

# From Fins to Limbs to Fins: Limb Evolution in Fossil Marine Reptiles

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**Limb osteology and ontogenetic patterns of limb ossification are reviewed for extinct lineages of aquatically adapted diapsid reptiles. Phylogenies including these fossil taxa show that paddle-like limbs were independently derived, and that the varied limb morphologies were produced by evolutionary modifications to different aspects of the limb skeleton. Ancient marine reptiles modify the limb by reducing the relative size of the epipodials, modifying the perichondral and periosteal surface of elements distal to the propodials, and evolving extremes of hyperphalangy and hyperdactyly. Developmental genetic models illuminate gene systems that may have controlled limb evolution in these animals.** © 2002 Wiley-Liss, Inc.

**KEY WORDS:** ontogeny; phylogeny; mosasaurs; ichthyosaurs; plesiosaurs

## INTRODUCTION

Recent discoveries in the fields of paleontology and developmental genetics have generated a research renaissance into the patterns and processes of vertebrate limb evolution. The newly discovered fossils have shown that the earliest tetrapods had more than five fingers and toes [Coates and Clack, 1990], while developmental genetics has revealed the underlying gene systems that control limb patterning [Sordino et al., 1995; Cohn and Tickle, 1999]. Not too surprisingly, research and hypothesis construction on the evolutionary developmental

biology of the limb have focused on tetrapod limb origins and the fin-to-limb transition [Shubin et al., 1997; Coates and Cohn, 1998, 2000; Wagner et al., 2000]. However, an equally intriguing aspect of tetrapod limb evolution has received relatively little attention: the secondary radiation of tetrapods back into aquatic environments—the fin-to-limb-to-fin transition. The recolonization of the water has occurred repeatedly in distantly related tetrapod lineages, and in each case involves a major morphogenetic reorganization of the limb to a paddle-like, or fin-like, structure. Among living groups of tetrapods, this process of secondary radiation and morphogenetic evolution has produced the specialized limbs of cetaceans, seals, sea lions, manatees, walruses, and sea turtles. The fossil record also provides evidence of aquatic adaptation and extreme morphological specialization of the limbs in a number of extinct lineages of diapsid reptiles (Fig. 1): mosasaurs, ichthyosaurs, plesiosaurs, pliosaurs, their basal sauropterygian cousins, and extinct crocodylians.

Our understanding of the fin-to-limb-to-fin transition is surprisingly good, due for the most part to the excellent fossil preservation provided by aquatic depositional environments. We have superb fossils documenting stratigraphic, or temporal, sequences of morphological changes to the limb skeleton as animals continued to adapt to their environments. We also have an excellent fossil record preserving complete growth series for many species; these data are excellent sources of information on the patterns of limb ossification through ontogeny.

For example, we currently recognize that the earliest diapsid reptiles (i.e., reptiles with two temporal fenestrae) are from rocks that are approximately 310 million years old. These early four-legged terrestrial animals for the most part resembled modern lizards. In 260-million-year-old rocks, we find evidence of aquatic adaptations in diapsids. Over the next 200 million years, numerous groups of diapsids return to aquatic habitats and subsequently modify their skeletal systems for aquatic locomotion, principally the limb skeleton. Sixty-five million years ago, the last of the giant marine diapsids became extinct; in less than 10 million years, whales filled the ecological and morphological gap.

In this article, I will review current hypotheses of diapsid phylogeny as well as the basics of cartilage and

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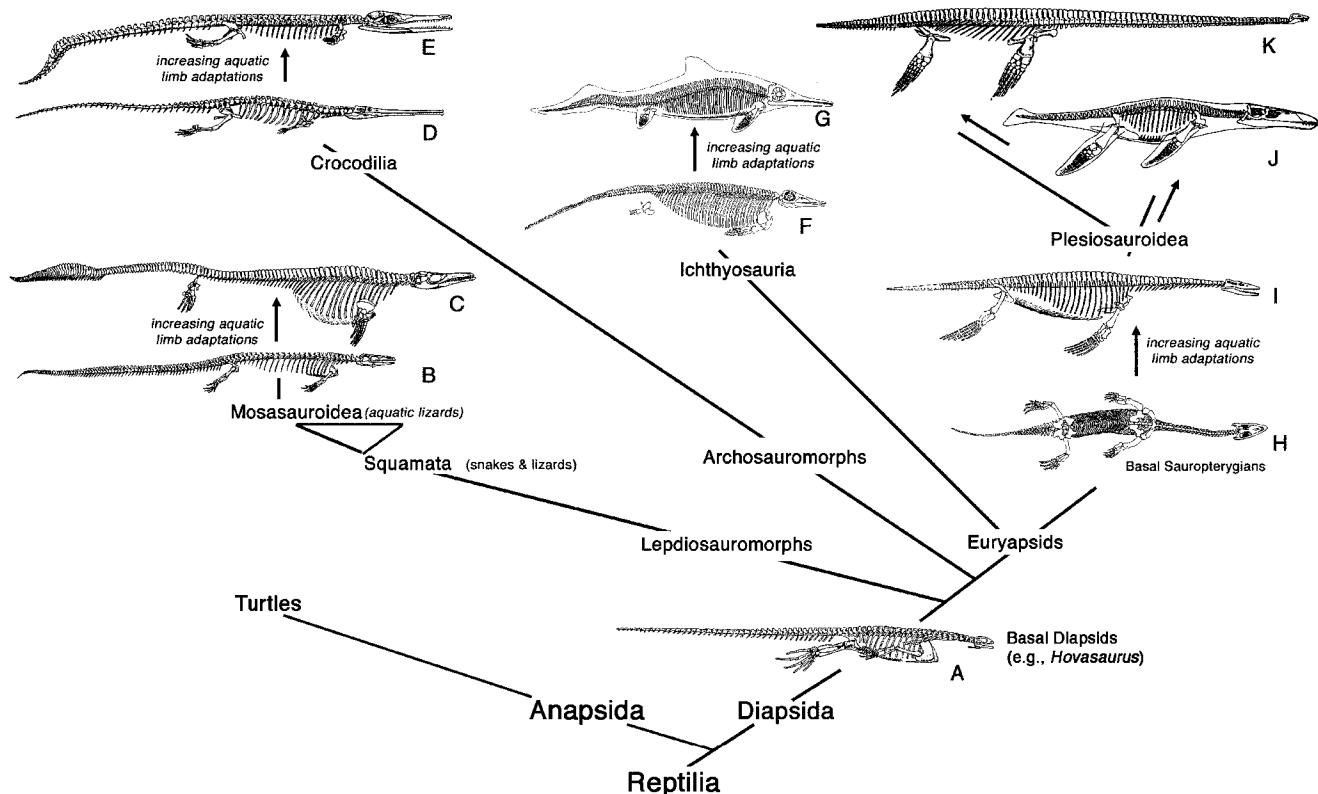


Fig. 1. Phylogenetic relationships of diapsid reptiles derived from cladistic analysis of Caldwell [1996a]. **A:** *Hovasaurus*, basal diapsid, Upper Permian [Currie, 1981; Caldwell, 1994]. **B:** *Aigialosaurus*, basal mosasaurid, Cenomanian, Upper Cretaceous [deBraga and Carroll, 1993]. **C:** *Plotosaurus*, mosasaurine mosasaur, Maastrichtian, Upper Cretaceous [Russell, 1967]. **D:** *Steneosaurus*, basal marine mesosuchian crocodile, Upper Jurassic [Carroll, 1988]. **E:** *Geosaurus* Upper Jurassic [Fraas, 1902].

**F:** *Utatusaurus*, basal ichthyosaur, Triassic [Carroll, 1988]. **G:** *Mixosaurus*, ichthyosaur, Upper Triassic [Carroll, 1988]. **H:** *Generalized basal sauropterygian*, Upper Triassic [Carroll, 1988]. **I:** *Pistosaurus*, basal plesiosaurian, Upper Triassic [Carroll, 1988]. **J:** *Liopleurodon*, pliosaur, Upper Jurassic [Taylor, 1993]. **K:** *Alzadasaurus*, elasmosaurid plesiosaur, Upper Cretaceous.

bone morphogenesis. Both topics contextualize my review of the available fossil data on limb osteology, ontogeny, and evolution in five groups of semiaquatic to obligatorily aquatic diapsids. These five groups include the basal diapsid *Hovasaurus boulei*, the mosasauroids (a large and diverse group of small- to giant-sized marine lizards that lived during the Upper Cretaceous period), the sauropterygians (a large group of small to giant marine reptiles with fusiform bodies and long necks that appear in the Triassic and go extinct at the end of the Cretaceous), the ichthyosaurs (a diverse group of marine reptiles with a dolphin-like body form that appear in Lower Triassic and go extinct in the Upper Cretaceous), and the metriorhynchid crocodiles (a group of marine crocodiles, distantly related to extant crocodiles, that appear in the Early Jurassic and go extinct by the Early Cretaceous).

### DIAPSID PHYLOGENY: CERTAINTIES AND UNCERTAINTIES

A phylogenetic pattern is the necessary prerequisite for formulating process hypotheses on the evolutionary transformation of morphology. Selection of a phylogenetic hypothesis profoundly affects the distribution of characters and thus the subsequent evolutionary hypotheses of morphological change.

For example, the hypothesis of relationships presented here (Fig. 1) is derived from the cladistic analysis of diapsids conducted by Caldwell [1996a]. Caldwell's study reviewed the data and hypotheses of Rieppel [1993a, 1994] and revised his phylogenetic scheme by adding ichthyosaurs to the analysis (excluded by Rieppel). The study by Caldwell [1996a] was the first cladistic analysis, complete with published data matrices, to include ichthyosaurs in an analysis of overall diapsid interrelationships.

The phylogenetic hypotheses of Caldwell [1996a] and Rieppel [1993a, 1994] are very different and suggest different scenarios for the evolution of limbs in aquatic diapsids. Rieppel's [1993a, 1994] phylogenetic scheme, and that presented in subsequent analyses [deBraga and Rieppel, 1997; Rieppel and Reisz, 1999], found turtles to be diapsid reptiles in a group including lizards and snakes. Using Rieppel's phylogeny excludes any analysis of ichthyosaurs limbs while concomitantly forcing the analysis of turtle limbs. The choice of any one phylogeny over another clearly affects the evolutionary study of an organ system.

Problematic relationships not examined by Caldwell [1996a] include the ingroup relationships of mosasaurs. It is commonly agreed on that mosasaurs are squamate reptiles (lizards and snakes), though controversy exists concerning their specific squamate relative [Russell,

1967; Caldwell, 1999]. In contrast, there is little debate on the relationships of metriorhynchid crocodiles. They are considered to be mesosuchian crocodiles nested within the Archosauromorpha [Parrish, 1993].

Turtles are not here considered as diapsids despite the arguments of Rieppel [1993a, 1994], deBraga and Rieppel [1997], and Rieppel and Reisz [1999]. Caldwell [1996a] explicitly tested Rieppel [1993a] hypothesis by alternately including/excluding turtles and ichthyosaurs from tests of the data matrices; only when ichthyosaurs were excluded from the matrix, and turtles included, did turtles remain within diapsids in the position hypothesized by Rieppel [1993a]. Caldwell's [1996a] cladistic analysis of diapsid phylogeny reconstructed Ichthyosauria as the sister group of the Sauropterygia; this clade, the Euryapsida, formed a more inclusive clade with the Archosauromorpha, both of which are the sister group of Lepidosauromorpha.

The diapsid nature of sauropterygians (plesiosaurs, pliosaurus, nothosaurs, and placodonts) and ichthyosaurs has not been easily recognized [Jaekel, 1910; Kuhn-Schnyder, 1967; Tarsitano, 1983; Sues, 1987; see also the literature review in Caldwell, 1996a] as diapsids historically were diagnosed by the possession of both a supratemporal and lateral temporal fenestra. Ichthyosaurs and sauropterygians possess a supratemporal fenestra, but the cheek is either solid or emarginated, not fenestrate as in other diapsids. This supposed non-diapsid character complex was used to establish membership for both groups within the Euryapsida (Colbert [1955]) by both Romer [1968] and McGowan [1973]. On the basis of the presence or absence of the lateral temporal fenestra, classifications of the Euryapsida have variably contained ichthyosaurs, sauropterygians, placodonts, *Araeoscelis*, *Trilophosaurus*, *Protosaurus*, *Prolacerta*, and even lizards; all of these groups are now recognized as diapsids that either do not possess a lower temporal bar, have an emarginated cheek, or have a solid cheek.

Presently, ichthyosaurs, sauropterygians, mosasaurs, and marine crocodiles are all considered diapsid reptiles. Each of these groups contains derived members that independently evolve aquatically adapted limbs.

### CARTILAGE AND BONE MORPHOGENESIS: A BRIEF REVIEW

Bone-forming precursor cells can be broadly divided into endochondral and perichondral chondrocytes. During limb morphogenesis, these two cell types form condensation foci that will ultimately form the cartilage precursors of the limb skeleton. For long bone elements, endo- and perichondral chondrocytes migrate to, and differentiate within, distinct regions in the condensing focus [Wolpert and Tickle, 1993]. The result is that the chondrocyte types are arranged in specific patterns relative to each other. During early chondrogenesis, cells of the incipient perichondrium are aligned parallel to the long axis of the element, while those of the incipient endochondrium are oriented at right angles to the long axis of the element [Rooney et al., 1984]. In contrast, chondrocytes in non-long bone elements, such

as carpals and tarsals, do not form symmetrical patterns relative to each other. There is no obvious differential orientation between surficial (perichondral) and internal (endochondral) chondrocytes.

The dumbbell shape of long bone elements, as opposed to irregular-shaped non-long bone elements, i.e., mesopodials, potentially results from the differential orientation of endochondral chondrocytes relative to the encasing perichondral chondrocytes [Wolpert and Tickle, 1993]. Therefore, the perichondrium may mechanically restrict the growth and shape of the endochondrium in long bone elements, whereas for irregular mesopodial elements, bone shape may be related to the absence of a differentiated perichondrium.

In general, long bones begin ossification prior to non-long bone elements; this offset establishes the observable phenomenon of delayed mesopodial ossification where the propodials, epidrodials, and metapodials have ossified periosteally, while the mesopodials are still formed of cartilage. The ossification of mesopodials is endochondral (exceptions, which will be discussed below, include fossil crocodiles where some "mesopodials" have evolved characteristics of a long bone). Ossification begins in the middle of the cartilage and spreads nonsymmetrically toward the margins of the element. Mesopodial ossification is significantly delayed relative to all other limb bones; this phenomenon is observed in most tetrapods [Rieppel, 1992a, 1992b]. A second delay is noted for long bones where ossification begins in the perichondrium and produces the aforementioned sheath or collar of compact, lamellar bone along the length of the shaft (periosteal bone). Once perichondral ossification has been initiated, ossification of endochondral chondrocytes occurs within the shaft [Rieppel, 1992a, 1992b].

Patterns of ossification specifying differences between endochondral and perichondral ossification, and the elements in which ossification begins, are important to understanding developmental and evolutionary alterations to limb morphology. If the perichondrium is important in determining the shape of an element [Wolpert and Tickle, 1993], then alterations to element development will affect its shape and function. Further, the relative amount of endochondral or perichondral bone, and the nature of an element's articulations, will also affect the function of the element and of the limb. If such changes are exaggerated over geological time, then the effect is evolutionary modification of morphology leading to the distinction of new groups of organisms.

### BASAL DIAPSID: PRIMITIVE CONDITION

#### Basal Diapsids

*Hovasaurus boulei*, and a number of other early diapsids not discussed here [Caldwell, 1994], are found in 260-million-year-old (Upper Permian) rocks outcropping in southwestern Madagascar [Piveteau, 1926; Carroll, 1981; Currie, 1981]. These rocks are interpreted as having been deposited in rift valley lakes and rivers [Cliquet, 1957]. *Hovasaurus boulei* is known from a large number of complete, articulated skeletons that preserve a superb growth series of carpal and tarsal

ossification sequences; this diapsid also shows aquatic adaptations such as lateral flattening of the tail [Currie, 1981]. The following is a review of Caldwell's [1994] ontogenetic limb ossification data for *Hovasauros*.

*Hovasauros boulei* (Fig. 2) shows ontogenetic ossification patterns of the primary axis and digital arch consistent with those observed in living lepidosaurs [Rieppel, 1992a, 1992b, 1993b, 1993c, 1993d, 1993e]. There are no ossified carpals or tarsals in the smallest individuals. However, when carpal ossification begins, the following sequence is found: ulnare, distal carpal four, intermedium, lateral centrale, distal carpal three or one. The sequence of ossification of the remaining carpals is highly variable. Tarsal ossification proceeds according to the sequences astragalus/calcaneum, distal tarsal four, distal tarsal three, centrale, distal tarsals two, one, or five. As was noted by Shubin and Alberch [1986] for chondrogenic patterns, limb ossification is highly constrained along the primary limb axis and at the postaxial initiation of the digital arch. Variation is observed preaxially along the digital arch and with respect to the postaxial development of the fifth digit.

Reference to *Hovasauros* as representative of the basal diapsid condition (Fig. 1) highlights the potential conservatism of limb development patterns. By exten-

sion, and in association with a phylogeny, ontogenetic data provide insight on the conservatism of the underlying genetic controls on limb development.

**MOSASAUROIDS: GIANT MARINE LIZARDS**

Mosasauroid squamates (aigialosaurs and mosasaurs) are a temporally and spatially diverse group of extinct marine lizards that achieved their greatest adaptive and taxonomic diversity in the Upper Cretaceous [Russell, 1967; deBraga and Carroll, 1993; Bell, 1997]. The limb and girdle skeletons of aigialosaurs closely resemble those of other fossil and modern terrestrial lizards in both structure and proportions [Caldwell, 1996b]. In contrast, mosasaur limbs are proximally shortened and have broad paddle-like meso- and metapodia; the carpus and tarsus display delayed mesopodial ossification that persists late into adult development. Delayed mesopodial ossification makes it possible to study the mesopodial ossification patterns in giant-sized adult mosasaurs despite the rarity of juveniles and the absence of embryos [Russell, 1967; Bell, 1997]. Here I review the data on patterns of limb skeleton formation in mosasaurs presented by Caldwell [1996b].

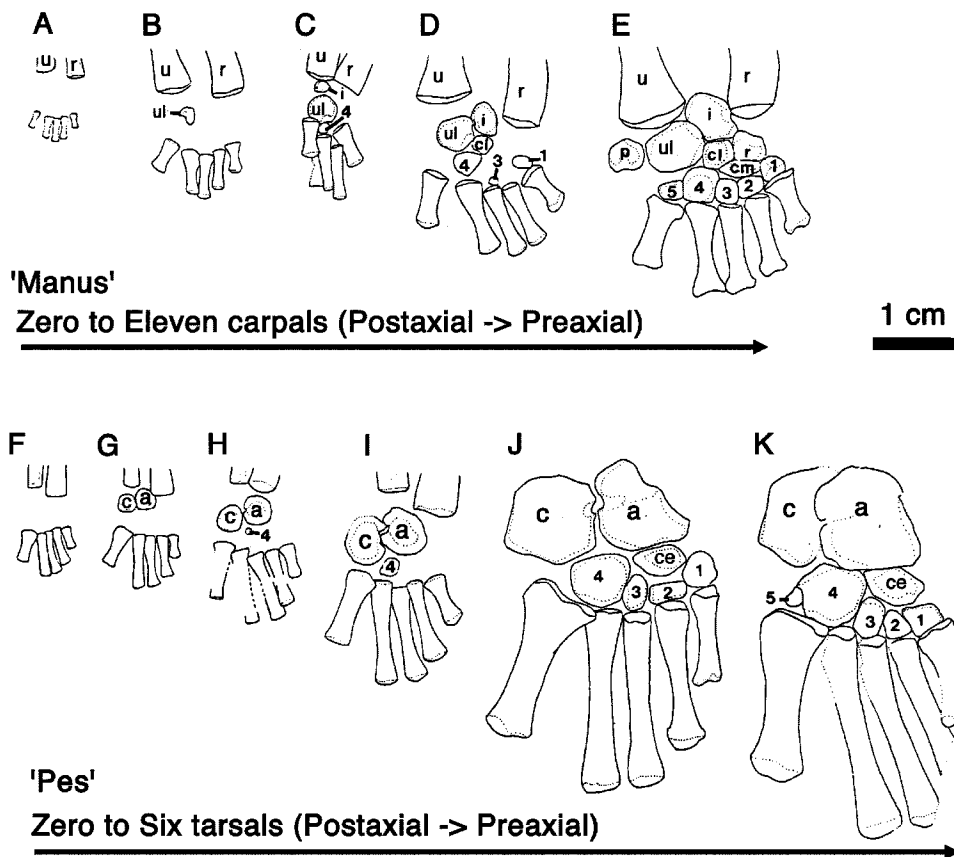


Fig. 2. Carpal/tarsal ossification patterns through the ontogenetic series of *Hovasauros boulei*. Some illustrations are reversed for ease of comparison: **A-E**: Carpals. **F-K**: Tarsals. Scale bar = 1 cm. Abbreviations: a, astragalus; c, calcaneum; ce, centrale; cl, lateral centrale; cm, medial centrale; F, femur; f, fibula; H, humerus; i, intermedium; lcp, lateral calcaneal process; p, pisiform; r, radius; ra, radiale; t, tibia; u, ulna; ul, ulnare; 1-5, distal carpals and tarsals; i-v, metacarpals and metatarsals. Illustrations modified from Caldwell [1994].

**Ossification Sequences and Phylogeny**

Caldwell [1996b] examined the known carpal and tarsal ossification patterns for 13 genera of fossil mosasaurs and aigialosaurs and noted that a complete ontogenetic sequence of mesopodial ossification could not yet be found for any one genus and/or species. However, Caldwell [1996b] did report on partial sequences for various species of mosasaurs and at various stages of adult development.

From among the varied subfamilies of mosasaurs, Caldwell [1996b] noted that large (10–12 m) adult tylosaurine mosasaurs show one- and two-element stages for both the carpus and tarsus (Fig. 3A, B, and I). Platecarpine mosasaurs (5–10 m) show three-, four-, and five-element stages for the carpus (Fig. 3C–E) and a three-element stage in the tarsus (Fig. 3J). Five- and

seven-element stages are known for the carpus of plioplatecarpines (Fig. 3G), and *Ectenosaurus* (Fig. 3F) shows a six-element stage of carpal ossification. Seven to eight elements in the carpus (Fig. 3H) and three in the tarsus (Fig. 3K) characterize all mososaurines (*Clidastes*, *Mosasaurus*, etc., ranging in size from 5 to 15 m).

Caldwell [1996b] mapped these partial sequences for different mosasaur taxa onto a phylogeny, treated the resultant patterns of phylogenetic reduction in the reverse, i.e., as an ontogenetic sequence of ossification, and proposed from this reverse phylogeny a hypothetical mesopodial ossification sequence (Fig. 3). It was reasoned that if tylosaurines have the least ossified mesopodia, and platecarpines, plioplatecarpines, ectenosaurus, and mososaurines have mesopodia where ossified elements increase by consistent sequential addition from a tylosaurine-like pattern, then mesopodial

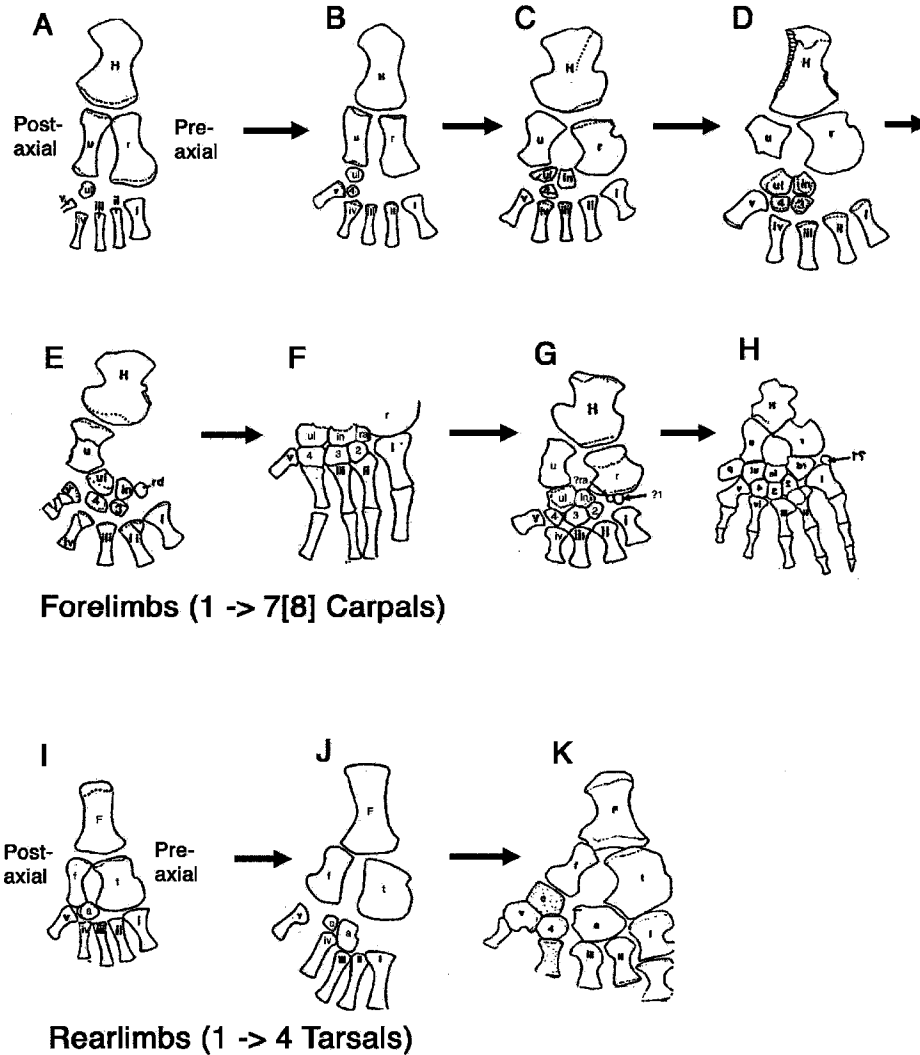


Fig. 3. Hypothetical carpal and tarsal ossification sequences of Mosasaurs. **A–H:** Carpal ossification sequences derived from partial sequences available for *Tylosaurus* (first and second figures) and *Platecarpus* (third, fourth, and fifth figures), followed by *Ectenosaurus* and *Plioplatecarpus*, and finally the seven- and eight-element stages of *Clidastes*. Most of the direct sequence data are available for “russellosaurines”; mososaurine sequences

are almost completely hypothetical. **I–K:** Tarsal ossification sequences are derived from *Tylosaurus* (first and second figures) and *Mosasaurus* (third figure); in this case any other mosasaur with an articulated rearlimb shows the three element stage, presumed here to be the final stage of tarsal ossification. For abbreviations, see legend for Figure 2. Illustrations modified from Caldwell [1996b].

ossification in mosasaurs proceeded from one to seven carpals and one to three tarsals. Caldwell [1996b] suggested the following carpal ossification sequence: ulnare, distal carpal four (dc4), intermedium, dc3, radiale or dc2, dc1 or pisiform and dc5. For the mosasaur tarsus, Caldwell [1996b] presented the following ossification sequence: astragalus, distal tarsal four and/or calcaneum.

More importantly, Caldwell [1996b] noted that the mosasauroid pattern of ossification did not differ from the general patterns noted for carpal and tarsal ossification in the Permian diapsids *Thadeosaurus*, *Hovasaurus*, and *Claudiosaurus* [Caldwell, 1994]. Caldwell [1996b] further noted that skeletal paedomorphosis was a dominant heterochronic pattern in mosasaurid evolution, and that continued preaxial reduction of mesopodial ossification through phylogeny had resulted in the deletion of ossified elements from the preaxial portion of the ossification sequence. Based on the shared primitive aspects of conserved lepidosauromorph sequences [Caldwell, 1994], mosasaur specializations include variations on the degree of ossification, the number of ossified elements, and the number of preaxial/terminal deletions in the digital arch sequences.

#### SAUROPTERYGIAN LIMBS: OSTEOLOGY AND OSSIFICATION PATTERNS

Sauropterygians are characterized by a number of specialized morphologies related to locomotion and

feeding in aquatic habitats [Taylor, 1992, 1993; Rieppel, 1994]. Placodonts, considered to be the basal-most sauropterygians, show few aquatic adaptations of the limb skeleton and were likely bottom-walkers that did not swim well. In other basal sauropterygians such as eusauropterygians and pachypleurosaurs (Fig. 1), aquatic locomotion is thought to have occurred by anguilliform movement of the axial skeleton with some thrust being generated by the forelimbs [Storrs, 1993]. The body of these animals is elongate and bears short, flattened limbs (Fig. 1). Locomotion in more derived sauropterygians, such as plesiosaurs and pliosaurus (Fig. 1), is thought to have been a form of underwater flying or rowing where the limbs served as the primary source of propulsion [Godfrey, 1984; Nicholls and Russell, 1991]. The plesiosaur body was shaped like a flat-bottomed boat with elongate, paddle-like limbs whose skeleton differs significantly from that of basal sauropterygians.

#### Basal Sauropterygians: Limb Osteology

The limbs of nonplesiosaurian sauropterygians (i.e., those early marine reptiles considered to share a common ancestor with plesiosaurs and pliosaurus, such as placodonts, nothosaurs, and pachypleurosaurs) are very similar to the limbs of more basal diapsids (compare Fig. 2 with Fig. 4). The manus and pes are well developed, both are modestly proportioned compared to the rest of the limb, and the propodials and epipodials are of similar proportions to a conservative terrestrial limb.

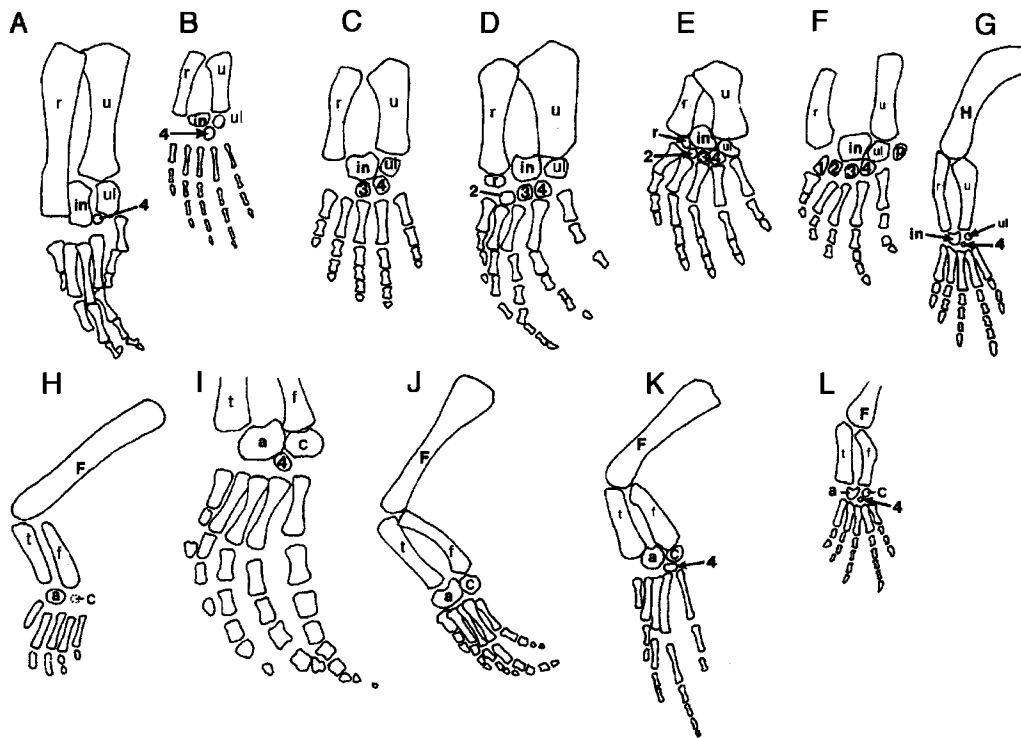


Fig. 4. Forelimbs and rearlimbs of Triassic sauropterygians. Some images are reversed to allow easier comparisons. **A:** Forelimb of *Neusticosaurus*. **B:** Forelimb of *Nothosaurus*. **C:** Forelimb of *Paranotosaurus*. **D:** Forelimb of *Ceresiosaurus*. **E:** Forelimb of *Lariosaurus*. **F:** Forelimb of *Proneusticosaurus*. **G:** Forelimb of *Simosaurus gaillardoti*. **H:** Rearlimb of *Lariosaurus*. **I:** Rearlimb of *Ceresiosaurus*. **J:** Rearlimb of *Serpianosaurus mirigiolensis*. **K:** Rearlimb of *Psilotracheosaurus toepflichi*. **L:** Rearlimb of *Simosaurus gaillardoti*. For abbreviations, see legend for Figure 2. Illustrations modified from Caldwell [1997a].

As was noted by Caldwell [1997a], in terms of limb ossification, basal sauropterygians show delayed mesopodial ossification and a consistent pattern of postaxial to preaxial, and proximal to distal, ossification through the digital arch (Fig. 4).

**Adult Plesiosaur Limb Osteology**

Despite the relative ease of comparing morphology and ossification patterns between basal sauropterygians and basal diapsids [Caldwell, 1997a], similar comparisons for plesiosaurs are problematic (compare Fig. 4

with Fig. 5). From an evolutionary perspective, aquatic adaptation in plesiosaurs resulted in substantial modifications to many components of the limb skeleton, making ready identifications difficult.

The limb skeletons of the Lower Jurassic plesiosaurs, *Plesiosaurus hawkinsi* and *Plesiosaurus brachypterygius*, are very similar (Fig. 5A, B, G, and H) and show that the humerus and femur are roughly the same size. The radius/ulna and tibia/fibula are much smaller than the propodials and an important morphological landmark, the antebrachium, is still present. The postaxial margins of the ulna and fibula have been modified to

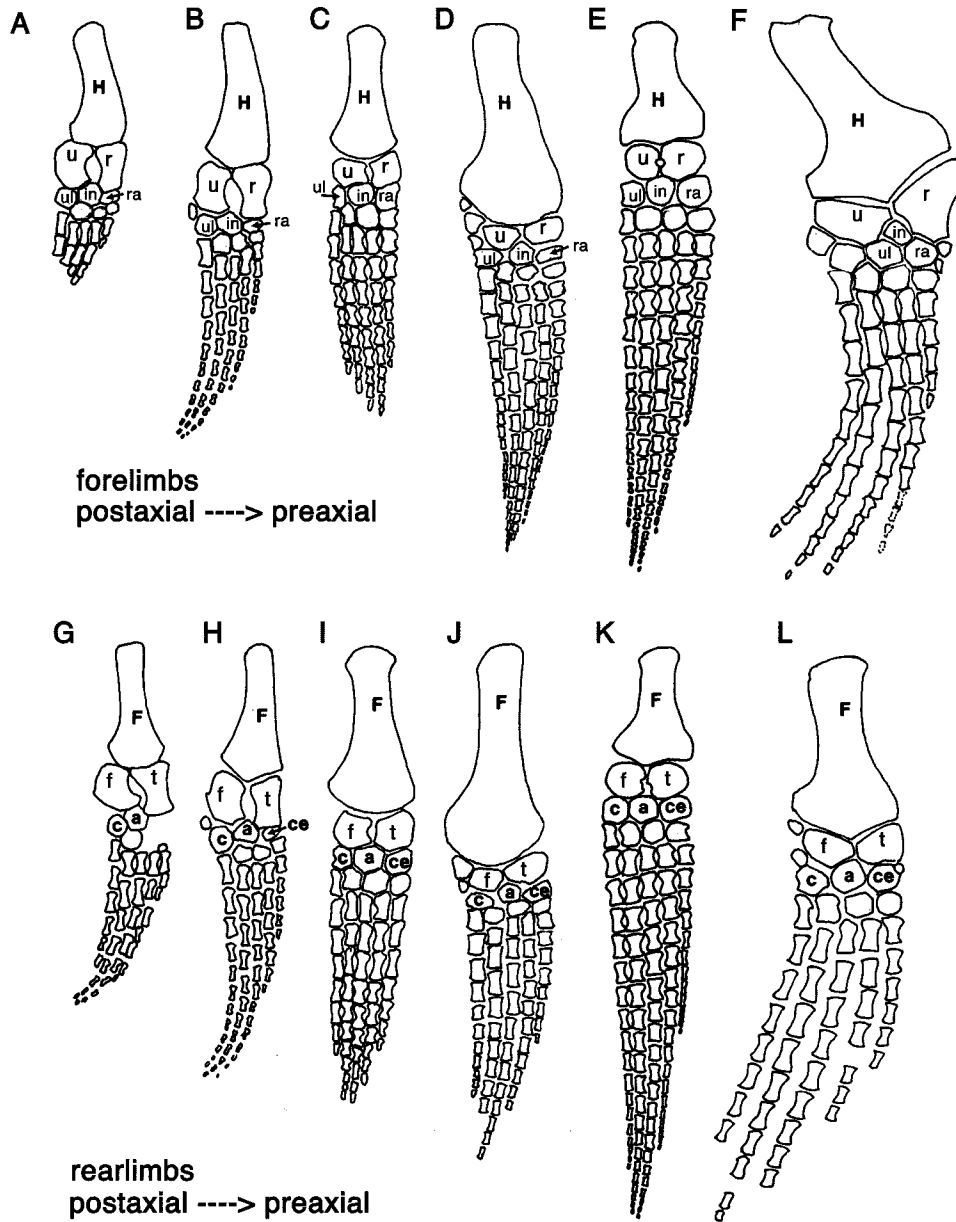


Fig. 5. Forelimbs and rearlimbs of Lower Jurassic to Upper Cretaceous plesiosaurs and pliosaurs. **A:** Forelimb of *Plesiosaurus hawkinsi*. **B:** Forelimb of *Plesiosaurus brachypterygius*. **C:** Forelimb of *Peloneustes philarchus*. **D:** Forelimb of *Dolichorhynchops osborni*. **E:** Forelimb of *Cryptoclidus eurymerus*. **F:** Forelimb of *Alzadasaurus pembertoni*. **G:** Rearlimb of *Plesiosaurus hawkinsi*. **H:** Rearlimb of *Plesiosaurus brachypterygius*. **I:** Rearlimb of *Peloneustes philarchus*. **J:** Rearlimb of *Dolichorhynchops osborni*. **K:** Rearlimb of *Cryptoclidus eurymerus*. **L:** Rearlimb of *Alzadasaurus pembertoni*. For abbreviations, see legend for Figure 2. Illustrations modified from Caldwell [1997a].

form an arc-shape; the usual shape of the bone is like an elongate dumbbell (see *Hovasaurus* (Fig. 2) or more basal sauropterygians (Fig. 4)).

Patterns of mesopodial ossification comparable to those of basal sauropterygians are not known for Lower Jurassic plesiosaurs [Caldwell, 1997a], though it is certain that mesopodial ossification occurred postaxially to preaxially (Fig. 5G). The absence of preaxial ossification also indicates the presence of delayed mesopodial ossification.

Hyperphalangy, where the number of phalanges increases significantly over the plesiomorphic formula, is also a characteristic feature of plesiosaur limbs. This condition appears in stratigraphically early plesiosaurs such as *Plesiosaurus brachypterygius* (rearlimb phalangeal count of 5-6-11-11-11) and persists in later plesiosaurs. This feature contrasts with the primitive, reduced, or slightly increased phalangeal counts observed in basal sauropterygians (Fig. 4).

The forelimbs (Fig. 5C–F) and rearlimbs (Fig. 5I–L) of the plesiosaurs *Peloneustes philarchus* (U. Jurassic) and *Dolichorhynchops osborni* (U. Cretaceous), and the plesiosaurs *Cryptoclidus eurymerus* (U. Jurassic) and *Alzadasaurus pembertoni* (U. Cretaceous) show a number of features in common. The humerus/femur is less than half the length of the rest of limb. The manus/pes is extremely elongate due to an increase in the number of phalanges (hyperphalangy) and the radius/ulna and tibia/fibula are extremely reduced in size. The antibrachial space is lost or significantly reduced in size, and the number and identity of carpals/tarsals are obscured either by loss or by alterations to their morphology. The principal difference between Upper Jurassic and Cretaceous plesiosaurs and plesiosaurs is the presence/absence of the perichondral bone on the margins of the radius/ulna and tibia/fibula. The plesiosaur *Peloneustes* (Fig. 5C and I) possesses well-formed margins on the radius/ulna and tibia/fibula that frame the antibrachial space. Perichondral bone is present on the preaxial margin of the radius in the plesiosaur *Cryptoclidus* (Fig. 5F). The same morphology is apparent in *Alzadasaurus*, though the antibrachial space is much smaller than in *Peloneustes* (Fig. 5E and K). In the plesiosaur *Dolichorhynchops* (Fig. 5D and J), the perichondral bone is absent from the margins of the tibia and fibula. Unlike Lower Jurassic plesiosaur species (Fig. 5A, B, G, and H), later plesiosaurians do not show evidence of delayed mesopodial ossification. However, the distinct long bone features of the metacarpals/metatarsals and phalanges versus the rounded shapes of the carpals and tarsals would seem to suggest that at some level a delay in ossification was present.

### Plesiosaur Ossification Patterns

The only plesiosaur taxon for which a partial limb ossification pattern is available is the Upper Jurassic cryptoclidid, *Cryptoclidus eurymerus* [Caldwell, 1997a]. However, even this partial sequence gives no insight on a specific pattern. Rather, what is clear from the available growth stages is that delayed mesopodial ossification is still present in *Cryptoclidus*, though

not as delayed as in basal sauropterygians. As noted above, *Cryptoclidus* shows a high degree of altered perichondral bone morphogenesis on the margins of the epi-, meso-, and metapodials. Linked to these bone modifications is an altered ossification sequence of the radius/ulna, tibia/fibula, and some metacarpals and metatarsals [Caldwell, 1997a]. This is significant in terms of tetrapod limb ossification patterns as it suggests that ossification sequences may be linked to differences in the timing of perichondral versus endochondral ossification.

## ICHTHYOSAUR LIMBS: OSTEOLOGY AND OSSIFICATION PATTERNS

### Adult Ichthyosaur Limb Osteology

Comparison of the limb osteology of the advanced ichthyosaur *Stenopterygius* (Fig. 6) to that of the basal diapsid *Hovasaurus* (Fig. 2) shows a large number of features unique to ichthyosaurs. In *Stenopterygius*, the humerus and femur are easily identified, though both are extremely short compared to *Hovasaurus*. The radius/ulna and tibia/fibula are short, rounded elements that have lost their long bone morphology. Carpal elements of *Stenopterygius*, preaxially (anterior to the limb axis) to postaxially (posterior to the limb axis), are the radiale, intermedium, ulnare, pisiform (proximal row), and distal carpals 1–4 (distal row). Tarsal elements, preaxially to postaxially, are the centrale, astragalus, calcaneum (proximal row), and distal tarsals 1–3 (distal row). There are four manal digits for which metacarpals are identified based on their articulation with distal carpals 1–4 (Fig. 6). Elements of the fifth digit are not ossified in all specimens. Two forms of variation are noted: the metacarpal and more proximal elements do not always ossify, and the number of ossified elements varies. The manus also possesses a supernumerary digit (Fig. 6D, I–K, and N) located between digits 3 and 4 (S3-4); this digit is considerably shorter than the five principal digits and never articulates with the distal carpal row. Elements of the supernumerary digit do not always ossify, but when they do the number of ossified elements varies between individuals. The pes is not discussed here, as it does not significantly differ from the manus except that it does not possess a supernumerary digit.

### Ichthyosaur Ossification Patterns

As was noted by Caldwell [1997b], the more advanced groups of ichthyosaurs (e.g., *Stenopterygius*) no longer present delayed mesopodial ossification; in fact, the mesopodials are highly ossified in embryos and appear to ossify in sequence with the remainder of the metapodium [Caldwell, 1997b]. Limb element ossification patterns follow a continuous proximal-to-distal sequence from the propodial elements through to the terminal elements of the first to the fourth digit in the manus and the first to third digit in the pes. The fifth manal and fourth pedal digit begin ossification later than more preaxial digits and also show evidence of proximal addition of elements near the distal

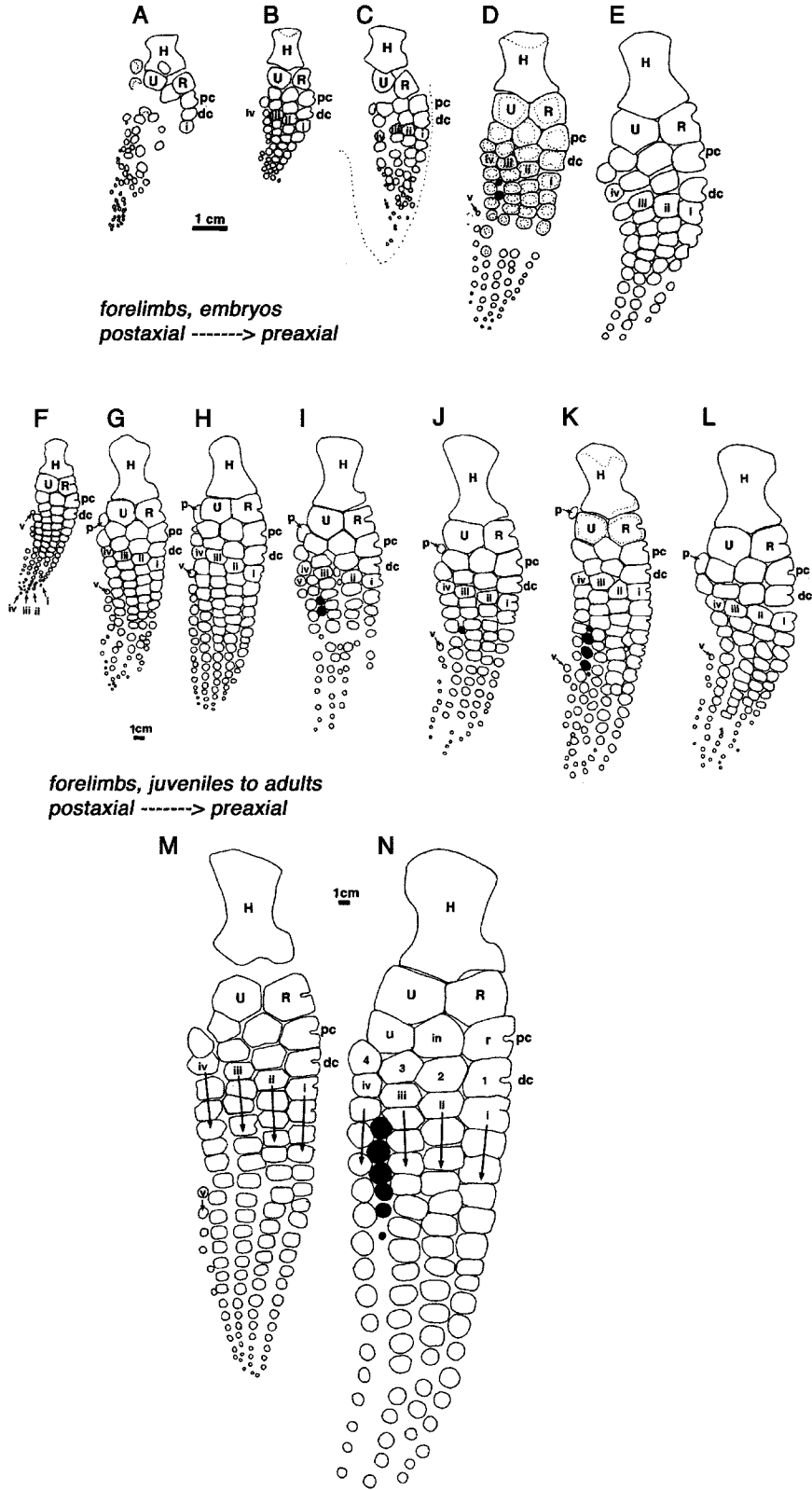


Fig. 6. Ichthyosaur forelimb osteology and ontogeny, embryos to adults, *Stenopterygius* sp. (Toarcian; Lower Jurassic), including one embryonic specimen of *Ichthyosaurus* cf. *communis* (Hettangian; Lower Jurassic). **A–E**: Forelimb osteology/ontogeny of embryonic *Stenopterygius*. **F–N**: Forelimb osteology/ontogeny of adult *Stenopterygius*. Elements in black are digital elements from the supernumerary digit S3–4. For abbreviations, see legend for Figure 2. Illustrations modified from Caldwell [1997c].

mesopodial row in a manner consistent with delayed ossification of the fifth distal mesopodial in other diapsids. Ossification of manal elements in the supernumerary 3-4 (S3-4) digit and the fifth digit appear interdependent; if one or the other is highly ossified, ossification of the other is retarded.

**MODIFIED PERICHONDRAL OSSIFICATION**

Caldwell [1997c] reported on ontogenetic and stratigraphic changes to bony limb elements that reflect evolutionary changes to the mechanisms, and thus developmental genetics, of bone morphogenesis (see above discussion of bone and cartilage morphogenesis). Both plesiosaurians (plesiosaurs and pliosaurs) and ichthyosaurs alter their limb morphologies by modifying the development of perichondral bone tissues (Figs. 7

and 8) on epipodial and metapodial elements [Caldwell, 1997c]. The modification of metapodial element shape is most pronounced in ichthyosaurs where all epipodial and metapodial elements lose their hourglass shape and become flattened discs (Figs. 6 and 8). For all taxa showing modifications to the shape of the epi-, meso-, and metapodial elements, it is important to note that phylogenetically and ontogenetically, modifications to these elements proceeds proximal to distal, and postaxial to preaxial, through the limb field.

**Plesiosaurs: Limb Osteology and Perichondral Bone Loss**

Plesiosaurs show similar progressive trends toward perichondral bone loss as do ichthyosaurs. The notable difference is that the most derived plesiosaur limbs

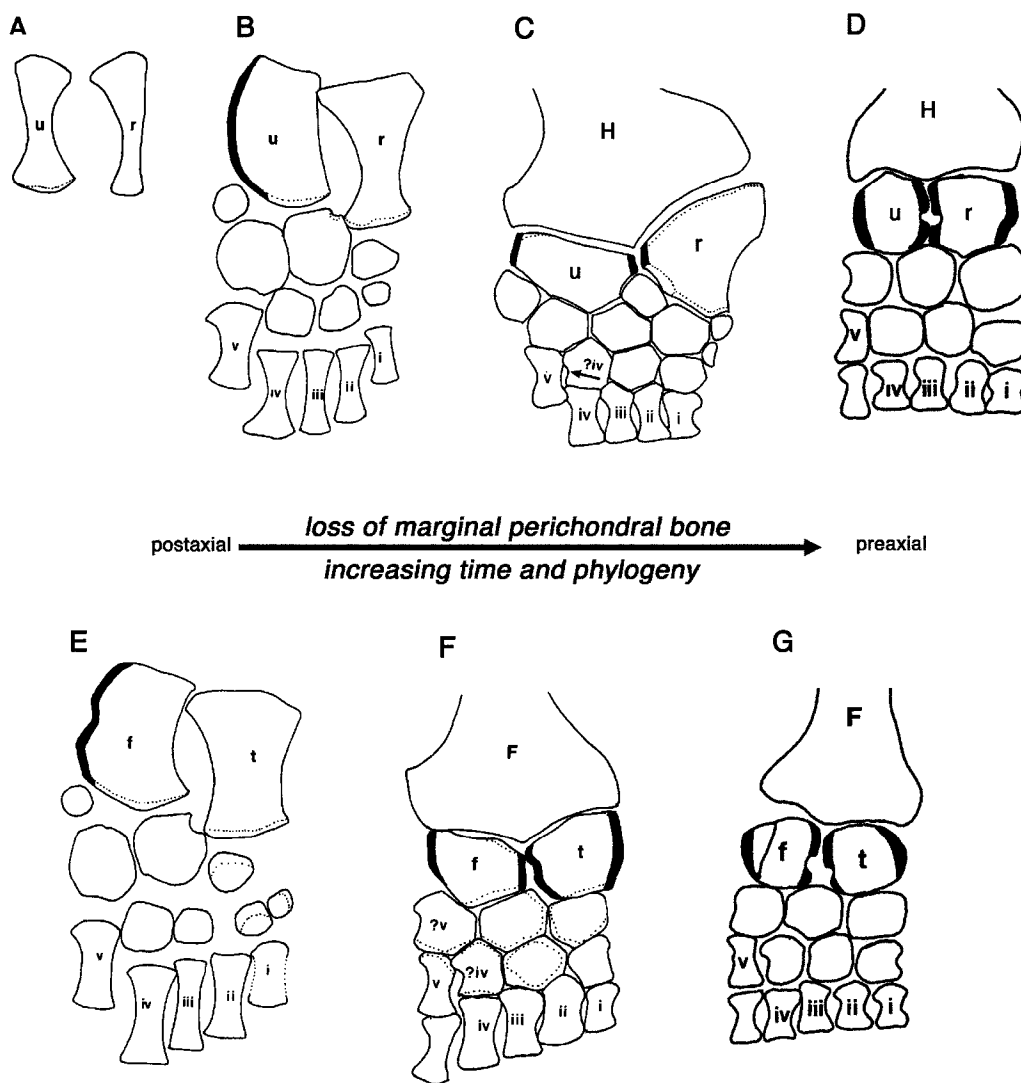


Fig. 7. Limbs of four plesiosaur taxa showing phylogenetic patterns of marginal perichondral bone loss. Shaded regions indicate where perichondral bone has been lost from the margins of an element. **A:** Forelimb of *Pistosaurus longaeus* (Anisian; Middle Triassic). **B:** Forelimb of *Plesiosaurus dolichodirus* (Lower Jurassic). **C:** Forelimb of *Cryptocleidus eurymerus* (Middle Jurassic). **D:** Forelimb of *Alzadosaurus pambertoni* (Campanian; Upper Cretaceous). **E:** Hindlimb of *P. dolichodirus* (Lower Jurassic). **F:** Hindlimb of *Cryptocleidus eurymerus* (Middle Jurassic). **G:** Hindlimb of *A. pambertoni* (Campanian; Upper Cretaceous). For abbreviations, see Figure 2. (Illustrations modified from Caldwell [1997b]).

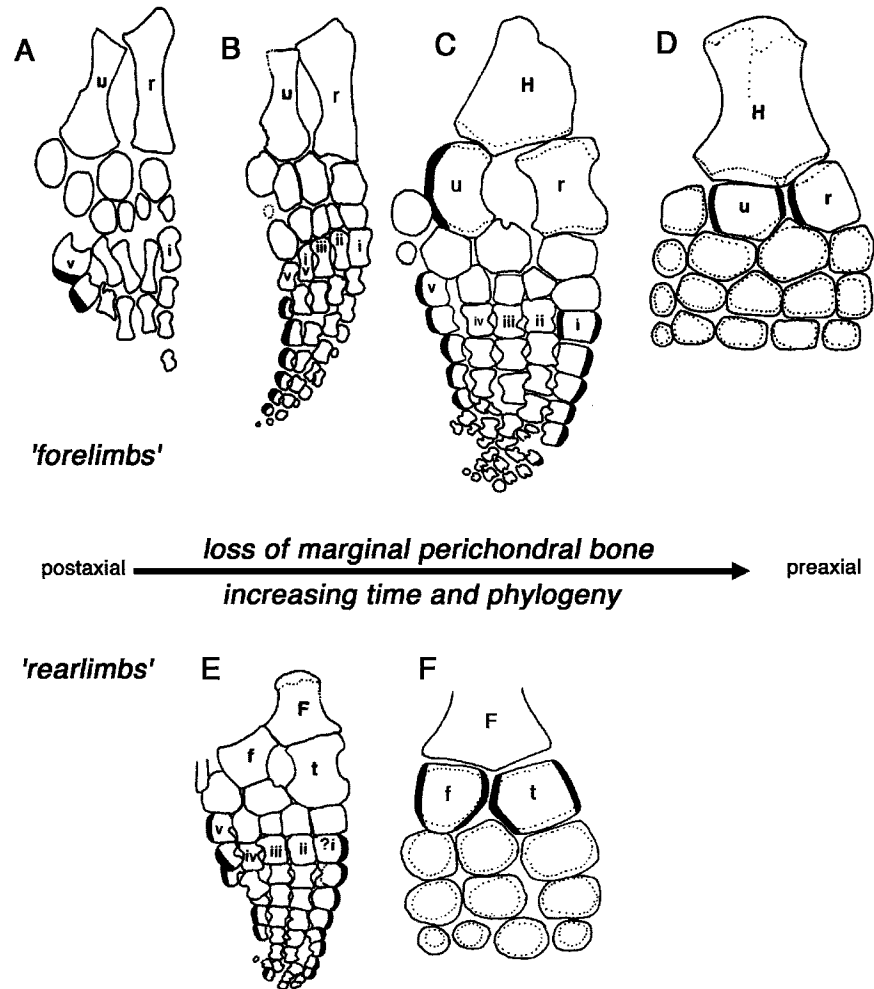


Fig. 8. Limbs of ichthyosaurs showing phylogenetic patterns of postaxial to preaxial loss of perichondral bone. Blackened regions indicate where perichondral bone has been lost from the margins of an element that possessed that tissue in terrestrial neodiapsids. In later ichthyosaurs, all elements distal to those with shaded margins have lost perichondral bone. **A:** Forelimb of *Grippia* sp. (Scythian; Lower Triassic). **B:** Forelimb of

*Parvinatorator wapitiensis* (Lower to Middle Triassic). **C:** Forelimb of *Mixosaurus cornelianus* (Anisian-Ladinian; Middle Triassic). **D:** Forelimb of *Ophthalmosaurus icenicus* (Callovian; Upper Jurassic). **E:** Hindlimb of *M. cornelianus* (Anisian-Ladinian; Middle Triassic). **F:** Hindlimb of *O. icenicus* (Callovian; Upper Jurassic). For abbreviations, see legend for Figure 2. Illustrations modified from Caldwell [1997b].

(Fig. 7C, D, F, and G) show perichondral bone loss from only a few of the most proximal and postaxial phalanges; perichondral bone is usually retained along at least one margin.

What is interesting about the evolution of sauropterygian limbs, in light of perichondral bone loss, is that this phenomenon only arises in plesiosaurs (derived sauropterygians). In the primitive plesiosaurian *Pistosaurus*, there is no evidence of modifications to perichondral bone on long bones. When modification of perichondral development is obvious in plesiosaurs, it appears along the postaxial margins of the ulna and fibula, but not the metapodials (compare with ichthyosaurs; Fig. 8). Phylogenetic loss of perichondral bone in the Plesiosauroidea and Pliosauroida is largely restricted to the radius/ulna and tibia/fibula. The result is limb bones that are ichthyosaur-like (compressed and rounded as seen in *Alzadasaurus*; Fig. 7D and G). *Cryptoclidus* shows an intermediate stage where the

only remaining perichondral margin is found on the preaxial margin of the radius (Fig. 7C and F).

### Ichthyosaurs: Limb Osteology and Perichondral Bone Loss

The phylogeny of perichondral bone loss from long bone element margins is most exaggerated in Jurassic ichthyosaurs and can be considered a feature shared by three ichthyosaur families: Ichthyosauridae, Stenopterygiidae, and Leptopterygiidae.

Earlier ichthyosaurs, of Triassic age, show varying degrees of perichondral bone loss from the long bone elements of the digits (Fig. 8A and B). *Mixosaurus* (Fig. 8C and F) shows the earliest loss of perichondral bone from the ulna, though there is some possibility that similar loss affected the postaxial margin of the ulna in *Cymbospondylus* [Sander, 1989]. Subsequent evolution, leading to continued loss of perichondral bone, affects

the margins of the remaining upper limb bones, with the exception of the humerus, and the margins and morphologies of the remaining digits 4 through 2.

What cannot yet be ascertained is the sequence of bone loss in digits 4 through 2, i.e., whether or not the sequence continued from 1 through to 4, or the reverse. The outgroup condition, and therefore the polarity of loss leading to the condition in Jurassic ichthyosaurs, cannot be determined from existing phylogenies of Triassic and Jurassic taxa. However, it is concluded from the sequence and pattern of perichondral bone loss in the digits that alterations to limb morphology occurred by perturbing development in at least three ways: deletion to the end of the sequence, i.e., loss of perichondral bone from the first digit, or at the extremes, loss of the first, and successive alterations to digits 2, 3, and 4; modifications at the start of development, i.e., perichondral bone loss from proximal and postaxial elements such as the ulna; and loss of perichondral bone from the fifth digit, or at the extremes, loss of the digit.

It is significant that the first and fifth digits show evolutionary modifications prior to the onset of modifications (ontogenetic and/or phylogenetic) in other distal limb bones. The first digit is the last element to appear as a chondrogenic [Shubin and Alberch, 1986] and osteogenic center [Rieppel, 1992a, 1992b; Caldwell, 1994]. The fifth digit does not chondrify or ossify in sequence with elements of the digital arch. Why the loss of perichondral bone occurred in the digits prior to loss in epipodial elements is unknown. This is not the condition observed in plesiosaurs.

In general, perichondral bone loss affected the limbs of ichthyosaurs in a postaxial-to-preaxial direction across the limb and mesopodium. This pattern is consistent with patterns of ossification noted for terrestrial neodiapsids [Caldwell, 1994], and for patterns of chondrogenesis from which the postaxial position of the primary axis of limb development was recognized [Shubin and Alberch, 1986].

## FOSSIL MARINE CROCODILES

### Limb Osteology and Perichondral Bone Loss

Perichondral bone is absent from the radius, ulna, and first metacarpal in the paddle-like forelimb of the fossil marine metriorhynchid crocodile *Geosaurus* [Fraas, 1902; Caldwell, 1997c]. *Geosaurus* and other metriorhynchid crocodiles are crocodylian archosaurs included within the clade Archosauromorpha (Fig. 1).

Perichondral bone loss in *Geosaurus* (Fig. 9B) is convergent with the loss observed in ichthyosaurs and plesiosaurs (Fig. 1). What is unique about the *Geosaurus* condition is the outgroup state of terrestrial crocodylians from which it is derived [Parrish, 1993]. Fossil and extant crocodylians have perichondral bone on the margins of forelimb mesopodials: the radiale and ulnare (Fig. 9A). Perichondral bone is also present on the epipodials and metapodials. However, the presence of perichondral bone on the proximal bones of the mesopodium is unique to archosaurs among diapsids.

Therefore, perichondral bone loss in *Geosaurus* includes not only the radius, ulna, and first metacarpal,

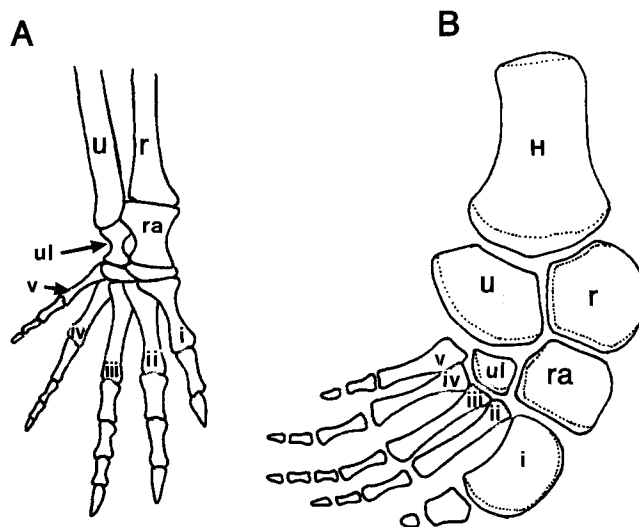


Fig. 9. Forelimbs of fossil and modern crocodylians. **A:** *Alligator* (modern). **B:** *Geosaurus* (Upper Jurassic). For abbreviations, see legend for Figure 2. Illustrations modified from Caldwell [1997b].

but also the radiale and ulnare. This is a very different state than that observed in ichthyosaurs and plesiosaurs. *Geosaurus* limbs show a very unique derived condition from an unusual state of perichondral ossification in terrestrial crocodylians. The metriorhynchid condition deserves special attention relative to other crocodylians, to other archosaurs (birds and dinosaurs), and, finally, to other archosauromorphs and neodiapsids.

### SUMMARY: PERICHONDRAL BONE LOSS

As a transformation series, the taxic distribution of perichondral bone loss in the aquatic diapsids reveals a pattern of loss that closely follows the axes and sequences of limb ossification/development in other fossil and extant terrestrial diapsids [Rieppel, 1992a, 1992b; Caldwell, 1994]. In plesiosaurs, initiation of loss begins on postaxial epipodial elements, usually on the postaxial margins of those elements, and spreads preaxially and distally across the epipodium and onto some postaxial metapodials through ontogeny and phylogeny. In ichthyosaurs, loss of perichondral bone is initiated on the shafts of the first and fifth digits. This is followed by loss from the postaxial epipodials and across the epipodium in a preaxial direction. Loss continues across the metapodium and down the length of the hand and foot, until all elements distal to the humerus develop without a bony perichondral sheath.

### DEVELOPMENT, EVOLUTION, AND GENETICS

Aquatically adapted diapsid limbs present an evolutionary mosaic of morphological modifications as compared to the terrestrial limb of the basal diapsid *Hovasaurus*. For example, mosasaurs (Fig. 3) show limited hyperphalangy, a decrease in relative size of the propodials, an increase in the size of the manus/pes,

and a reduction in the number of tarsals. Advanced ichthyosaurs evolve the extremes of hyperphalangy and hyperdactyly, radically alter the morphogenesis of perichondral bone on all elements distal to the propodials, decrease the size of the propodials, and increase the size of the manus and pes. Plesiosaurs and sauropterygians evolve limb skeletons that are intermediate in their modifications as compared to mosasaurs and ichthyosaurs. In short, the evolution of aquatically adapted limb morphologies among diapsid reptiles has involved many different modifications to many different parts of the limb. Therefore, if phenotype has been modified in differing limb regions over evolution, it indicates very clearly that genotype, that is, the pattern controlling gene systems that build limbs, has also been differentially modified both within the limb of a species and between the limbs of species.

Current research on limb developmental genetics has demonstrated the importance of homeobox gene complexes to limb pattern formation. The individual and overlapping expression domains of a number of genes in the *HoxA11–13* and *HoxD11–13* complexes are necessary for the formation and organization of the distal regions of the limb bud (epipodials through to metapodials) [Zakany et al., 1997]. Mouse mutants misexpressing these genes present modified limb skeleton morphologies ranging from epipodial truncations or oligodactyly (absence of expression products) to extremely elongated digital elements (increased amount of expression products). Misexpression or absence of other genes associated with limb patterning, such as Sonic Hedgehog (*Shh*) or Indian Hedgehog (*Ihh*), results in preaxial polydactyly [Yang et al., 1998; Chiang et al., 2001]. A scheme proposed by Zakany et al. [1997] also involved Hox gene complexes in the development of both oligo- and polydactylous limbs. Expression of only *HoxA*, but not *HoxD*, in the distal region of the limb bud produced polydactylous limbs, while expression of *HoxD* only is modeled to produce an oligodactylous limb with elongate digital elements and digits.

It is interesting to consider a model of developmental evolution in marine diapsids by referring to several of the proximate mechanisms of morphogenesis elucidated by modern developmental biology. Hyperdactyly (polydactyly) in ichthyosaurs may very well have evolved from the evolutionary fixation of misexpressed *Shh* or *Ihh* in association with the isolated expression of *HoxA11–13*. Hyperphalangeal conditions might be explained by heterochronic alterations to the length of time that expression products of normal genes are active; hyperphalangy may also be a dose-dependent phenomenon. Likewise, the reduction of ossified elements in mosasaur paddles (loss of the fifth digit) might reflect prolonged *HoxD* expression in the absence of *HoxA*. Other modifications to the limb skeleton of aquatic diapsids remain problematic in terms of their developmental genetic or proximate causes (e.g., modified perichondral chondrocyte formation). However, in the context of a phylogenetic hypothesis (Fig. 1), patterns of developmental evolution emerge from the wealth of available paleontological and neontological data on limb osteology and ontogeny.

## CONCLUSION

From Owen's [1849] platonistic examination of the essential "nature of limbs" to the typological-transformist search for pattern-controlling genes and structural homologies, researchers have been fascinated by a simple empirical observation: commonality of limb organization and structure. The limb morphologies of tetrapods that made the fin-to-limb-to-fin transition are no exception. As Owen [1849] noted, the basic "essentialist" elements of the limb remain, as do the highly conserved gene systems controlling limb morphogenesis.

It is this latter reality that makes the study of adaptive evolution so intriguing. Aquatic adaptation and limb evolution revolves around independent and constrained morphological and developmental solutions to an equally constrained problem: efficient locomotion and adaptive fitness in watery environments. The question arises as to what constrains the evolution of an organ system and why gene complexes are so highly conserved? Why are hopeful monsters a lovely idea but seemingly nonexistent on close observation? Whatever the ultimate evolutionary answer may be, it is abundantly clear from genetics and palaeontology that at some level, any one individual of a species is limited by its inheritance; it is unlikely that I will ever sprout wings, as I do not currently have them and my mother, her mother, and our collective early ancestors did not have them. Were organisms not somewhat constrained by their genealogical inheritance (genotype and the resultant possible phenotypes), then the recovery of phylogenetic history by reference to morphology and molecules would be impossible, as would the understanding of evolutionary morphogenesis and development.

It is this form of logic, rationale, and method that I have applied in this analysis of aquatic diapsid limb evolution. These highly modified, highly adapted swimming reptiles inherited the genes and morphologies of their 260-million-year-old terrestrial ancestors. Within the parameters of that genetic and phenotypic information set, that is, Owen's essential features of the tetrapod limb, mosasaurs, crocodiles, ichthyosaurs, and plesiosaurs became secondarily aquatic and evolved aquatically adapted limbs. These reptiles reconstructed the morphogenetic endpoint of an ancient limb system through as yet poorly understood temporal and spatial modifications to their developmental genetic pathways.

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