FUNCTION AND PHYLOGENY IN SAUROPTERYGIAN (DIAPSIDA) EVOLUTION

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ABSTRACT. The Sauropterygia includes the Pachypleurosauria and Nothosauriformes. The nothosauriforms are here defined as the Plesiosauria, Placodontia, and relatively plesiomorphic taxa historically known as “nothosaurs.” The Suborder Nothosauria is paraphyletic and no longer tenable. Placodonts possess numerous autopomorphies which conceivably developed following the pachypleurosaur-nothosauriform divergence and are related to their aberrant, bottom-dwelling habits. The functional evolution of the Sauropterygia was dominated by locomotor adaptations for an aqueous environment. The physics of buoyancy and hydrodynamics were the primary mitigating factors. Feeding strategy played a subordinate role in evolutionary direction. Ancestral history of the clade constrained most of its representatives to limb-dominated (paraxial) propulsion, after this format was adopted by early sauropterygians. The forelimbs at least, were probably used in symmetrical, paired strokes by all members of the group. “Nothosaurid” locomotion, deriving drag and lift thrust from the limbs, was functionally antecedent to the plesiosaur swimming style. Plesiosaurs used all four limbs, perhaps simultaneously, to generate a large component of lift-based thrust. For reptiles, this was an unusual functional response to a secondary invasion of the sea.

INTRODUCTION

The groups of fossil marine reptiles comprising the Sauropterygia Owen, 1860, have long been known and yet remain poorly understood. The first sauropterygians to be recognized and described (as in Cope, 1821; Meyer, 1839; Owen, 1854, 1860) were members of the Plesiosauria de Blainville, 1835. This group spanned much of the Mesozoic, was globally distributed, and includes spectacular long- and short-necked swimming reptiles. All plesiosaurs are characterized by two pairs of highly modified, hyperphalangic limbs variously described as “paddles,” “flippers,” or “wings” (fig. 1A). The latter name reflects the widely held belief that the limb-dominated (paraxial) propulsion of these animals was subaqueous “flight” (Brown, 1981; Frey and Riess, 1982; Halstead, 1989; Massare, 1988; Robinson, 1975; Tarsitano and Riess, 1982; Taylor, 1981).

Certain less derived Triassic reptiles, sometimes considered ancestral to plesiosaurs, are now known to be an unnatural, paraphyletic assemblage of plesiomorphic sauropterygians (Rieppel, 1987a, 1989; Storrs, 1990, 1991; Sue, 1987a; Taylor, 1989; Tschanz, 1989). These animals, primarily from the Old World, once formed the Suborder Nothosauria Seeley, 1882. The Pachypleurosauria Sanz, 1980, however,

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is a natural clade and includes the least derived sauropterygians known
Pachypleurosaurids were generally small (up to 1 m in length), lacertiform
inhabitants of paralic (marginal marine) realms, and exhibited relatively
subtle aquatic adaptations. Other "nothosaur"-grade sauropterygians
were often larger but retained the primitive lacertiform habitus (fig. 1B).
All "nothosaurs" apparently represent a similarly constrained functional
response to reinvasion of the aquatic environment. Most "nothosaurs," as
well as plesiosaurs, were probably piscivorous, although cephalopods
may also have been an important part of some diets (Halstead, 1989;
The Placodontia Zittel, 1890 appear related to undisputed sau-
ropterygians but pursued a divergent functional strategy from those of
other forms (Storrs, 1990, 1991). The placodonts, all of Triassic Old
World distribution, probably dwelt largely on the nearshore marine
bottom, feeding on benthic invertebrates such as molluscs (Colbert,
1967, 1980; Peyer and Kuhn-Schnyder, 1955; Pinna and Nosotti, 1989; Romer,
1966). Many have a "shell" of dermal armor, and most possess a battery
of crushing teeth on the palate. Like plesiosaurs, they are generally large
(over 1 m in length), and advanced forms often exhibit moderately
specialized limbs (fig. 1C).
While numerous sauropterygian genera have long been recognized,
their systematic relationships are only now beginning to be clarified by
the use of rigorous phylogenetic analysis (Riepe1, 1987a, 1989; Schmidt,
This clarification of phylogeny is a necessary precursor to any understand-
ing of functional evolution. The presumed origin of sauropterygians in
the Permian, and their diversification in the Mesozoic, was probably a
sequence of varied adaptive strategies to different ecological opportuni-
ties. The key to this sequence was their secondary invasion of aquatic
environments. Knowledge of intragroup relationships can suggest to
what degree convergence, divergence, and parallelisms existed in the
functional responses of sauropterygians. It also allows evaluation of the
importance of ancestral history relative to functional pressure in clade
evolution. For example, the group's overall functional similarity appears
related to a single solution for exploiting the aqueous environment,
developed at a very early point in its history. Only later was this solution
variously elaborated on with the partitioning of old, or invasion of new,
ecological niches.
After a discussion of sauropterygian phylogeny, this essay will exam-
ine the possible factors that may have influenced the evolution of sau-
ropterygian reptiles. In particular, the functional morphology of various

Fig. 1. Typical marine reptile types of the clade Sauropterygia. (A) The plesiosaur
ThaumatOSaurus in ventral aspect, approx 3 m long; gastralia and limb girdles evident (after
Fraas, 1910); (B) the plesiomorphic "nothosaurid" Corosaurus in dorsal aspect, approx
1.5 m long (after Storrs, 1991); (C) the placodont Placochelys in dorsal aspect, approx 2.5 m
long; carapace prominent (after Jaccel, 1907).
sauropterygians and the role of functional constraint as a driving factor in their locomotory evolution will be considered. How the constraints of ancestry and development have potentially influenced this evolution will also be discussed briefly.

SAUROPTERYGAN RELATIONSHIPS

It is now believed that the sauropterygians comprise a monophyletic clade which had its origin among primitive terrestrial diapsids. The move to an aquatic, ultimately marine, habitat for the group must therefore represent a secondary invasion of the sea. Romer (1974) voiced reservations that this was the case but, as he himself noted, there was virtually no consensus on the group's ancestry at the time of his writing. The works of Jackel (1910), Kuhn-Schnyder (1962, 1963a, 1967, 1980), and Carroll (1981) have now, however, indicated the likelihood of sauropterygian descent from "eosuchian"-grade, diapsid reptiles. Younginiformes represent a useful outgroup for analysis of sauropterygian relationships (Rieppel, 1987a; Storrs, 1991; Sues, 1987a). Sues (1987a) supported the inclusion of Sauropterygia within Benton's (1985) Neodiapsida and Lepidosauromorpha.

Carroll (1981) invoked several apparent synapomorphies of Cladiosaurus, a small aquatic "eosuchian" from the Upper Permian of Madagascar, and sauropterygians to link the two taxa. These include the reduction of the suborbital and interpterygoid fenestrae, the loss of the transverse pterygoidal flange, the apparent loss of the subtropical arcade and coincident reduction of both the jugal and quadratojugal, an unossified sternum, reduced propodial epicondyles, and a transformed (to a notch) ectepicondylar foramen. These characters have caused some workers (Rieppel, 1987a; Schmidt, 1987; Storrs, 1991; Tschanz, 1989) to consider Cladiosaurus to be a plesiomorphic sister taxon to the Sauropterygia. Benton (1985) and Evans (1988) acknowledged the diapsid affinities of Cladiosaurus but placed it outside Benton's (1985) Archosauromorpha/Lepidosauromorpha dichotomy. They did not, however, examine sauropterygian relationships. Rieppel (1989) concluded that Cladiosaurus is the plesiomorphic sister to sauropterygians plus Archosauromorpha and Lepidosauromorpha. It is probable, therefore, that Cladiosaurus represents a suitable structural analog for the type of animal that gave rise to the Sauropertygia.

The stratigraphic position of Cladiosaurus and those of primitive neodiapsids such as younginiforms indicate a minimum time of divergence for the sauropterygian lineage as Upper Permian, although early sauropterygians are poorly represented by fossil material (see Storrs, 1991). By definition, clades originate at least by the earliest appearance of a sister group member. Unequivocal sauropterygian synapomorphies are a single temporal fenestra (homologous to the upper opening of diapsids), no supratemporal, postparietal, tabular, or lachral; retracted nares, a large retroarticular process on the mandible, no trunk vertebral intercentra, three or more sacral vertebrae, no sternum, a
divided scapulocoracoid, pectoral and thyroid fenestration, and most remarkably, a scapula that lies superficially to the clavicle (Storrs, 1991).

The most “primitive,” but not the earliest, confirmed sauropterygians are the Pachypleurosauria. They are represented by numerous genera (such as Neusticosaurus, Dactylosaurus, and Keichousaurus) from the Middle Triassic Tethyan province, particularly Europe and China, which form a natural clade at the base of the Sauropterygia (fig. 2). Pachypleu-

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**Fig. 2.** Cladogram of hypothetical sauropterygian relationships depicting positions of representative taxa and outgroups (modified from Storrs, 1991). *Cladosaurus* is used as the sister taxon of the Sauropterygia. Several presumably valid pachypleurosaur and “nothosaurid” genera are not included due to insufficient data for these forms. See Storrs (1991) for a discussion of the status of all described “nothosaur” genera. * = metataxon.
rosaurs are characterized by the loss of the ectopterygoid (Rieppel, 1989). Other significant features may include the presence of an impedance-matching middle ear (indicated by a ventral quadrate projection for suspension of the tympanum), a trend for supratemporal fenestra reduct- 

tion, a general "pachyostotic" thickening of the ribs, and a narrowing of the distal ends of the sacral costae (Rieppel, 1989; Storrs, 1991). That all have upper temporal openings smaller than the orbit does not define the group (as in von Huene, 1956; Peyer, 1934; Saint-Seine, 1955; Schmidt, 1987), for this is a plesiomorphic characteristic.

The remaining "nothosaurs" (Nothosauridae Baur, 1889 (in Zittel, 1890), now discarded) display a variety of synapomorphies linking them in hierarchical fashion with the plesiosaurs (Rieppel, 1989; Storrs, 1991; Sues, 1987a). This "nothosaurian" assemblage (for example, Simosaurus, Nothosaurus, and Lariosaurus) undoubtedly contains the nearest sister taxon to the Plesiosauria. "Nothosaurids" are known from North America, Europe, Africa, and Asia and range from Scythian to Carnian in age (fig. 3). Together with placodonts, the "nothosaurids" and plesiosaurs form a clade designated Nothosauriformes by Storrs (1991). Tschanz's (1989) Eusauroptrygia is similar but excludes the placodonts. The nothosauriforms share the presence of a large supratemporal fenestra, a posterolateral process of the frontal, an elongate jugal extending caudad from the orbit, a robust mandibular symphysis, platycoelous vertebrae, and a strongly curved humerus (reversed in plesiosaurs), all of which are derived characters (Storrs, 1991). Virtually all nothosauriforms are of relatively large size. This is a significant distinction when contrasted with the average size of pachypleurosaurs. Rieppel (1989), Storrs (1990, 1991), Sues (1987a), and Tschanz (1989) have shown that large "notho-
saurids" and pachypleurosaurs do not form a single, monophyletic group and that the paraphyletic Nothosauria must be abandoned. Tschanz (1989) adopted a restricted concept of the Nothosauria, but this is perhaps unwise in light of the strong historical connotations of this taxonomic name.

The aberrant Placodontia (for example, Placodus, Cyamodus, and Paraplacodus) are presumed to represent a divergent lineage of Triassic nothosauriforms (Storrs, 1990, 1991). They are, however, notable for possession of procumbent, incisiform anterior dentition; molariform posterior and palatal dentition, normally separate pterygoids, a prominent coronoid process, possible hyposphene/hypantrum vertebral articulations, and a robust body frequently armored with dermal ossifications (Drevermann, 1933; Owen, 1858; Peyer and Kuhn-Schnyder, 1955; Storrs, 1991; Sues, 1987b). These autapomorphies say nothing about their higher order relationships and may have arisen following the establishment of the nothosauriform clade. Relationships within the seemingly monophyletic placodonts have not been determined. Placodont anatomy, taxonomy, and systematics are poorly understood, and the group requires substantially more study.

The plesiosaurs (for example, Plesiosaurus, Alzadasaurus, and Liopleurodon) display the derived features of their highly transformed limbs,
generally elongate necks and stout thoraces, and (with the one known exception of *Brachauchenius*) foramina subcentralia in their vertebrae. Plesiosaurs seemingly reverse the sauropterygian derivations of a solid palate and a straight clavicular arch with a sharp anterolateral "corner" (Storrs, 1991). Here too, relationships within the monophyletic Plesiosauria have yet to be rigorously examined. The traditional Plesiosauroidae (Gray, 1825) Welles, 1943 and Pliosauroidea (Seeley, 1874) Welles, 1943 (long- and short-necked forms, respectively) may or may not be valid monophyletic groups.

**EVOLUTIONARY CONSTRAINTS**

In addition to the limitations imposed upon the direction of clade evolution by environmental conditions and adaptive selection, other constraining factors also play a significant role in the phylogenies of...
organisms (Alberch, 1980; Gould, 1980; Maynard Smith and others, 1985; Seilacher, 1970). Carroll (1985) examined the various roles of ancestry, development, and function in the evolutionary direction of secondarily aquatic diapsids, including the sauropterygians. In many ways, these factors are complexly interrelated and hierarchical. Carroll’s (1985) study of sauropterygians, however, was necessarily limited by the overall breadth of his topic, that is, all aquatic diapsid reptiles. Which constraints have played a role in sauropterygian evolution, and what has been their relative importance?

Constraints of ancestry in a clade limit the available solutions to an ecological problem. Its constituent organisms must work with the constraint of preexisting anatomy from which to build new morphotypes. For example, secondarily aquatic marine mammals are constrained by the evolutionary history of their terrestrial mammalian forebears to a vertically oriented plane of undulation. Thus, whale vertebrae flex primarily up and down relative to each other and scarcely at all side to side. Even aquatic mammals using paraxial propulsion (limb-dominated locomotion), such as sea lions, have this constraint in the primary direction of vertebral column flexure (that is, vertical plane of movement). Conversely, spinal undulation in lower tetrapods is invariably accomplished in the horizontal plane because of the lateral undulatory history of plesiomorphic sister groups (for example, Rhipidistia). Ancestral constraints undoubtedly also influenced the descent of the Sauropterygia, a discussion of which appears below.

Constraint of development similarly restricts an organism’s morphology to a pattern dictated by the developmental history (embryological and postembryological) of the individual. Numerous types of developmental influences may affect a lineage’s history (Maynard Smith, and others, 1985). To the extent that developmental constraints are inherited, they are reminiscent of ancestry. A unique effect of development can be seen, however, in the limited structural types which may be produced in organisms by heterochrony (changed developmental timing and/or rates). Domestic dog breeds, for example, dramatically illustrate the results of artificially selected, neotenic development (Copping and Coppinger, 1982; Coppinger and Smith, 1983; Wayne, 1986). Breeder selection for juvenile personality attributes also consistently produces mature individuals with large heads and floppy ears as a consequence. These are not characters known to have existed in any adult ancestor but rather are found in all juveniles of the canine clade. They are characters linked by the developmental program of dogs to the artificially selected characters. Selection is not acting directly upon the former. Human evolution may also have included a major neotenic component, as adult humans exhibit notable phenotypic similarities to juvenile chimpanzees, our closest extant sister taxon (Gould, 1977; Montagu, 1981; Vrba, Denton, and Prentice, 1989) [although Shea (1988) objects to certain aspects of this idea]. [Maynard Smith and others (1985) caution that comparison of allometric relationships can not always rule out the possibility of adaptive (selective) value for a trait.]
Typically, heterochrony acts in mosaic fashion, as do many other important evolutionary forces. While heterochronic development is undoubtedly a major source of lineage change (see McKinney, 1988), ontogenetic history, particularly at the embryonic level, is exceedingly difficult to document among fossils. Brief discussions of sauropterygian heterochrony have been presented by Brown (1981), Carroll (1988), Carroll and Gaskill (1985), McNamara (1988), Storrds (1991), and Sues (1987a). For example, the similarity of juvenile sauropterygian pectoral girdles and propodials to the adult conditions in relatively plesiomorphic taxa, and the progressive retention of skeletal cartilage in most lineages are notable examples. The description by Andrews (1910) of ontogenetic stages for the plesiosaur Cryptoclidus (Cryptocleidus) shows that the pectoral girdle elements are relatively small in juveniles and that the longitudinal pectoral bar of the adult has not yet formed. In these and other regards, the juvenile girdle is much like those of adult “nothosaurs” and placodonts (fig. 4). This may be an example of peramorphosis (addition to form) in the plesiosaur lineage. Similarly, sauropterygian propodials, particularly the humeri, show progressive additions in shape (that is, peramorphosis) to the apparent ancestral condition. Thus juvenile

![Diagram of sauropterygian pectoral girdles](image)

Fig. 4. Sauropterygian pectoral girdles in ventral aspect illustrating shape and proportional variation. Not to scale. (A) Juvenile of the plesiosaur Cryptoclidus (after Andrews, 1910); (B) the pachypleurosaur Neusticosaurus (after Carroll and Gaskill, 1985); (C) the placodont Placodus (after Drevermann, 1933); (D) the “nothosaurid” Ceresiosaurus (after Kuhn-Schnyder, 1963b), (E) adult of the plesiosaur Cryptoclidus (after Andrews, 1910).
"nothosaur," placodont, and plesiosaur humeri resemble one another, as each resembles the adult "eosuchian" humerus. "Advanced" plesiosaurs and placodonts substantially modify the primitive condition as adults. Paedomorphosis (the retention of ancestral juvenile characters in the adult) may exist in plesiosaurs, in as much as some advanced genera (such as *Alzadasaurus*) seemingly reduce limb girdle ossification relative to plesiomorphic taxa like *Plesiosaurus*. Likewise, certain "nothosaur" genera (like *Lariosaurus* and *Serpianosaurus*) exhibit marked reductions in the number of ossifications in the carpus and tarsus. The condition of reduced ossification is widespread among aquatic reptiles and has been referred to as "aquatic neoteny" by de Ricqlès (1975) and Rieppel (1987b).

Functional constraints are placed on the evolution of groups by the physical parameters of an organism's operation and environment. Only certain structural solutions are functionally viable under a particular set of environmental conditions. No bird can fly, for instance, unless the aerodynamic qualities of its wings and the strong, yet lightweight configuration of its skeleton, allow enough lift to counter gravity. Physical laws constrain animals that fly to specific shapes and volume-to-mass ratios, to which this activity is subordinate. Birds, bats, insects, and pterosaurs fly with nonhomologous structures, all of which, however, conform to a generally similar pattern. Swimming animals meet with similar functional constraints, but the fluid medium of their environment (water) is significantly denser than air. The basic relationships of lift, drag, gravity, and bouyancy, as they affect swimming bodies on the scale of vertebrates, are summarized in figure 5. How the various sauropthygian groups have reacted to functional pressures, and, indeed, how their responses vary, seems to have been important in their evolution.

Carroll (1985) showed that aquatic diapsids were not severely constrained as a group by the effects of ancestral history, because related forms fall into different structural categories. Similar aquatic adaptations, furthermore, have evolved independently on several occasions. Carroll's (1985) categories, therefore, often contain members of several higher order taxonomic divisions. The categories themselves, however, are not rigorously defined. Nevertheless, Carroll (1985) suggests that each is distinct, they do not form part of an anatomical spectrum, and that relatively few intermediate stages exist among aquatic diapsids. The implication is that constraints of similar habits and function produced structural convergences in many relatively unrelated clades.

In a broader sense than size or shape, however, ancestry constrains most secondarily aquatic tetrapod swimmers to axial (undulatory) locomotion (Webb and Blake, 1985). The relatively few tetrapods that swim primarily with their limbs do so because of other predominant factors. Penguins, for example, are constrained by ancestral bird history. They possess a stiff thorax, short tail, and large wings which have merely been adapted for use in water. Sea turtles also rely for swimming upon forelimb strokes which are symmetrically applied, but only because their
shell (an ancestral development) prevents body flexion. Paraxial propulsion is, therefore, an obvious necessity. The historical constraint of axial locomotion was also overcome in the Sauropetergia, for plesiosaurs were obviously paraxial swimmers, as discussed below. Other sauropetergians may likewise have favored their limbs over sinusoidal undulations of the trunk and tail. Why should this be so? The ancestral and functional aspects of sauropetergian locomotory evolution thus deserve special attention.

FUNCTIONAL MORPHOLOGY OF THE SAUROPTERYGIA

Most sauropetergians (some placodonts excluded) were greatly streamlined to reduce total drag during swimming. Few other conclusions regarding sauropetergian function can be so readily made. Many recent workers have examined the functional morphology of various sauropetergian groups (Alexander, 1989; Carroll and Gaskill, 1985; Frey and Riess, 1982; Godfrey, 1984; Halstead, 1989; Massare, 1988; Nicholls and Russell, 1991; Pinna and Nosotti, 1989; Robinson, 1975, 1977; Sanz, 1980; Schmidt, 1984, 1986; Storrs, 1988, 1991; Tarsitano and Riess,
1982; Taylor, 1986). However, these discussions have usually focused on the most transformed and spectacular members of the clade, the plesiosaurs. As indicated by their highly elaborated, hyperphalangic, limbs; supernumerary ossifications adjoining the epipodials and mesopodials (incipient polydactyly?), loss of intralimb flexibility, increased thoracic rigidity, frequent lengthening of the neck, and shortening of the tail, locomotion by these marine reptiles was limb-dominated (paraxial). Not so obvious is the mechanism by which the limbs provided thrust. In other words, was the limb-generated thrust of plesiosaurs drag- or lift-based?

Historically, the analogy of plesiosaurs using their limbs as oars or paddles, that is, drag-based propulsors, was in great favor (Halstead, 1969; Newman and Tarlo, 1967; Romer, 1966; Tarlo, 1957, 1959b; Watson, 1924, 1951; Williston, 1914). The limbs were thought to displace volumes of water with broad sweeps back toward the body. With drag harnessed in this manner, an equal and opposite reaction would propel the animal forward. A feathered return stroke provided little or no additional thrust, and thus overall progression was discontinuous. Numerous types of swimming vertebrates use drag to create thrust, whether produced by the action of the limbs or by undulation of the tail (Braun and Reif, 1985; Gray, 1968; Webb and Blake, 1985). A strictly drag-based, fore and aft, propulsive stroke of the plesiosaur limb, however, is not strongly supported by anatomical or functional evidence, especially the distally tapering limbs and their hydrofoil shape. A hydrofoil is the most efficient structure for the creation of lift in water (Rayner, 1985). Neither would the glenoid and acetabulum of plesiosaurs easily allow the limbs to be held with their broadest surfaces normal to movement (Nicholls and Russell, 1991).

It was, furthermore, often imagined that long-necked plesiosaurs spent much of their time rowing about the surface of the sea using swan-like necks as “hunting platforms” from which sharp eyes could detect passing fish (Conybeare, 1824; Fraas, 1910; Koken, 1893). This latter idea is now regarded as fanciful [see Shuler, 1950, and Williston, 1914, for historical discussions]. Plesiosaur necks lacked the flexibility required for them to be used this way. The faces of the centra were essentially flat, and the neural arches and spines left little room for movement. Furthermore, the presence of gastroliths (“stomach stones”) in most, if not all, elasmosaurs, for example, suggests that ballast (Darby and Ojakangas, 1980) was needed to maintain a neutrally buoyant position within the water column. Modern crocodiles use stomach stones as an important buoyancy compensator (Cott, 1961), and numerous other modern swimmers also ingest stones (M. A. Taylor, in preparation). This is not to assert, however, that gastroliths functioned only in this manner. A dual purpose scenario for plesosaur gastroliths, perhaps as grinding aids to digestion, may be imagined. Interestingly, the short-necked, large-headed pliosaurs (whether monophyletic or not), with their probably different lifestyle from elasmosaurs, have rarely been reported with any significant number of gastroliths. This may be related to different functional regimes for long- and short-necked plesiosaurs.
Pliosaur hindlimbs are larger than the forelimbo, while the reverse is true in elasmosaurs, and each group had differently proportioned propodials and limb girdles elements (Halstead, 1989). The different tooth types in some small and large headed forms also suggest distinct feeding habits (Massare, 1987). Williston (1906) briefly noted the association of "pebbles" (gastroliths) with the polycotylid pliosaurs Polycotylus and Trinacromerum, but this has not been more recently confirmed. In fact, many pliosaurs certainly lacked gastroliths as, indeed, Williston (1903) suggested. Williston (1906) may have been misled, because "Polycotylus" ischiadicus Williston, 1903, for example, was later identified as an elasmosaur (Williston, 1906; Storrs, in press; Welles, 1943). In any event, bouyancy compensating stones or not, few obligatory vertebrate swimmers spend much of their time at the water's surface. Most workers believe that pliosaurs were restricted to the water column for most of their activity.

More recently, a proposal by Robinson (1975) that pliosaurs were subaqueous "fliers," like penguins (Baudinette and Gill, 1985; Clark and Bemis, 1979) and sea turtles (Walker, 1971, 1974; Zangerl, 1953), has gained widespread acceptance (Brown, 1981; Frey and Riess, 1982; Halstead, 1989; Robinson, 1977; Tarsitano and Riess, 1982; Taylor, 1981). This hypothesis envisions the limbs of pliosaurs as "wings," providing lift-based thrust through the hydrofoil action of continuous, up and down, figure-eight style, propulsive strokes. Lift is generated by the limb through asymmetry of the "wing" and its inclination relative to its movement through the water (see fig. 5). Naturally, the use of four limbs rather than two is proposed for pliosaur "flight." This is essentially a reworking of an idea set forth by Fraas (1905) and accepted by Abel (1908, 1912). Kurtén (1968) also suggested that pliosaurs must have "flown" subaquously. Tarlo (1957) implied the use of lift-based propulsive strokes for only the forelimbs of pliosaurs. Lift-based thrust through "wing"-like movement is suggested by the hydrofoil shape of the limbs and especially their distal taper. The distal ends of oars are expanded to maximize drag (Alexander, 1989; Nicholls and Russell, 1991; Robinson, 1975). Conversely, "wings" require favorable (that is, high) aspect ratios (long, tapering shapes) to minimize lift induced drag (Rayner, 1985), which results from the input of kinetic energy to the water through trailing vorticities produced at the "wing" tip (fig. 6). Plesiosaur limbs also had increased potential as hydrofoils (through transverse section asymmetry and larger functional surfaces), because of the soft tissue that formed their trailing edges. These edges, extending beyond the skeletal components of the limb, are occasionally preserved as skin impressions (Halstead, 1989; Robinson, 1975, Tarlo, 1957).

Godfrey (1984), however, convincing demonstrated that plesiosa- rian limb girdles did not have the significant vertical components (that is, fixed scapular process, acromion, sternum [although Nicholls and Russell (1991) propose an unusually positioned, unossified sternum], or vertically oriented corocoid) required to brace the limbs against the rib cage and vertebral column during strict underwater "flight." Neither did they have attachment surfaces for large abductor musculature, nor could
the plesiosaur limb be lifted above the horizontal plane as in penguins and sea turtles (Nicholls and Russell, 1991; Tarsitano and Riess, 1982; Williston, 1903). An intermediate functional model was proposed (Godfrey, 1984), whereby periodic thrust pulses were generated by an asymmetrical down and aft power stroke. Elements of this stroke combined both lift- and drag-based thrust. The hydrofoil shape and presumed attitude of the limb and a feathered return stroke all created lift. Drag-based thrust was generated during caudal adduction of the limb, near the end of its downward power stroke. Frey and Riess (1982) and Tarsitano and Riess (1982) also stressed that the recovery stroke was largely passive [Rayner (1985), in fact, proposes that plesiosaurs may have swallowed stones to counteract excessive vertical force resulting from passive up strokes]. This hypothesized method of swimming is akin to that used by modern day sea lions (English, 1976; Feldcamp, 1987) and combines elements of both “rowing” and “flight.” As in otariids, the power strokes of opposite limbs would have been applied simultaneously for maximum efficiency. Fore and hind limb pairs probably also operated in phase, although Frey and Riess (1982) envisioned alternately paired strokes. They believed that synchronous power strokes of the hind limbs would be adversely affected by turbulence from the fores. Halstead (1989), however, argued that trailing vorticities were not a problem, if plesiosaurs followed a wave-like path through the water. Alexander (1989), moreover, suggests that out of phase hind limb strokes might be less efficient than simultaneous operation of all limbs.

The aquatic locomotion of “nothosaurs” has received less attention than has that of plesiosaurs. A long held assumption is that these essentially lacertiform animals were undulatory propulsors, using a long,
sinuous tail as the major thrust organ. For example, Carroll and Gaskill (1985) note that “nothosaur” forelimbs are modified from the terrestrial condition, but on the basis of their study of “Pachypleurosaurus” [= Neusticosaurus according to Sander (1989)], and especially its large tail, conclude that axial propulsion dominated “nothosaur”, or at least pachypleurosaur, locomotion. The crux of their argument is that the relative proportions of tail, body, and limbs are suggestive of caudal propulsion as in crocodilians (Manter, 1940) and iguanids (Bartholomew, Bennett, and Dawson, 1976). Carroll (1988), Kuhn-Schnyder (1987), Peyer (1931), Sues (1987a) and Sues and Carroll (1985) accept the tail as the primary locomotory organ in “nothosaurs” while agreeing with Carroll and Gaskill (1985) that the forelimbs, nevertheless, played an important role intermediate between that of primitive sprawling tetrapods and plesiosaurs. This intermediate role was regarded as drag-based “paddling” or “rowing.”

All “nothosaur” forelimbs exhibit adaptations for aquatic life that, in general, serve to increase the functional surfaces (whether drag- or lift-based) of the limb as is typical for paraxial swimmers. In “nothosaurs” these include a distal flattening and occasional distoventral cupping of the humerus, broadening of the distal extremity of the humerus and often of the entire ulna, shortening and flattening of both epipodials, reduced intralimb flexibility, and frequent hyperphalangy. Such modifications do not suggest an aid in drag reduction or streamlining, were the limbs to be held passively against the body of an axial swimmer. Neither are the limbs well adapted for efficient terrestrial travel [to what extent “nothosaurs” could have traveled on land, if at all, is unknown; various authors have promoted some amphibious ability for them (Carroll and Gaskill, 1985; Colbert, 1980; Peyer, 1931; Schmidt, 1984; Williston, 1914)]. The forelimbs of “nothosaurs” must, therefore, have played a major role in aquatic locomotion. It has been unclear whether this role was in primary propulsion or only steering. Certainly, many marine tetrapods which swim by undulation (whales, mosasaurs, ichthyosaurs, thalattosuchians) show aquatic limb adaptations that would aid them in maneuvering. However, the curvature of the “nothosaurid” humerus and the ovoid shape of its proximal end make it unlikely that the forelimbs could be drawn completely against the body or readily rotated. The restricted movements of the “nothosaur” forelimb suggest a limited utility in directional control. Whales, for example, have a great deal of motion of the glenoid joint. Sanz (1976, 1980) and Schmidt (1984, 1986) argued that “nothosaurs” relied mostly upon their limbs for swimming but could not agree upon the style of movement (“flight” versus “rowing,” respectively). Carroll and Gaskill (1985) state only that the relatively robust forelimbs, with their specialized pectoral arch (much as in plesiosaurs), are indicative of a posteriorly directed limb stroke of some kind.

“Nothosaurs” of all types, like plesiosaurs, possessed comparatively rigid thoraces. Their largely flat vertebral faces, broad neural arches, subrectangular neural spines, accessory articulations, and densely packed
gastralia (ventral ribs) all served to limit body flexion (plesiosaurs accomplish this without accessory vertebral articulations—a derived character). Indeed, all complete, articulated “nothosaur” skeletons are preserved with virtually no curvature of the thorax. This trunk rigidity of “nothosaurs” was probably disadvantageous to undulation of any part of the vertebral column, because propulsive undulations in vertebrate axial swimmers are normally generated anteriorly of the tail. Most undulatory swimmers propagate waves along the entire body during locomotion, even though wave amplitudes may be relatively greater in the tail than the thorax (Alexander, 1982; Hildebrand, 1974; Rayner, 1985; Webb and Blake, 1985). No secondarily aquatic tetrapod uses only its tail for generation of propulsive undulations. Likewise, the long anterior caudal ribs of “nothosaurs” reduced flexibility at the base of the tail where most needed if the tail was used for continuous thrust. The long, relatively flexible necks of these animals would also have been a hinderance to axial propulsion, because vertebrate undulation is most efficient when anteriormost wave amplitudes are minimized. A movable neck would counteract any propulsive undulations of the tail through the energetically wasteful creation of “lateral recoil,” as part of the force acting upon the body tended to rotate the head (Webb and Blake, 1985). All vertebrates, both modern and extinct, which demonstrably swim by undulation of the vertebral column have extremely short necks. Although plesiosaur necks were probably less flexible than those of “nothosaurs,” they could not have grown as long as they did unless associated with a paraxial swimming style. Thus, it is likely that “nothosaurs” used their forelimbs, at least, with which to swim. Finally, the inflexible nature of the “nothosaur” thorax prevented alternating limb movements of the “sprawling” tetrapod kind, dictating that only symmetrically applied strokes were possible. Carroll (1988), Carroll and Gaskill (1985), and especially Sues and Carroll (1985) also found that lateral truncal flexion was significantly restricted in “Pachypleurosaurus” and Dactylosaurus as a prerequisite to symmetrical limb movements in advanced “nothosaurs” and plesiosaurs (where trunk flexion was entirely eliminated).

Storrs (1988, 1991) has suggested that the forelimbs of the plesiomorphic nothosauriform Corosaurus, and by analogy those of most “nothosaurids,” provided a dominant paraxial thrust which was functionally antecedent to that of plesiosaurs. Much of the movement of the forelimbs of Corosaurus was restricted to the horizontal plane, although some down stroke was also possible. As in plesiosaurs, the appendicular girdles of “nothosaurs” are expanded primarily in the horizontal plane with little vertical contribution. The relationships of the pectoral girdle elements are thus largely identical between the two “groups.” The combined drag/lift swim strokes of otariids and plesiosaurs (following Godfrey, 1984) probably also existed in “nothosaurid” locomotion. Detailed reconstruction of forelimb and pectoral girdle musculature of Corosaurus shows that similar movements and attitudes of the forelimbs
were likely, although the drag component probably overshadowed that of lift (Storrs, 1991). The aspect ratios of “nothosaurian” limbs provided less favorable lift to lift induced drag ratios than did those of plesiosaurs, so the relative importance of the thrust components (drag and lift) must have been different. The lift-based component of the power stroke was less efficiently created in “nothosaurs” because of the lesser distal taper to their limbs (figure 7). Furthermore, the vertical range of movement of the “nothosaurian” forelimb was limited by the configuration of the glenoid/humerus articulation so less lift was generated by any downward stroke (Storrs, 1991). Nevertheless, the “feet” of “nothosaurs” are relatively longer and narrower than are the broad “paddles” of non-“flyers.” The greater mechanical efficiency of plesiosaur subaqueous propulsion may have been achieved by abandonment of terrestrial locomotion, which was perhaps rudimentarily retained in “nothosaurs.”

The hindlimbs of “nothosaurs” were less specialized than the forelimbo, often smaller, and also less restricted in the range of movement possible (Storrs, 1991). They nevertheless possessed robust musculature associated with sturdy ventral plates of the pelvis, thus a powerful rowing stroke may have been possible. The hindlimbs probably provided acces-
sory thrust, but their more plesiomorphic morphology suggests less of a role. They may exhibit slight hyperphalangy (for example, Ceresiosaurus and Lariosaurus), but the femur is less robust than the humerus and does not exhibit flattening or broadening. The epipods of the hindlimb are also less modified from the terrestrial condition than are the ulna and radius, while the pelvis is also not highly specialized. These differences in the fore- and hindlimbs of “nothosaurs” suggest a greater role for the hindlimb in either terrestrial locomotion or, more probably, subaquous directional control. Submarine steering could have been largely accomplished by the attitude of the hindlimbs as it is in Alligator (Manter, 1940). The tail of “nothosaurs” probably augmented and modified the thrust (for quick starts and turns) produced by the limbs. This method of swimming foreshadowed the type to appear in plesiosaurs where input from the tail was negligible. Increased reliance on, and selection for, modified limbs made “nothosaurid” locomotion the functional ancestor of plesiosaur swimming.

While the longer tails of pachypleurosaurs may have played a greater part in swimming than they apparently did in nothosauriforms, pachypleurosaurs must also have used their forelimbs for some subaqueous propulsion (Carroll, 1988; Carroll and Gaskill, 1985; Storrs, 1991; Sues and Carroll, 1985). Their forelimbs possess all the aquatic adaptations discussed above except a broadly curved humerus and, occasionally, the possible exception of hyperphalangy. Pachypleurosauro pectoral girdles show a broad similarity in construction and proportion to most “nothosaurid” pectora and therefore, are likely to have functioned in a similar manner. The retention of a long tail in secondarily aquatic animals, as seen in plesiomorphic sauropterygians, is not necessarily an adaptation but may be merely held over from the ancestral condition. The tails of “nothosaurs” in general are not especially deep, nor laterally compressed, as is typical for sculling vertebrates.

Swimming ability in placodonts has been examined in more than just a cursory fashion only by Pinna and Nosotti (1989). Most authors (for example, Colbert, 1967, 1980; Peyer and Kuhn-Schnyder, 1955; Williston, 1914) have reasonably assumed a bottom-dwelling, slow-moving habit for this group which Pinna and Nosotti (1989) confirm. It appears from the general morphology of the Placodontia that they swam predominantly, if not exclusively, with their appendages as the stout, often armored trunk of most placodonts precluded a great deal of body flexion or undulation. Thus, it seems that most sauropterygians, with the possible exception of the most primitive forms, relied overwhelmingly on paraxial propulsion. This is a relatively unusual form of locomotion for aquatic reptiles.

SAUROPTERYGIAN FUNCTIONAL EVOLUTION

Because the morphologies of pachypleurosaurs and “nothosaurids” are far less removed from the condition in the hypothetical terrestrial ancestor of sauropterygians than is that of plesiosaurs, they seemingly
shed light on the functional evolution of the latter group. While not directly ancestral to plesiosaurs, the appendicular skeletons of the known “nothosaurs” are partially analogous to them and to their structural predecessor and may be indicative of the steps that led to the successful invasion of a new functional niche.

Carroll and Gaskill (1985) and Sues (1987a) have already discussed the possible functional relationship between “nothosaurs” and plesiosaurs, particularly with regard to pachypleurosaurus and Pistorosaurus, respectively. They imagine a succession of locomotory advances from strict undulatory propulsion using lateral tail movements, through increased forelimb use in propulsion, to the strictly limb-mediated swimming of plesiosaurs. A radical central nervous system shift from the ancestral program of terrestrial, undulatory “sprawlers” to the symmetrical, simultaneous limb strokes of advanced sauropterygians is implied (Carroll, 1984, 1985; Carroll and Gaskill, 1985; Sues and Carroll, 1985). I have argued here that symmetrical strokes of the forelimbs were probably the primary means of thrust in all sauropterygians. Symmetrical limb adduction would have made increased neck length a possibility for the early sauropterygians, because unlike the case in axial propulsion, a long, flexible neck would not have hindered forward progress, as discussed above. With continued modification of the limbs (especially increased hyperphalangy, distal tapering, and decreased intralimb mobility), shortening and stiffening of the thorax, and reduction of the tail, “nothosaur”-like animals became ideal functional precursors for plesiosaurs.

The origin of plesiosaurs probably coincided with the complete abandonment of the land and/or paralic environs. Storrs (1991) and Sues (1987a) have suggested that the habitats of plesiomorphic versus derived sauropterygians (pachypleurosaurus versus “nothosaurids” versus plesiosaurs) corresponded to a nearshore to offshore gradient, although most plesiosaurs (that is, those from the Jurassic and Cretaceous) were not contemporaries of the “nothosaurs” (Pistorosaurus is an Anisian plesosaur, while isolated plesiosaur remains are common in the Rhaetian). No “nothosaur” is known after the Carnian. Likewise, no placodont is known to have survived beyond the Triassic. Placodonts were nearshore forms and also diverged relatively early from “nothosaurids” and plesiosaurs (Storrs, 1991). Mazin (1987) attributes the extinction of sauropterygians in nearshore habitats to a global cycle of oceanic transgression and regression at the end of the Triassic.

Why did elongate, secondarily aquatic reptiles such as the early sauropterygians develop a limb-dominated method of aqueous propulsion rather than the typical undulatory swimming style of lizards, crocodilians, and others? The basic ingredients of undulatory behavior were already in place in the terrestrial locomotion of primitive “sprawlers,” and presumably in the hypothetical sauropterygian ancestor. Axial propulsion was probably obligatory for the amphibious, immediate ancestors of the Sauropterygia because of this strong ancestral constraint. Theoretically, these were coastal animals exploring a new environmental niche in
the search for a new food or shelter resource (Benton, 1979; Colbert, 1967). Most reptile lineages readily adapt to life in the water (Carroll, 1984; Seymour, 1982) but, in so doing, bring with them the "sprawling" constraint, so that the overwhelming majority of reptilian swimmers are undulators. Notably, sea turtles and penguins have overcome their lateral undulatory history because of functional considerations, as discussed previously. How have sauropterygians done so?

Carroll and Gaskill (1985) have proposed that after the advent of habitual aquatic behavior, temporary limb and appendicular girdle reduction may have taken place in the sauropterygian precursor in an attempt to decrease drag. Subsequent limb enlargement and restructuring of the sauropterygian pectoral girdle into its unique format might have been driven by the need for occasional terrestrial forays (Carroll and Gaskill, 1985), or a bottom dwelling/feeding mode of life (Schmidt, 1986). For example, the stout dermal arch elements of most "nothosaurs," with their medial positions relative to the scapulae, may have protected the front of the body when on land (Carroll and Gaskill, 1985). Both reduction and reclamation of the appendicular skeleton can be imagined to have occurred by subtle developmental rate/shape changes in the early ontogeny of a basal sauropterygian, just as the reversal of position of the ribs and scapulocoracoids in Testudines is undoubtedly a result of a developmental shift at the base of that lineage. Limb-dominated propulsion in "nothosaurs" might have been advantageous in maneuvering along and/or pushing off from the substrate, either on land or on the sea floor (Carroll and Gaskill, 1985; Schmidt, 1986). As a result, the forelimbs especially were "preadapted" (exapted of Gould and Vrba (1982)] for swimming. In this case, it could have been adaptive pressure for modified limb function that overcame the constraint of ancestral undulation in sauropterygians. This argument explains the increased use of the limbs but seemingly not their new symmetrically coordinated movements.

Another possibility attends the requirement in many habitually aquatic animals of neutral buoyancy. Its development in sauropterygians may have simultaneously determined their transition to paraxial swimming. Organisms able to maintain a static water column depth with minimal effort (that is, are neutrally buoyant) are usually at a distinct energetic advantage over those that cannot. The means of buoyancy compensation likewise depends on selection of mechanisms for their economy of energy (Alexander, 1982). Gravity exerts a constant downward pull on all objects that, in most free swimmers, must be overcome in order to prevent sinking. Positive thrust opposite to gravity helps to do this but at a distinct energetic cost. A fortuitous counterbalance exists for secondarily aquatic tetrapods in the vertebrate lung, particularly, which imparts to them a natural positive buoyancy. The density of swimming reptiles and the air in their lungs may be substantially lower than that of water (depending upon temperature; approx 1.025 g/ml for salt water). Extreme buoyancy, however, can also be at odds with locomotion within the water column. Ideally, a hydrostatic or neutrally buoyant condition
may be attained whereby the forces of gravity and buoyancy effectively cancel each other out and play an insignificant role in midcolumn swimming position and behavior (Rayner, 1985). A neutrally buoyant animal may choose a relatively stable position within the water column where thrust is needed only to overcome drag and none for the maintenance of depth. Thus for swimming reptiles, and, to an even greater degree, bottom dwellers, some mechanism for decreasing natural buoyancy is often desirable. A variably buoyant condition may be attained by adjustment of the volume of lung gas. This may occur at the water's surface or during dives, as air in the lungs is compressed as a consequence of increasing depth (Seymour, 1982). A passive and more permanent solution involves the elaboration of dense skeletal elements or the ingestion of ballast. Crocodilians, for example, may use gastroliths for ballast just as plesiosaurs probably did, as noted above.

While plesiosaurs (although perhaps not pliosaurs) certainly swallowed stones, no plesiomorphic sauropterygian (that is, “nothosaur”) has been discovered with unequivocal gastroliths [Sander (1989) describes single sand grains in the thoraces of only two of hundreds of individuals of Neusticosaurus]. Like plesiosaurs, however, “nothosaur” ribs and especially their gastralia are dense and frequently thickened, or “pachyostotic.” Ventral ribs are part of the ancestral package of all reptiles, but they are often reduced or lost. In all sauropterygians the gastralia are particularly large and dense. Sauropterygian limb girdles are also constructed of dense, heavy bone. The tight, heavy ventral basket composed of these elements was probably a buoyancy compensator as first suggested by Nopcsa (1923). It was the development of such ventral baskets that greatly reduced, if not eliminated, thoracic flexion in the early sauropterygians. Therefore, the attainment of negative or neutral buoyancy in this way would have given paraxial propulsion added importance and provided the impetus that made functional need more compelling than heritage. Symmetrical, limb-dominated propulsion in the Sauropodygia may indeed have been developed by necessity. I believe that this is the most plausible scenario for the origin of the sauropterygian locomotor format.

Following the change to nonundulatory swimming, and thus fundamental neurological transformation, sauropterygians were constrained to paraxial propulsion. From that point on in their history, a new ancestral constraint operated from which they did not emerge. New morphotypes would have exploited the paraxial format as enabled by the availability of new environments. In the case of plesiosaurs, the move to the open sea could have been sufficient. Enlarged ventral girdle components and long, narrow limbs (with favorable, that is, high aspect ratios) which were nearly identical front and rear were then fully developed. In fact, phylogenetic modification of limb dimensions for the attainment of a favorable aspect ratio is seen throughout the fossil history of sauropterygians. The “primitive” pachypleurosaur limb gives way to increased hyperphalangy, distal tapèr, and intralimb rigidity in many “nothosaurids”
and placodonts and is "perfected" in plesiosaurs (see figs. 1 and 7). As a result of the high degree of specialization of the plesiosaur locomotory apparatus, they were seemingly successful in broader geographic and stratigraphic ranges than were their nearshore cousins, thus their survival when "nothosaurs" and placodonts became extinct in the Late Triassic. A further division of available niches enabled short-necked plesiosaurs (pliosaurs) to be pursuit predators whereas stealth, agility, and surprise strikes from a static position may have been normal for the long-necked varieties (Massare, 1988). Neck length and relative head size are also reflections of prey preference/size.

Placodonts remained constrained to paraxial swimming too. In fact, the armor of Cyamodus, Henodus, Placochelys, and Psephoderma, for example, further prevented body undulations, although their "shells" seemingly arose after the use of their limbs became dominant. Paraxial propulsion was not a hinderance to bottom feeding, and the prominent dermal armor of some genera may also have contributed to an overall negative buoyancy. Placodont skeletons contain dense, "pachyostotic" bone, while gastroliths were apparently lacking. The many unique features of placodonts, noted above, may have arisen following the pachypleurosaur/nothosauriform divergence. Placodonts could then have evolved such characters independently of other forms because of their occupation of an unusual ecologic niche. Function and feeding strategy assumed new importance for the placodonts, and this is reflected in their crushing dentition and other autapomorphies. Likewise, functional pressures involved in aquatic respiration and piscivory presumably constrained the other sauropterygians to retracted nares and sharp, homodont dentition, to name but a few examples.

CONCLUSION

To reiterate, the foregoing discussions and the work of Godfrey (1984) in particular, suggest that the model of underwater "flight" for plesiosaur paraxial locomotion is not a perfect one. Rather, it is probable that the plesiosaurian power stroke combined elements of "flight" and subaqueous "rowing" with both vertical (lift-based) and fore and aft (drag-based) components. Robinson (1975) was correct in highlighting the hydrofoil-shaped limbs of plesiosaurs. Their distally tapering configuration created a relatively high aspect ratio for each limb and thus minimized trailing vorticity and lift-induced drag. Nonetheless sea lions, with limbs constructed in a functionally similar pattern, do not rely exclusively upon lift-based thrust. A horizontal component of the plesiosaur limb power stroke probably generated propulsive drag as in otariids. An inertial gliding phase may have existed between periodic power strokes, again as in sea lions (English, 1976; Godfrey, 1984). At least in pliosaurs, this gliding phase would have been relatively unencumbered by drag because of their comparatively small surface to mass ratio (less likely in elasmosaurs whose long necks increased surface area relative to mass). Such a style of locomotion, and the general plesiosaur habitus, had
its origin at least by the lowermost Middle Triassic (the first known appearance of *Pistosaurus*) and remained largely unchanged until the time of sauropterygian extinction at the terminal Cretaceous. Changes did occur in neck length, head size, tooth type, and limb proportions. These changes were related to feeding strategy and prey selection. Unquestionably, the plesiosaur habitus was a very successful one representing a well adapted morphotype for a specific environment. The environment was the open sea and the midwater column, and the form of locomotion was the unique one of paraxial thrust symmetrically produced by two pairs of appendages.

“Nothosaurs,” with their modified forelimbs, probably functioned in a similar way, although less efficiently and with the forelimbs as the dominant pair of appendages. The tail, largely on the basis of the restricted trunk flexibility, was most likely only an auxiliary thrust organ, used for quick starts and steering. The hindlimbs were also important in maneuvering. As in plesiosaurs, the “nothosaur” pattern, once achieved, remained relatively constant with little additional locomotory innovation during its history (although feeding strategy and correlated morphology also varied here). Unlike plesiosaurs, however, the “nothosaurs” constitute an unnatural, paraphyletic assemblage of related animals. Their overall morphological similarity is plesiomorphic. Maintenance of this similar habitus, nevertheless, was probably also functionally mediated. It too, was successful in a narrow range of environments, probably all paralic (marginal marine) habitats, occupied by these creatures. When advanced “nothosaur”-like animals extended their geographic range to more offshore marine habitats, they became ideal functional precursors for plesiosaurs.

Placodonts apparently originated among more plesiomorphic “nothosaurian” animals, carrying their paraxial locomotion to a bottom-dwelling lifestyle. The forelimbs were initially dominant, but the hindlimbs may have played a more important role in advanced forms. The placodonts later embellished the basic sauropterygian bauplan with numerous autapomorphies (for example, crushing dentition and dermal armor) related to their new mode of life.

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