Origin and Early Evolution of Vertebrate Skeletonization

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ABSTRACT Data from living and extinct faunas of primitive vertebrates imply very different scenarios for the origin and evolution of the dermal and oral skeletal developmental system. A direct reading of the evolutionary relationships of living primitive vertebrates implies that the dermal scales, teeth, and jaws arose synchronously with a cohort of other characters that could be considered unique to jawed vertebrates: the dermoskeleton is primitively composed of numerous scales, each derived from an individual dental papilla; teeth are primitively patterned such that they are replaced in a classical conveyor-belt system. The paleontological record provides a unique but complementary perspective in that: 1) the organisms in which the skeletal system evolved are extinct and we have no recourse but to fossils if we aim to address this problem; 2) extinct organisms can be classified among, and in the same way as, living relatives; 3) a holistic approach to the incorporation of all data provides a more complete perspective on early vertebrate evolution. This combined approach is of no greater significance than in dealing with the origin of the skeleton and, combined with recent discoveries and new phylogenetic analyses, we have been able to test and reject existing hypotheses for the origin of the skeleton and erect a new model in their place. Microsc. Res. Tech. 59:352-372, 2002. © 2002 Wiley-Liss, Inc.

WHAT CAN AN ARCANE DISCIPLINE LIKE PALEONTOLOGY OFFER TO A WORLD OF MOLECULAR BIOLOGY?

Opinions on the significance of fossils differ greatly. Traditionally, paleontology has provided the only key to the past through the discovery of fossil ancestors to living groups and the only means of incorporating a temporal perspective ("deep time") to our understanding of the timing and tempo of evolutionary events. Quite rightly, this view has been challenged in recent decades with the application of more rigorous methods of uncovering the evolutionary relationships of living and fossil groups (phylogenetic systematics or "cladistics") and the impact of molecular biology on systematics, developmental biology, and estimating temporal distance between living taxa (the "molecular clock" hypothesis). It has been argued that ancestors can never be identified unequivocally (Engelmann and Wiley, 1977) and, thus, the main significance of paleontological data has apparently been lost. Further, some authors have argued that fossils are of only secondary importance to extant organisms because the former can only be interpreted in light of the latter (Patterson, 1977; Nelson, 1978). Following this line, Patterson (1981) argued that fossils had no influence on establishing the relationships among living organisms.

These commentaries have led to an extended period of introspection among the paleontological community heralding a more rigorously scientific approach to the incorporation of fossil data into evolutionary biology. Although a number of criticisms were justified, others have been rejected or qualified. Systematic studies of the relationships between major animal and plant groups have revealed that paleontological data are key to correctly resolving the interrelationships of living taxa, e.g., seed plants (Doyle and Donoghue, 1987; Donoghue et al., 1989), freshwater fishes (Wilson, 1992), tetrapods (Gauthier et al., 1988), and mammals (Novacek, 1992). This obtains because fossils help to prevent the identification of homoplasy as homology in living members of distantly related groups and identify homologies that might not otherwise be recognized as such. The importance of paleontological data is now widely acknowledged among contemporary systematists and the assimilation with data from living organisms is leading to radically different hypotheses for the origin of major groups in comparison to those based exclusively on data from living organisms.

The importance of fossil data in other spheres of evolutionary biology remains contentious. The classification of extant and extinct taxa alongside one another has led to the discovery of different patterns of character evolution. In large part this is restricted to the evolution of gross skeletal characters in that it is only the mineralized components of organisms that are readily fossilized. Nevertheless, these data can prove critical in informing developmental studies that seek to resolve macroevolutionary problems such as the origin of fins (Coates and Cohn, 1998, 1999) and limbs (Coates, 1991) among vertebrates.

Thus, even in a world of molecular biology, paleontology continues to make a unique and essential contribution to evolutionary biology through the correct

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resolution of evolutionary relationships and the discovery of taxa that exhibit combinations of anatomical characteristics not met with among the living biota. In some research areas, paleontology can make a further, more direct, contribution to understanding the evolution of development. There is no better example of this than the origin and evolution of development of vertebrate skeletal systems and there are a number of reasons. First, because oral and dermal skeletal tissues are invariably mineralized, they are readily entrained within the fossil record. Second, to a degree the developmental history of these tissues is recorded in their relationship to incremental growth lines, their topological relationships, and in the position and polarity of cell spaces incorporated within the mineralized matrix of the tissues. Third, these data can be readily reconciled with knowledge of developmental processes in laboratory animals. Finally, and of greatest importance, the organisms in which the mineralized skeleton first evolved are long extinct and there are no living relatives that can be taken as proxies in experimental analysis; for this reason alone, we have no recourse but to paleontology if we are to understand the origin and early evolution of the vertebrate skeleton, from both pattern and process perspectives. Thus, although fossils are open to fewer avenues of experimental observation, the data that are obtainable can be studied in just the same way as in living organisms.

Given that neither paleontology nor "neontology" can arrive at correct conclusions independently, there is nothing to lose and much to gain from breaking down the long-standing divisions between these two groups of scientists. From this perspective, it is perverse that groups of scientists should aim at resolving the same evolutionary problems and yet circumscribe their sources of data on the basis of those organisms that have living representatives versus those organisms that have none.

SKELETAL SYSTEMS

Debate over the origin of the vertebrate skeleton has revolved around the issue of which group is the first to exhibit evidence of skeletonization and/or mineralization (e.g., Romer, 1933; White, 1946; Sansom et al., 1992; Purnell and von Bitter, 1992; Purnell, 1995; Smith et al., 1996a,b; Young et al., 1996; Donoghue and Aldridge, 2001). What has been left behind in this discussion is a distinction between the different skeletal systems (see, e.g., Couly et al., 1993), a distinction that has been argued to be as old as the earliest evidence of skeletonization (cf. Nelson, 1970; Patterson, 1977). There are at least two distinct skeletal systems: the dermoskeleton (widely perceived to encompass teeth, scales, fin spines, etc.), and the endoskeleton (the braincase, branchial skeleton, axial and appendicular skeletons) (Fig. 1) and it has been argued that although elements of the skeleton can be interchangeably derived from either system, the two systems have remained distinct throughout vertebrate phylogeny (Patterson, 1977).

The endoskeleton may be further divided into splanchnocranial (sometimes inappropriately termed the viscerocranium), neurocranial, axial, and appendicular components, although these distinctions have not been considered in hypotheses concerning the origin



Fig. 1. The head of *Eusthenopteron foordi*, a sarcopterygian fish, demonstrating the different skeletal systems (after Jarvik, 1980). Neurocranium, dark gray; splanchnocranium, light gray; dermoskeleton, unshaded but margins between the cranial dermal bones are outlined in black.

and evolution of the skeleton. Concerning the head alone for a moment, the splanchnocranium and neurocranium may be distinguished topologically, but chiefly on their embryological origin. The splanchnocranium is derived exclusively from neural crest, while the neurocranium is derived largely from paraxial mesoderm, but with a neural crest-derived prechordal component. Kuratani et al. (1997) argue that the prechordal component of the neurocranium is more appropriately considered a premandibular component of the splanchnocranium, and its development is certainly regulated in a manner that is more akin to the mandibular arch than any component of the neurocranium. We will follow this distinction in our consideration of skeletal evolution.

Recently, it has been argued that components traditionally allied to either a uniform dermoskeleton or endoskeleton belong to a third distinct system, an "oral" skeleton (= splanchnocranium) (Fig. 1; Smith and Coates, 1998, 2000, 2001). This hypothesis rests with a reconsideration of the developmental basis of tooth development. Although teeth have traditionally been considered part of the dermoskeleton on the basis that they are borne by dermal bones, endoderm is a prerequisite for tooth development (Graveson et al., 1997), whereas it is not implicated in the development of comparable structures (scales) in the dermoskeleton and, thus, teeth may more appropriately be considered part of the endoskeleton, and the splanchnocranium in particular. Although the authors of this challenging hypothesis argue for a disassociation between the evolution of teeth and jaws, the splanchocranium as a whole appears to have a history that is both developmentally and phylogenetically distinct from other vertebrate skeletal systems, and so the distinction between teeth and oral scales may well reflect this largerscale distinction. However, whereas the distinction between the endoskeleton and dermoskeleton has been deemed to be absolute and fundamental, the origin of the distinction between oral and dermoskeletal odontogenic systems has not been considered. Below we explore the origin and pervasiveness of the distinction between splanchnocranial and dermoskeletal dental elements during vertebrate phylogeny. Further, we will



Fig. 2. Diagrammatic representation of the various groups of living and fossil chordates considered in this study. 1. Sessile tunicate. 2. Cephalochordate. 3. Hagfish. 4. Lamprey. 5. Conodont. 6. Heterostracan. 7. Arandaspid. 8. Astraspis. 9. Anaspid. 10. Thelodont. 11. Galeaspid. 12. Osteostracan. 13. Placoderm. 14. Chondrichthyan. 15. Acanthodian. 16. Primitive actinopterygian. 17. Sarcopterygian. [Color figure can be viewed in the online issue, which is available at www.interscience. wiley.com.]

examine the evolution of the skeleton taking into consideration the hypothesis that the skeleton is a mosaic of distinct endo- and dermoskeletal systems, exploring the implications that this distinction has for various hypotheses for the origin and early evolution of the skeleton among basal vertebrates. First, we must consider the interrelationships of the living and extinct groups of jawless and jawed vertebrates, but before this we introduce the various groups of basal vertebrates and their kin and outline their characteristics germane to a discussion of skeletal evolution.

DRAMATIS PERSONAE Invertebrate Relatives of the Vertebrates

The phylum to which humans and all other vertebrates belong is the phylum Chordata. The Chordata also includes two or three groups (depending on how the Vertebrata is defined) in addition to vertebrates. These are the tunicates (sea squirts; Fig. 2.1) and the cephalochordates (the amphioxus; Fig. 2.2). Neither group exhibits good evidence of skeletonization; only the ascidiacean and soberacean tunicates are able to secrete biomineralized tissues. These occur in the form of microscopic spicules embedded in the tunic wall or as amorphous pellets with a variety of mineralogies (Lambert et al., 1990). Cephalochordates exhibit limited evidence of unmineralized skeletonization, in the form of the small imbricating cartilaginous rods that support the buccal cirri and the external openings of the pharynx (e.g., DeBeer, 1937).

Jawless Wonders

Hagfishes (Fig. 2.3) and lampreys (Fig. 2.4) are basal vertebrates that are distinguished from more derived living groups by the primary absence of jaws. Although vertebrates, both groups lack many characteristics that might generally be perceived characteristically vertebrate, such as any form of mineralized skeleton or paired fins. There has been considerable debate over the nature of the living jawless vertebrates, not least their relationship, but also in consideration of how the anatomy of living forms may or may not be representative of Paleozoic antecedents.

Chordates are clearly dominated by the vertebrates. Vertebrates in their turn are dominated by the jawed

vertebrates, but it has not always been so. Living jawless vertebrates are just two conservative groups among a plethora of jawless groups known from the Paleozoic fossil record (545-250 million year ago). Jawed vertebrates did not attain their numeric dominance over jawless vertebrates until the Upper Paleozoic. Thus, if we were to compare current vertebrate diversity to that of, for instance, the Silurian (428-418 million years before present), we would see a complete reversal of this pattern of dominance (compare Figs. 3 and 7). Of greater significance in our quest to examine the origin and early evolution of vertebrate skeleton, the fossil record reveals that, in contrast to the "naked" hagfishes and lampreys, the vast majority of jawless vertebrates were extensively skeletonized and, thus, the living representatives of this grade of organization are entirely unrepresentative of their extinct relatives.

Fossil jawless vertebrates are dominated by the "ostracoderms" (Fig. 2.6–2.12), so-called because they are characterized by an extensively developed mineralized dermal skeleton. In some groups the dermal skeleton is composed of individual scales in a manner comparable to living sharks, in others only the trunk and tail are covered by discrete scales, while the head and portion of the trunk immediately adjacent is encased in relatively few large plates that are sometimes fused to form a head "capsule." The most pertinent difference between "ostracoderms" and the living jawless vertebrates is in their ability to synthesize a mineralized dermal skeleton; neither grade of organization includes a mineralized vertebral skeleton.

The anaspids (Figs. 2.9, 5.7) are a relatively small group that shares many anatomical similarities to lampreys, such as the morphology of the caudal fin and the apparent single nostril. Anaspids differ from lampreys in the possession of paired ventro-lateral fins, a mineralized dermal skeleton composed of hundreds of small scales, and a "mandibular" plate that acted in a dorsoventral orientation rather than the bilaterally acting "rasping tongues" of hagfishes and lampreys.

Conodonts (Fig. 2.5) are the first group of skeletonizing vertebrates to make an appearance in the geological record. The gross anatomy of conodonts is common to hagfishes and lampreys, but conodonts differ most significantly in the possession of a complex array of dental elements (Fig. 5.1, 5.4) that occupied an internal (buccopharyngeal) position. No dermoskeleton was present and thus the conodonts are set apart from all other "ostracoderm" groups. The homologies of the tissues comprising the dental elements have been the subject of vigorous debate (Dzik, 1986; Sansom et al., 1992, 1994; Kemp and Nicoll, 1995a,b, 1996; Sansom, 1996; Schultze, 1996; Smith et al., 1996a; Donoghue, 1998; Donoghue and Chauffe, 1999; Donoghue et al., 2000; Donoghue and Aldridge, 2001) but homology with vertebrate hard tissues is supported on the basis of fabric, structure, topological and inferred developmental tissue relationships, their arrangement into tissue complexes, and phylogenetic congruence. Conodont dental elements are considered to be composed of dentine (Fig. 5.3) and enamel (Fig. 5.2).

Galeaspids (Fig. 2.11) are a diverse group that exhibits an anatomy that is superficially similar to the osteostracans, but galeaspids appear to primitively lack paired fins and are easily distinguished from osteostracans on the presence of a large rostral olfactory opening in the cranial dermoskeleton that continues through to the oralo-branchial chamber. The dermoskeleton can be divided into cranial and postcranial divisions. The cranial skeleton is composed of two or more large plates that are probably fused together in branchial area of the animal. The composition of the cranial skeleton is not well understood, although published data indicate that it is composed of acellular bone and an internal unmineralized cartilaginous endoskeleton lined with perichondrally ossified acellular bone (Janvier, 1990; Zhu and Janvier, 1998). The postcranial skeleton is very poorly understood and nothing is known of its histological composition.

The heterostracomorphs are dominated by the heterostracans (Figs. 2.6, 5.8), which are a very diverse group characterized by a cephalothoracic dermal skeleton composed of two or more large plates that enclose the body; although some of the component plates are fused together, more usually they abut against one another. The trunk and tail dermoskeleton is composed of diamond or lath-shaped overlapping scales. All components of the dermoskeleton are composed of a superficial layer of dentine, acellular bone, and, in some taxa, enameloid, arranged in discrete tubercles or ridges; this overlies a middle layer of acellular bone that either exhibits a gross spongy texture or is organized into discrete osteons onto which the pulp cavities of the superficial layer open. The basal layer is also composed of acellular bone arranged in sheets that unite the osteons.

The remaining heterostracomorphs are Astraspis (Figs. 2.8, 5.5), Eriptychius (Fig. 5.6), and the arandaspids (Fig. 2.7). Arandaspids are numerically abundant but are taxonomically restricted to two taxa, from the Ordovician of Australia and South America. Arandaspids are anatomically very similar to heterostracans but differ chiefly in the condition of the exhalent gill openings. The dermoskeleton is structurally very similar to that of heterostracans, but poor preservation precludes precise determination of the tissue types (Gagnier, 1993). Astraspis also differs from heterostracans chiefly on the basis of the exhalent branchial openings, and possesses a dermoskeleton that is also composed of acellular bone, dentine, and enameloid, but the bone exhibits a spongy macrostructure in contrast to the vaulted structure of the dermoskeleton in heterostracans and arandaspids (Sansom et al., 1997). *Eriptychius* is known from disarticulated scales, scale fragments, and one small area of articulated squamation (Denison, 1967); the gross anatomy of this taxon is completely unknown. The overall structure of the dermoskeleton is similar to Astraspis, although enameloid is not present and some skeletal fragments include endoskeletal globular cartilage (Fig. 6.2) (Denison, 1967).

Osteostracans (Figs. 2.12, 5.9) are a very diverse group that encompasses a wide range of anatomical designs, including forms that possess paired (pectoral) fins as well as forms that do not. Osteostracans are characterized by a completely fused head capsule composed of dentine and cellular bone. Osteostracans are one of the few groups of jawless vertebrates to possess a mineralized endoskeleton which is limited to the head and shoulder girdle and composed of unmineralized to mineralized cartilage lined with cellular perichondral bone (Stensiö, 1927).

Thelodonts (Fig. 2.10) possess a dermoskeleton of numerous minute scales that give these animals a shark-like appearance. The individual scales are composed of dentine and, possibly, acellular bone. At least some thelodonts also exhibit a skeleton composed of minute scales lining the buccopharynx and, possibly, associated with the gills (van der Brugghen and Janvier, 1993; Donoghue and Smith, 2001). The function, developmental origin, and phylogenetic significance of these structures remains equivocal. Thelodonts possess paired (pectoral) appendages, although whether these structures are homologous to true fins, or else are merely "flaps," remains the subject of debate.

Primitive Jawed Vertebrates

The basal living groups of jawed vertebrates are the chondrichthyans (Figs. 2.14, 6.1, 6.3–6.6; sharks and rays), actinopterygians (Fig. 2.16; ray-finned fishes) and sarcopterygians (Fig. 2.17; lungfishes, coelacanths, and tetrapods—including humans), the latter two comprising the Osteichthyes (bony fishes); all groups possess an axial and appendicular endoskeleton.

Chondrichthyans possess a dermal skeleton composed of microscopic scales (Fig. 6.1) that each develop from single dental papillae, as do the teeth. The remainder of the skeleton, the endoskeleton, is almost entirely cartilaginous, although some living groups exhibit perichondral bone lining the cartilage. If extinct members of the group are considered, this condition is by no means representative of chondrichthyans as a whole. Living chondrichthyans are only a derived vestige of the total group diversity and, as a rule, most chondrichthyans were more heavily skeletonized, with a greater proportion of perichondral bone and a dermal skeleton including scales that continued to grow throughout life, each scale composed of numerous dental units that appeared in succession (e.g., Zangerl, 1966, 1968; Figs. 6.3–6.6). Available evidence suggests that the oldest known chondrichthyans (not necessarily the most primitive) lacked teeth (Sansom et al., 1996, 2000, 2001).

Primitive osteichthyans, such as Polypterus and Latimeria, possess a dermal skeleton including growing scales that are composed of numerous dental units that are added in succession and teeth that are replaced from below in a manner more comparable to our own than to the pattern of replacement exhibited by chondrichthyans. The primitive osteichthyan endoskeleton is also heavily skeletonized, although more derived members of the clade, particularly among the actinopterygians, exhibit evidence of secondary reduction in calcification of the skeleton. The generalized pattern of osteichthyan endoskeletal development is for skeletal elements to pass from a cartilaginous, through perichondral to endochondral pattern of ossification. Thus, skeletal reduction among actinopterygians has been accounted for by heterochrony. The fossil record of primitive osteichthyans bears this pattern out.

There are two principle extinct groups of primitive jawed vertebrates: acanthodians (Fig. 2.15) and placoderms (Fig. 2.13). The dermoskeleton of acanthodians is guite conservative throughout the group: a trunk and tail skeleton composed of numerous diamondshaped composite scales and a cranial dermoskeleton composed of a number of plates of unknown composition: the dermoskeleton also includes fin spines. The oral skeleton is variable and teeth are present in only one of the many acanthodian subgroups, the ischnacanthids. Ischnacanthids possess two types of teeth: symphyseal tooth whorls and marginal jaw-borne teeth (Ørvig, 1973; Denison, 1978). All elements of the dermoskeleton and oral skeleton are composed of dentine and cellular bone, no enamel-like tissues are present (contra Richter and Smith, 1995). The endoskeleton, which includes axial and appendicular components, is composed of cartilage, lined with perichondral bone, and permeated by endochondral bone.

Placoderms possess a dermal skeleton that occurs in two divisions, much like the dermoskeleton of osteostracans. The trunk and tail skeleton is made up of numerous diamond-shaped scales, while the cranial and immediately postcranial skeleton is united into a single head capsule composed of a number of large plates united by scarf joints. Both divisions of the dermoskeleton are composed of dentine and cellular bone. The oral skeleton of placoderms is unusual in that although most taxa possessed a biting dentition, there is no evidence of teeth or tooth-like tissues except for small dentine tubercles present on the lingual margin of the jaw bones in some taxa (Ørvig, 1980). The jaw bones provide a self-sharpening biting surface. The endoskeleton includes a perichondrally ossified brain case, often with distinct sensory capsules; the axial and appendicular skeletons are also perichondrally ossified (Denison, 1978).

INTERRELATIONSHIPS OF LIVING AND EXTINCT GROUPS OF JAWLESS AND JAWED VERTEBRATES

Recovering evolutionary patterns is impossible outside of a framework of evolutionary relationships and, thus, to a greater or lesser extent, all evolutionary hypotheses stand or fall with the systematic framework on which they are based. This is problematic because resolution of the interrelationships of the living and extinct groups of jawless and jawed vertebrates have proven intractable ever since the first endeavors were undertaken. There are essentially two main hy-potheses: the "ostracoderms" comprise two principal groups, the "pteraspidomorphs" and "cephalaspido-morphs," dominated respectively by the heterostracans and osteostracans, to which the living hagfishes and lampreys are attributed, respectively. Further, these groups share a common ancestor to the exclusion of jawed vertebrates; all three main groups share a common ancestor unknown and shrouded in the depths of deep time (Stensiö, 1927, 1958, 1964, 1968; Jarvik, 1980; Bjerring, 1985). The main alternative view is set against the framework of cyclostome paraphyly and posits that the "ostracoderms" are also paraphyletic (although there may be local monophyletic groups), with some taxa more closely related to jawed vertebrates that others (Janvier, 1981, 1996a.b: Forev and Janvier, 1993; Donoghue et al., 2000). It should be noted that there are a number of iterations about these extremes. Further, cyclostome monophyly/paraphyly

and "ostracoderm" monophyly/paraphyly are not mutually dependent and it has been demonstrated that "ostracoderm" paraphyly stands even if cyclostome monophyly is imposed (Donoghue et al., 2000).

The main source of contention lies with the manner in which the hypothesis of relationships is inferred. Cyclostome and "ostracoderm" monophyly are resolved from morphological datasets only when particular emphasis is placed on characters that are inferred to have greater evolutionary significance than others, relying on a priori knowledge of the hypothesis of relationships that is to be recovered (e.g., Stensiö, 1958). Cladistic analyses require no such assumptions and consistently resolve "ostracoderms" as paraphyletic (e.g., Janvier, 1981). For this reason, we follow cladistic methodology in assembling a systematic framework against which to examine the origin and early evolution of the vertebrate skeleton.

Building on earlier work (Janvier, 1981; Forey and Janvier, 1993, 1994; Forey, 1995; Janvier, 1996a,b), Donoghue et al. (2000) and Donoghue and Smith (2001) have undertaken the most recent and inclusive cladistic analyses of the interrelationships of living and extinct lower vertebrates and a summary of the results are presented in Figure 3 (refer to the original articles for the data on which these hypotheses are based). This hypothesis supports the view that both cyclostomes and "ostracoderms" are paraphyletic, with the "ostracoderms" resolved as more closely related to living jawed vertebrates than either hagfishes of lampreys; conodonts are resolved as basal members of this "ostracoderm" lineage. In terms of systematic classification, these results have a number of significant implications, particularly if we are to follow the dictates of phylogenetic systematics. While it is permissible to continue formal recognition of paraphyletic groups, there is now widespread acceptance that only monophyletic groups should be recognized. Although paraphyletic groupings serve a useful purpose in reflecting grades of organization, the divisions between which also reflect significant evolutionary events in the phylogeny of life (Cavalier-Smith, 1998), they also serve to obscure the evolutionary relationships between these groups. The situation is particularly problematic with fossil taxa, where classifications based on extant taxa are defined on the basis of a suite of characters that all members of the group possess. Fossil taxa invariably possess subsets of these characters, but not all of the characters and, hence, they fail to qualify as members of the group. But these character suites were acquired in sequence, rather than concurrently, during the evolutionary history of a group since its divergence from the lineage leading to its nearest living relative; fossil taxa record this sequence of character acquisition and they are clearly more closely related to the group with which they share a subset of the defining characters than to any other. Rather than separating them into a distinct paraphyletic group, thus, emphasizing an evolutionary episode not represented by extant taxa, cladistic classification provides a means of reflecting their evolutionary relationship to their nearest living relatives. "Crown" groups define all the living members of a group and all extinct members derived from the common ancestor of the living members of the group; the "stem" group defines the extinct



Fig. 3. Phylogenetic relationships between the groups of chordates considered in this study. The black bars across the top refer to the various taxonomic groups and grades of organization used; lettered nodes refer to significant events in the various chordate and vertebrate skeletal systems. A: Origin of the earliest skeleton in the vertebrate lineage—a splanchnocranium. B: Anatomical development of the splanchnocranium in concert with its takeover by neural crest; origin of a neurocranium. C: Further development of the splanchnocranium and neurocranium, origin of neural elements in the axial endoskeleton. D: Origin of mineralized splanchnoskeletal elements the odontode, origin of dentine. E: Origin of a mineralized dermal

skeleton—multicomponent scales are primitive, origin of dermal bone. **F**: Origin of perichondral bone, origin of a mineralized endoskeleton. **G**: Origin of cellular dermal and endoskeletal bone, origin of an appendicular endoskeleton, splanchnocranial ossification-proper. **H**: Origin of a mineralized axial endoskeleton, ventral vertebral elements, centra (arcocentra), origin of "teeth." **I**: Dental elements consistently associated with the splanchocranium including branchial arches. **J**: neurocranium composed of distinct ossifications, splanch nocranium well ossified. **K**: origin of endochondral bone, dermoskeleton, and endoskeleton well ossified. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

taxa that are more closely related to the crown group than to the nearest living relative of the crown group (Hennig, 1966; Jefferies, 1979). The total group encompasses both the stem and crown group (Jefferies, 1979).

The application of cladistic classification to the hypothesis of relationships presented in Figure 3 would circumscribe conodonts and the "ostracoderms" as the stem-group to the crown-group Gnathostomata (note that Gnathostomata does not equate to jawed vertebrates because placoderms, basal jawed vertebrates, are not mem-

bers of the crown group; Fig. 3). While it is possible to give the stem and crown-groups distinct names (e.g., de Queiroz and Gauthier, 1992), this would serve only to recognize a paraphyletic group and it is common practice to recognize only the total group with a formal name (Smith, 1994). Thus, conodonts, the "ostracoderms," and all jawed vertebrates fall within the total group Gnathostomata; all living jawed vertebrates and all extinct taxa derived from the common ancestor of jawed vertebrates comprise the crown group Gnathostomata, while stem group Gnathostomata is composed of conodonts, "ostracoderms," and placoderms.

With this systematic framework and vocabulary in place, it is possible to infer the significance of the various living and fossil groups to tracing the evolution of the various organ systems through the phylogeny of early vertebrates.

INVERTEBRATE NONCHORDATE ORIGIN OF VERTEBRATE SKELETONIZATION?

Many classical attempts to unravel the origin of vertebrate skeletonization have considered the skeletal systems of nonchordates as possibly reflecting an "ancestral" condition (Moss, 1964, 1968). These rest with the assumption that vertebrates, or chordates, shared a common ancestor with any other clade of animals that itself possessed a mineralized skeleton, and while, e.g., brachiopods and bryozoans were included within the deuterostomes, this remained a possibility. However, this scenario is no longer appropriate, given the revolution in our understanding of metazoan relationships that has occurred with the rise of molecular phylogenetics (e.g., Field et al., 1988; Peterson and Eernisse, 2001). Brachiopods and bryozoans have been expunged from the Deuterostomia and, with molluscs, annelids, etc., constitute the protostome superclade Lophotrochozoa (Halanych et al., 1995); chaetognaths and nemerteans have similarly been expelled from among the deuterostomes and, together with arthropods etc., comprise the other protostome superclade Ecdysozoa (Aguinaldo et al., 1998). Skeletal biomineralization is now envisaged to have arisen independently in a great number of distinct lineages during the so-called "Cambrian explosion" which, originally perceived as the major diversification event in metazoan evolutionary history, is now becoming widely reinterpreted as a less significant phase of widespread skeletonization, possibly coincident with a rise in predation (see e.g., Bengtson, 1998; Peterson et al., 1997). The origin of a skeleton in chordates represents but one of these many experiments with skeletonization among metazoans and, thus, it would appear that their relatives offer few clues to the plesiomorphic condition of the chordate skeleton. Perhaps the only important legacies of chordate evolutionary history germane to the origin of a skeleton are the conserved regulatory genes that are integral to the development of the skeleton and other organs, both in chordates and other metazoans (e.g., BMPs, FGFs, Shh, etc.).

One specific hypothesis (Jefferies, 1986) argues that the plesiomorphic chordate skeleton was a mesodermal calcitic tissue called stereom, which comprises the skeletons of all living and fossil echinoderms (e.g., Smith, 1980). This, the "calcichordate" hypothesis, interprets an extinct group of organisms as stem-chordates and craniates, rather than following the convention of recognizing them as stem- or crown-echinoderms (e.g., Philip, 1979; Gee, 2001). Like echinoderms, "calcichordates" possess a stereom skeleton and, thus, the calcichordate hypothesis requires this skeleton to have been lost at least three times in the lineages leading to cephalochordates, tunicates, and craniates, respectively (see Gee, 1996 for an outline of the debate). Assuming that this theory is correct, there is little to compare between the mesodermal skeletal tissues of chordates and echinoderms (e.g., the non-neural crestderived cartilages of the living jawless vertebrates are noncollagen-based, while stereom is permeated by extrinsic collagen fibers). However, there are problems with the theory and it has been argued that even if the anatomical interpretations of "calcichordates" are accepted, they fail a test of phylogenetic congruence (Peterson, 1995; but see Jefferies, 1997). And, further, the interpretation of "calcichordate" anatomy has not been undertaken without the a priori assumption that these organisms are either chordates or echinoderms, precluding appropriate testing of whether a chordate, echinoderm, or plesiomorphic deuterostome milieu is the most appropriate framework.

Given that we are attempting to trace the evolutionary history of chordate skeletonization, it would not be appropriate to turn aside from the "calcichordates" on the flimsy reasoning that there is equivocation over their precise place in the tree of life. However, it is our opinion that the weight of evidence suggests that the "calcichordates" are either members of the total-group Echinodermata, or else that they occupy a more plesiomorphic position among deuterostomes (cf. Gee, 2001). Thus, in the knowledge that stereom is not germane to our understanding of chordate skeletal evolution, we will turn aside from the "calcichordates."

THE ENDOSKELETON: SKELETONIZATION AND CALCIFICATION

"Evolutionary and developmental histories...seem to tell the same story; ontogeny appears to recapitulate phylogeny, and there is seemingly ample reason to justify current belief in the primitiveness of cartilage. It is, however, highly probable that this pretty picture is a delusion and the reverse of the true situation. Modern evidence suggests that bone, not cartilage, was the primitive skeletal material; that cartilage originally was not an adult tissue but a purely embryonic one, evolved in connection with the development of internal skeletal elements; and that the presence of cartilage in the adult is indicative not of a primitive condition but of a paedogenesis, the retention in the adult of an embryonic stage of the skeletal development" (Romer, 1942, p. 394).

As can be inferred from the above quote, the views on the origin of the vertebrate skeleton from the early 20th century were based on a direct reading of the Scala naturae of living vertebrates. It posited that the skeleton was primitively unmineralized and cartilaginous, as exemplified by the "lowest" of living vertebrates, and exhibited a pattern of progressive calcification through phylogeny. This all changed with the discovery of the "ostracoderms" that, in a paradigm of ancestor-worship and phylogenetic reconstruction via "phyletic trends," provided a basis for the reinterpretation of the Scala naturae. Following Stensiö's (1927) hypothesis that the "ostracoderms" were ancestors of the living jawless vertebrates, Romer (1933, 1942, 1963, 1964, 1967) argued that the skeleton was primitively heavily mineralized and the phyletic trend within all vertebrate lineages was one of skeletal reduction. The naked "agnathans" were deemed little more than neotenic "ostracoderms," wholly unrepresentative of the skeletal characteristics of their ancestral kin.



Fig. 4. Cranial endoskeletons of the living jawless vertebrates. 1. Hagfish (after Marinelli and Strenger, 1956). 2. Lamprey (Marinelli and Strenger, 1954).

Current understanding of the interrelationships of living and extinct jawless and jawed vertebrates demands that the perception of the origin and evolution of the vertebrate skeleton turns full-circle. Stensiö's perception of the relationships between living and extinct jawless vertebrates has largely been rejected in favor of another where hagfishes, at the very least, are appreciated as primitively lacking a mineralized skeleton. Recent analyses suggest that lampreys, too, are primitively naked (Forey and Janvier, 1994; Forey, 1995; Janvier, 1996a,b; Donoghue et al., 2000; Donoghue and Smith, 2001; however, unpublished results suggest that this may be an artifact of character coding strategies). These conclusions are supported by the fossil record of both groups (hagfishes: Bardack, 1991, 1998; lampreys: Bardack and Zangerl, 1968, 1971; Janvier and Lund, 1983; Lund and Janvier, 1986; although this fossil record is limited to a period of a few million years in the midst of an inferred evolutionary history extending over 500 million years). Further, the presence of systematically distinct, primitively naked, and uncalcified jawless vertebrates (Myllokunmingia and Kunmingella) in the Early Cambrian (Shu et al., 1999), all of which possessed a branchial and/or cranial endoskeleton, provides compelling support for the original model for a primitive vertebrate skeleton. Finally, outgroup analysis suggests that the origin of this skeleton may extend deeper into chordate phylogeny than the most primitive vertebrates or craniates.

Basal Vertebrates and the Invertebrate Chordates: Origin of the Skeleton

Within the systematic framework presented in Figure 3, the earliest evidence of a skeleton is afforded by the cartilaginous rods that support the buccal cirri and gill arches in cephalochordates (DeBeer, 1937). In hagfishes, skeletal elements are similarly limited to the endoskeleton, although an integrated cranial and branchial cartilaginous skeleton is present, as well as a cartilaginous caudal fin skeleton (Fig. 4a; Marinelli and Strenger, 1956; Wright et al., 1998; Robson et al., 2000; putative vertebral elements described by Gadow and Abbott 1895 are fused fin rays). Lampreys exhibit greater evidence of skeletal development in the form of a compartmentalized cranial, branchial, axial, and tail skeleton (Fig. 4b; Marinelli and Strenger, 1954; Robson et al., 1997). Putative homologies between the elements comprising the endoskeleton of hagfishes and lampreys are dubious (Holmgren and Stensiö, 1936), and even more so between these two groups and cephalochordates. Thus, it is difficult to ascertain the gross structure of the primitive vertebrate skeleton; nevertheless, the endoskeletons of these taxa are united by their biochemical structure. Unlike the cartilages of living jawed vertebrates, which are collagen-based, the endoskeletal cartilages of cephalochordates, hagfishes, and lampreys are entirely noncollagenous and are composed of matrix proteins that are more similar to one another, and to the cartilages of protostomes, than to those of jawed vertebrates (Wright et al., 2001). Thus, it is possible to conclude that the earliest representation of skeletonization in the vertebrate lineage was a noncollagen-based unmineralized cartilaginous endoskeleton associated with the pharynx: the splanchnocranium (node A in Fig. 3). The evidence from hagfishes, lampreys, and the fossil naked jawless vertebrates from the Cambrian (Shu et al., 1999) indicate that among the earliest vertebrates the splanchnocranium was enlarged and was embryologically derived from neural crest (Langille and Hall, 1988a). The embryological origin of the cephalochordate skeletal elements is obscure but has been presumed to be nonneural crest, following the axiom that neural crest is a synapomorphy of vertebrates. However, recent discoveries of cell populations that exhibit similar fates and patterns of homeotic gene expression among invertebrate chordates (Holland et al., 1996; Holland and Holland, 1998, 2001; Manni et al., 2001; Sharman et al., 1999) and even nonchordate deuterostomes (Baker and Bronner-Fraser, 1997) suggest that this assumption may warrant further investigation. Lampreys and hagfishes possess a further component to their splanchnocranium, the lingual cartilages, that appear to have no corollary in jawed vertebrates. Nevertheless, the lingual cartilages are deemed to be a general character of vertebrates (Janvier, 1981; Jefferies, 1986) and, thus, it is possible to conclude that the latest common ancestor of hagfishes, lampreys, and jawed vertebrates (node B in Fig. 3) would also have possessed a splanchnocranium that included lingual cartilages.

The neurocranium appears to have no corollary among invertebrate chordates and its earliest representation is met with among basal vertebrates. In jawed vertebrates, neural crest contributes to the development of the trabeculae, nasal capsule (components that, following Kuratani et al. [1997], we accept to be a part of the splanchnocranium rather than the neurocranium) and part of the otic capsule; other components are derived from mesodermal mesenchyme. Neural crest contribution to the trabeculae has been demonstrated in lampreys (Langille and Hall, 1988a), but these elements comprise part of the lamprey neurocranium, contradicting the hypothesis that the redefined neurocranium is entirely derived from mesodermal mesenchyme (Kuratani et al., 1997), at least primitively, but Kuratani et al. (2001) argue that this cartilage is more appropriately considered homologous

to the parachordals, or a mandibular arch element, of jawed vertebrates; they also contend with the neural crest origin of lamprey "trabeculae" based on Johnels' (1948) study on the development of the lamprey head skeleton. Experimental support for neural crest contribution to the otic capsule is equivocal, and no data are available for the nasal capsule. The mesodermal origin of other elements of the neurocranium among the earliest vertebrates is supported by normal development in neural crest extirpation experiments (Langille and Hall, 1988a).

The absence of an axial endoskeleton in cephalochordates is in accordance with an absence of sclerotome from which axial skeletal elements develop in jawed vertebrates and the absence of expression of the amphioxus ortholog of the vertebrate sclerotome genetic markers Pax-1 and Pax-9 (AmphiPax-1/9; Holland et al., 1995) in somite development. Shimeld and Holland (2000) argued for cooption of Pax gene expression into somite development in explaining the origin of sclerotome and, thereby, the axial skeleton; this was probably contingent upon Noggin and SHH, which are required for the initiation and maintenance of Pax-1 expression in sclerotome induction (Fleming et al., 2001). In hagfishes the somites are known to differentiate into dermatome and myotome, but there is an absence of histological evidence for the presence of sclerotome (cf. Gorbman, 1997; Price, 1897) and this corresponds to the absence of an axial skeleton. Lampreys are the most plesiomorphic chordates to exhibit myotomal differentiation, including a sclerotomal component, and in corollary, they are also the most plesiomorphic group to possess axial skeletal elements. This is limited to neural vertebral elements that occur for much of the length of the trunk as paired rods or arches surmounting the notochordal sheath; caudally the elements are fused into a plate that is connected to the caudal fin rays. The paired arcualia are positioned intrasegmentally (Brand-Saberi and Christ, 2000) and, thus, the phenomenon of "resegmentation" (Remak, 1850) is one that has evolved after the divergence of lampreys from gnathostomes, and prior to the origin of crown-gnathostomes. The absence of centra and intervertebral discs can be linked to the lack of expression of *Bapx1*, which is required for their normal development in jawed vertebrates (Lettice et al., 2001). Lamprey vertebral elements have been considered homologous to the neural arcualia of living jawed vertebrates (Gadow and Abbott, 1895; Borkhvardt, 1978; Shute, 1972), and both are derived from sclerotome (Tretjakoff, 1926). We may conclude, therefore, that the axial skeleton is secondary to the splanchnocranium and neurocranium, and appeared in hand with the origin of sclerotome, after the divergence of hagfishes and lampreys.

Lampreys afford the earliest evidence of skeletal calcification within the vertebrate lineage (Langille and Hall, 1993).

Gnathostome Stem-Lineage

The gnathostome stem-lineage is composed of all extinct groups of jawless and jawed vertebrates that lie in a phylogenetic position intermediate to the living lampreys and living jawed vertebrates. This includes all of the "armored" jawless vertebrates, known in the vernacular as the "ostracoderms," plus at least one extinct group of jawed vertebrates, the placoderms. The mineralized tissues that comprise their skeletons confer a much better fossil record than the "naked" jawless vertebrates. However, there are a number of drawbacks to this fossil record. First, although the mineralized tissues preserve many anatomical details, the absence of mineralized tissues in living jawless vertebrates ensures that these characters are of little use in resolving the interrelationships of "cyclostomes" and "ostracoderms." Second, "ostracoderms" and their kin do not preserve details of the unmineralized components of skeleton, save as outline impressions. Thus, the fossil record provides little data on the subsequent evolution of the endoskeleton prior to the origin of jawed vertebrates. Nevertheless, we can infer from the absence of a mineralized splanchnocranium in any stem-gnathostome, bar conodonts, and thelodonts, that the condition expressed by lampreys is representative of all prejawed vertebrates; this is supported by indirect evidence of an unmineralized branchial skeleton in heterostracans (Janvier and Blieck, 1979), and the preservation of carbonized outlines of putatively cartilaginous branchial skeletons in a number of anaspid-like forms (Arsenault and Janvier, 1991; Woodward, 1900; Stensiö, 1939; Ritchie, 1960, 1968) that compare favorably to the branchial skeleton of lampreys. It is likely also that this skeleton was composed of the same or similar noncollagen-based cartilage. Further, it is possible that a neurocranium was lacking entirely among basal stem-gnathostomes such as the heterostracans, which show evidence of a close association between the inner surface of the dermal skeleton and the brain, sensory organs, and gill pouches (Janvier, 1996b).

As mentioned, conodonts are one of only two stemgnathostome groups that exhibit any evidence of endoskeletal mineralization, given that the conodont feeding elements are deemed to have occupied a buccopharyngeal position (Purnell and Donoghue, 1997). This is potentially of great significance, first, because conodonts are the basal members of the gnathostome stem-lineage and, second, this skeleton is limited to dental elements composed of a stereotyped suite of vertebrate dental tissues (Fig. 5.1-5.4; Donoghue, 1998; Donoghue and Aldridge, 2001). Although teeth and tooth-like structures have generally been considered part of the dermal skeleton $\bar{b}ecause$ they are borne by dermal jaw bones, it has recently been determined that endoderm is required for dental development and, thus, teeth may more appropriately be considered part of the endoskeleton. Such a hypothesis can only be adequately tested by examining the phylogenetic history of oral dental elements. A number of other stemgnathostome groups also exhibit evidence of dental skeletal elements associated with the mouth, but these appear to be structurally confluent with the dermoskeletal dental elements (e.g., ascending lamina and oral plates of heterostracans, Kiaer [1932], Watson [1954], Broad and Dineley [1973], Purnell [2002]; pre-oral field of osteostracans, Janvier [1985a,b]). At least some thelodonts also possess mineralized dental elements in association with their oral cavity, pharynx, and/or branchial skeleton (van der Brugghen and Janvier, 1993; Donoghue and Smith, 2001). Nevertheless, given the scheme of relationships presented in Figure 3, there is no phylogenetic support for homology between



Fig. 5. Skeletal structure of the major groups of stem-gnathostomes. 1. Rostral view of the feeding elements of an ozarkodinid conodont with the major element divisions labeled. 2. Enamel-like crown tissue of a conodont dental element. 3. Dentine basal tissue of a conodont dental element. 4. Longitudinal section through a conodont dental element demonstrating the relationship between the two main structural divisions—an upper "crown" and a lower "basal body." 5. Light micrograph of a superficial tubercle in the dermoskeleton of the Ordovician heterostracomorph *Astraspis*; note the fine caliber unbranched dentine tubules and the overlying stellate enameloid cap. 6. Nomarski interference optical micrograph of a tubercle in the dermoskeleton of the Ordovician heterostracomorph *Eryptychius*; note the broad, branching dentine tubules and the absence of a hypermineralized capping tissue. 7. Electron micrographs of an etched section through a dermoskeletal scale of an anaspid, under progressively higher magnification. 8. Electron micrographs of an etched section through the dermoskeleton of a cyathaspid heterostracan, under progressively higher magnification; note the vallted structure that dominates the histology. 9. Electron micrographs of an etched section through the dermoskeleton of a thyestidian osteostracans, under progressively higher magnification; note the sharp distinction between the lamellar bone, which comprises more than half of the structure, from the overlying bone and dentine; dentine tubules branch profusely to form a dense terminal network that encompasses the whole of the outer surface.



Fig. 6. 1. Section through the dermoskeleton of a Recent shark; the dermoskeleton is composed exclusively of thousands of discrete dental units. 2. Nomarski interference optical micrograph of the globular calcified cartilage that comprises the (?neurocranial) endoskeleton of the Ordovician heterostracomorph *Eriptychius*. 3. Nomarski interference optical micrograph of a horizontal thin section through

the dermoskeletal scale of one of the earliest chondrichthyans known from the fossil record; the taxon, as yet unnamed, has been recorded from the Late Ordovician of North America. 4-6. Electron micrographs of three scales from an unnamed chondrichthyan from the Late Ordovician of North America.

the oral skeleton (versus extra-oral) of conodonts and thelodonts and the teeth and oral denticles of crowngnathostomes. We will explore these data further after reviewing the evolution of the dermoskeleton.

The controversy surrounding conodont and thelodont oral skeletal elements notwithstanding, lampreys are the earliest members of the vertebrate lineage to exhibit evidence of endoskeletal calcification (Langille and Hall, 1993), in both the neurocranium and splanchocranium, although there is little more than circumstantial evidence to indicate that this extends beyond in vitro conditions (e.g., Bardack and Zangerl, 1971). There is equivocal evidence of a mineralized endoskeleton among the heterostracomorphs: globular calcified cartilage is found in association with one of the heterostracomorphs, *Eriptychius* (Fig. 6.2; Denison, 1967), although the topological distribution of the tissue is unknown; arandaspids possess ocular skeletal elements that resemble endoskeletal sclera of jawed vertebrates (Gagnier, 1993). The earliest firm evidence of endoskeletal calcification in the fossil record is afforded by the galeaspids (Janvier, 1996a,b; Zhu and Janvier, 1998) and osteostracans (Stensiö, 1927), which are among the most derived of all stem-gnathostomes. In both, the known endoskeleton is composed of a single mass of largely unmineralized cartilage lined with perichondral bone (acellular in galeaspids, cellular in osteostracans) that comprises the neurocranium, enclosing the branchial area (although probably not including the branchial arches), and the heart and scapular area in osteostracans. Globular calcified cartilage is also present in both groups. Given the absence of distinct divisions in the cranial endoskeleton of galeaspids and osteostracans, recognizing homologies

to the endoskeleton of jawed vertebrates and living jawless vertebrates is problematic. It has been proposed, however, that the entire skeleton is neurocranial, a characteristic comparable to placoderms (e.g., Stensiö, 1964; although Stensiö also argued that the ridges on the roof of the branchial chamber of osteostracans incorporated the branchial arches and, thus, implicitly assumed that the osteostracan endoskeleton also included the splanchnocranium—a view contested by Janvier, 1985a).

There is little evidence of a further development of the axial endoskeleton beyond that expressed by lampreys until after the origin of jawed vertebrates. Indeed, the only evidence of an axial endoskeleton is in heterostracans and osteostracans that exhibit impressions in the base of the dorsal dermal skeleton that indicate the presence of unmineralized neural arcual elements (Janvier and Blieck, 1979). It should be noted that there is no evidence for the absence of hemal arcual elements. Although anaspids, thelodonts, and osteostracans all possess pectoral appendages, only the constricted pectorals of osteostracans bear any comparison to the pectoral fins of jawed vertebrates, to which they have been homologized. None of these groups exhibit any evidence of an appendicular endoskeleton (the axial and appendicular endoskeletal elements described from the osteostracan Alaspis rosamundae by Belles-Isles [1989] are extremely dubious).

Evolution of the Splanchnocranium Between Jawless and Jawed Vertebrates

Given the absence of evidence to the contrary, it must be assumed that all "ostracoderms" possessed a lampreylike splanchnocranium. It is pertinent, therefore, to consider homology between the lamprey and crown-gnathostome endoskeletons. While it is possible that the neurocrania of hagfishes, lampreys, galeaspids, osteostracans, and jawed vertebrates may be considered homologous at a gross level, attempts to derive homology between the splanchnocrania of these taxa has proven more problematic (e.g., Holmgren and Stensiö, 1936). Although the branchial skeleton of lampreys is derived from neural crest (Langille and Hall, 1988a), as in living jawed vertebrates (Langille and Hall, 1988b), this is outweighed as an inference of homology by evidence suggesting that the splanchnocrania of lampreys and living jawed vertebrates are independently acquired skeletal complexes or, rather, that the splanchnocranium of crown-gnathostomes is neomorphic (cf. Schaeffer and Thomson, 1980). The latter view equates well with evidence indicating that the splanchnocrania of lampreys and jawed vertebrates have a common embryological origin from molecular developmental data on the patterning of the neural crest streams in lampreys and jawed vertebrates such as mouse and chick. For instance, in attempts to resolve the origin of the gnathostome jaw, Kuratani and co-workers have demonstrated stereotyped crown-gnathostome expression patterns of regulatory genes in neural crest cells and configurations of crest-derived mesenchyme occupying anatomically equivalent sites in lampreys (Kuratani et al., 1999, 2001; Horigome et al., 1999; Ogasawara et al., 2000; Myojin et al., 2001), which they use to suggest homology between these regions in the two groups at certain stages of development. Thus, for instance, it is possible to identify a homologous population of mandibular arch crest-derived mesenchyme in lampreys (Horigome et al., 1999). However, beyond an early stage of development, which they term the vertebrate "phylotype," there is no simple correspondence between the development of lamprevs and crown-gnathostomes and. thus, there is no simple homology between the gnathostome jaw and anatomical structures in lampreys, ammocoete or adult. Rather, there has been a systematic rearrangement of craniofacial mesenchyme that precludes traditional one-to-one structural homologies, such as between the jaw of jawed vertebrates and the velar apparatus of lampreys ("ontogenetic repatterning," sensu Wake and Roth, 1989). In this scenario, the jaw and velum could only be considered homologs in the sense that they are both derivatives of a homologous "mandibular" population of neural crest-derived mesenchyme (see also Köntges and Lumsden, 2000, for the implications of inferred rhombomeric fate mapping for homologies between the lamprey splanchnocranium and the mandibular arch skeleton). The same appears to be true of the postmandibular pharyngeal arches, where ontogenetic repatterning of mesenchymal migration lies at the heart of the topological difference in the relationship between the gills and gill arches in living jawed and jawless vertebrates (Kimmel et al., 2001; these authors inappropriately attempt to resolve homology between the resulting skeletal structures). However, it is important to remember that the entire gnathostome stem-lineage lies between these conditions and it is possible, even likely, that the rearrangement of craniofacial mesenchyme occurred, in part or in whole, prior to the origin of a jaw. This will only be resolved if paleoembryology lives up to its ultimate promise (e.g., Zhao and Bengtson, 1999).

Jawed Vertebrates and Crown-Gnathostomes

The origin of a more characteristic vertebrate endoskeleton, composed of a mineralized neurocranium, splanchnocranium, axial and appendicular skeletons, can be attributed, rather paradoxically, to the origin of jawed vertebrates rather than to the origin of vertebrates (cf. Gans and Northcutt, 1983). Placoderms are a large basal clade of jawed vertebrates (terminal stemgnathostomes) that exhibit a great range of endoskeletal characteristics. Like in osteostracans, the neurocranium is a single ossification (although in some taxa the olfactory capsules are a distinct ossification), composed of mineralized or unmineralized cartilage and lined with perichondral bone in most groups; Denison (1978) also recorded endochondral ossification. Placoderms also afford evidence of a number of firsts in vertebrate skeletal development; they are the earliest vertebrates to exhibit evidence of ossification of the splanchnocranium-proper (i.e., in distinction to the oral dental elements of conodonts and thelodonts) in the form of an ossified mandibular arch skeleton and hyoid; there is little evidence of ossification of the branchial arches; the first evidence of dermal bone association with the splanchnocranium in the form of dermal jaw-bones that support small dental elements in some, but not all groups; the earliest evidence of an ossified axial skeleton, although it is not preserved in many groups, presumably because it was not mineralized. Where ossified, the vertebral elements are composed of perichondral bone, including both neural and hemal arches, and centra produced through the extension of the arcualia in some taxa, a condition common to many basal crown-gnathostome groups (Arratia et al., 2001). Given that centra are present in placoderms (Arratia et al., 2001), the prerequisite expression domain of Bapx1 (Lettice et al., 2001) must have been established within the gnathostome stem-lineage, rather than at the origin of living jawed vertebrates. It is not possible to constrain the earliest phylogenetic appearance of ventral vertebral elements because stem-gnathostome arcualia were unmineralized and the presence of dorsal arcualia can only be inferred from impressions in the occipital region of the dermoskeleton. Nevertheless, it is clear from their presence in placoderms that ventral vertebral elements were incorporated into the vertebrate bodyplan prior to the origin of crown-gnathostomes.

The combined characteristics of placoderms and chondrichthyans should provide the key to further resolving the condition of the endoskeleton in the latest common ancestor of all jawed vertebrates (node H in Fig. 3). The characteristics of living chondrichthyans are divergent from placoderms, in that bone is almost entirely absent from the endoskeleton (although there are thin layers of perichondral bone lining the cartilage in some living chondrichthyan taxa). Fossil representatives of basal chondrichthyans are more akin to placoderms, in that perichondral bone is more widespread.

The generality of a more extensively mineralized endoskeleton amongst basal gnathostomes is supported by the next major group of jawed vertebrates in the gnathostome lineage, the acanthodians. Acanthodian anatomy is poorly known except for some of the youngest representatives of the group. In these taxa the endoskeleton is more extensively mineralized than in either placoderms or chondrichthyans. The neurocranium exhibits various degrees of ossification and is only well developed among some of the stratigraphically youngest acanthodians, such as Acanthodes, where it is composed of perichondral bone in a number of distinct ossifications (Heidtke, 1990) in a manner more comparable to osteichthyans. The palatoquadrate and meckelian cartilages exhibit variable histology, from entirely calcified cartilage to entirely perichondral bone, and intermediates (Ørvig, 1951, 1967a,b; Jessen, 1973). The branchial arches are also well ossified and support gill rakers, composition unknown. The axial skeleton is composed of neural and hemal arches composed of perichondral bone (Miles, 1970).

All more derived vertebrates comprise the Osteichthyes, which very clearly exhibits great variation in skeletal morphology and composition. Basal osteichthyans are more typical of the vast majority of jawed vertebrates than are any of the more primitive vertebrate groups. The endoskeleton is largely composed of perichondral bone and endochondral bone exhibits much greater distribution even among primitive mem-bers of the basal osteichthyan groups. Throughout osteichthyan phylogeny there is evidence of greater integration of the splanchnocranium, neurocranium and dermatocranium. Functional integrity of the head is maintained through phylogeny due the modular nature of cranial neural crest and its derivatives, patterned on the basis of its rhombomeric origin; the "modules" generate integrated units of muscle and the skeletal elements to which the muscle attaches, and all derivatives

of a specific rhombomere are innervated by the same nerve (Köntges and Lumsden, 1996, 2000).

Thus, overall, the phylogenetic appearance of endoskeletal tissues marries with their successive appearance in the development of osteichthyans (cartilage > perichondral bone > endochondral bone). However, many osteichthyan groups exhibit evidence of reduced endoskeletal mineralization, particularly the actinopterygians, actinistians, and dipnoans (e.g., Moss, 1964). From this it is clear that Romer was not entirely incorrect in his observation of trends of skeletal reduction through vertebrate phylogeny, although like all evolutionary trends, it was merely a generalized and oversimplified abstraction of the real pattern of skeletal evolution, which is much more complex.

DERMOSKELETON

The earliest evidence of dermal skeletonization is met with in the "ostracoderms" (stem-gnathostomes) and represents the chief characteristic that unites the group with jawed vertebrates, to the exclusion of the hagfishes and lampreys. The dermoskeleton does not exhibit great variability in its composition, although the gross structural arrangement of the tissues can be quite variable. There are two main components to the dermoskeleton: dental units composed of dentine, bone of attachment and enamel or enameloid in some taxa; an underlying layer of dermal bone that can be differentiated into spongy or cancellar layers overlying a sheet-like basal lamellar bone layer (e.g., Fig. 5.8). Neither component is always present. The dermoskeleton can also be divided into cranial and postcranial divisions that exhibit differences in patterning and tissue distribution.

Correlation between characteristics of the dermoskeleton and evolutionary relationships suggest that the skeleton arose de novo in a single step such that even in the most basal "ostracoderms" it is already an extensive, fully-encasing body armor. A number of authors have suggested that this is an implausible hypothesis and that the known fossil record of skeletal evolution must be woefully incomplete (e.g., White, 1946). Nevertheless, this is all that a strict reading of the fossil record and early vertebrate phylogeny suggests. The heterostracomorphs, basal members of the 'ostracoderms," possess a cranial dermoskeleton composed of relatively few large plates that are either fused or composed of numerous smaller closely associated units (Fig. 5.8). The superficial layer is composed of individual dental units (Fig. 5.8, lower field) that are either fused to each other at their margins or else united by an underlying layer of spongy bone. These units are composed of bone of attachment, dentine, and, in some taxa, an enameloid cap. In most groups the underlying bone layer has a vaulted structure enclosing expansive cavities into which the dentine pulp cavities open. The vaulted structure is produced by the internal apposition of layers of acellular bone in a manner comparable to osteons and, thus, the lamellar structure of the floor and walls of this layer are continuous. The underlying floor of the vaulted layer is also composed of laminar acellular bone that was accreted by apposition from below, thereby uniting the otherwise discrete osteons. The postcranial dermoskeleton exhibits a comparable structure, organized into a series

of discrete overlapping to nonoverlapping scales. This histology is probably general for basal stem-gnathostomes, as the dermoskeletons of groups such as the anaspids (Fig. 5.7) and thelodonts are variations on this theme. The anaspid dermoskeleton (Fig. 5.7) remains enigmatic, but available data suggests that it is comparable to the basal acellular bone layer of the heterostracan dermoskeleton (Gross, 1937, 1958). Conversely, the thelodont dermoskeleton is composed solely from isolated dental units and is, therefore, comparable only to the superficial layer of the heterostracan skeleton. The dermoskeleton of galeaspids is also enigmatic, although available evidence also indicates that it is comparable to the spongy or lamellar acellular bone layer of the heterostracan dermoskeleton (Janvier, 1990; Zhu and Janvier, 1998; the putative record of enameloid in galeaspids is spurious).

The most significant evolutionary step in the phylogeny of the dermoskeleton among the ostracoderms, after the origin of the dermoskeleton itself, is the origin of cellular bone, which is first met with in osteostracans (Fig. 5.9); tissue distribution in this group is otherwise comparable to other ostracoderms. The placoderm dermoskeleton is much akin to the condition in osteostracans except that placoderms record the first unequivocal evidence of incorporation of the components of the dermoskeleton into the splanchnocranium in the form of the dental plates that also include dental elements composed of dentine, in some taxa. Placoderms are the earliest group in vertebrate phylogeny to exhibit patterned cranial dermal bones, although attempts to relate these to osteichthyan dermal bones (Graham-Smith, 1978) have generally been unsuccessful. Subsequent evolution of the dermoskeleton is quite conservative and is characterized by a motif of reduction; although basal representatives of both main clades of osteichthyans bear an extensive dermoskeleton, derived members of both clades generally do not. This is manifest in two distinct ways by the two lineages. Although dental components of the dermoskeleton are lost in both lineages, among actinopterygians the skeletal evolution is characterized by reduced mineralization, rather than reduced skeletonization (e.g., Meunier, 1987; Meunier and Huysseune, 1992); among sarcopterygians the postcranial dermoskeleton is entirely absent in even basal members of crown group Tetrapoda, which has led to spurious conclusions regarding the plesiomorphic nature of the dermoskeletal system (see Smith and Hall, 1990).

In summary, the evolution of the dermoskeleton concerns the patterning of two main variables, the superficial dental units, composed of dentine and sometimes augmented by enamel or enameloid, and bone, and a deeper unit composed of bone from which the main structure of the dermoskeleton is composed. The distinction between these two dermoskeletal systems has long been recognized (e.g., Westoll, 1967), but a distinction between the two on developmental grounds has only recently been determined (Smith and Hall, 1990, 1993).

The evolution of specific tissues types is far more complex and correlation between grades of enamel, enameloid, dentine or bone, and phylogeny, indicates that many tissue grades are convergent. For instance, orthodentine-grade dentines are met with in heterostracomrophs (Fig. 5.5, 5.6, 5.8) and jawed vertebrates, but taxa with a systematic position intermediate of these groups (e.g., osteostracans, Fig. 5.9; thelodonts) possess dentines that are organized in a manner more typical of bone (mesodentine) (see Smith and Sansom. 2000, for expansion); enameloid is present in heterostracomorphs (Fig. 5.5, 5.8), but in no other stem-gnathostomes. This phenomenon has been confronted before and explained in two ways. Halstead (1982) argued that the hypothesis of relationships was incorrect and adjusted the phylogeny such that histological (and other contentious characters) were in greater accord; Schaeffer (1977) did not consider evolutionary relationships in great detail, but implicitly accepted that the phylogeny was correct and argued that this pattern reflected something significant about the nature of the how developmental systems, such as the component skeletal systems, evolve. Taking the dental module as an example, which had been conceptualized into a developmental unit called the "odontode" by Ørvig (1967a,b, 1968, 1977), Schaeffer argued that the dermoskeleton was a "single, modifiable morphogenetic system" and through changes in the action of components of this "morphogenetic system," any of the constellation of dermoskeletal tissues could be produced, singularly or in combination. Schaeffer's hypothesis benefits from independent phylogenetic support (although it would be difficult to falsify a random pattern!) but it is also grounded in experimental data (see, e.g., Lumsden, 1987; Smith, 1995). However, given Smith and Hall's (1990, 1993) observations on the bicomponent nature of the dermoskeleton, which extends as far back in development to segregated populations of neural crest cell derivatives, it is likely that Schaeffer's view of the dermal skeleton is overstated. The dermoskeleton is probably a good deal less flexible than the apparently random patterns of tissue grade would otherwise suggest; much of the absence of pattern probably arises from a failure to differentiate between odontogenic and skeletogenic systems within the dermoskeleton when recording the occurrence of tissue types. We are currently attempting to remedy the situation.

COEVOLUTION OF THE DERMAL AND ENDODERMAL SKELETAL SYSTEMS: RECIPROCAL ORIGINS?

It is clear from a combined paleontological-neontological perspective that the earliest vertebrate skeleton was an entirely unmineralized cartilaginous splanchnocranial endoskeleton. This skeleton appears to have been non-neural crest-derived (contra Smith and Hall, 1990; but keep in mind the potential implications of Holland et al., 1996!) and the secondary dominance of neural crest in the patterning and development of the splanchnocranium must be a secondary vertebrate innovation, explaining why many aspects of pharyngeal arch development are non-neural crest-dependent (Veitch et al., 1999; see Graham and Smith, 2001, for an excellent commentary). The splanchnocranium was also the site of the earliest mineralized skeleton in the form of conodont elements composed of dental tissues arranged in a manner comparable to the teeth of jawed vertebrates. A key element of the early mineralized skeleton, but aside from conodonts and thelodonts,

odontodes are found exclusively in a dermal position in stem-gnathostomes. This leads to only two possible conclusions: the odontode developmental module and its component tissues have been converged upon in the two distinct skeletons and in a number of distinct lineages, or else the switch from endoskeletal to dermoskeletal odontodes in the earliest ostracoderms, and the subsequent phylogenetically distinct occurrences of endoskeletal odontodes, represent a shift and extension in the expression topology (heterotopy) of a homologous developmental module. On face value, the latter is by far the most plausible hypothesis but it is perplexing given the axiom that the endoskeleton and dermoskeleton have distinct development and phylogenetic origins (Patterson, 1977). Smith and Coates (1998, 2000, 2001) have explicitly discriminated between dermoskeletal and oral (endoskeletal: splanchnocranial) odontodes, extending to a stage in vertebrate phylogeny that predates the origin of jaws, at the very least. The evolutionary origin of this distinction is enigmatic, but when placed in a phylogenetic framework expression topology suggests that there was no distinction between dermal and endodermal odontodes at this early stage in the evolution of vertebrate skeletonization.

The subsequent evolution of the oral and extra-oral skeletons is simpler. The key patterning characteristics of the oral dental skeleton (site-specific morphological polarity and prefabricated replacement) are not only apparent among the earliest dentate jawed vertebrates, but also in the apparently homoplastic oral dental apparatuses of conodonts (Donoghue, 1998) and thelodonts (van der Brugghen and Janvier, 1993; Smith and Coates, 2001). It is likely that this is because both characters are subtle (albeit fundamental) modifications of the characteristics of dermoskeletal odontodes (cf. Halstead Tarlo and Halstead Tarlo, 1965). Although more complex dental morphologies are explored through subsequent vertebrate phylogeny, the dental developmental characters established at the earliest stages of skeletal evolution change little, if at all.

The loss of dental elements in the dermoskeleton of all but the most basal actinopterygians provides a useful perspective on the evolutionary/developmental relationship between the dermoskeleton and splanchnocranium. Sire et al. (1998) and Sire (2001) have described the secondary appearance of dental elements in the dermocranium of two distantly related teleosts. These authors compared the structure of these dermal "tooth-like" denticles to the oral teeth and found that the only characters that distinguish between the two sets of dental elements, other than their topology, arise entirely from the effects of function on development. While it remains possible that the dermal odontodes result from the resurrection of a plesiomorphic condition of the actinopterygian dermal skeleton, this scenario is far less likely than a heterotopic shift in expression of endoskeletal odontodes. Indeed, it is only the axiomatic distinction between dermal and endodermal skeletal lineages that argues against this hypothesis; in an alternative perspective on the same data, the hypothesis of a distinction between dermal and endodermal skeletons is rejected on the basis of the evidence at hand.

These data provide evidence of a mechanism for heterotopic shifts in the expression topology of odontodes between the endoskeleton and dermoskeleton, and against the veracity of the dermoskeletal/endoskeletal distinction which may have much wider implications for the phylogeny of the cranium in particular. However, this equivocation over the veracity of the endoskeleton as a skeletal system independent of the dermoskeleton encompasses only the odontogenic component. Aside from a vicarious odontogenic system, the dermoskeleton, neurocranium, splanchnocranium, axial and appendicular skeletal systems may otherwise be considered distinct and discrete in both developmental and evolutionary perspectives.

ORIGIN OF THE VERTEBRATE SKELETON, EVOLUTIONARY SCENARIOS, AND SKELETONIZATION VERSUS CALCIFICATION

A number of distinct hypotheses have been erected to explain the events surrounding the origin of the "vertebrate skeleton" (see Ørvig, 1968, and Donoghue and Aldridge, 2001, for a review). These may be summarized into two main groups: hypotheses based on the physiology of living primitive vertebrates and invertebrate chordates, and hypotheses based on the proposed functional significance of the earliest vertebrate skeletons. Physiology-based hypotheses are many and varied, arguing that the skeleton arose as a barrier to osmosis (Marshall and Smith, 1930; Smith, 1932), for ion storage (Gans and Northcutt, 1983; Northcutt and Gans, 1983; Griffith, 1987, 1994; Westoll, 1942), as a reservoir of biolimiting elements (Pautard, 1961; Urist, 1963, 1964; Halstead Tarlo, 1964a; Halstead, 1969), as a buffer (Ruben and Bennett, 1980) or a disposal site for waste by-products (Berrill, 1955).

Functional hypotheses argue either for an origin of the skeleton linked to sensory enhancement (e.g., Thomson, 1977), or protection (Romer, 1933, 1942). The sensory-driven hypothesis is based on two main observations. First, in many early vertebrate groups (heterostracans, osteostracans, lungfishes) the dermoskeleton is permeated by a complex system of canals (the so-called "pore canal system") that open to the outer surface through a dense array of pores that have an outline morphology that strongly resembles the morphology of ampullary organs in extant chondrich-thyans (e.g., Gross, 1956; Thomson, 1975, 1977). Second, phosphate is an effective electrical transducer (Northcutt and Gans, 1983). On this basis a number of authors have argued that the earliest vertebrate skeleton functioned either to house and enhance electroreceptive organs (Gans and Northcutt, 1983, 1985; Northcutt and Gans, 1983; Gans, 1988, 1989, 1993) and/or to maintain spacing between mechanoreceptors (Lumsden, 1987). In contrast, the protection or "armor" hypothesis is based on the contrast in gross morphology of the dermoskeleton in the "ostracoderms" (taxa that we would now identify as stem-gnathostomes) to less heavily skeletonized groups of primitive jawed vertebrates and entirely "naked" living jawless vertebrates. In its original conception (Romer, 1933), the armor hypothesis combines these observations with diversity data on the "ostracoderms" and eurypterids ("sea scorpions"), which are popularly deemed to have

been the top predators of their day. The romanticism of an evolutionary shift from "meek filter feeders into fearsome predators" (Postlethwaite et al., 1998, p. 345) has made this hypothesis more compelling than the data upon which it is based would otherwise provide and, thus, the "armor" hypothesis is the most widely accepted for the origin of the vertebrate skeleton.

The systematic framework presented in Figure 3 and the analysis of the skeletal evolution presented above provides a means of testing between the available hypotheses for the origin of the skeleton and the evolutionary scenarios that are built upon them. First, it is clear that all the main hypotheses for the origin of the skeleton overlook the point that the vertebrate skeleton has an invertebrate origin and that it not linked to developing an osmotic barrier, ion storage, or the storage of biolimiting elements, the earliest phylogenetic appearance of the skeleton is not linked to buffering acid by-products, disposing of waste products, sensory reception, or protection. Rather, the earliest representation of the vertebrate "skeletal system" relates entirely to feeding and respiration. To an extent, this conflates skeletonization with calcification, but the distinction between the two is hard to draw (e.g., Langille and Hall, 1993; Meunier and Huysseune, 1992) since they are interdependent, as can be evidenced by the fact that in most jawed vertebrates development of the embryonic endoskeleton proceeds without calcification until much of the structure has been established. Until the origin of the dermoskeleton, to which all the existing hypotheses relate, the evolution of skeletonization within the vertebrate lineage was all endoskeletal, and almost entirely splanchnocranial. And given that the first appearance of the odontode was splanchnocranial (conodonts) it could be argued that, so far as developmental modules are concerned, the key innovations of the dermoskeleton were already established in the splanchnocranium.

Even if we do choose to distinguish between skeletonization and mineralization, and emphasize mineralization as the key character in denoting the origin of the vertebrate skeleton, traditional models for the origin of the skeleton may still be rejected. The physiology-based hypotheses are difficult to reject ultimately because they are difficult to test. Hypotheses that argue the primitive mineralized skeleton served as a reservoir are potentially testable on the observation of resorption and, thus, recovery of mineral deposits; evidence of resorption in the vertebrate skeleton is a relatively derived phenomenon and there is no convincing evidence below the level of osteostracans (see, e.g., Denison, 1952) and the most derived of all heterostracans (Gross, 1935; Halstead Tarlo, 1964a), both of which are only remotely related to the earliest mineralized vertebrates. The "osmotic barrier" hypothesis may also be rejected on the basis that the earliest mineralized skeleton is not dermal, and the earliest dermoskeletons exhibit high permeability (Halstead Tarlo, 1964b). Similarly, the sensory enhancement hypothesis may also be rejected on the basis that the earliest known mineralized tissues are dental and not associated with the positioning or enhancement of cutaneous sensory receptors. Given the presence of mechanoreceptors superficially mounted within the unmineralized dermis of hagfishes (Fernholm, 1985; Braun

and Northcutt, 1997, 1998) and lampreys (Kleerekoper, 1972), a mineralized dermoskeleton is not a prerequisite for maintaining an effective sensory interface with the environment; it is likely that this condition persisted among basal stem-gnathostomes, in which there is little evidence of a cutaneous sensory system except for irregular grooves in the surface of the dermoskeleton. Furthermore, those organisms in which an electrosensory system has been interpreted as present (osteostracans and heterostracans by Denison, 1951, osteostracans and heterostracans by Denison, 1964; Thomson, 1977; Northcutt and Gans, 1983; Northcutt, 1985) are only remotely related to the earliest dermoskeletonized vertebrates, and evidence for the presence of an electroreceptive system in the derived organisms is actually far from convincing (cf. Bemis and Northcutt, 1993).

With the rejection of all of the above, we are left with little other than Romer's (1933) ever-popular "skeletonfor-armor" hypothesis. The data on which the hypothesis was erected, co-occurrence of filter feeding basal vertebrates and predatory eurypterids, is now no longer persuasive. Nevertheless, were it not for conodonts, the current phylogenetic pattern of skeletal characteristics among stem-gnathostomes and their living jawless relatives would provide strong and compelling support for this hypothesis.

Conodonts squarely fill White's (1946) "gap" between the naked cyclostomes and armored "ostracoderms," both in terms of phylogenetic relationships and skeletal characteristics. With only one significant exception, conodonts have an anatomy that is typical of lampreys, a suite of characters that can be considered general for primitive vertebrates, for they are also shared in large part by the hagfishes. However, that one significant exception sets conodonts apart from the cyclostomes is the critical character that unites conodonts, "ostracoderms," and jawed vertebrates to the exclusion of the "cyclostomes": a mineralized skeleton. Functional data from conodonts indicate that the elements performed relatively sophisticated feeding functions and that the organisms were predators on macrophagous prey (Purnell, 1995; Donoghue and Purnell, 1999). In the systematic framework presented herein, these data imply a scenario for the origin of the skeleton that is diametrically opposed to the hitherto prevalent "armor" hypothesis. Rather than arguing that the skeleton evolved to protect filter-feeding early vertebrates from predation, the phylogenetic hypothesis presented herein argues in favor of a hypothesis in which the skeleton evolved first to perform a feeding function in a predator/scavenger, and was only secondarily coopted to perform a protective role among the "ostracoderms (Purnell, 1995)."

AND FINALLY, IN A WORLD WITHOUT FOSSILS...

Interpretations of character polarity in vertebrate skeletal evolution that do not entertain paleontological data are surprisingly common and it is perhaps now possible to appreciate the implications of such ignorance. Based on data from extant organisms alone, the gap between organisms with and without a mineralized skeleton would be even greater than "White's gap" between "ostracoderms" and living jawless vertebrates



Fig. 7. Phylogenetic relationships between the living groups of chordates considered in this study. The black bars across the top refer to the various taxonomic groups and grades of organization used; lettered nodes refer to significant events in the various chordate and vertebrate skeletal systems. A: Origin of a splanchnocranium. B: Development of the splanchnocranium and origin of a neurocranium and chondrocranium. C: Further development of the splanchnocranium, neurocranium and chondrocranium, origin of neural elements in the axial endoskeleton. D: Origin of a dermal skeleton, origin of a mineralized endoskeleton; origin of perichondral bone, origin of dentine, origin of enameloid, origin of jaws, origin of teeth, origin of an appendicular skeleton, development of the axial endoskeleton such that both neural and hemal elements are present. E: Origin of dermal bone, origin of endochondral bone, origin of dermal bone, origin of multicomponent scales and teeth. [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

(Fig. 7). Not only would a fully developed dermoskeleton be perceived to have been acquired de novo in a single evolutionary step but, coincidentally, the perception of the shift from jawless to jawed vertebrates would be interpreted as a single, fundamental reorganization of the generic anatomy of vertebrates. In concert with the appearance of the dermoskeleton, we would perceive the earliest jawed vertebrates to have also acquired a mineralized endoskeleton, very little of which corresponds to the neurocranial-splanchnocranial endoskeleton of lampreys or hagfishes. Indeed, possibly the only comparable elements of the endoskeletons of jawed and jawless vertebrates are their neural arcualia! Even the biochemical structure of main structural protein of the connective tissue protein is fundamentally dissimilar to the collagenous connective tissues of jawed vertebrates. Furthermore, both teeth and

jaws appear at the same stage as the first dermoskeleton, and the sophisticated patterning and regulatory characteristics of these skeletal systems would have been present from their very earliest expression. Appendicular skeletons, almost the entire axial skeleton, a distinct neurocranium, sclerotic ossicles, and endoskeletal sclera, would all appear concurrently, in a single step, and this list dwarfs in comparison to changes and derived characteristics of the brain, sensory system, etc. Indeed, this pattern of fundamental anatomical reorganization fits well with evidence of genome duplication at the origin of jawed vertebrates (Holland and Garcia-Fernandez, 1996; Sharman and Holland, 1996, 1998; Sharman et al., 1997), but this perception is probably also flawed for the same reason.

Without knowledge of stem-gnathostomes our perception of early vertebrate evolution, and the evolution of the various organ systems that comprise anatomy, would not just be incomplete, but incorrect. Nothing would be known of the diversity of tissue types and tissue combinations that are met with exclusively among the stem-gnathostomes, hinting at the nature of how developmental systems, such as the dermoskeletal system, evolve through experimentation immediately after their inception, and informing us of how subsequent skeletal diversity may or may not be constrained by earlier contingent events in evolutionary history. We would be unaware that there was a debate to be enjoyed over the topological origin of the dental developmental unit (the odontode), we would presume that the dermoskeleton was primitively patterned as isolated dental units rather than compound aggregates, and we would conclude that dermal bone is a derived characteristic of osteichthyans, rather than a relatively primitive feature of stem-gnathostomes. Such details are just that, but they can be critical not only to the proper understanding of the evolution of organ systems and their developmental basis. Together they can provide for very different perceptions of macro-evolutionary events, such as the origins of vertebrate skeletons.

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