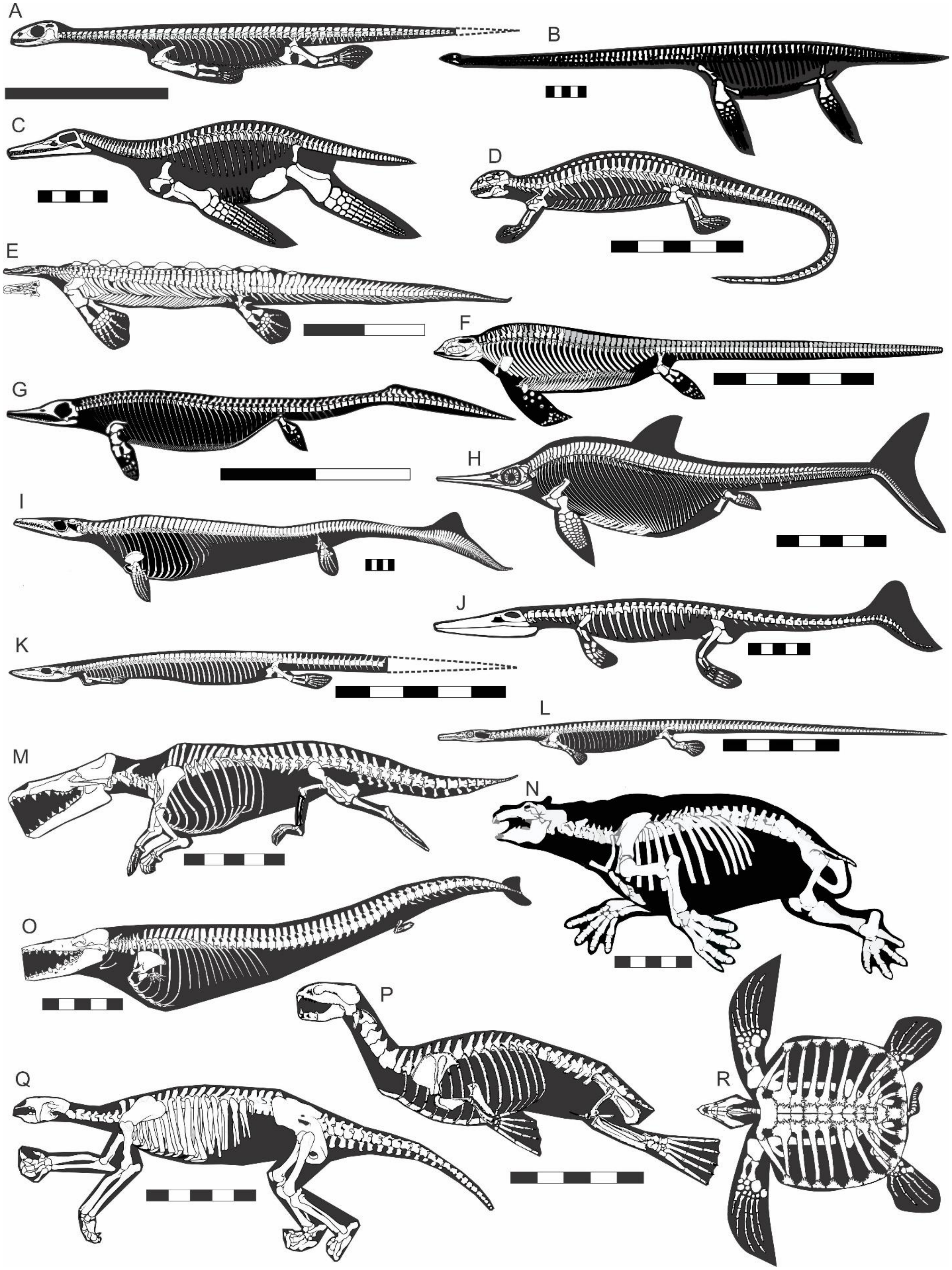
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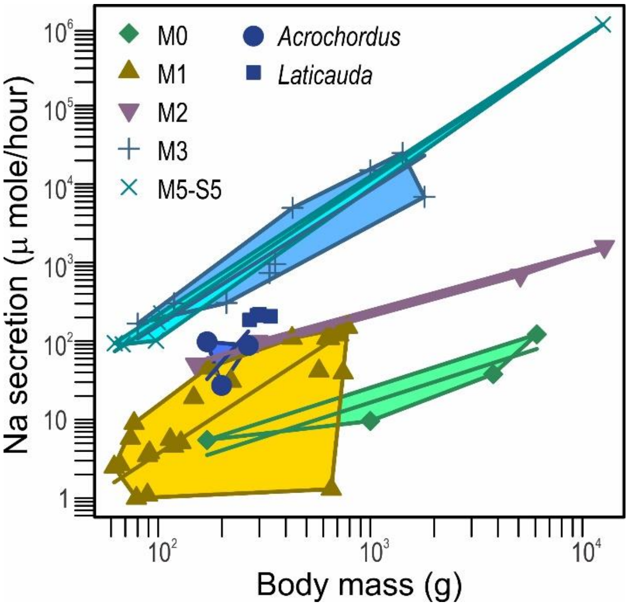

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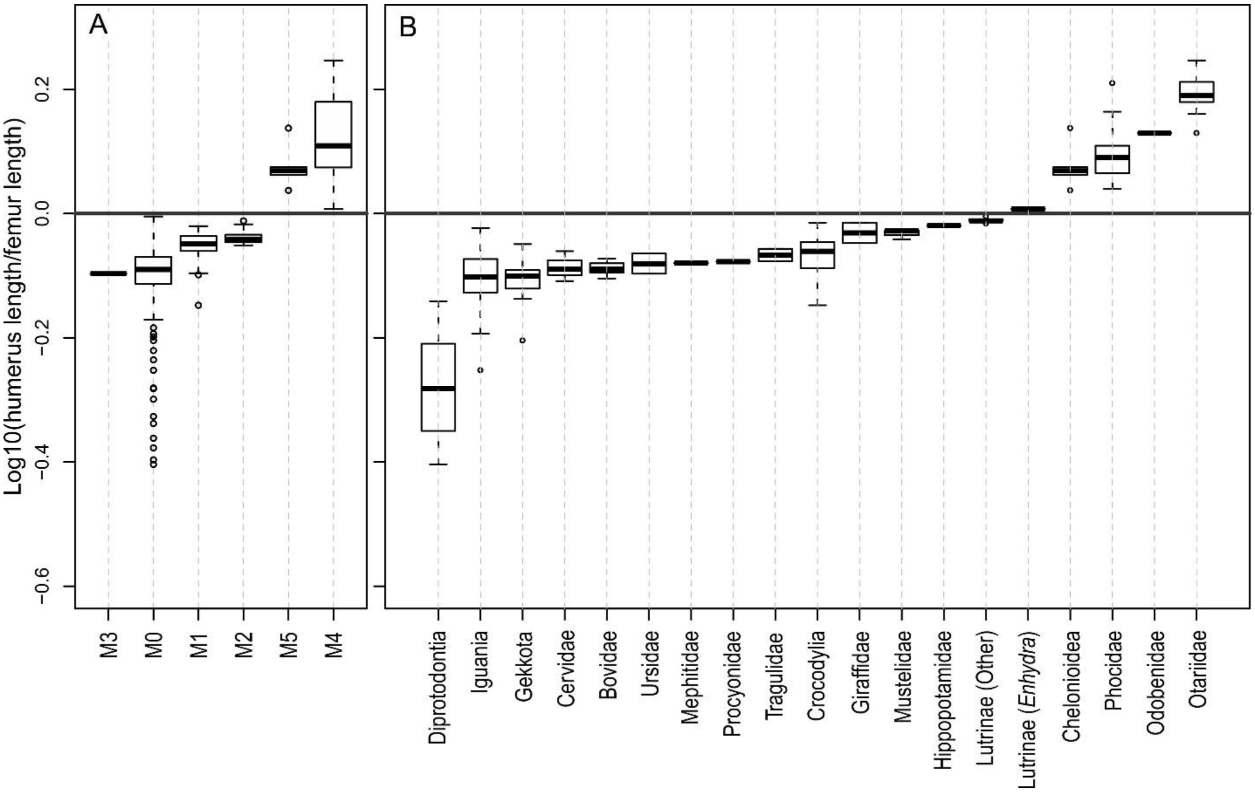

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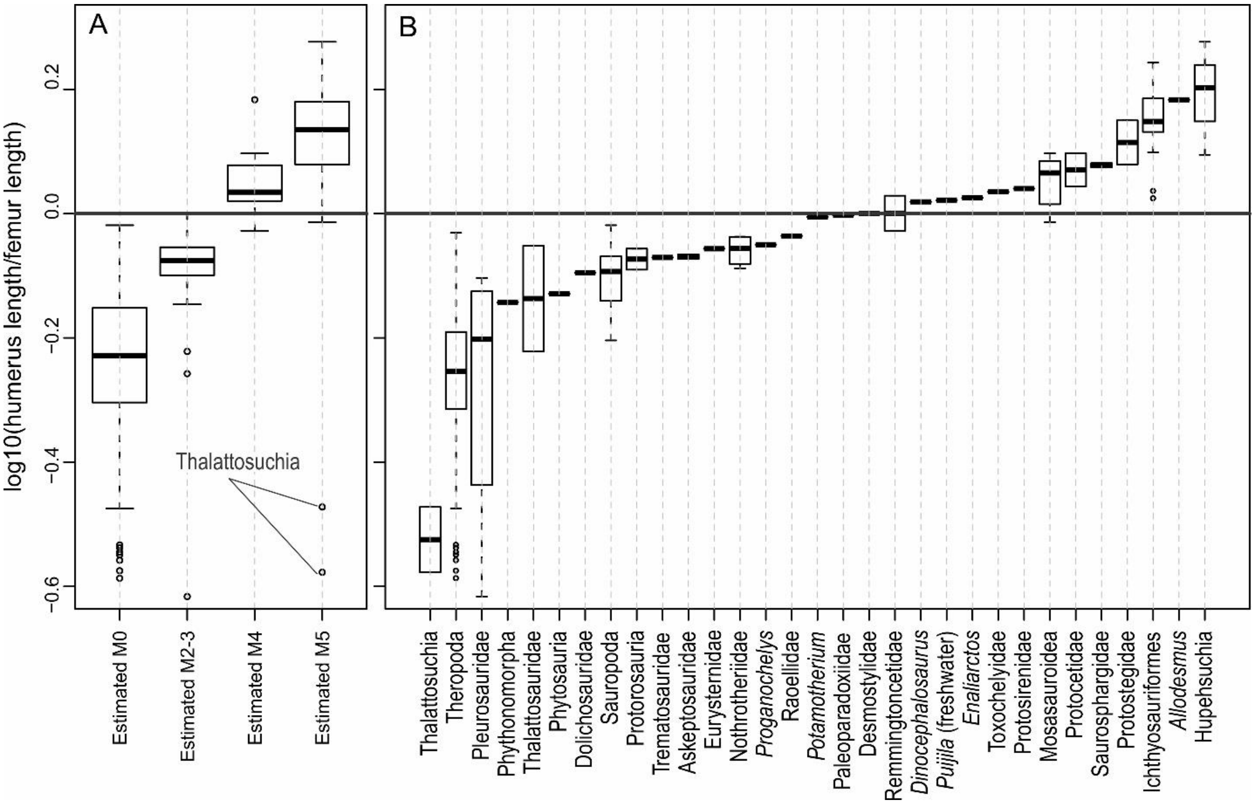

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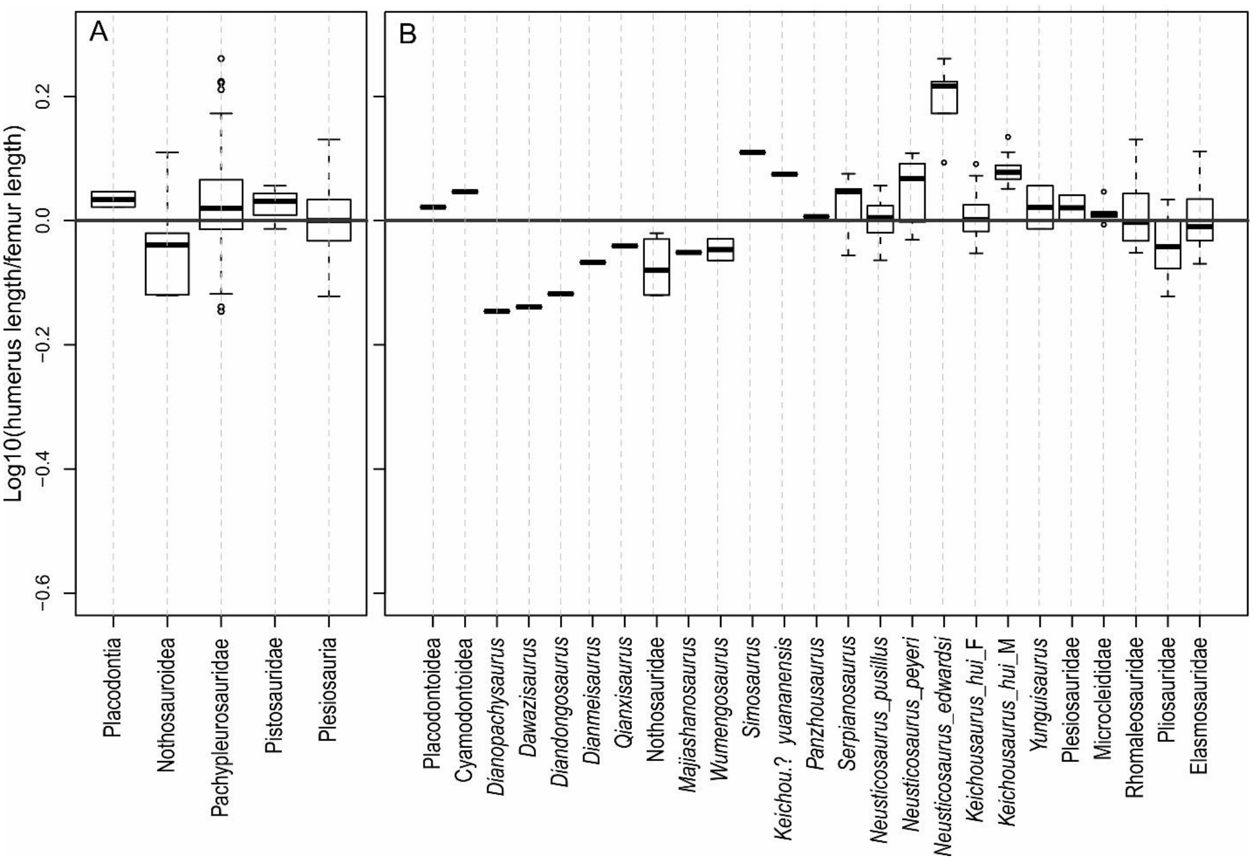

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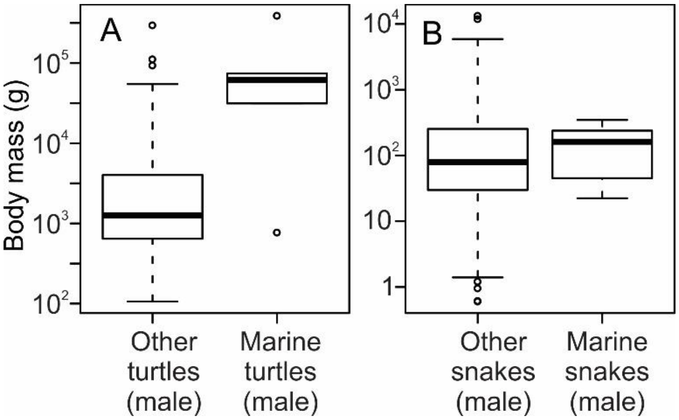

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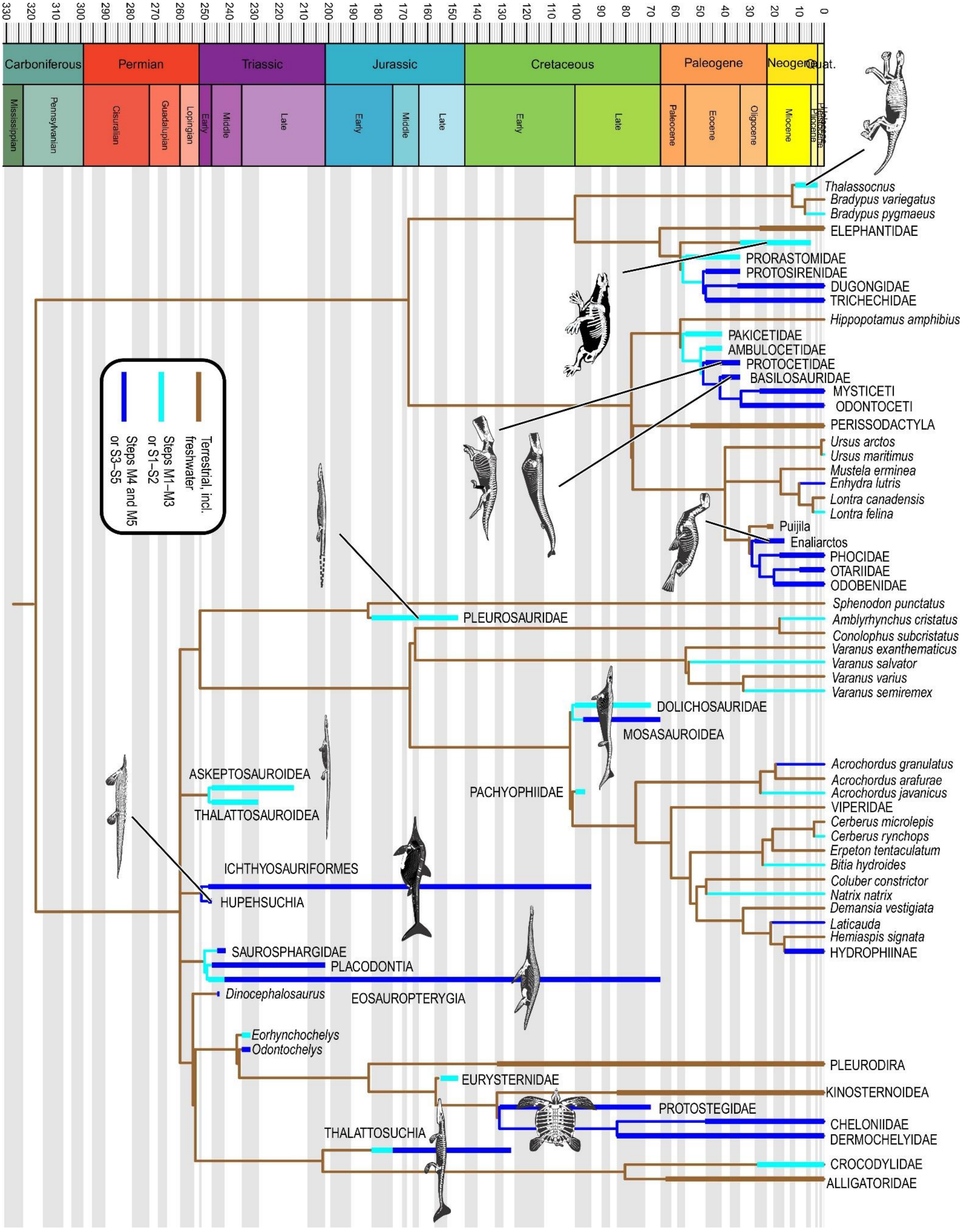

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10
0
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Paleogene
Neogene
Quat.
Mississippian
Pennsylvanian
Cisuralian
Guadalupian
Lopingian
Early
Middle
Late
Early
Middle
Late
Early
Late
Paleocene
Eocene
Oligocene
Miocene
Pliocene
Pleistocene
Terrestrial, incl. freshwater
Steps M1–M3 or S1–S2
Steps M4 and M5 or S3–S5
Thalassocnus
Bradypus variegatus
Bradypus pygmaeus
ELEPHANTIDAE
PRORASTOMIDAE
PROTOSIRENIDAE
DUGONGIDAE
TRICHECHIDAE
Hippopotamus amphibius
PAKICETIDAE
AMBULOCETIDAE
PROTOCETIDAE
BASILOSAURIDAE
MYSTICETI
ODONTOCETI
PERISSODACTYLA
Ursus arctos
Ursus maritimus
Mustela erminea
Enhydra lutris
Lontra canadensis
Lontra felina
Puijila
Enaliarctos
PHOCIDAE
OTARIIDAE
ODOBENIDAE
Sphenodon punctatus
PLEUROSAURIDAE
Amblyrhynchus cristatus
Conolophus subcristatus
Varanus exanthematicus
Varanus salvator
Varanus varius
Varanus semiremex
DOLICHOSAURIDAE
MOSASAUROIDEA
ASKEPTOSAUROIDEA
THALATTOSAUROIDEA
PACHYOPHIIDAE
Acrochordus granulatus
Acrochordus arafurae
Acrochordus javanicus
VIPERIDAE
Cerberus microlepis
Cerberus rynchops
Erpeton tentaculatum
Bitia hydroides
ICHTHYOSAURIFORMES
HUPEHSUCHIA
Coluber constrictor
Natrix natrix
Demansia vestigiata
Laticauda
Hemiaspis signata
HYDROPHIINAE
SAUROSPHARGIDAE
PLACODONTIA
Dinocephalosaurus
EOSAUROPTERYGIA
Eorhynchochelys
Odontochelys
PLEURODIRA
EURYSTERNIDAE
KINOSTERNOIDEA
PROTOSTEGIDAE
CHELONIIDAE
DERMOCHELYIDAE
THALATTOSUCHIA
CROCODYLIDAE
ALLIGATORIDAE

Table 1. Marine adaptations in extant marine tetrapods. See Section III for definitions of marine adaptation Steps M1–M5 (for marine animals excluding snakes) and Section IV for Steps S1–S5 (for marine snakes). Blank cells indicate absence, whereas ? indicates lack of information. Species diversity per colonization was calculated by dividing the total number of species by the minimum number of marine colonizations in each category.

			Aquatic adaptation steps			**Haline adaptation steps**					
Marine adaptation step	**Common name**	**Scientific name**	**A1: at least occasional locomotion in water**	**A2: absence of terrestrial travel**	**A3: fully aquatic lifestyle except for reproduction**	**H1: diet of at least some food originating in brackish or saline marine water**	**H2: diet of at least some food collected directly in sea water**	**H3A: water balance maintenance without terrestrial fresh water**	**H3B: completely marine diet**	**Marine species**	**Species diversity per unique colonization event**
M1b	Crabeating frog	*Fejervarya cancrivora*				+				1	1.13
M1b	Japanese macaque	*Macaca fuscata*				+				1	
M1c	American alligator	*Alligator mississippiensis*	+			+				1	
M1c	Broad-snouted caiman	*Caiman latirostris*	+			+				1	
M1c	Freshwater crocodile	*Crocodylus johnstoni*	+			+				1	
M1c	Pig-nosed turtle	*Carettochelys insculpta*	+	?		+				1	
M1c	Northern river terrapin	*Batagur baska*	+	?		+				1	
M1c	Painted terrapin	*Batagur borneoensis*	+	?		+				1	
M1c	Long-tailed monkey	*Macaca fascicularis*	+			+				1	

M2	Diamondback terrapin	*Malaclemys terrapin*	+			+	+			1	1.11
M2	Saltwater crocodile	*Crocodylus porosus*	+			+	+			1	
M2	American crocodile	*Crocodylus acutus*	+			+	+			1	
M2	Rusty monitor	*Varanus semiremex*	+			+	+			1	
M2	Asian water monitor	*Varanus salvator*	+			+	+			1	
M2	Fishing cat	*Prionailurus viverrinus*	+			+	+			1	
M2	Marine otter	*Lontra felina*	+			+	+			1	
M2	North American river otter	*Lontra canadensis*	+			+	+				
M2	Eurasian otter	*Lutra lutra*	+			+	+				
M2	Human	*Homo sapiens*	+			+	+			1	
M3	Marine iguana	*Amblyrhynchus cristatus*	+			+	+	+		1	1.0
M3	Polar bear	*Ursus maritimus*	+			+	+	+		1	
M4	Sea otter	*Enhydra lutris*	+	+		+	+	+	+	1	17.0
M4	Pinnipeds	Pinnipedia	+	+		+	+	+	+	33	
M5	Modern sea cows	Sirenia	+	+	+	+	+	+	+	3	32.7
M5	Sea turtles	Chelonioidea	+	+	+	+	+	+	+	7	
M5	Modern whales	Neoceti	+	+	+	+	+	+	+	88	
S1a	Reticulated python	*Python reticulatus*	+							1	4.3
S1c	Java file snake	*Acrochordus javanicus*	+			+				1	
S1c	Indo-Australian water snakes	Homalopsinae 1	+			+				11	
S2	Indo-Australian water snakes	Homalopsinae 2	+			+	+			4	4
S3	Sea kraits	*Laticauda* spp.	+	+		+	+		+	8	8
S4	Little file snake	*Acrochordus granulatus*	+	+	+	+	+		+	1	1
S5	Sea snakes	Hydrophiinae	+	+	+	+	+	+	+	70	70

Table 2. Osteological and ecological features correlated with marine adaptation steps in extant marine tetrapods. See Section II for definitions of marine adaptation steps M1–M5. COM, centre of mass.

Marine adaptation step	**Common name**	**Scientific name**	**Anterior shift of COM: humerus longer than femur**	**Pronation/supination mechanically impossible or very difficult**	**Carpal/tarsal bones flattened and packed**	**Elbow/knee joint surfaces flattened or slightly biconcave**	**Forearm–wrist/shin–ankle joint surfaces flattened or slightly biconcave**
M1b	Crabeating frog	*Fejervarya cancrivora*					
M1b	Japanese macaque	*Macaca fuscata*					
M1c	American alligator	*Alligator mississippiensis*					
M1c	Broad-snouted caiman	*Caiman latirostris*					
M1c	Freshwater crocodile	*Crocodylus johnstoni*					
M1c	Pig-nosed turtle	*Carettochelys insculpta*					
M1c	Northern river terrapin	*Batagur baska*					
M1c	Painted terrapin	*Batagur borneoensis*					
M1c	Long-tailed monkey	*Macaca fascicularis*					
M2	Diamondback terrapin	*Malaclemys terrapin*					
M2	Saltwater crocodile	*Crocodylus porosus*					
M2	American crocodile	*Crocodylus acutus*					
M2	Rusty monitor	*Varanus semiremex*					
M2	Asian water monitor	*Varanus salvator*					
M2	Fishing cat	*Prionailurus viverrinus*					
M2	Marine otter	*Lontra felina*					
M2	North American river otter	*Lontra canadensis*					
M2	Eurasian otter	*Lutra lutra*					
M2	Human	*Homo sapiens*					
M3	Marine iguana	*Amblyrhynchus cristatus*					
M3	Polar bear	*Ursus maritimus*					
M4	Sea otter	*Enhydra lutris*	+				
M4	Pinnipeds	Pinnipedia	+				
M5	Modern sea cows	Sirenia	+	+			
M5	Sea turtles	Chelonioidea	+	+	+		
M5	Modern whales	Neoceti	+	+	+	+	+

Table 3. Fossil marine tetrapods and their ecological and anatomical features. ‘C’ stands for highly cartilaginous mesopodials.

			Anterior shift of COM—Humerus longer than femur	**Pronation/Supination mechanically impossible or very difficult**	**Carpal/tarsal bones flattened and packed**	**Elbow/Knee joint surfaces flattened or slightly biconcave**	**Forearm–wrist/Shin–ankle joint surfaces flattened or slightly biconcave**	**Non–marine fluvial fossil record**	**Inferred Step**
Temnospondyli	Trematosauridae		–	–	–	–	–	+	M1–2
Diapsida incertae sedis	Ichthyosauromorpha	Hupehsuchia	+	+	+	+	+	–	M5
		Nasorostra	+	+	C	+	+	–	M4–5
		Chaohusaurus	+	+	C	+	+	–	M5
		Non-parvipelvian Ichthyopterygia	+	+	+	+	+	–	M5
		Parvipelvia	+	+	+	+	+	–	M5
	Saurosphargidae		+	–	(+)	–	–		M4
	Sauropterygia	Placodontia	+	–	C	–	–	–	M4
		Nothosauroidea	–	–	C	–	–	–	M2–3
		Pachypleurosauridae	(+)	–	C	–	–	–	M2–4
		Wangosaurus	(–)	–	C	–	–	–	M2–3
		Yunguisaurus	(+)	+	C	+	+	–	M5
		Plesiosauria	(+)	+	+	+	+	+	M5
	Thalattosauria	Askeptosauridae	–	–	C	–	–	–	M2–3
		Thalattosauridae	–	–	C	–	–	–	M2–3
Lepidosauromorpha	Sphenodontia	Pleurosauridae	–	–	–	–	–	–	M2–3
		Ankylosphenodon	(–)	–	–	–	–	–	M2–3
	Dolichosauridae		–	–	–	–	–	–	M2–3
	Mosasauroidea	basal forms	?	–	–	–	–	–	M2–3

		Mosasauridae	(+)	+	+	+	+	+	M5
Archosauromorpha	incertae sedis	*Dinocephalosaurus*	+	–	C	–	+	–	M4
	Tanystropheidae	*Macrocnemus*	–	–	–	–	–	–	M2–3
		Tanystropheus	–	–	–	–	–	–	M2–3
	Pseudosuchia	*Qianosuchus*	–	–	–	–	–	–	M2–3
		Ticinosuchus	–	–	–	–	–	–	M2–3
		Sikannisuchus	?	?	?	?	?	–	M2–3
	Phytosauria	*Diandongosuchus*	–	–	–	–	–	–	M2–3
		Mystriosuchus	–	–	–	–	–	+	M1–2
	Thalattosuchia	Basal forms							M2–3
		Metriorhynchidae	–	+	+	+	+	–	M5
	Testudines	*Eorhynchochelys*	–	–	–	–	–	–	M2–3
		Odontochelys	+	–	–	–	–	–	M4
		Solnhofia clade	–	–	–	–	–	–	M2–3
		derived Pan-Chelonioidea	+	?	+	–	+	–	M5
Mammalia	Sirenia	*Pezosiren*	–	–	–	–	–	–	M2–3
		Protosirenidae	+	–	–	–	–	–	M4
	Carnivora	*Enaliarctos*	+					–	M4
		Allodesmus	+					–	M4
	Desmostylia							–	M4?
	Cetacea	Pakicetidae	–	–	–	–	–	+	M1–2
		Ambulocetidae	–	–	–	–	–	–	M2–3
		Remmingtoncetidae	+?	–	–	–	–	–	M4
		Protocetidae	+	–	–	–	–	–	M4
		Basilosauridae	+	+	+	–	+	–	M5
	Pilosa	*Thalassocnus*	–	–	–	–	–	–	M2–3

Table 4. Minimum species diversity of selected marine tetrapod clades, excluding cetaceans and pinnipedomorphs for which high diversities are established based on extant species alone (Table 1). * total number of species-level operational taxonomic units in relevant phylogenetic analyses in the cited publications.

Clade	**Number of species**	**Reference**
Sauropterygia + Saurosphargidae	190*	Li *et al.* (2014); Neenan *et al.* (2015); Jiang *et al.* (2019); Madzia & Cau (2020)
Ichthyosauromorpha	114*	Chen *et al.* (2014*a*); Moon (2017); Huang *et al.* (2019)
Thalattosuchia	78*	Young *et al.* (2020)
Mosasauroidea	46*	Jiménez-Huidobro & Caldwell (2019)
Sirenia (stem + crown)	40*	Domning *et al.* (2017); Perini *et al.* (2019)
Chelonioidea (stem + crown)	34*	Evers *et al.* (2019); Gentry *et al.* (2019)
Thalattosauria	22*	Druckenmiller *et al.* (2020)
Desmostylia	13	Matsui & Tsuihiji (2019)
Eurysternidae	8	Anquetin *et al.* (2017)
Thalassocnus	4	Peralta-Prato & Solórzano (2019)
Pleurosauridae	3	Carroll (1985)
Odontochelys	1	Li *et al.* (2008)
Eorhynchochelys	1	Li *et al.* (2018)