research. Several general approaches have been developed, including logic, rules, semantic networks, and frames. The flexibility and precision of mathematical logic make it both a useful method and a standard of comparison for alternative representation schemes. Rules provide a modular and uniform mechanism that has proved to be popular for both expert systems and psychological modeling. Semantic network representations simplify certain deductions (such as inferences through taxonomic relations) by reflecting them directly in a network structure. Frames generalize this notion, providing structures or frameworks for organizing knowledge. A good overview of these topics and further references are given in A. Barr and E. A. Feigenbaum, Eds. [*Handbook of Artificial Intelligence* (Kaufman, Los Altos, Calif., 1981), vol. 1].

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Neural Crest and the Origin of Vertebrates: A New Head

Carl Gans and R. Glenn Northcutt

Summary. Most of the morphological and functional differences between vertebrates and other chordates occur in the head and are derived embryologically from muscularized hypomere, neural crest, and epidermal (neurogenic) placodes. In the head, the neural crest functions as mesoderm and forms connective, skeletal, and muscular tissue. Both the neural crest and the epidermal placodes form special sense organs and other neural structures. These structures may be homologous to portions of the epidermal nerve plexus of protochordates. The transition to vertebrates apparently was associated with a shift from a passive to an active mode of predation, so that many of the features occurring only in vertebrates became concentrated in the head.

In the extensive discussions on the origin of vertebrates (*1–3*), there has been an emphasis on characters shared between early vertebrates (and their descendants), and other deuterostomes—particularly the protochordates (Table 1). This emphasis on similarities, and thus on characters that appear to be primitive for chordates, has masked some major differences between vertebrates and all other deuterostomes. Consideration of these disparities allows analyses of the functional shifts that seem to have occurred with the origin of vertebrates.

Our analysis of new data from developmental biology, neurobiology, functional morphology, and systematics leads us to propose the hypothesis that vertebrates have evolved from protochordate-like ancestors primarily by elaboration and differentiation of their epidermal nerve plexus and by muscularization of their hypomere. This hypothesis is supported by the observation that many of the sensory, integrative, and motor systems of vertebrates, as well as their supportive skeletal structures, are derived embryologically from neural crest and epidermal (neurogenic) placodes. In the process, these embryonic tissues form the anterior part of the head, most of which represents a new vertebrate unit.

The structural differences between protochordates and vertebrates are presented in Table 2, along with notes on the embryonic origins of the vertebrate structures. Consideration of the functions of these systems and of their phylogenetic development leads to a new interpretation of the phylogeny of the vertebrate head.

Comparison of Vertebrates and Protochordates

At some stage of their life history, all chordates show such apparently derived characters as a dorsal hollow nerve cord, a notochord, segmented muscles (in an unsegmented trunk), and a perforated pharynx (*1–3*). However, certain assumed correlates of these characters prove to be only superficially similar in different chordate types (Table 3). For instance, although protochordates and vertebrates both have a pharynx, that of vertebrates differs (i) in having a cartilaginous rather than a collagenous skeleton (*4, 5, 8*), (ii) in pumping water with the branchiomeric muscles rather than cilia (*1*), and (iii) in having gills and internal, muscular aortic arches, both of which are lacking in protochordates (*6–8*). Similarly, although the myotomes of the axial musculature are staggered in cephalochordates, those of vertebrates lie in symmetrical pairs. In addition, the trunk muscle cells of cephalochordates extend to the nerve cord, where the motor endplates lie. In contrast, the motor endplates of vertebrates lie at the termination of peripherally passing spinal nerves (*9*). The differences between protochordates and vertebrates even affect superficially similar structures.

Vertebrates differ from other chordates because they are mobile predators, the predatory activities of which, whether or not utilizing jaws, inevitably involve the modified skeletal elements and muscles of the pharynx. This active predation is directed by an elaborate array of special sense organs and their integrating circuitry. Predation is supported by an advanced metabolic mechanism with specializations for exchange and

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distribution of respiratory gases. Although some of these attributes involve modification of preexisting portions of the protochordate anatomy, many other attributes concern structures that the vertebrates have assembled into the head. This "new" part of the head represents an addition that includes two suites of functional characters: (i) detection and capture of prey and (ii) the exchange and distribution of respiratory gases.

Clearly, vertebrates have a substantial suite of shared-derived characters that distinguish them from protochordates and from invertebrates (Table 2). The presence of these characters in itself is not a key to an understanding of vertebrate ancestry. Their occurrence is unexpected and demands an explanation of the transition that led to their development and the subsequent successful radiation of vertebrates. Because the differences involve multiple organ systems, it is appropriate to search for a common denominator that would allow an explanation of possible transitions between protochordates and vertebrates. We suggest that this common denominator is embryonic development.

Development of the Shared-Derived Characters

Analysis of the shared-derived characters of vertebrates (those advanced morphological attributes that characterize the group) indicates that these develop from one of three embryonic tissues: the hypomere, the neural crest, and the epidermal placodes (Table 2). The contribution of hypomere (the ventral, unsegmented lateral plate portion of the mesoderm) has long been recognized. What has not been emphasized is that most of the new hypomeric contributions reflect hypomeric muscularization in vertebrates. This muscularization leads primarily to the branchiomeric muscle of the pharynx (*10*), the muscle of the walls of the gut, and the muscular heart. Although hypomere is a feature of many deuterostomes, the occurrence of well-developed muscular layers is not (*1, 8*). The distribution of hypomeric muscle across deuterostomes (some echinoderms, enteropneust hemichordates, and vertebrates) suggests that muscle has evolved independently a number of times, from more primitive myoepithelial cells (*11*).

The neurogenic epidermal placodes are generally described as thickenings of the ectoderm at those cephalic sites at which sense organs will form; they actually originate from a zone adjacent to the anterior portion of the neural tube. The neural crest tends to be defined as paired strips of tissue, that lay adjacent to the edges of the neurectoderm and are folded inward along its sides during closure of the neural tube. Both epidermal placodes and neural crest are involved developmentally in many vertebrate sense organs, and neural crest has long been known to contribute to other vertebrate structures (*12, 13*). Some texts of developmental biology even list neural crest as a vertebrate character (*14*). The recent data in developmental biology obtained with the use of tritiated thymidine labeling and quail-chick chimeras have corroborated earlier findings, and these techniques have revealed that many other tissues derive from the neural crest and epidermal placodes (*15–19*) (Table 2).

Embryologically, both neural crest and epidermal placodes are found adjacent to the neurectodermal neural plate, in a zone surrounding its anterior and lateral edges. A number of developmental studies show that initially neural crest is incorporated into the neural tube, to form its dorsal-most alar closure; later neural crest migrates outward and comes to lie adjacent to the closed neural tube, immediately beneath the ectoderm (*20*). It migrates from here to highly specific locations in regions throughout the body (*15–19*). The epidermal (neurogenic) placodes, unlike neural crest, are restricted initially to the head. The placodes consist of a dorsolateral and ventrolateral series (*19, 21*). The dorsolateral series lies adjacent to the neural crest and forms special sense organs and possibly the adenohypophysis (*22*). The ventrolateral epibranchial placodes lie adjacent to the pharyngeal pouches and form the sensory ganglia of the cranial nerves that innervate the taste buds. The close spatial arrangement of neural crest and epidermal placodes in the developing embryo has led to the belief that these tissues are associated in some manner.

Table 1. Taxonomic overview of deuterostomes. These are bilateral organisms with the anus formed from blastopore, enterocoelous formation of coelom, indeterminate cleavage, and ciliated larva (*4*).

Phylum Echinodermata
Phylum Pogonophora
    Beard worms
Phylum Hemichordata* (*6*)
    Includes acorn worms (enteropneusts) and pterobranchs
Phylum Chordata*
  Subphylum Urochordata
    Includes tunicates, thalaceans, and larvaceans
  Subphylum Cephalochordata
    Amphioxus
  Subphylum Vertebrata
    Superclass Agnatha
      Includes lampreys and hagfish
    Superclass Gnathostoma
      Includes bony and cartilaginous fishes, amphibians, reptiles, mammals, and birds

*The term "Protochordata" includes all chordates except vertebrates.

Relation of Neural Crest to Epidermal Placodes

Although developmental studies reveal that the shared-derived characters of vertebrates arise from a limited number of embryonic tissues, these studies do not provide insights into the phylogenetic origin of these tissues nor into the selective pressures that may have produced the changes. However, all these shared-derived characters are involved with the functions of gas exchange or the detection, ingestion, and processing of food. Specifically, the structures developing from neural crest and placodes (Table 2) are involved significantly with sensory and integrative functions. This again raises the question of the relation between neural crest and epidermal placodes.

Placodes and neural crest have many parallel characteristics (*15–19, 21*). Both are derivatives of ectoderm and can migrate. Both form sensory neurons and special sense organs. Both produce or induce extracellular mucopolysaccharides as an extracellular matrix. Both must interact to form many structures. Placodes differ from neural crest in that they occur only in the head; in contrast, the tissues derived from neural crest arise along the trunk and tail as well. Only placodes form sensory receptors, whereas only the neural crest forms motor neurons (*15–19*).

The similarities suggest that the tissues are somehow associated, either ontogenetically or phylogenetically. The differences suggest that placodes are not part of the neural crest, and that they do not induce, nor are they induced by, neural crest. It would seem most likely that these two embryonic tissues are parallel derivatives of a single precursor, presumably a precursor that was involved in the formation of sensory, integrative, and motor tissues of protochordates.

The sensory, integrative, and, to a large extent, motor systems of hemichordates and protochordates reside in an epidermal nerve plexus. This plexus has a variable degree of mid-dorsal condensation, infolding, and cephalization (*23,* *24*). However, adult urochordates have secondarily simplified the centralized nervous systems seen in their larval stages (*24*).

Other deuterostomes have not only an epidermal nerve plexus, but also a perivisceral one. The embryonic origin of the perivisceral plexus has not been investigated fully; however, it is usually conceded that neurons in metazoans arise only from ectodermal tissues (*24*). If this is the case, then the perivisceral plexus probably arises from ectodermal cells and migrates into the wall of the gut. Apparently, the embryonic precursors of the peripheral nerve plexuses of deuterostomes are migratory, a property characteristic also of neural crest and epidermal placodal tissues. These considerations are consistent with the suggestion that parts of the central nervous system and special sense organs of vertebrates arose phylogenetically by a condensation and elaboration of the diffuse epidermal nerve plexus characteristic of other deuterostomes.

Origin of the Skeletal System

Although the differences in their sensory systems are profound, perhaps the most striking difference between vertebrates and protochordates is the possession of a head skeleton in the former. The head skeleton is composed of cartilage and calcified tissues (bone, dentine, and enamel). Both protochordates and vertebrates have an epithelial notochord for support, but in vertebrates the notochord extends only to the level of the basicranial fenestra, rather than to the rostral tip of the head as in protochordates. The extensive cranial skeleton of vertebrates arises embryologically from a pharyngeal skeleton (derived from neural crest), an integumentary skeleton (derived from neural crest and sclerotomal mesoderm), an anterior neurocranium (derived from neural crest), and a posterior neurocramium (derived from neural crest and sclerotomal mesoderm, respectively) as well as olfactory (neural crest), optic (neural crest), and otic (neural crest and sclerotomal mesoderm) sensory capsules (*12, 17, 18, 25*). It seems noteworthy that the rostral portion of the skull is entirely of neural crest origin.

Ostracoderm agnathans seem to have had all of the cephalic skeletal components seen in modern vertebrates (*26*). However, the best preserved portion of their skeletons is the ossified integumentary armor. The external surface of this armor apparently consisted of a dentinous layer, sometimes with a surface coating of an enamel-like material. The deeper layers of the dermal armor were bony, with the middle layer of each plate perforated by many more vascular and collagen-filled channels than the innermost one. Although many of the shared-derived vertebrate characters arise from neural crest and epidermal placodes, and are related to sensory or integrative functions, the supportive tissues form a major category that initially seems unrelated to neural function. However, both neural crest and placodal tissues are involved in the secretion of proteoglycans, that is, mucopolysaccharides (*15, 17, 27–29*). Moreover, it is possible that at first occurrence these tissues were associated with a sensory rather than a supportive function.

Table 2. Shared-derived characters of vertebrates. Abbreviations: NC, neural crest; P, epidermal placodes; H, hypomere; MH, muscularized hypomere; DH, food detection and ingestion; G, gas exchange; F, food processing.

Character	Embryonic origin*	Associated functions
Nervous system		
Cranial nerves with sensory ganglia	NC, P	DH, G
Trunk nerves with sensory ganglia	NC	DH
Peripheral motor ganglia	NC	G, F
Forebrain	NC?	DH, F
Paired special sense organs		
Nose	P	DH
Eyes (accessory organs)	NC? (P)	DH
Ears	P	DH
Lateral line mechanoreceptors	P	DH
Lateral line electroreceptors	P	DH
Gustatory organs	NC, P	DH
Pharyngeal and alimentary modifications		
Cartilaginous bars	NC	DH, F, G
Branchiomeric muscle	MH	DH, F, G
Smooth muscle of gut	MH	F
Calcitonin cells	NC	G
Chromaffin cells—adrenal cortex	NC	DH, F
Circulatory system		
Gill capillaries	H	G
Muscularized aortic arches	NC	G
Muscular heart	MH	G
Skeletal		
Anterior neurocranium and sensory capsules	NC	DH, F
Cephalic armor and derivatives	NC	DH

*See references (*15–19, 21, 27*).

Table 3. Some spurious similarities between vertebrates and protochordates (*1, 3, 8*).

Character	Complication
Anterior brain	Only occurs in vertebrates. Nonneural in cephalochordates
Sense organs	Although sense organs occur in both groups, protochordates have only simple, peripheral and central receptors, and lack the complex paired peripheral sense organs characteristic of vertebrates
Pharyngeal skeleton	Formed of cartilage in vertebrates; only contains collagen and chitin in protochordates
Transport of water	Pumped through pharynx by muscle in vertebrates Driven by ciliary movement in protochordates
Gas exchange surfaces	Capillary gill expansions in vertebrates No pharyngeal specializations in protochordates
Aortic arches	Muscular-walled in vertebrates; nonmuscular, covered with collagen in protochordates
Food transport	By muscular peristalsis in vertebrates; by ciliary motions in protochordates

Transduction Enhancement

The larval stages of most deuterostomes are ciliated, and it appears that these cilia have both sensory and motor functions (*30*). Previous studies suggest that the sensory receptors of most vertebrates represent modified ciliated cells (*31*). The mechanoreceptive neuromasts of the vertebrate lateral line system have many of the properties presumed to characterize primitive ciliated sense organs. However, the lateral line systems of lampreys (*32*), all cartilaginous fishes, and primitive bony fishes have an additional class of modified ciliated receptors, namely, the electroreceptive ampullary organs, which are capable of detecting weak electric fields (*33*). In view of the distribution of electroreceptors, it seems likely that the earliest vertebrates also possessed ampullary electroreceptive organs. Furthermore, a number of fossil fishes had a pore-canal system, consisting of supposed electroreceptors (*34*). The flask-shaped cavities of the pore-canal system were lined with dense enamel-like tissues, as was the surface of the dentinous protrusions of the integumentary armor. These enamel-like tissues, as well as the underlying bone, are formed of crystalline hydroxyapatite deposited on a collagenous matrix. It has been suggested that the high resistivity of this crystalline material increased the sensitivity of electroreception (*35*).

The development of the deep bony layers of the integumentary armor could have developed later as a consequence of the formation of the dentinous and enamel-like tissues. Consequently, bone initially may have functioned to maintain the spacing of the peripheral detectors rather than to facilitate receptor sensitivity (*36*).

Cartilage differs from bone by having proteoglycans, rather than hydroxyapatite matrix deposited on the collagenous frame. These proteoglycans are histochemically similar to the material of the gelatinous cupulary organs of the mechanoreceptive neuromasts (*28*). We suggest that mechanoreception was a primary function of this material. Analysis also indicates that the proteoglycans of the pharyngeal basket may initially have been secreted by pharyngeal deformation detectors. Later in evolution, proteoglycans became more widespread and increased the elastic storage capacity of the pharyngeal skeleton (*37*). Both bone and cartilage apparently spread from their primary association with the integumental and pharyngeal skeleton. Both appear as derivatives of neural crest in the facial skeleton, involving chondrification and ossification of the sensory capsules and braincase. More important, both appear in the postotic cranium and in the axial and appendicular skeletons, all of which are formed of mesodermal sclerotome without neural crest or placodal contributions (*38*). Apparently, the capacity to deposit proteoglycans and hydroxyapatite, perhaps in association with fibronectins (*39*), involves a shift of the secretory or inductive capacity among cell lineages. The potential for such change of tissue specificity has now been observed, for instance, for enzymes among populations and even species of *Drosophila* (*40*).

These considerations suggest that skeletal materials arose from neural crest in the pharynx and integument of the head and that they later appeared in the cranial capsule and still later in the postotic skeleton. They support the concept that the postotic skull and the vertebral and appendicular systems arose first in gnathostomes and that the situation seen in Recent agnathans is, in this sense, not degenerate but primitive (*41*).

The relative antiquity of cartilage and bone remains in dispute (*42*). If cartilage is viewed as a material that initially aided transduction-amplification and only later became involved with facilitation of the elastic recoil of the pharynx, it was presumably involved in the shift of the pharyngeal structures from filter-feeding to ventilation (*43*). The probable role of the neural crest in this shift to ventilation is further indicated by its contribution to the muscular aortic walls and the sensory neurons involved in proprioception (*15–19*). The enhancement of gas exchange in the pharynx must have preceded the reduction of diffusional gas exchange across the integument, which would have been a corollary of any extensive bony armor. It follows, then, that the primary cartilage of the pharynx must have arisen earlier than dermal bone. Apparently, cartilage later developed a role as an embryonic supportive tissue, particularly in zones of articulation (*44*). The skeletal tissues thus appear to be derivatives of sensory transducers, but also show a strong association with the enhancement of gas exchange.

The New Head

The preceding arguments suggest that most novel vertebrate characters were derived by modification of preexisting embryonic tissues in protochordates. Hypomeric muscularization seems to be a common phenomenon, as is the origin of the neural tissues from the ectoderm. However, it is more difficult to understand why the neural crest should function like mesoderm in the anterior head. This is clearly the most striking change coincident with vertebrate origins; to make a crude analogy, the vertebrate head may be conceived as an addition to the existing body of protochordates.

Although there have been many studies of vertebrate head segmentation, they disclose no simple pattern and investigators disagree about mechanisms and their significance (*45*). There are at least two segmentation series, the epimeric and the hypomeric one. Yet, such rostral structures as the dermal bones and the anterior neurocranium do not fit either series. The formation of these new structures by an elaboration and modification of the unsegmented embryonic nerve plexus seems to be consistent with the absence of a clear segmental pattern. Thus, the existing segmentation of the head of protochordates was not disturbed; instead, the capsules associated with the special sense organs and the proliferation of the anterior end of the nerve cord developed anterior to the rostralmost notochordal tip and its flanking epimeres (somites and segmented blocks of dorsal mesoderm).

Both series of truly segmented structures seen in vertebrates then are retentions from a protochordate level of organization. The epimeric segmentation derives from the muscularization of body tissues for locomotion, and the branchial segmentation from hypomeric modification for filter-feeding. The origin of vertebrates did not involve any further segmentation. According to this view all expressions of segmentation of the nervous system relate to the existing epimeric and hypomeric segmentation of the mesoderm.

Even though the basic developmental sequences remain unchanged, the utilization of neural crest tissues would permit major structural modifications. Thus, gastrulation and its attendant redistribution of mesodermal tissues, including the chordamesoderm, need not be reorganized (*46*). Instead, the modification may have been concentrated in the ectoderm and all of the observed changes would involve the ectoderm and its interactions with other tissues. Anterior prolongation utilized the matrix-forming capacity of the epidermal nerve plexus; it did not increase the number of anterior mesodermal segments or cause their rostral elaboration. Many of the complications encountered when attempting to establish a simple solution to the "segmentation" of the prootic head, therefore, only reflect the fact that much of this region is intrinsically unsegmented. The epidermal modifications provided a framework for an array of sequential, but not segmentally, arranged structures.

Scenario

When the shared-derived characters for vertebrates are contrasted with the characters of chordates, it appears that vertebrates arose gradually from animals resembling ciliated filter-feeding protochordates that used muscular propulsion in their adult stages (Fig. 1). Apparently, such organisms resembled Recent cephalochordates. They had a notochord that could be bent by the sequential and alternating contraction of myotomal muscles, and a pharyngeal basket with a skeleton of collagenous branchial bars. These animals also seem to have been filter-feeders that transported both a mucous strip and water currents by ciliary propulsion and to have utilized a ciliated endoderm to transport food down the gut. Presumably, they obtained their respiratory gases by diffusion across the pharyngeal walls and the body surface. Further, their circulation involved only myoepithelial pumping action at the base of the aortic arches; they lacked both a central heart and capillaries on the surface epithelium of the pharyngeal bars (*47*). These organisms may have differed from modern cephalochordates in having a far more extensive epidermal nerve plexus (*48*).

The primary shift to a vertebrate condition apparently involved a modification of the filter-feeding mechanism to a mechanism that permitted use of selective predation and made larger prey items accessible. To the extent that larger prey was available in the environment, its capture would not only have increased the range of nutrients, but established advantages for increased predator size and consequently for increased metabolic output; an improvement of the mechanism for gas exchange would then have acquired a substantial advantage.

This improvement was accomplished by muscularization of the hypomere into "branchiomeric" muscle and by the capacity for muscular deformation of the pharynx. Also, there was replacement of collagenous pharyngeal bars by more elastic cartilaginous ones that permitted elastic recoil, using the energy stored during muscular pharyngeal deformation (*43*). In parallel, there was subdivision of the circulatory system into capillary beds beneath the gill epithelia, muscularization of the aortic arches, the development of a central heart and circulating erythrocytes. Also, the wall of the gut became muscularized and this increased the capacity to deal with larger prey items in a larger lumen utilizing extracellular digestion. All of these changes involved the development of new sensory, integrative, and motor controls, which apparently were centralized by expanding the neural tube to form the spinal cord and hindbrain. At this stage the paired and external special sense organs developed, as well as a central integrative capacity for utilizing the increased information they provided.

A further level of modification involved the enhancement of electroreception and its development into a major sensory modality capable of detecting distant and hidden prey. The key change was the enhancement of the detecting capability of the system by the deposition of hydroxyapatite. These deposits led first to dentinous and enamel-like tissues, to maintain the spatial orientation of the sensory receptors. The development of such a bony base, including the ossification of the neurocranium, clearly occurred late in the transition to the vertebrate condition, as the first recognizable agnathans already had all major sense organs, brain divisions, and cranial nerves (*26*). Ossification, then, is the latest rather than an early indicator that the vertebrate grade has been attained—an achievement that had been preceded by acquisition of most of the aspects that we identify as shared-derived characters of vertebrates.

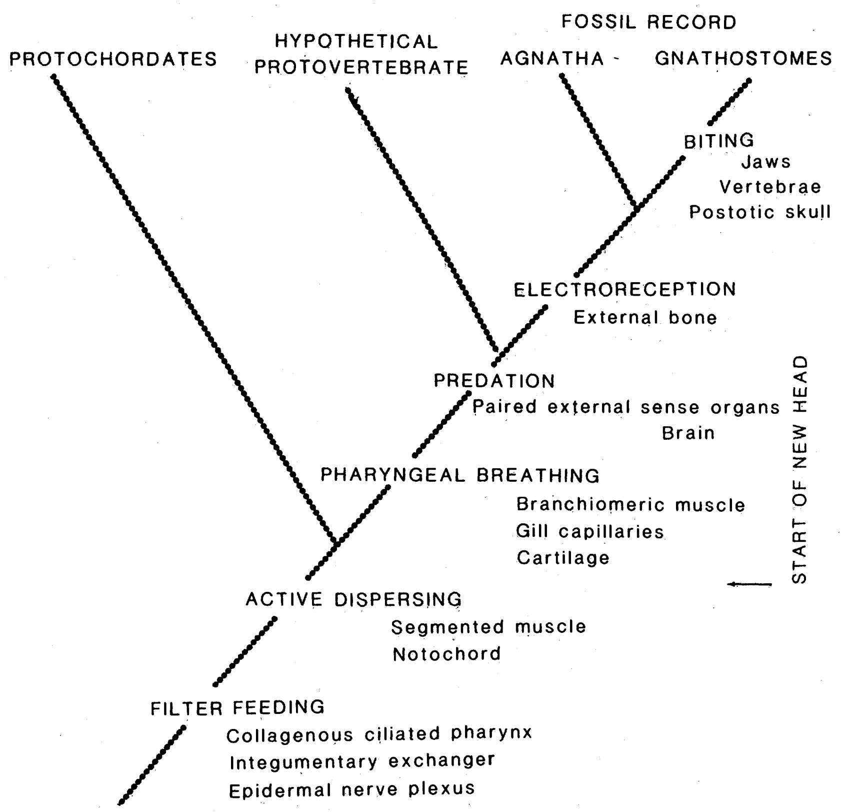

Fig. 1. Hypothesized structural and functional transitions in vertebrate evolution. The postulated functional states (capitals) precede the modified structures (lower case letters) involved with them.

This sequence of modifications suggests how a shift from filter-feeding to active predation could allow and facilitate an increased metabolic rate (*49*) and the structural correlates thereof. Many of these modifications probably occurred in postmetamorphic adults rather than in the early embryonic stages of the protovertebrates. Metamorphosis occurs in all protochordates and most anamniotic vertebrates; hence, it presumably occurred in the transitional forms. Thus, the larval stages of the earliest vertebrates likely retained some level of ciliation, filter-feeding, and other aspects, interpreted here as conservative protochordate characters.

While these modifications were being evolved, the new sense organs and the integrative specializations of the new vertebrates apparently developed anterior to the existing nerve tube. Thus, most of the vertebrate head and brain lies anterior to the tip of the notochord. Most of the new tissues and organs, as well as their surrounding and supportive elements, derive embryologically from tissues that formerly gave rise only to the epidermal nerve plexus. This change accounts for many of the differences in the organization of the structures between the vertebrate head and the trunk; much of the head represents an addition and does not represent a modified portion of the existing trunk (*50*).

The final stage would have involved the modification of the anterior gill bars into the articulated jaws, characterizing gnathostome animals. The "new" head, formed in the preceding stage, is homologous only to that portion of the gnathostome head which lies anterior to a line passing through the otic region; the (mesodermal) postotic skull develops as part of the transition to gnathostomes. Furthermore, the gnathostome condition is marked by such associated specializations as discrete teeth and by the first appearance of true vertebrae. At this level, the scattered segmental cartilages of agnathans are transformed into the more complex and articulating vertebral arches that later provide replacement of the notochord. As vertebrae appear to have arisen only at the gnathostome level, it may be appropriate to resurrect the name and implied concept Craniata for the agnathans plus gnathostomes, now referred to as the Vertebrata.

Alternatives and Implications

There should be little or no disagreement about the structures we consider vertebrate nor about their embryonic origins. Furthermore, there is likely to be little disagreement about the present biological roles of these vertebrate elements. Alternative views are possible about the phylogenetic sequence in which these vertebrate characters appeared and about their phyletically early functions or their advantages at the time of origin.

It could be argued that rather than being selected by the advantages associated with active predation, many of the characters only reflect a shift to larger size of animals that retained filter-feeding. However, the sensory structures, which so obviously characterized even the earliest vertebrates, are distance receptors, and elsewhere only occur in actively predacious animals. Even more profound disagreements might concern the possible origins of neural crest and placodes, and the reality of their homology to the epidermal nerve plexus of other deuterostomes. They might be homoplastic and have independently evolved from ectodermal tissues.

Although phyletic hypotheses cannot be tested directly, predictions that follow from them are subject to test. If our hypothesis is correct, ectodermal placodes and neural crest should share more similarities with epidermal nerve plexus than any one of them does with other ectodermal derivatives. This would not be expected if they were all separate and independent derivatives from ectoderm. The possibility could be checked as soon as monoclonal antibodies against neural crest or placodal tissues become available.

There are also other identified biochemical markers, such as the S-100 protein which already has been demonstrated in numerous crest-derived tissues (*51*). If we are correct, some such substances should also occur in tissues derived from the placodes and in the epidermal nerve plexus of protochordates (but not in ectoderm generally). Obviously, the compounds of interest are those which are neither common properties of all ectoderm nor of only one of the three tissue types.

The general hypothesis offered here may allow a reexamination of various conflicting views regarding issues, such as coelom formation and the putative sister group of the Chordates. Also it has important bearing on the issue of head segmentation, because the theory invalidates the traditional view that branchiomeric cranial nerves are serial homologs of the dorsal spinal ones. It also raises questions about the origin and subsequent evolution of the paired sense organs, as well as the possibility that the forebrain and its paired evaginations, which form the epiphysis, paraphysis, and eyes, arose later in phylogeny than the remainder of the central nervous system.

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35. Many modern fishes insulate their electroreceptors by placing them into canals lined with doubly layered pavement epithelia connected by tight junctions and coated by layers of collagenous fibers; however, it has been noted that the resistivity of dentine is equivalent to that of the soft insulating tissues (*34*).
36. Once such integumentary calcification had progressed to the level of continuous plates it would obviously have further advantages, such as predator deterrence, ion storage, and others tabulated by L. B. Halstead [*Proc. Malacol. Soc. London* **38**, 552 (1969)].
37. A similar type of sensory mechanism apparently exists in amphioxus in which sensory cells are embedded in the deforming notochord [Q. Bone, *J. Comp. Neurol.* **115**, 27 (1960)].

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43. The earliest branchiomeric muscles were likely involved only in pharyngeal contraction, with expansion, that is, the return to the primary shape, driven by elastic recoil. Two-phase pumping, such as seen in Recent gnathostome fishes, in which each phase is driven by independent action of different muscles, probably arose much later.
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47. Indeed, the blood flow proceeds through aortic arches that are embedded in the collagenous supportive bars, rather than running immediately beneath the epithelium, as in vertebrates (*9*).
48. Such an epidermal nerve plexus has been observed in the ectodermal lining of the cephalochordate atrium [Q. Bone, *Philos. Trans. R. Soc. London Ser. B* **243**, 241 (1961)]; it is not clear whether and how far the plexus extends over the remainder of the body in larval and adult cephalochordates.
49. J. A. Ruben and A. F. Bennett, *Nature (London)* **286**, 886 (1980); *ibid.* **291**, 411 (1981).
50. In this context, we note the articulation of the jaws to the neurocranium; the jaw articulation generally marks a position homologous to the most rostral extent of the protochordate head.
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52. This set of concepts has been discussed with many colleagues and any list of acknowledgements is likely to be incomplete [we cite many of them in (*3*)]. The present manuscript benefited from comments by R. H. Denison, G. C. Gorniak, N. Kemp, D. Noden, R. A. Nussbaum, P. Pridmore, G. R. Smith, and L. Trueb. The concepts noted in this article were first presented at the 1981 meeting of the Society for Vertebrate Paleontology on 29 October, Ann Arbor, Michigan. Supported by NSF grant DEB 80-03678 and DHEW PHS grants 1RO1 DEO 5112-03 (to C.G.) and NS 11006 and EY 02485 (to R.G.N.).

The "Decade of the Environment" in the U.S.S.R.

Philip R. Pryde

Ten years ago there appeared the first American monographs having as their goal the establishment of the status of environmental protection activities in the U.S.S.R. (*1, 2*). Their conclusion, based on a systematic review of the major categories of natural resources, was that the state of the environment in the Soviet Union was not significantly different in most respects from that in the United States. In both countries environmental protection and the prudent use of natural resources is accorded a high official priority; in both countries major pollution and waste problems arise more from the inherent nature of economic processes than from the country's political or economic system; both countries are working to reduce waste and pollution as much as possible; and both countries are finding the latter difficult to accomplish because of the high cost of pollution abatement measures or an inadequate level of field inspection and enforcement.

The objective of this article is to examine the state of resource conservation and environmental protection in the U.S.S.R. at the beginning of the 1980's, as compared to the early 1970's. Without question, much environmental improvement took place in the Soviet Union over the past 10 years, but in what areas were significant advances realized and in what areas not? In the United States, the 1970's were the "decade of the environment"; was this also the case in the U.S.S.R.?

Economic Imperatives

Both environmental degradation and environmental improvement normally take place at a slow but steady pace, often involving imperceptible changes over a short time span. In the Soviet Union in the 1970's, however, these changes were influenced by two economic events of particular concern. The first was a general downturn in what had been for three decades an unbroken and vigorous rate of industrial expansion (from about an 8 percent annual increase from 1965 to 1970 to about 4½ percent from 1975 to 1980). The second was the worldwide energy crises of 1973 and 1979, from which the Soviet Union was not entirely isolated. Both events have given new impetus to the subject of resource conservation in the U.S.S.R. and will help put the rest of the discussion into perspective.

The downturn in average annual rates of increase in Soviet industrial production has been accompanied by a clearly stated need to improve the efficiency with which natural resources are used. Soviet spokesmen acknowledge that such improvement would not be difficult, and the 1972 studies cited many lamentations in the Soviet press over wasteful practices in such industries as petroleum extraction and timber harvesting (*1*, pp. 96–106). Particularly common were the burning off of large quantities of wellhead gas and the carrying out of inadequate reforestation measures. The situation apparently has improved only marginally, and leading journals still frequently protest, for example, the waste of natural gas that accompanies the extraction of petroleum and coal (*3*).

The situation prompted a front page article in *Pravda* in 1981 (*4*) which presented a resolution calling for more efficient use of natural resources. It was frankly stated that "compared to the best world indices, we expend greater amounts of raw materials and energy per unit of national income. . . . [T]he CPSU Central Committee and the USSR Council of Ministers consider it necessary to fundamentally improve all efforts to economize and make efficient use of raw materials, supplies, fuel, and power in all branches of the national economy" (*4*). As one response to this, an increased emphasis on recycling, especially of newspapers and municipal wastes, has taken place in the past 10 years, paralleling similar efforts in the United States.

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