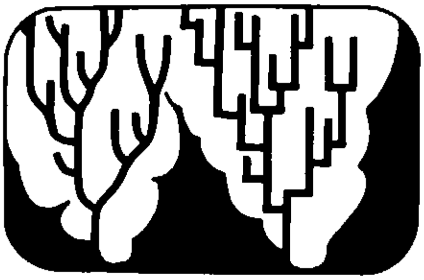

# PALEOSCENE #2.

# Physical and Biological Constraints on the Pattern of Vertebrate Evolution

Robert L. Carroll
*Redpath Museum*
*McGill University*
*859 Sherbrooke St. W.*
*Montreal, Quebec H3A 2K6*

## Introduction

Darwin (1859) argued that all evolutionary change could be explained by natural selection acting on variations within populations. He felt that this process led to the emergence of new species and could account for all organic diversity.

If variation and selection were the only factors influencing the direction and rate of evolution, one might expect a nearly uniform and continuous distribution of anatomical patterns and general adaptive types in both space and time (Figure 1). In contrast, study of both the modern fauna and the fossil record shows that most organisms can be grouped into a relatively small number of major structural patterns and clearly distinct ways of life.

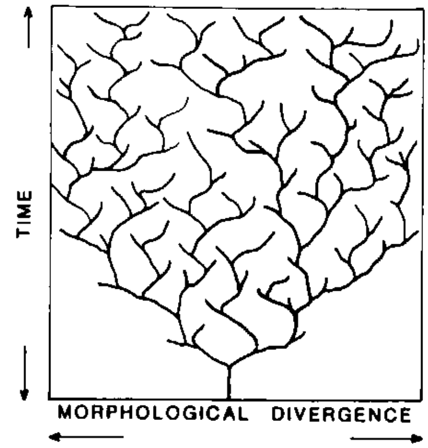

**Figure 1** *Hypothetical radiation of a group in which there are no constraints. All potential morphotypes are produced by natural selection acting on random variation. Morphological change proceeds at a uniform rate.*

Within the modern fauna, vertebrate classes and orders are clearly distinct from one another and very few extant genera and species cannot be readily classified in one group or another. There are certainly no living animals that might be considered intermediate between amphibians, reptiles, birds and mammals. Among mammals, the only group for which there is current dispute over its ordinal classification is the family Tupaiidae (tree shrews), which has been allied with both primates and insectivores (Luckett, 1980).

The high degree of adaptation of all modern species for distinct ways of life made it difficult for biologists to conceive of the idea of evolution prior to the writings of Darwin. Darwin became convinced of the fact of evolution through his knowledge of the geographical distribution of plants and animals and the basic structural similarities of all major groups, revealed through the study of comparative anatomy and developmental biology. He assumed that the fossil record would eventually demonstrate a continuous sequence of intermediate forms, showing the gradual development of all structural changes and linking all taxonomic groups.

The fossil record was very poorly known in the nineteenth century, and paleontologists, including Owen, Cuvier, Agassiz, and Dawson (1977) were among the strongest opponents of evolutionary thought. To them, the fossil record showed the same pattern as that exhibited by the modern flora and fauna, that is, a series of very distinct groups, without intermediates.

Knowledge of the fossil record has greatly improved during the twentieth century. Some major groups, such as reptiles and mammals, are known from more fossil than modern genera. We now have a fairly complete record of the major events in vertebrate history during the Cenozoic and Mesozoic and at least a rough outline for the Paleozoic.

Surprisingly, the fossil record still shows a pattern of a relatively small number of major groups which are clearly distinguishable from one another. Fossil intermediates between major groups are known, but they are rare. The fossil record does not show a continuous spectrum of adaptive types, nor a uniform pattern of progressive change over time (Gould and Eldredge, 1977). In contrast, vertebrate history is dominanted by a number of rapid radiations, followed by the long-term persistence of a relatively few adaptive types (Figure 2). Groups such as the therapsids include some families that were structurally and physiologically intermediate between ancestral and descendant groups, but the majority of included families represent clearly divergent lineages. The radiation of therapsids was clearly separate from that of both pelycosaurs and mammals, and was based on a different combination of structural and physiological characteristics.

The fossil record of vertebrates in the Cenozoic is certainly sufficiently complete to demonstrate that the conceivable universe of organisms is distributed in a discontinuous manner in both space and time. A similar pattern is evident in the Mesozoic and Paleozoic, where it is accentuated by the relative incompleteness of the record which results in a bias toward the discovery of common, long-lived and widespread species.

How can this heterogeneous pattern be explained?

Does it demonstrate basic inadequacies in selection theory as developed by Darwin?

What other, non-Darwinian, factors might be responsible?

The history of vertebrates suggests that there are limits to the powers of natural selection. Evolution acts at different rates on different structures and at different times in different groups. Some groups appear to exhibit little evolutionary change, and many conceivable structures and adaptive patterns never appear, or contribute little to species diversity.

The term evolutionary constraint may be applied to any factors that limit the expression of the full spectrum of morphological and adaptive patterns that might be conceived as resulting from adaptive radiation.

Several, somewhat overlapping, categories of constraints may be recognized:

1. Environmental constraints. Factors that are external to the organism, including both other species and the physical environment.
2. Intrinsic constraints. (a) Developmental processes; (b) Factors related to the materials of which the body is composed and the physiological properties of biological systems.

## Environmental Constraints

The most obvious explanation for the discontinuous distribution of organisms is to be found in the heterogeneity of the environment. Throughout vertebrate history, the vast majority of organisms have been adapted to particular environments and ways of life. Almost all can be described as being primarily aquatic, terrestrial or aerial. Within these broad physical environments, further habitat subdivision can be recognized on the basis of currents, salinity, climate, etc. Biological factors such as trophic level and specific diets define particular ways of life.

The physical and biological environments of any one habitat result in selection for features that are nearly always disadvantageous in other environments or ways of life. This leads to the perpetuation and intensification of particular anatomical and physiological specializations. Hence, among mammalian groups, basic adaptations such as herbivory, insectivory, and carnivory tend to be perpetuated within a lineage so that most members of the major mammalian orders have retained characteristic morphologies for 50-60 million years.

The basic constancy of major groups is attributed to stabilizing selection. As long as the adaptive zone is well defined by physical and biological factors, selection will act to limit any structural and behavioural changes that might potentially lead to different ways of life. Adaptive zones are not defined solely by external factors, however, but are recognized by the nature of the organisms that inhabit them.

Changes in biological factors such as competition or predation that favour an adaptational shift would alter the direction of selection and might lead to a markedly different way of life. Significant shifts have occurred in many well-established groups. Among the mammalian carnivores for example, the most significant change has been toward an obligatory aquatic way of life which occurred separately among the ancestors of seals and the sea lions and walruses (Tedford, 1977). Their basically predatory role was retained, however.

Adaptation to biological aspects of the environment is an every changing process, since all other organisms (including members of the same species) are changing as well. Physical aspects of the environment, in contrast, may be essentially constant and lead to particular, optimal solutions. That a specific structural pattern is optimal can be judged in several cases by the convergent achievement of very similar structures in groups with different ancestry. A clear example is provided by the body form in rapidly-swimming sharks, bony fish and ichthyosaurs (Figure 3).

The optimal shape for rapidly-swimming animals can be established from principles of hydrodynamics and the constraints of the vertebrate body plan (Lighthill, 1970). The fastest swimming modern bony fish belong to the family Carangidae, typified by the tuna. The body plan, termed thunniform, is characterized by a spindle-shaped trunk and a high, lunate tail. The body is laterally compressed to resist lateral movement and the force of muscle contraction is concentrated at the base of the tail. A nearly identical body form was achieved by Jurassic ichthyosaurs and by several groups of sharks, the first as early as the Upper Devonian. Among marine mammals, the cetaceans exhibit a similar body form.

There are differences between the swimming adaptations of these groups but they can be attributed to their distinct ancestry. The most clear cut difference is between cetaceans and other fast-swimming vertebrates. Locomotion in both fish and reptiles is produced primarily by lateral undulation of the trunk and tail. One of the major changes accompanying the origin of mammals was the elimination of lateral undulation of the trunk and the elaboration of dorsoventral undulation. When the ancestors of whales went back to the water, effective locomotion involved the evolution of a horizontal fluke, rather than a vertical caudal fin, as occurred in the ancestry of ichthyosaurs.

The bony support of the tail in sharks and ichthyosaurs differs in its orientation. Its dorsal orientation in sharks and the flat, rather than rounded, ventral surface of the body can be related to the fact that sharks are heavier than water and would sink if they did not swim constantly and use the forelimbs and front of the trunk as hydrofoils to produce lift. The reversed heterocercal tail of ichthyosaurs may have served to keep the front of the body, buoyed up by the lungs, from raising in the water. The body of the tuna and other fast-swimming bony fish has nearly neutral buoyancy, and the caudal fin is almost completely symmetrical. Despite these differences, the body profile of rapidly-swimming members of all these groups is remarkably similar in shape. There is clearly an optimal body form for rapid swimming.

Between groups, specialized aquatic locomotion provides an excellent example of convergence. Within groups, it demonstrates changing evolutionary rates and stasis. From the Lower Jurassic into the Upper Creta-

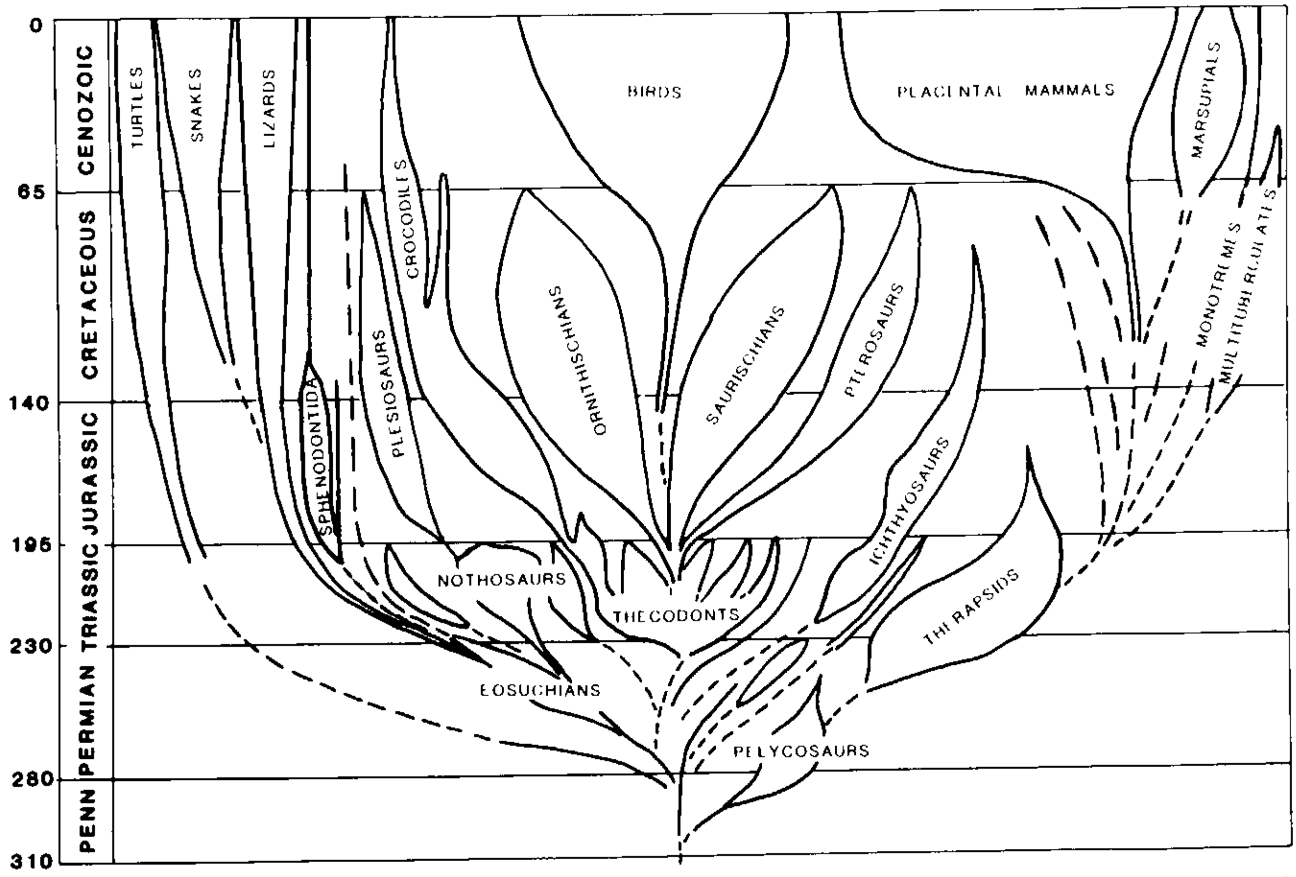

**Figure 2** *Radiation of amniotes (reptiles, birds, and mammals) since the Carboniferous. In contrast with Figure 1, evolution is strongly episodic, with a series of rapid radiations followed by long-term maintainance of relatively similar patterns of morphology and adaptation.*

ceous (approximately 120 million years) ichthyosaurs exhibit a nearly constant body form. The fossil record of ichthyosaurs in the Triassic is incomplete, but it appears to have required about 40 million years to achieve the pattern of advanced ichthyosaurs (McGowan, 1983).

Active flight similarly constrains the body form to a particular pattern, and nearly identical structures were achieved separately by flying reptiles (the pterosaurs) and birds (Figure 4).

Physical constraints of the environment are clearly sufficient to explain why particular structural patterns may be achieved fairly quickly and persist for long periods of time.

## Development Constraints

Developmental constraints have been viewed as somewhat independent from the selection hypothesis since they act to limit the amount of variability that is available.

Alberch (1980), Gould (1980), Williamson (1981) and Bonner (1982) have argued that the course of evolution may be significantly restricted by inherent limitations of developmental processes. As an example, Alberch and Gale (1985) cited distinct developmental differences in the expression of digits in frogs and salamanders which have persisted over a period of more than 200 million years.

An analogous situation is evident in the pattern of carpal and tarsal formation in reptiles. The sequence of ossification of the bones of the wrist and ankle is well documented in late Permian reptiles on the basis of growth series of several species (Currie, 1982; Currie and Carroll, 1984).

In the carpus, the first bone to appear is the ulnare, followed by the fourth distal carpal and the intermedium, then the lateral centrale, distal carpals 1 and 3, followed by the radiale, medial centrale, and distal carpals 2 and 5, and last of all, the pisiform. In the tarsus, the astragalus and calcaneum appear first, followed by the fourth distal tarsal, the centrale, distal tarsals 3, 1, and 2, and finally the fifth distal tarsal, which may then fuse with the fourth.

These early genera were near the base of a large radiation leading to all modern reptiles (other than turtles) and a number of extinct aquatic groups. Early members of the aquatic lineages show a reduction in the number of carpals and tarsals to provide greater flexibility of the wrist and ankle and to reduce weight. The first elements to be lost were the last elements to be ossified in the more primitive group. It appears to be a general rule of development that the last elements to appear are the most subject to change and loss. It may be considered a developmental constraint that predicts, in a general way, the pattern of the carpus and tarsus in many groups of secondarily aquatic reptiles. This is clearly shown by the nothosaurs (Figure 5). It is also evident in primitive members of more advanced groups, including plesiosaurs and ichthyosaurs. It is not an absolute constraint, however. Advanced plesiosaurs and ichthyosaurs have a clearly different pattern of the limbs which overcomes this constraint with the development of new elements and significant changes in proportions and configuration. The primitive distinction between elements of the lower limb and the hand and foot are lost, and some ichthyosaurs also lose the serial pattern of the digits (Figure 6).

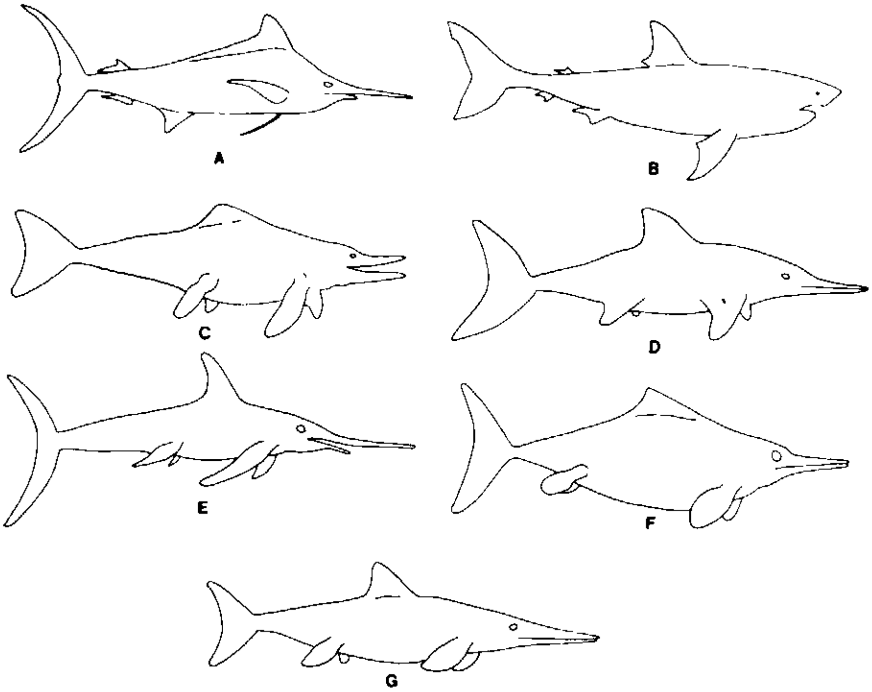

**Figure 3** *Body outline of rapidly-swimming aquatic vertebrates. (A) The marlin, a living teleost bony fish. (B) a predaceous shark. C-G, a variety of ichthyosaurs: (C)* Ichthyosaurus, *Lower Liassic, Lower Jurassic; (D)* Stenopterygius, *Upper Liassic, Lower Jurassic; (E)* Eurhinosaurus, *Upper Liassic; (F)* Ophthalmosaurus, *Upper Jurassic and Lower Cretaceous; (G)* Platypterigius, *Upper Cretaceous. These ichthyosaurs differ somewhat in fin proportions and the configuration of the skull and jaws, reflecting different degrees of manoeuvrability and feeding habits, but the general body form has remained nearly constant for 120 million years in response to the constraints of rapid swimming. (Outlines of ichthyosaurs adapted from McGowan, 1983).*

Another developmental "rule" that is broken among secondarily aquatic reptiles is that which states that limb reduction begins with the most distal elements and proceeds proximally (Wolpert, 1983). This pattern is followed in nothosaurs, with reduction of the digits and then the distal limb elements, while the humerus and femur remain large. In contrast, the number of phalanges and the total length of the hand *increase* in plesiosaurs and ichthyosaurs, while the distal limb elements are reduced. The humerus and femur remain large in plesiosaurs, but are much reduced in ichthyosaurs.

Unfortunately, little is yet known of the way in which developmental processes are controlled among vertebrates (Bonner, 1982; Goodwin *et al.*, 1983; Raff and Kaufman, 1983). It is not possible to outline what changes may be possible and which are prohibited. Holder (1983), in a general discussion of constraints on limb development, points out that no current model can explain specific changes in localized regions of the limbs. On the other hand, Hinchliffe and Griffiths (1983) described mutations that have very specific effects, and suggest that the pattern of the carpus and tarsus are directly amenable to selection.

On the basis of currently available evidence, it is difficult, if not impossible, to determine whether conservative developmental patterns are a constraint on evolutionary change, or conversely, reflect long-term stabilizing selection. This may depend on the particular trait and group under consideration. One may attribute the overall constancy of the vertebrate body plan to some inherent aspects of development. Such pervasive features of vertebrate anatomy might also be termed historical constraints. Among tetrapods, the paired limbs always show the same general pattern, but this is not a basic vertebrate constraint since cartilaginous and bony fish show many different arrangements of the fin skeleton.

Presumably, long-term selection can eliminate some developmental pathways, thus forever eliminating some originally possible directions of adaptation. Limbs and other major features that are lost are probably never regained.

Another type of constraint that may be noted in aquatic reptiles is the basic way in which propulsive force is generated. This may be considered either a behavioural constraint, or a structural or developmental constraint of the central nervous system. Primitive reptiles retain from their fish ancestors a mode of propulsion based on lateral flexure of the trunk and tail. This force is translated to the limbs in primitive tetrapods, but continues to depend primarily on the axial musculature. Most secondarily aquatic reptiles, including ichthyosaurs, mosasaurs, marine crocodiles and lizards, retain this behavioural system as they reduce their limbs. Two groups break this constraint. Both sea turtles and plesiosaurs rely primarily on their limbs for propulsion and they are used symmetrically, rather than alternately as was the case in primitive terrestrial reptiles. The turtles are obliged to use their limbs rather than their trunk for propulsion since it is immobilized by a rigid shell.

The ancestors of plesiosaurs, the Triassic nothosaurs, retain a more normal, lizard-like body form. As in other secondarily aquatic reptiles, the limbs are reduced and they relied primarily on the tail for propulsion (Carroll and Gaskill, 1985). The forelimbs were presumably not initially used in aquatic propulsion since their inherently asymmetrical movement would drive the head and anterior trunk from side to side, interfering with forward movement.

Plesiosaurs are characterized by much larger limbs than those of nothosaurs and a much more rigid trunk. Their limbs must have been used symmetrically for forward locomotion. The substantial anatomical gap between nothosaurs and plesiosaurs may be accounted for by behavioural and developmental constraints of the locomotor system.

The fossil record of sauropterygians is very incomplete during the Upper Triassic, but isolated vertebrae and limb bones show a transition between the typical nothosaur pattern and that of plesiosaurs. The nature of the change in body proportions, which is one of the most significant factors that separate these two groups, has not been documented. The origin of plesiosaurs also involved a switch in habitat from shallow, near shore, to more open ocean. Unfortunately, deposits that reflect this range of habitats are poorly known from this time interval.

As in the case of the ichthyosaurs, the typical plesiosaur pattern, once evolved, was maintained for approximately 120 million years. The length of the head and neck varies greatly, but not the relative length of the limbs and trunk.

**Structural and Physiological Constraints**
There are some aspects of organisms that show little if any significant variability and thus are not amenable to change in response to selection. They may be considered the most clear-cut examples of evolutionary constraints.

Most activities of vertebrates are associated directly with the skeletal and muscular systems whose fundamental units show ex-

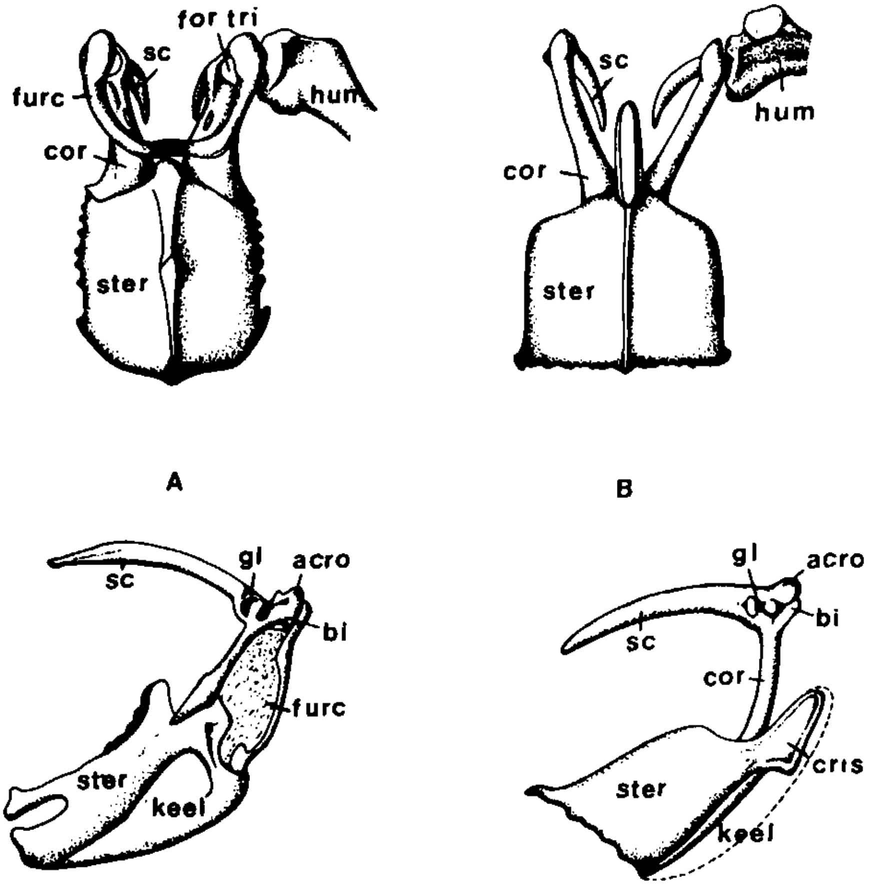

**Figure 4** *Pectoral girdle of a bird (**A**) and a pterosaur (**B**) in ventral and lateral views, showing high degree of structural similarity. Abbreviations:* **acro**, *acrocoracoid process;* **bi**, *biceps tubercle;* **cor**, *coracoid;* **cris**, *cristospine;* **for tri**, *foramen triosseum;* **furc**, *furcula;* **gl**, *glenoid fossa;* **hum**, *humerus;* **keel**, *sternal keel (partially cartilaginous in the pterosaur);* **sc**, *scapula;* **stern**, *sternum. Principal differences include the absence of the furcula in the pterosaur. Its function may be partially taken by the cristospine that extends anteriorly from the sternum. In the absence of a furcula, there is no foramen triosseum in the pterosaur, but the acromial process of the scapulocoracoid would serve as a pulley for the reorientation of the tendon of the supracoracoid muscle, as in birds. (From Padian, 1983).*

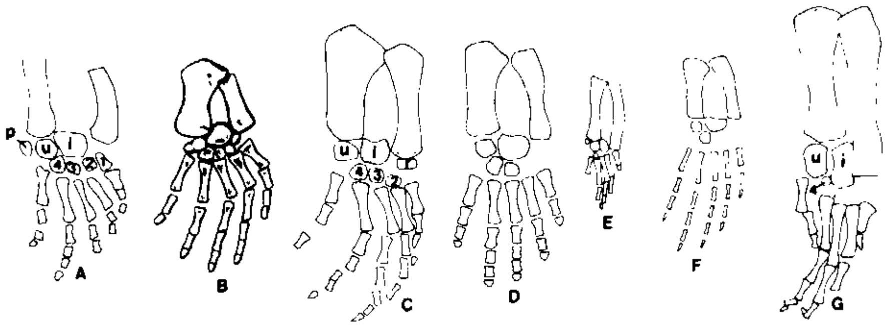

**Figure 5** *Forelimb of nothosaurs showing different patterns of the carpus. These correspond in a general way to the sequence of ossification of the carpals in primitive eosuchians. (**A**) Proneusticosaurus; (**B**) Lariosaurus; (**C**) Ceresiosaurus; (**D**) Paranothosaurus;(**E**) Dactylosaurus; (**F**) Nothosaurus;(**G**) Pachypleurosaurus; the number of phalanges is reduced from the primitive reptilian formula of 2, 3, 4, 5, 3 to 1, 2, 3, 4, 3. Abbreviations:* **i**, *intermedium;* **p**, *pisiform;* **r**, *radiale;* **1-5**, *distal carpals. The medial and lateral centrale, present in primitive reptiles, are missing in all these genera. (From Carroll, 1985).*

tremely limited variability. Although the configuration and distribution of bone and cartilage differ greatly among the vertebrate groups, their strength per unit area is essentially constant (Hildebrand, 1982). Selection may act to make the most effective use of their physical properties, but their strength under tension, compression or shear cannot be significantly altered.

The distribution of bone and cartilage can be adjusted to take advantage of the relative strength of bone and the relative lightness and compressibility of cartilage. The elaboration of cartilage as the only endoskeletal material in sharks and their allies presumably precludes the evolution within that group of the complex feeding structures common to bony fish which require the greater strength of bone.

The strength of muscle contraction is also restricted within narrow limits. The arrangement of the fibres and some aspects of their physiology are variable, but all muscles exert a force of approximately 2-3 kg $cm^{-2}$ of cross-section, measured at right angles to the orientation of the fibres. The degree by which a muscle contracts, and the amount that it can be stretched without damage are also closely limited. Muscles can contract only about 30% of their resting length, and are capable of stretching by approximately 50% of their resting length. Change in the size and proportions of the skull and appendicular skeleton are closely constrained by these properties of the muscles.

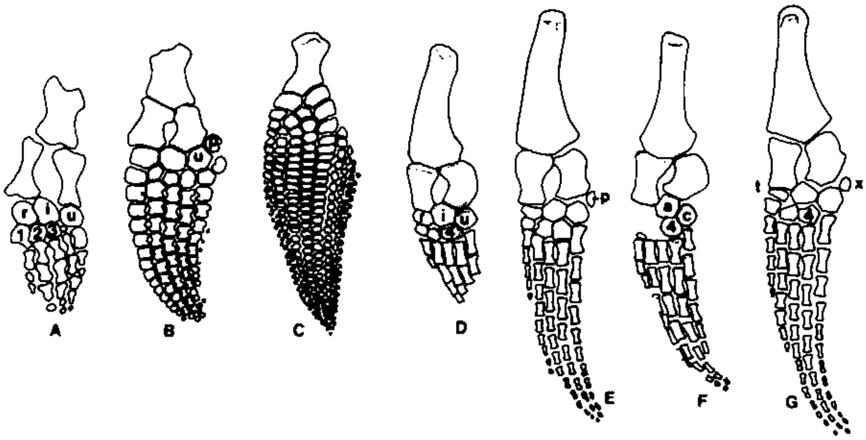

**Figure 6** *Limbs of ichthyosaurs and plesiosaurs. (A) the ichthyosaur* Chaohusaurus; *(B)* Mixosaurus; *(C)* Ichthyosaurus; *(D) forelimb of* Plesiosaurus triatarsostinus; *(E) forelimb of* Plesiosaurus brachypterygius; *(F) rear limb of* Plesiosaurus triatarsostinus; *(G) rear limb of* Plesiosaurus brachypterygius. *Abbreviations:* **a**, *astragalus;* **c**, *calcaneum;* **t**, *(a new bone in the position of the tibiale of amphibians);* **x**, *neomorphic element in the tarsus comparable to the pisiform of the carpus; others as in Figure 5. (From Carroll, 1985).*

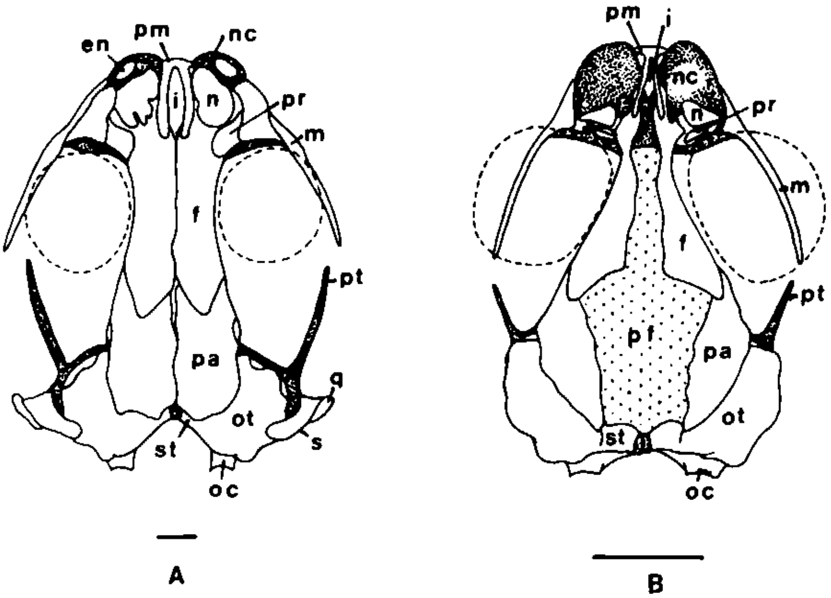

**Figure 7** *Skulls of two closely-related salamanders, showing striking differences in the pattern of the dermal bones to accommodate the great relative increase in size of the sense organs as a result of the smaller absolute size of the skull. (A)* Pseudoeurycea goebeli; *(B) the much smaller species,* Thorius narisoualis. *Scale bars = 1 mm. Abbreviations:* **en**, *external naris;* **f**, *frontal;* **fp**, *frontoparietal fontanelle;* **i**, *internasal fontanelle;* **m**, *maxilla;* **n**, *nasal;* **nc**, *nasal capsule;* **oc**, *occipital condyle;* **ot**, *otic capsule;* **pa**, *parietal;* **pm**, *premaxilla;* **pr**, *prefrontal;* **pt**, *pterygoid process;* **q**, *quadrate;* **s**, *squamosal;* **st**, *synotic tectum.*

Perhaps the most general structural constraints are those associated with the relationships between linear dimensions, surface area and volume. If one considers the vertebrate body as a roughly cubical structure, doubling of linear dimensions results in squaring the surface area, while the volume increases as the cube of linear dimensions. Since the weight-bearing capacity of bone and the force generated by muscles are both proportional to cross-sectional area, the muscles and bones of the limbs must increase faster than linear dimensions to support and move a heavier body.

This factor also affects processes such as heat gain and loss, and exchange of respiratory gasses and nutrient molecules across membranes, all of which occur at an essentially constant rate that is proportional to surface area. Increased body size requires a disproportionate elaboration of the area of the gills or lungs for gas exchange, and the area of the intestinal surface for absorption of food. The rate of heat loss and gain, and water loss are correspondingly reduced in animals with larger bodies.

Metabolic rate within a particular group increases in proportion to approximately the .75 power of the body weight (Schmidt-Nielsen, 1975). Requirements for food, oxygen and elimination of metabolic waste increase faster than linear dimensions, although not at the rate of volume increase. Gould (1975a) has demonstrated a direct relationship between occlusal area of the cheek teeth and body size in a variety of mammals. The tooth size increases at a significantly faster rate than linear measures of the skull.

All changes in proportions related to change in absolute size are termed allometric, and are of great significance in constraining the general body form of vertebrates (Gould, 1966, 1974, 1975b).

The relative size of the sense organs of the head provides a striking example of a structural constraint. Both the eye and the otic capsule are significantly larger, relative to other features of the head, in small vertebrates. This is related to physical factors that restrict their practical size within fixed limits. The rate of fluid flow is restricted in small tubes and hence the diameter of the semicircular canal varies only slightly over a great range of body weights (Jones and Spells, 1963). The dimensions of the rods and cones of the eye are limited by the interference pattern of the waves of light which set bounds to the production of a clear retinal image (D'Arcy Thompson, 1966). In tiny vertebrates, the eye and otic capsule dominate the structure of the skull (Figure 7). This greatly influences the configuration of the surrounding skeletal elements. The development of the bones conforms to the earlier established pattern of the sense organs (Hanken, 1984). The bones can thus change very significantly in shape without any corresponding genetic change in the mechanism that controls bone formation. Presumably the manifest changes in the details of skull structure are governed by one factor, selection for smaller body size.

The reorganization of the skull in relationship to reduced body size has been an important factor in the early evolution of lepospondyls and modern amphibians (Carroll and Holmes, 1980), primitive reptiles (Carroll, 1970), modern lizards, and possibly ancestral snakes (Rieppel, 1984).

Hanken (1985) notes that changes in development leading to rapid ossification at small body size in plethodontid salamanders greatly increase variability, opening up the possibility for extensive adaptative radiation. A similar change, resulting in precocious ossification, may have been an important factor in the emergence of amniotes and lepospondyl amphibians in the Carboniferous.

## Summary

Environmental and intrinsic constraints help to explain why evolution has not resulted in a continuous spectrum of adaptive forms in space and time. The discontinuous pattern of adaptive types might not be predicted directly from Darwinian selection theory, but it is easily understood in relationship to a heterogeneous environment and limiting factors inherent to all organisms. On the basis of our current knowledge of the history of vertebrates, no clearly non-Darwinian factors are necessary to explain their evolution.

## Acknowledgements

I wish to thank Mrs. Pamela Gaskill for her help with the illustrations, and Dr. Hans-Dieter Sues for critical reading of the manuscript. This work has been supported by grants from the Natural Sciences and Engineering Research Council of Canada.

## References

Alberch, P., 1980, Ontogenesis and morphological diversification: American Zoologist, v. 201, p. 653-667.

Alberch, P. and Gale, E.A., 1985, A developmental analysis of an evolutionary trend: digital reduction in amphibians: Evolution, v. 39, p. 8-23.

Bonner, J.T., 1982, Evolution and Development: Springer-Verlag, New York, 357 p.

Carroll, R.L., 1970, Quantitative aspects of the amphibian-reptilian transition: Forma et Functio, v. 3, p. 165-178.

Carroll, R.L., 1985, Evolutionary constraints in aquatic diapsid reptiles: Special Papers in Palaeontology, v. 33, p. 145-155.

Carroll, R.L., and Gaskill, P., 1985, The nothosaur *Pachypleurosaurus* and the origin of plesiosaurs: Royal Society of London, Philosophical Transactions, v. B309, p. 343-393.

Carroll, R.L. and Holmes, R., 1980, The skull and jaw musculature as guides to the ancestry of salamanders: Zoological Journal of the Linnean Society, v. 68, p. 1-40.

Currie, P.J., 1982, *Hovasaurus boulei*, an aquatic eosuchian from the Upper Permian of Madagascar: Palaeontologia africana, v. 24, p. 99-168.

Currie, P.J. and Carroll, R.L., 1984, Ontogenetic changes in the eosuchian reptile *Thadeosaurus*: Journal of Vertebrate Paleontology, v. 4, p. 68-84.

D'Arcy Thompson, W., 1966, On Growth and Form, Abridged Edition, Bonner, J.T., ed.: Cambridge University Press, Cambridge, United Kingdom, 346 p.

Darwin, C., 1859, The Origin of Species: John Murray, London, 502 p.

Dawson, J.W., 1977 (reprint of 1890 edition), Modern Ideas of Evolution: Shea, W.R. and Cornell, J.F., eds., Neale Watson Academic Publications, Inc., Prodist, New York, 240 p.

Goodwin, B.C., Holder, N. and Wylie, C.C., 1983, eds.,Development and Evolution: The Sixth Symposium of the British Society for Developmental Biology, Cambridge University Press, Cambridge, United Kingdom, 437 p.

Gould, S.J., 1966, Allometry and size in ontogeny and phylogeny: Biological Review, v. 41, p. 587-640.

Gould, S.J., 1974, The origin and function of "bizarre" structures: antler size and skull size in the "Irish Elk", *Megaloceros gigantus*: Evolution, v. 28, p. 191-220.

Gould, S.J., 1975a, On the scaling of tooth size in mammals: American Zoologist, v. 15, p. 351-362.

Gould, S.J., 1975b, Allometry in primates, with emphasis on scaling and the evolution of the brain: Contributions to Primatology, v. 5, p. 244-292.

Gould, S.J., 1980, The evolutionary biology of constraint: Daedalus, v. 109, p. 39-52.

Gould, S.J. and Eldredge, N., 1977, Punctuated equilibria: the tempo and mode of evolution reconsidered: Paleobiology, v. 3, p. 115-151.

Hanken, J., 1984, Miniaturization and its effect on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia: Plethodontidae). I. Osteological variation: Biological Journal of the Linnean Society, v. 23, p. 55-75.

Hanken, J., 1985, Morphological novelty in the limb skeleton accompanies miniaturization in salamanders: Science, v. 229, p. 871-874.

Hildebrand, M., 1982, Analysis of Vertebrate Structure: John Wiley and Sons, New York, 654 p.

Hinchliffe, J.R. and Griffiths, P.J., 1983, The prechondrogenic patterns in tetrapod limb development and their phylogenetic significance: *in* Goodwin, B.C., Holder, N. and Wylie, C.C., eds., Development and Evoluion: the Sixth Symposium of the British Society for Developmental Biology, Cambridge University Press, Cambridge, United Kingdom, p. 99-121.

Holder, N., 1983, Developmental constraints and the evolution of vertebrate digit patterns: Journal of Theoretical Biology, v. 104, p. 451-471.

Jones, G.M. and Spells, K.E., 1963, A theoretical and comparative study of the functional dependence of the semicircular canal upon its physical dimensions: Royal Society of London, Proceedings, v. B157, p. 403-419.

Lighthill, M.J., 1970, Aquatic animal propulsion of high hydromechanical efficiency: Journal of Fluid Mechanics, v. 44, p. 265-301.

Luckett, W.P., 1980, ed., Comparative Biology and Evolutionary Relationships of Tree Shrews: Plenum Press, New York, 314 p.

McGowan, C., 1983, The Successful Dragons: Samuel Stevens, Toronto and Sarasota, 263 p.

Padian, K., 1983, A functional analysis of flying and walking pterosaurs: Paleobiology, v. 9, p. 218-239.

Raff, R.A. and Kaufman, T.C., 1983, Embryos, Genes and Evolution. The Developmental-Genetic Basis of Evolutionary Change: Macmillan Publishing Company, Inc., New York, 395 p.

Rieppel, O., 1984, Miniaturization of the lizard skull: its functional and evolutionary implications: *in* Ferguson, M.W.J., ed., The Structure, Development and Evolution of Reptiles: Symposia of the Zoological Society of London, v. 52, p. 503-520.

Schmidt-Nielsen, K., 1975, Animal Physiology. Adaptation and Environment: Cambridge University Press, Cambridge, United Kingdom, 699 p.

Tedford, R.H., 1977, Relationship of pinnipeds to other carnivores: Systematic Zoology, v. 25, p. 363-374.

Williamson, P.G., 1981, Morphological stasis and developmental constraint: real problems for neo-Darwinism: Nature, v. 294, p. 214-215

Wolpert, L., 1983, Constancy and change in the development and evolution of pattern: *in* Goodwin, B.C., Holder, N. and Wylie, C.C., eds., Development and Evolution: The Sixth Symposium of the British Society for Developmental Biology, Cambridge University Press, Cambridge, United Kingdom, p. 47-57.

Accepted, as received, 28 February 1986.