

## 2. Homologies and Evolutionary Transitions in Early Vertebrate History

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### ABSTRACT

The major two morphological gaps in extant euchordate anatomy, the cephalochordate-vertebrate gap and the cyclostome-gnathostome gap, are reviewed in light of paleontological data to illustrate possible cases of evolutionary transitions in euchordate evolution. The Early Cambrian mylokunmingiids probably possessed neural crest- and epidermal placode-derived structures, but display character combinations that suggest they are stem vertebrates and, possibly alongside yunnanozoans, contribute to fill the cephalochordate-vertebrate gap. Although hagfishes and lampreys are known since the Carboniferous, their relationships to the other fossil jawless vertebrate taxa remain obscure. Euphaneropids and possibly anaspids display some lamprey-like features that may turn out to be general for the clade that includes lampreys and gnathostomes. Among the jawless stem gnathostomes ("ostracoderms"), osteostracans are currently regarded as the closest relatives to jawed gnathostomes, but share with lampreys some unique and strikingly similar characters, such as the structure of the nasohypophysial complex, that are currently regarded as homoplasies and therefore overlooked in narratives about early vertebrate evolution. The characters that support the current theories of vertebrate interrelationships are briefly reviewed and discussed. Despite some incongruent character distributions, "ostracoderms" provide a means for establishing the sequence in which gnathostome characters appeared. Finally, the question of the origin of jaws is discussed in light of recent data provided by developmental biology. Current vertebrate phylogenies, coupled

with process-based narratives inferred from developmental data, may provide scenarios of evolutionary transitions. However, returning to problematical characters that display incongruent distribution patterns and searching for more data of good quality are probably more rewarding in the long term to generate new phylogenies.

### Transitions and Character Transformations

Science has long turned to fossils as evidence for evolutionary transitions through time, particularly those transitions associated with the rise of the major vertebrate clades. *Vertebrate Paleontology and Evolution*, by Robert L. Carroll (1988), is a perfect example of the defense and justification of evolutionary paleontology, and is therefore widely used for teaching purposes. Like many of us, Carroll joined the cladistic revolution, but he did not argue much with the critics of paleontological data, even when fossils were under heavy fire, notably after the famous (or, to some, infamous) article by Rosen et al. (1981) about lungfish-tetrapod relationships. He pragmatically relies on characters—that is, the anatomical structures as we actually see them, and their homology—as evidence for relationships, but geological time remains his guide. Such paleontology-based scenarios of evolutionary transition, as the paired fin-limb transition or the rise of the mammalian middle ear, through a long series of “transitional” fossil forms are thus Carroll’s favorite subjects. In the 1980s, Carroll and I were in different camps. He believed in the power of fossils as direct evidence for evolutionary transitions and evolution through time. In contrast, I considered that the antiquity of fossils was not a particular property that gave them any more weight: fossils were merely useful additional sources of characters, yet less informative than extant organisms in terms of actual observable data.

His reservations about certain issues in cladistics notwithstanding, Carroll published his first (and so far only) computer-assisted cladistic analysis of the choanates, with particular reference to early fossil tetrapods (Carroll, 1995). As a coeditor of the volume in which this article appeared, I remember Carroll sending me a note that alluded to his skepticism as to the trees he obtained. The conclusion of his article clearly showed that his preference goes to actual, chronologically ordered series of fossils, and ended with a quote from Scott and Janis (1993:300): “[C]omputer programs, . . . like the White Queen, can believe six impossible things before breakfast.” Surprisingly, this echoed the criticism by Platnick et al. (1996:245) of standard parsimony and Farris’s optimization, which considers all possible most-parsimonious cladograms, even though some are impossible things.

Now, I would perhaps write a somewhat similar conclusion as Carroll’s (1995) regarding current cladistic computer programs. The weight of optimization, probabilities, and statistics in phylogeny reconstruction seems to eclipse the consideration of the characters and their definition, limitation, composition, or coding. There are more

and more trees, some of which, although most parsimonious, make no sense in terms of plausible character distribution. However, the main problem lies in the fact that from these innumerable trees, optimizations generate ancestral character states at nodes. Programs therefore produce a series of virtual evolutionary transformations that are ultimately described and discussed as if they were actually observed from the fossil record or by any other material means. This strikingly recalls the evolutionary tradition of reconstructing hypothetical intermediates. The difference is that because of the mixture of homoplasy and homology (and missing data) in most data sets, the ancestral character states are now a consequence of optimizations from "data that are always significantly less than perfect" (Nelson, 1994:111). Such trees are said to be predictive, but are these virtual transformations mere predictions, amenable to a test by actual organisms, be they extant or fossil? Theoretically, yes, but their frequently poor or variable support at nodes and successive changes from one analysis to the other make them be quickly forgotten, before any test turns up. A strict consensus of most parsimonious trees that would display a majority of unresolved nodes would be dismissed as meaningless or poorly resolved, whatever the strength of the support to the few nodes it may display. Yet such poorly resolved trees are sometimes the best ones that can reasonably be obtained, and on the basis of which one may seriously investigate further. Kearney (2002) pointed out the contradiction between the search for fully resolved trees and the inevitable biases that result from optimization of missing data in fossil taxa. She offered the same solution: a consideration of the few, robust nodes, and a return to the characters that show conflicting distributions.

In common with many cladists of the 1980s, I was inclined toward considering evolutionary transitions as more or less plausible tales that could only be inferred from character distribution. Nevertheless, evolutionary transitions from ancestor to descendent could not be narrated without any appeal to paraphyly, and thus these transitions did not cope with phylogenetic systematics. In other words, the story that gnathostomes could be derived from "agnathans" was pointless, because "agnathans" do not exist as a taxon. Moreover, an evolutionary transition process requires an adaptationist scenario, generally constructed on the basis of an array of functional, environmental, or paleoenvironmental arguments, the core of which is the organism-environment interaction. Systematics is not supposed to use such causal explanations for justifying one particular theory of relationships, but once character transformation is invoked, they become necessary.

The notion of character transformation, from a plesiomorphic to one or more apomorphic states, has been regarded by Nelson (1994:127) as the last remnant of the evolutionary approach in cladistics. Saying that, for example, the jaws are derived from "non-jaws," be it the velar skeleton of lampreys or anything else, is just as uninformative as saying that the gnathostomes are derived from "agnathans." Although such statements still frequently appear in text-

books, they merely remain a veil thrown over ignorance, i.e., the ignorance of the precise homologue of jaws in any other taxon (Kuratani et al., 2002). Nelson's view is thus that only the presence of a character in different organisms or taxa (i.e., the same part of the organisms, sometimes with different names) has a meaning in term of systematics. One can tell whether a character is, or is not, but saying that it *was not* and then *is* is already a first step toward an imaginary process of evolutionary transition. Here begins the search for possible transformation processes based on such kinds of data, as ontogeny, biomechanics, or intermediate forms, generally fossils.

I might have had different views were I working on such remarkable evolutionary series as early synapsids. However, my experience of early jawless vertebrates was extremely frustrating in this respect. All the taxa I could consider, be they extant (hagfishes, lampreys, gnathostomes) or extinct (e.g., arandaspid, heterostracans, galeaspids, osteostracans), were clades (with the possible exception of thelodonts), long recognized as such, and any evolutionary transition or ancestor-descendent relationship between one group and others was ruled out. All that the fossil data and character distribution told me was that if gnathostomes evolved from jawless vertebrates, their closest relatives were some "ostracoderms"—that is, fossil jawless vertebrates possessing a calcified endo- and exoskeleton, but showing no evidence for incipient jaws, pre-jaws, or anything else, and currently referred to as *stem gnathostomes* (Donoghue et al., 2000). At any rate, there was no clear evidence that "agnathans" in general, and "ostracoderms" in particular, were clades. The anatomically informative fossil clades that are currently available and relevant to this question are barely more numerous than they were about a century ago, with the notable exception of galeaspids. All that we have are different tools for assessing character distributions, the most important of which is that absence means nothing.

The way I have been considering fossils during the past two decades or so was therefore necessarily different from the once classical, evolutionary approach that was based on assumptions about character transformations and ancestor-descendent relationships between higher taxa ordered through time. To me, it is an interesting exercise to write about evolutionary transitions in early vertebrates. In fact, these transitions, if any, only rest on an apparent hierarchy of certain homologues, less and less general in distribution, but there is no taxon among either jawless vertebrates or early gnathostomes that can be referred to as a fossil *transitional form* (by the virtue of their unique character combination)—reputations that have been bestowed on organisms such as *Panderichthys*, *Acanthostega*, or *Archaeopteryx*.

gnathostome Euchordata (a name that predates Myomerozoa [Bjerring, 1984; see Carter, 1957]—i.e., cephalochordates and vertebrates) is desperately scarce. For example, all the characters that are currently used for reconstructing the progressive acquisition of the gnathostome body plan are known from such fossil jawless vertebrate taxa as heterostracans, galeaspids, and osteostracans, which are generally much derived in other respects (the so-called evolutionary dead ends). This situation compares to what would be the reconstruction of the evolutionary process that gave rise to the structure of eutherian mammals by only using such fossil taxa as edaphosaurs, dinocephalians, and dicynodonts. In addition, a long segment of early euchordate and vertebrate evolution took place before the rise of a mineralized skeleton and thus concerns organisms that are either rarely fossilized, or, if fossilized at all, provide little reliable information. Nevertheless, without these few fossil taxa, generally early Paleozoic in age, our conceptions of the relationships between the major present-day vertebrate taxa would perhaps be the same as those currently accepted, but our knowledge of the order in which the less and less general characters appeared throughout time would be virtually lacking (Donoghue and Sansom, 2002), unless inferred from the development of extant taxa, following von Baer's law.

The justification for the search for evolutionary transitions is the existence of gaps (generally morphological) in the overall resemblance of taxa. Without these gaps, evolutionary transitions would be as obvious as ontogeny, and thus their elucidation would be theoretically pointless. The major two morphological gaps among extant euchordates are between the cephalochordates and the vertebrates (in the classical sense; that is, including hagfishes, lampreys, and gnathostomes), and between the cyclostomes (hagfishes and lampreys, whatever their relationships) and the gnathostomes (Fig. 2.1).

How do we define such gaps and rate them as major? Here again, there is evidently the burden of anthropocentrism and subjectivity, as pointed out long ago throughout the cladist's criticisms of evolutionary systematics. In morphology, these gaps are regarded as the expression of disparity (however it may be measured), and in molecular systematics, they are assessed on the basis of large genetic distances (whatever this may actually mean). In fact, morphological gaps are assumed when no taxon can be used to demonstrate the imaginary transformations between two widely different taxa and when the latter lack readily recognizable homologies; that is, homologies that rest on "common sense" and can be used as a first theory of relationship with which to start an analysis (primary homologies, in the broad sense; de Pinna, 1991), such as the jaws of a cod and a cow, or pectoral fins and forelimbs. Thus, even though one may, on various grounds, assume homology between, say, the velar skeleton (or part of it) of lampreys and jaws of gnathostomes, there appears a broad morphological gap between these two taxa.

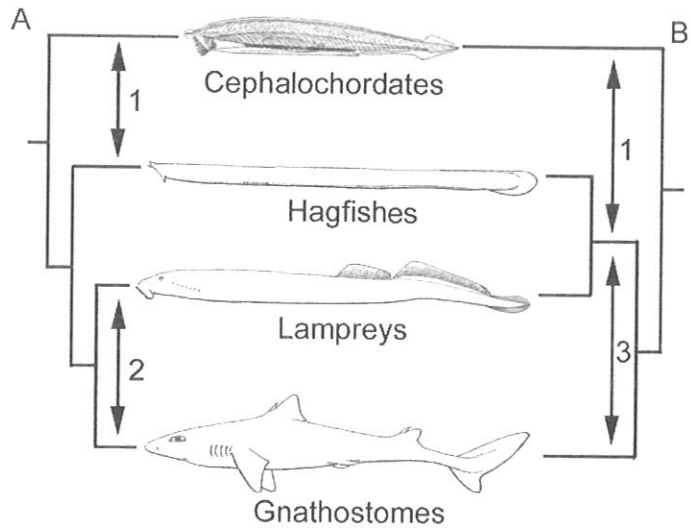


Figure 2.1. Two major morphological gaps in euchordate phylogeny. A, theory assuming cyclostome paraphyly; B, theory assuming cyclostome monophyly. 1, cephalochordate-vertebrate gap; 2, lamprey-gnathostome gap; 3, cyclostome-gnathostome gap.

The relationships between the three chordate groups (i.e., tunicates, cephalochordates, and vertebrates) have been the subject of debate during the past three decades. Although there has long been a consensus on the sister-group relationship between cephalochordates and vertebrates, Jefferies (1986) advocated sister-group relationships between tunicates and vertebrates, and recent works on the developmental genetics of tunicates provided evidence for a vertebrate-like condition in the latter, as to certain structures, notably the placodes (Mazet et al., 2005). Assuming that the sister-group relationship between cephalochordates and vertebrates is best supported by numerous anatomical, developmental, and molecular sequence data (Shimeld and Holland, 2000; Holland and Chen, 2001), there remains an impressive morphological gap between the two groups (1, Fig. 2.1). Therefore, attempts at reconstructing evolutionary transitions between the supposedly homologous characters of the two taxa remain largely imaginary (e.g., Butler, 2000), although ontogeny or developmental genetics may sometimes lend some support to one or the other of these inferred transformations, such as in the case of the median “eye” of cephalochordates and the paired eyes of vertebrates (Lacalli, 1996), or the placode precursors of tunicates and cephalochordates and the neurogenic placodes of vertebrates (Shimeld and Holland, 2000; Mazet et al., 2005). The cephalochordate-vertebrate gap begs at least two questions: first, how derived may cephalochordates be, relative to the common ancestor they shared with the vertebrates? And second, how much has the rise of the typical vertebrate neural crests and their adult derivatives contributed to give this gap an excessive importance?

The monophyly of extant cyclostomes is admittedly still debated (Delarbre et al., 2002), despite receiving increasingly strong

molecular support (Hedges, 2001; Mallatt et al., 2001; Furlong and Holland, 2002; Fig. 2.1B). In contrast, the paraphyly of the cyclostomes, with lampreys being the sister-group of the gnathostomes among present-day vertebrates (Fig. 2.1A), is strongly supported by morphological and physiological characters (Løvtrup, 1977; Janvier, 1978, 1996a,b; Dingerkus, 1979; Janvier and Blicek, 1979; Forey, 1984; Jefferies, 1986; Donoghue et al., 2000; Donoghue and Smith, 2001). I shall not enter this debate again here. All I can say is that if cyclostomes form a clade, either hagfishes are the most extraordinary example of reversion among vertebrates, or lampreys and gnathostomes are the most extraordinary example of evolutionary convergence (Delarbre et al., 2002). There is admittedly a current trend toward considering that reversion is underestimated in morphology-based phylogenies, and that molecular sequence-based phylogenies can pinpoint where extensive morphological reversions have occurred (e.g., Jenner, 2004). This argument overlooks the numerous biases that occur when comparing morphology-based trees, which are generally generated by parsimony programs, with sequence-based trees, which are generated by a wide range of methods that involve increasingly more complex models of evolution. Character losses do occur, and the processes through which they occur are sometimes complex, but postulating them as soon as a new tree turns up on the basis of an inferred gene evolution probability is, I think, an abuse of inference.

Curiously, and despite the morphological and physiological differences between hagfishes on the one hand and lampreys and gnathostomes on the other (Hardisty, 1982), few authors have ever alluded to any major gap at the "cyclostome" level of vertebrate phylogeny, because hagfishes and lampreys share much the same overall structure (such as eel-shaped body, single median "nostril," more or less pouch-shaped gills, retractable lingual apparatus, and horny teeth), which is assessed as general relative to the gnathostome condition in the framework of cyclostome paraphyly (Løvtrup, 1977; Janvier, 1981b) and is unique in that of cyclostome monophyly (Schaeffer and Thomson, 1980; Yalden, 1985).

Whatever the status of the cyclostomes, the morphological gap between the gnathostomes and either hagfishes or lampreys remains impressive (Fig. 2.1). For example, a glimpse at the endoskeletal skulls of a hagfish, a lamprey, and a gnathostome, such as a shark (Fig. 2.2), shows that very few primary homologies that can be readily assumed in all three taxa. In fact, only the skeletal olfactory and otic capsules, although quite different in shape in the three taxa, can be regarded as homologous, essentially because they surround sensory organs that are, in turn, regarded as unlikely to be homoplastic. Some more likely homologies are only shared by two of the three taxa, such as the velar skeleton or the lingual apparatus in hagfishes and lampreys, or the arcualia of the axial skeleton in lampreys and gnathostomes (Fig. 2.2).

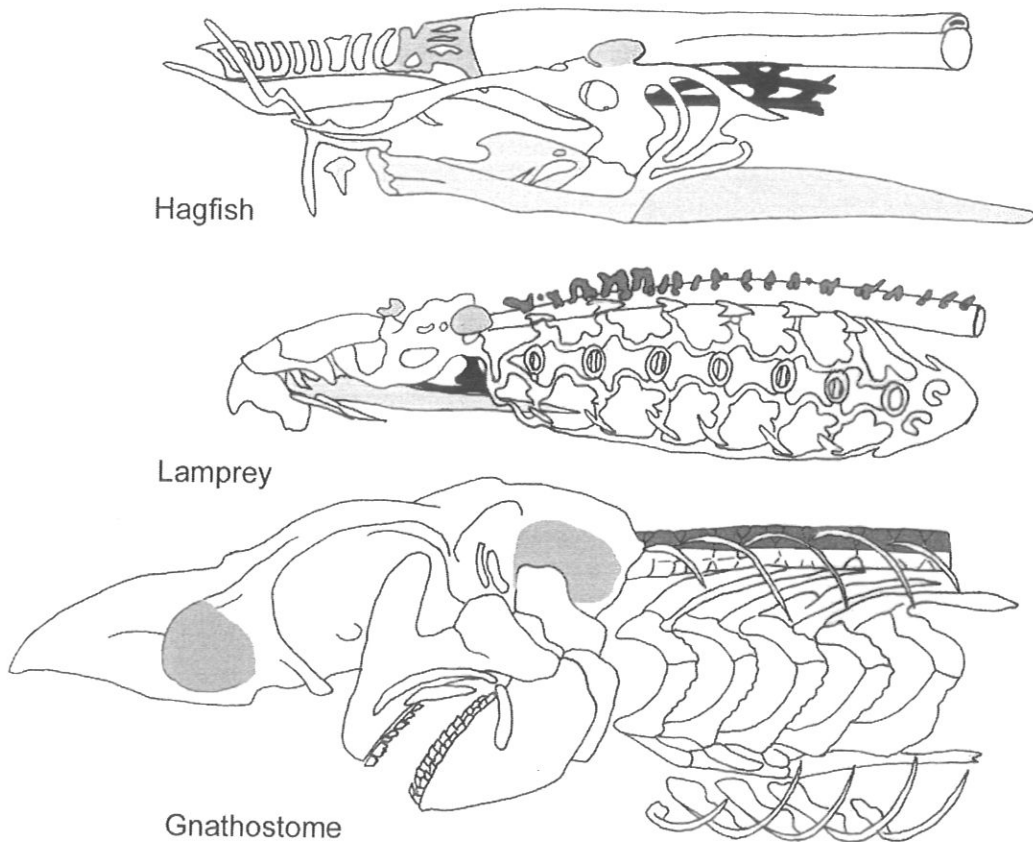


Figure 2.2. Skull in the three major vertebrate taxa: hagfish, lampreys, and gnathostomes (exemplified here by a shark), showing some of the presumably homologous characters. The “lingual apparatus” (light gray) and the velar skeleton (black) are unique to hagfishes and lampreys and have no undisputed homologue in gnathostomes. The dorsal arcualia (dark gray) are unique to lampreys and gnathostomes. The olfactory and otic capsules (medium gray) are the only parts of the skull that are unanimously regarded as homologues in all three groups. Modified from Janvier (1996b).

### Cambrian Euchordates and Presumptive Stem Vertebrates

Whether or not any fossil fills the cephalochordate-vertebrate gap remains unclear. Following the classical practice in paleontology, such fossils are generally looked for in the deep past of euchordate history, but on the vertebrate side of the gap, the earliest evidence for undisputed crown-group vertebrates are dermal armor fragments derived from arandaspids, from the Early Ordovician of Australia (Young, 1997). These, like other groups of “ostracoderms,” are regarded as more closely related to the gnathostomes than to either lampreys or hagfish, essentially because they possess dermal bone (Fig. 2.3H). In current phylogenetic studies, arandaspids are grouped with heterostracans and astraspids into a very weakly supported clade Pteraspidomorphi (Fig. 2.3H–J), and, more recently, as the sister-group to astraspids (Sansom et al., 2005). They are thus not the most inclusive taxon of the dermal bone-bearing vertebrates (Janvier, 1996a; Donoghue et al., 2000; Donoghue and Smith, 2001; Donoghue and Sansom, 2002).

Deeper in time, a number of Cambrian fossils have been tentatively referred to the vertebrates on the basis of either their overall morphology or the histological structure of their mineralized parts, when present (Bleick, 1991; Janvier, 1997; Smith et al., 2001). Apart



from the Myllokunmingiida (Fig. 2.3B), from the Early Cambrian of China (Shu et al., 1999, 2003a), none of them has yet been unanimously accepted as a vertebrate (Janvier, 2003). Among the presumed Cambrian vertebrates, two taxa have also received much attention during the last two decades: the euconodonts and *Anatolepis*.

### *Euconodonts*

Euconodonts are known from the Late Cambrian to the Triassic (Fig. 2.3F), but the only two genera known from articulated, or partially articulated, specimens (i.e., showing both the assemblage of the denticles usually referred to as *conodonts*, and the imprint of the head and body soft tissues) are Early Ordovician and Early Carboniferous in age, respectively (Briggs et al., 1983; Gabbott et al., 1995). It is nevertheless assumed that euconodonts, as a whole, may have displayed much the same overall morphology. Although the few morphological features described from the head and body imprints of the articulated euconodonts are rather convincingly euchochordate- and vertebrate-like (e.g., V-shaped myomeres; radials in caudal fin; large, paired optic capsules; Donoghue et al., 2000), most of the debates that arose in the 1990s about euconodont affinities were centered around the homology of the hard tissues that constitute their oral or pharyngeal denticles with those of the vertebrates. For reviews, see Aldridge and Purnell (1996), Schultze (1996), Donoghue and Aldridge (2001), and Kemp (2002). To date, there is no consensus on this question, but Donoghue et al. (2000) showed that hard tissue characters of euconodonts (i.e., whether they possess dentine, enamel, or bone) are not those that impose their position as crown-group vertebrates, and even as sister-group to "ostracoderms" plus gnathostomes in current vertebrate phylogenies. Euconodonts have also been regarded as the sister-group to either cephalochordates, crown-group vertebrates, hagfishes, or lampreys (see reviews in Aldridge and Donoghue, 1998; Donoghue et al., 2000), but an association with cephalochordates is less parsimonious because it would imply that the paired optic capsules either have appeared twice or are lost in cephalochordates. It has been pointed out that the myomeres of euconodonts seem to be V-shaped (as in cephalochordates), rather than W-shaped, as in crown-group vertebrates (and myllokunmingiids; see below), but this is probably an artifact of preservation (Donoghue et al., 2000). Euconodonts share with crown-group vertebrates the presence of median fin radials and are best placed as stem gnathostomes, notably on the basis of their ability to develop mineralized skeletal elements made of apatite (Fig. 2.3F).

### *Anatolepis*

*Anatolepis* is known from minute, tuberculate carapace fragments of Late Cambrian and Early Ordovician age; their histological structure recalls the classical vertebrate dentine (Smith and Sansom, 1995; Smith et al., 1996). However, none of the *Anatolepis* fragments recorded to date agrees with the structure of the individual dermal plates of the armor in classical "ostracoderm" taxa, nor

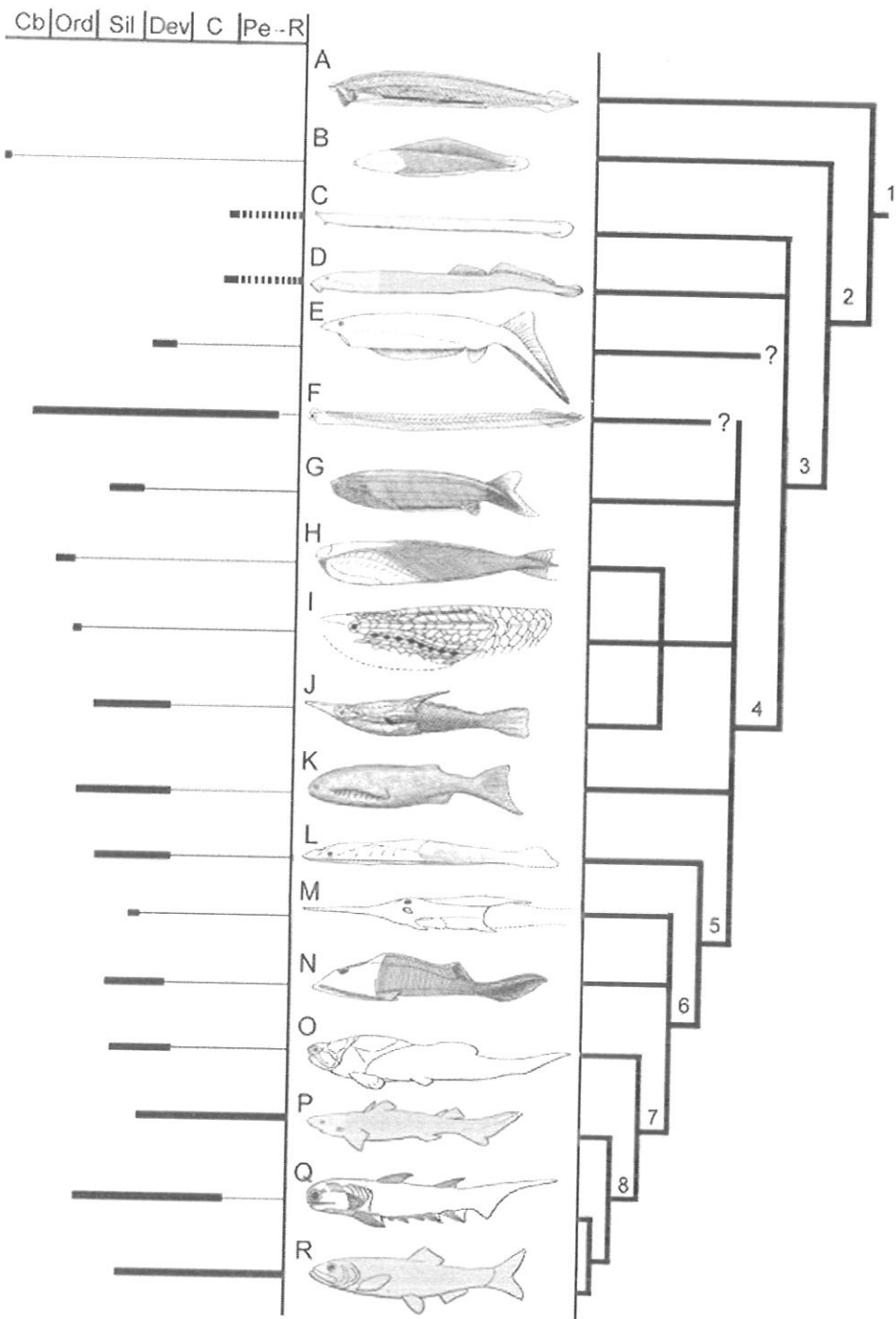


Figure 2.3. Synthesis (*not* a consensus tree generated by a computer program) of the major current theories of euchordate interrelationships (right), and stratigraphic distribution (thick bars, left) of the terminal taxa. All taxa are clades, except perhaps for thelodonts (K) and acanthodians (Q). Certain poorly known taxa (e.g., *Eriptychius*) are omitted. Extant taxa in gray. The conflict between the morphology- and molecular sequence-based theories regarding the hagfish-lamprey-gnathostome relationships is taken here into consideration, the relationships of the three groups being considered as unresolved. Taxa: A, cephalochordates;

do they show sensory-line canals or grooves that would be evidence for vertebrate epidermal placodes. In addition, some *Anatolepis* fragments are tubular in shape and have no equivalent in Paleozoic fishes. Yet Smith et al. (2001) tentatively compared them to the dermal bone sheath of the gill rakers in the extant whale shark. *Anatolepis* was once regarded as carapace fragments of an arthropod, but its histological structure apparently does not agree with this interpretation (Smith and Sansom, 1995). Currently, it is assumed that the name *Anatolepis* has been used for fragments of widely different origins, some of which may actually belong to arthropods, whereas others may belong to a vertebrate.

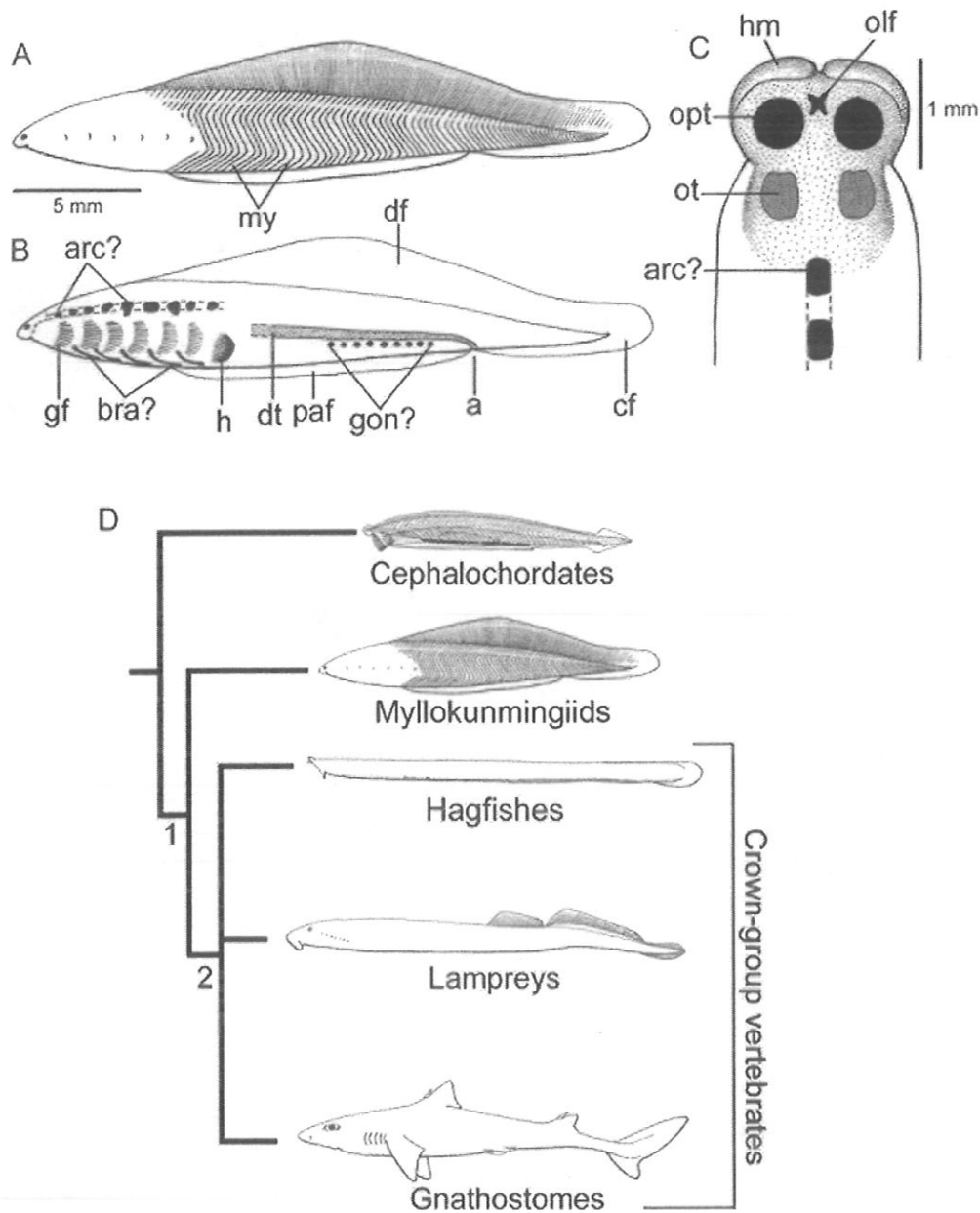
Admittedly, early evidence for dermal bone that can be readily referred to vertebrates known from articulated specimens may also display unusual histological structures, which differ from such classical vertebrate tissues as dentinous tissue (ortho-, meso-, and semi-dentine) or cellular bone. In anaspids and galeaspids, for example, the tubercles of the ornamentation are composed of a kind of acellular bone, and are thus entirely different from the dentinous tubercles of, for example, heterostracans, osteostracans, or gnathostomes. I even doubt that the galeaspid exoskeleton would have been referred to a vertebrate if complete head shields were not known. Thus, it cannot be ruled out that the early stages of the evolution of the vertebrate exoskeleton involved kinds of tissue structures outside the variation that we currently recognize in Paleozoic vertebrates. Judging from the histological structure of certain Ordovician vertebrate exoskeleton remains from Australia (Young, 1997), the United States (Sansom et al., 2001; Donoghue and Sansom, 2002), and Siberia (Karatajute-Talimaa and Smith, 2004), we can predict that entirely new types of histological structures may soon turn up in the earliest skeletonized vertebrates, and may make sense in systematics only

Figure 2.3. (continued)

B, Myllokunmingiida; C, hagfishes; D, lampreys; E, Euphaneropidae (also possibly included in the Anaspida); F, Euconodonta (relationships to or within the vertebrates still debated); G, Anaspida; H, Arandaspida; I, Astraspida; J, Heterostraci; K, Thelodonti (possibly nonmonophyletic); L, Galeaspida; M, Pituriaspida; N, Osteostraci; O, Placodermi; P, Chondrichthyes; Q, Acanthodii (possibly nonmonophyletic); R, Osteichthyes. Cb, Cambrian; Ord, Ordovician; Sil, Silurian; Dev, Devonian; C, Carboniferous; Pe-R, Permian to Recent. (A, C, D, J-R, after Janvier, 1996b; B, after Mallatt and Chen (2003a); E, based on pers. obs.; F, after Aldridge and Purnell, 1996; G, after Ritchie, 1964; H, after Gagnier, 1993a; I, based on Sansom et al., 2001).

Higher taxa and selected morphological characters inferred at nodes: 1, Euchordata (=Myomerozoa): chevron-shaped myomeres, endostyle, sinus venosus in blood vascular system, segmentally arranged spinal nerves; 2, Vertebrata: neural crest and epidermal placodes in development, olfactory, optic and otic capsules, gill filaments, W-shaped myomeres; 3, crown group Vertebrata: cartilaginous radials in fins, nonsegmental gonads; 4, Gnathostomata (in stem-based classifications): extensive dermal skeleton on head and body, well-developed cerebellum, well-developed vertical semicircular canals forming distinct loops; 5, unnamed taxon: perichondrally calcified endoskeleton, externally open endolymphatic ducts; 6, unnamed taxon: distinct pectoral fins and endoskeletal shoulder girdle, cellular perichondral and dermal bone, sclerotic ring and scleral ossification (unless present in arandaspids), slit-shaped external gill openings, epicercal tail (the latter four characters evidenced only in osteostracans among "ostracoderms"); 7, Gnathostomata (in apomorphy-based classifications): jaws, pelvic fins and girdles, nasal cavities opening to the exterior by separate nostrils and disconnected from Rathke's pouch; 8, crown group Gnathostomata: superior oblique muscle attached in anterior part of the orbit, adductor jaw muscles lateral to palatoquadrate.

Figure 2.4. (*opposite page*) A–C, attempted reconstruction of the myllokunmingiid *Haikouichthys ercaicunensis* Shu et al. (1999), from the Lower Cambrian of Chengjiang, China. A, reconstruction in lateral view (size and shape of external gill openings hypothetical); B, presumed internal structures in lateral view; C, stains of the head in dorsal view (from Janvier, 2003, modified and completed on the basis of new data on the fin and tail structure provided by Zhang and Hou, 2004). D, possible phylogenetic position of the myllokunmingiids. Characters at nodes: 1, neural crest and epidermal placodes in development, olfactory, optic and otic capsules, gill filaments, W-shaped myomeres; 2, cartilaginous radials in fins, nonsegmental gonads. Abbreviations used in figures: a, anus; af, anal fin; afac, canal for the facial artery; ama, anterior mesenteric artery; anc, annular cartilage; arc?, possible arcualia; asc, anterior semicircular canal; atr, atrium; bra?, branchial arches; bra1, first gill arch; bro, external branchial openings; brpl, branchial plates; cart, hypothetical cartilage plate bearing the dermal oral plates; cer, cerebellum; cf, caudal fin; cmvs, canal for the marginal vein sinus; cnhyd, circum-nasohypophysial depression; crhab, recess for the right habenular ganglion; cvcl, canal for the lateral head vein; da, dorsal aorta; da + oesc, canal for the dorsal aorta and the esophagus; dar, dorsal arcualia; dC, duct of Cuvier; dend, open endolymphatic duct; df, dorsal fin; df2, second dorsal fin; dt, digestive tract; el, epichordal lobe; exbrc, extrabranchial cartilages; gaimp?, possible gill-arch impressions; gf, gill filaments; gon?, possible gonads; gp, gill pouches; gs, gill slits; h, pericardial cartilage or heart; hl, ventral horizontal lobe of caudal fin; hm, anterior head margin (oral hood?); ht, impressions of horny teeth; hv, hepatic vein; hy, hyoid arch; hyhbrp, posterior hyoid hemibranch; hypc, hypophysial cavity; hyt, hypophysial tube; ic, canal for the internal carotid artery; lvsck, lateral velar skeleton; m, mouth; ma, mandibular arch; mdo, median dorsal opening; mins, pits for muscle insertion; ml, hypothetical levator muscle; mm, ectomesenchyme surrounding the mandibular mesoderm;.mvp, medial ventral processes for attachment of gill arches; mvs, marginal vein sinus; mvsk, medial velar skeleton; my, myomeres; nac, nasal cavity; nc, neural canal; nch, notochord; nchc, canal for the notochord; nho, nasohypophysial opening; nhplac, nasohypophysial placode; nhv, nasohypophysial valve; es, esophagus; ol, optic lobes; olf, olfactory capsule/organ; olfplac, olfactory placode; oltr, olfactory tract; opl, oral plates; opt, optic capsule; optf, optic fenestra; orb, orbit; oro, oral opening; orv, oral valve; ot, otic capsule; paf, preanal fin-fold; pc, piston cartilage; pcard, pericardial cavity; pef, pectoral fin; pefe, pectoral fin endoskeleton; pelf, pelvic fin; pelfrac, pelvic fin radials; pf, paired fin; pfrac, paired fin radials; pif, pineal foramen; pm, ectomesenchyme surrounding the premandibular mesoderm; psc, posterior semicircular canal; rhab, right habenular ganglion; Rp, Rathke's pouch; sc, single semicircular canal; sk, imprint of the skin; spi, spiracular canal; st, suspensory connective tissues for the esophagus; tc, tectal cartilages; tcl, tentacles; tel, telencephalic division of the brain cavity; var, ventral arcualia; vcl, lateral head vein or dorsal jugular vein (vena capitis lateralis); vel, velum; ven, ventricle; vfl, velar flap; vj?, possible ventral jugular vein; V2–3, maxillary and mandibular branches of the trigeminal nerve; VII, facial nerve.



when these isolated remains are assigned to articulated specimens. However, whatever vertebrate *Anatolepis* may turn out to be, it is probable that it will fall, according to current phylogenies, somewhere among “ostracoderms”—that is, stem gnathostomes.

#### *Myllokunmingiids*

The Myllokunmingiida (*Haikouichthys*, *Myllokunmingia*, and *Zhongjianichthys*; Shu et al., 1999; Shu, 2003), from the Lower Cambrian of Chengjiang, China, are probably the most convincing Cambrian vertebrates known to date, although lacking mineralized

tissues (Figs. 2.3B, 2.4). The differences among these three genera remain difficult to assess and may well be due to differences in size and preservation (Hou et al., 2002). However, their basic structure is now better known as a result of the discovery of about 500 specimens, referred to *Haikouichthys ercaicunensis*, which are preserved in different aspects and allow a more accurate reconstruction (Janvier, 2003; Shu et al., 2003a). To date, the identification of the myllokunmingiids as vertebrates has not been called into question. They provide quite convincing evidence for paired olfactory, optic and possibly otic capsules (olf, opt, ot, Fig. 2.4C), and six gills borne by skeletal arches (bra?, gf, Fig. 2.4B). This suggests the presence of epidermal placodes and neural crest-derived tissues, which are currently regarded as the most reliably unique vertebrate characters (Baker and Bronner-Fraser, 1997; Le Douarin and Kalcheim, 1999). Holland and Chen (2001) erected the taxon Cristozoa, i.e., organisms with neural crest, to accommodate the discovery of possible stem vertebrates, such as myllokunmingiids. In addition, their myomeres seem to display the characteristic W shape of the vertebrate myomeres, rather than the V shape in cephalochordates (Fig. 2.4A).

The first description of *Haikouichthys* and *Myllokunmingia* (Shu et al., 1999) raised questions about their having ventrolateral paired fins or fin folds, and the first phylogenetic analysis performed on the basis of only two specimens (referred to these two genera, respectively) suggested that *Myllokunmingia* was the sister-group of lampreys plus all other vertebrates except for hagfishes, whereas *Haikouichthys* appeared as the sister-group to lampreys (Shu et al., 1999; Donoghue et al., 2003). Further discoveries failed to provide evidence for paired fins in myllokunmingiids, and it is now clear that they all possessed a single median dorsal fin or fin fold, extending from the head to the tip of the tail (df, cf, Fig. 4A; Zhang and Hou, 2004). Ventrally, a similar median fin extends from the tip of the tail to the posterior limit of the branchial apparatus (paf, Fig. 2.4B), with an interruption at the level of the anus (a, Fig. 4B). There is thus a preanal skin fold (or fin fold), as in adult hagfishes, larval lampreys, and certain larval gnathostomes. One of the puzzling features in the first descriptions of the myllokunmingiids was the numerous, closely set, and forward-tilted radials in the dorsal fin (Shu et al., 1999; Janvier, 2003). This is at odds with the condition in vertebrates, where the dorsal fin radials are generally tilted backward. However, a recently discovered specimen shows a perfectly preserved body and tail, and demonstrates that these presumed radials become vertical at the midlength of the body, and then increasingly tilted backward toward the tip of the tail (Fig. 2.4A; Zhang and Hou, 2004). Moreover, this specimen suggests that the radials may in fact not be true radials (i.e., endoskeletal structures), but either epidermal folds or collagenous structures comparable to the ceratotrichia of the gnathostomes (Zhang and Hou, 2004). The lack of endoskeletal radials in the unpaired fins could thus suggest that myllokunmingiids are not crown-group vertebrates, which all have radials (Figs. 3, 4D;

Zhang and Hou, 2004). The position of the notochordal lobe, relative to the dorsal and ventral fin webs, is still unclear in myllokunmingiids, although the specimen described by Zhang and Hou (2004: fig. 1) seems to show a slightly larger dorsal web that could foreshadow the hypocercal condition of most present-day and fossil "agnathans" (Figs. 2.4, 2.12).

Another odd feature of myllokunmingiids is the structure of the gills (cf. Fig. 2.4B). These display relatively long, posteriorly directed, filamentous structures, which recall those also found in yunnanozoans. Whether these structures are gill rays supporting the gill filaments, or whether they armed the interbranchial septa and gill covers remains undecided. Zhang and Hou (2004) even suggested that the gill ray-like structures extended externally through the gill openings, the shape and size of which remain unclear. These structures are suggestive of the gnathostome gill rays, which are lacking in extant jawless vertebrates. Yet the recent discovery of numerous gill ray-like endoskeletal elements in the Late Devonian anaspid-like vertebrate *Euphanerops* (P. Janvier, pers. obs., 2004) suggests that this character is possibly more general than previously believed.

*Haikouichthys* displays, in the anterior part of the body, a number of more or less elongated, sinuous stains, which have been interpreted as imprints of cartilages, some being gill arches, others possibly arcualia of the vertebral column (arc? bra?, Fig. 2.4B; Shu et al., 2003b). This, however, should be considered with great reservation. Notably, the presumed arcualia would be anomalously large, relative to the size of the animal, and do not extend beyond the posterior limit of the branchial region. I assume that all these imprints are more likely derived from the branchial skeleton. The presence of a pericardial cartilage (or the heart proper), in the form of the well-marked stain at the rear of the branchial apparatus, is probable (h, Fig. 2.4B), although it is not ruled out that this stain was left by the liver, as is frequently observed in soft-bodied fishes preserved as imprints.

Myllokunmingiids show no clear evidence for a braincase, but specimens preserved in dorsal aspect display an unusually smooth area surrounding the sensory capsules, which suggests the presence of some kind of either cartilaginous or fibrous braincase (Fig. 2.4C), possibly comparable to the partly fibrous braincase of hagfishes. The peculiar bilobate anterior margin of the myllokunmingiid head (hm, Fig. 2.4C) somewhat resembles the cartilage of the oral hood of larval lampreys, but this is the only feature that could possibly suggest a closer relationship to lampreys than to any other chordate. Yet it also recalls the somewhat bilobate anterior head margin of yunnanozoans (Mallatt and Chen, 2003a: fig. 6A; see below). Although the olfactory organ of myllokunmingiids is small and apparently composed of two closely set nasal capsules (olf, Fig. 2.4C), there is no evidence that it opened dorsally and formed a nasohypophysial complex of the lamprey type.

The phylogenetic position of the myllokunmingiids remains ambiguous. It is still unclear whether they are crown-group or stem-group vertebrates. However, two characters could possibly support

the latter theory (2, Fig. 2.4D): the apparent lack of cartilaginous radials in the median fins, and the possible presence of serially arranged gonads. As a matter of fact, some specimens of *Haikouichthys* display, ventral to the imprint of the digestive tract (dt, Fig. 4B), a series of rounded stains, which have been interpreted as possible evidence for serially arranged gonads (gon?, Fig. 4B; Shu et al., 1999, 2003b; Hou et al., 2002). Such a structure of the gonads, also inferred in yunnanozoans (Mallatt and Chen, 2003a,b; see below), would recall the condition in the cephalochordates (also controversially recorded in the branchial region of certain enteropneust species) and is unknown in extant vertebrates. If such a condition of the gonads can ever be confirmed, then myllokunmingiids would show the first evidence of a combination of a reputedly unique cephalochordate character (serially arranged gonads) and reputedly unique vertebrate characters (head with paired sensory capsules, gill arches, W-shaped myomeres, etc.). It should nevertheless be pointed out here that these presumed gonad impressions in myllokunmingiids are remarkably well marked (Shu et al., 2003b: fig. 1J), as are also those of yunnanozoans (Mallatt and Chen, 2003a: figs. 10, 12), and strikingly recall the series of impressions left on the surface of the body musculature by the ventrolateral series of large slime glands of hagfish (Marinelli and Strenger, 1956: figs. 78, 82, 108). This is perhaps mere coincidence, but it is worth keeping in mind.

In sum, there is thus some support, albeit tenuous, to the theory that myllokunmingiids are the sister-group of the crown-group vertebrates, somehow filling the morphological gap between the cephalochordates and vertebrates.

#### *Yunnanozoans*

The Yunnanozoa are yet another taxon from the Early Cambrian of China, which has received much attention in connection with the question of vertebrate ancestry. Yunnanozoans (*Yunnanozoon* and *Haikouella*) are known from hundreds of exquisitely preserved specimens but remain the subject of heated controversies. They were first regarded as the closest fossil relatives to the vertebrates (Chen et al., 1995, 1999; Holland and Chen, 2001; Mallatt and Chen, 2003a,b), then to chordates or hemichordates (Shu et al., 1996), cephalochordates (Gould, 1995), and finally as stem deuterostomes, possibly related to the Cambrian vetulicolians (Shu et al., 2001, 2003b; Shu and Conway Morris, 2003). The detailed study of *Haikouella* by Mallatt and Chen (2003a), however, suggests some resemblance to larval lampreys in the organization of the head imprints. Yet these authors may have overinterpreted certain rather vague imprints, notably their claim that paired eyes, nostrils, and a brain are visible on the specimens (Mallatt and Chen, 2003a: fig. 7). Moreover, the very deep body and vertically straight myomeres of yunnanozoans are at odds with the V- or W-shaped myomeres of euchordates. In contrast, their elongated "gill rays" borne by the six gill arches resemble the gills of myllokunmingiids. To some extent, the deep body, straight myomeres, and shallow head



region of yunnanozoans also recall the aspect of the Middle Cambrian Burgess Shale fossil *Pikaia gracilens*, often referred to as a chordate or a vertebrate relative (Gould, 1995; Conway Morris, 1998). At any rate, yunnanozoans lack a number of characters uniquely shared by myllokunmingiids and vertebrates, such as the well-defined optic and olfactory capsules, but, like myllokunmingiids, they show some possible indication of serially arranged gonads (unless, as suggested above for the myllokunmingiids, these are impressions of ventral slime glands).

Considering some evidence for a relatively complex organization of the branchial apparatus, and despite their lack of chevron-shaped myomeres, yunnanozoans could thus possibly be euchordates, and more closely related to the myllokunmingiids and vertebrates than to the cephalochordates, as proposed by Mallatt and Chen (2003a,b). In such a case, they would also contribute in filling the morphological gap between the latter and the vertebrates, and provide a plausible example of an organism in which gill arch formation involved neural crest cell migration, before the appearance of epidermal placodes and thus vertebrate-like sensory capsules. However, the recent suggestion by Shu et al. (2003b) and Shu and Conway Morris (2003) that yunnanozoans represent stem deuterostomes is also worth considering as an alternative. It would imply that some of the characters regarded as unique to chordates or euchordates are, in fact, general for deuterostomes.

#### *Are There Fossil Cephalochordates?*

Strangely, it seems now that the main problem in euchordate evolutionary history is less with the early stages in vertebrate evolution than in those of their sister-group, the cephalochordates. Despite some dubious fossils either expressly referred to the cephalochordates (the Permian *Palaeobranchiostoma*; Oelofsen and Loock, 1981), or questionably so (e.g., *Emmonsaspis*; Resser and Howell, 1938; discarded by Conway Morris, 1993), there is no unambiguous evidence for fossil cephalochordates (Blicek, 1991). Molecular clock data, however reliable they may be (see criticisms by Donoghue et al., 2003), suggest divergence times between cephalochordates and vertebrates that can be as early as 750 Ma ago (e.g., Hedges, 2001). Thus, theoretically, cephalochordates (or stem cephalochordates) are likely to occur as early as the Cambrian, but we may be unable to recognize them, unless they are some of the mitrates, as claimed by Jefferies (1986). Between the mid-nineteenth and mid-twentieth centuries, the lack of an organized head in cephalochordates has been variously regarded as either primitive or the result of degeneracy. For example, Holmgren and Stensiö (1936: fig. 206) reconstructed a hypothetical ancestral cephalochordate that superficially looks like a naked osteostracan lacking paired eyes, and more recently, Bjerring (1984) figured a branching diagram where cephalochordates are the sister-group to a clade Agnatha (thereby implying an unlikely number of either losses in cephalochordates, or convergences between "agnathans")

and gnathostomes). Current molecular phylogenies and developmental data demonstrate quite clearly that cephalochordates are not nested within the vertebrates (see Holland and Chen, 2001). Nevertheless, as pointed out above, it remains undecided how much their anatomy has been modified since their divergence from the lineage that led to the vertebrates. Despite their possibly having neural crest and placode precursors (Holland et al., 1996; Shimeld and Holland, 2000; Holland and Holland, 2001; Holland and Chen, 2001), they show no evidence for migrating neural crest cells, and thus they are unlikely to have developed a skull with gill arches (in the vertebrate sense) in their evolutionary history. To date, cephalochordates are thus the only major deuterostome group for which there are no undoubted fossil data.

#### *Evolutionary Transition in Stem Vertebrates*

There is thus a slight possibility that myllokunmingiids and, less likely, yunnanozans are stem-group vertebrates that have diverged before the common ancestor to all extant vertebrates and after the cephalochordate-vertebrate divergence (Figs. 2.3, 2.4D). Do these taxa illustrate an evolutionary transition? Not really, because myllokunmingiids are morphologically very close to crown-group vertebrates. Whether yunnanozoans branch off deeper in euchordate phylogeny or are stem deuterostomes remains debated. As a whole, the gap between the cephalochordates and crown-group vertebrates remains void, or almost so. However, because we are in the realm of speculation, it is also possible that myllokunmingiids (assuming that they actually are "cristozoans") tell us that the gap in question may not have been that large, and that once the neural crest and epidermal placodes gained their role in head morphogenesis, the so-called vertebrate *Bauplan* turned up in perhaps no more time than the rise of paired limbs from fins. Such a simplistic scenario is probably doomed to be refuted by recent research on the presumed placode homologues of tunicates, which throws a new light on the diversity and early role of these developmental characters (Mazet et al., 2005).

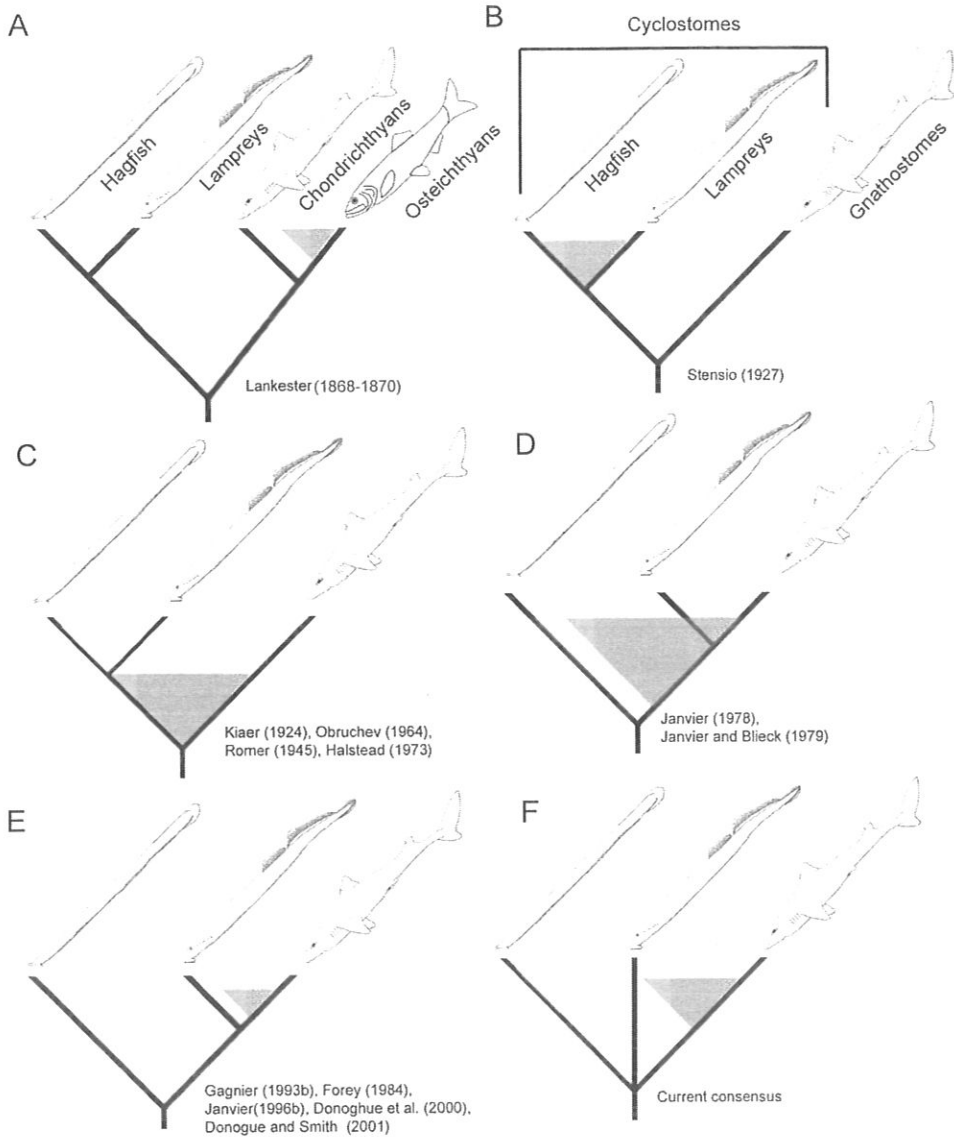
It is also possible that we pay excessive attention to myllokunmingiids because they have a very early age. Would we do the same if they were merely Carboniferous in age? After all, some Carboniferous Konservat-Lagerstätten have yielded peculiar soft-bodied vertebrate-like fossils (such as *Pipiscius*, *Gilpichthys*, and *Conopiscius*; Bardack and Richardson, 1977; Briggs and Clarkson, 1987) that may also turn out to be stem-group vertebrates.

#### **Whence the Cyclostomes?**

Whether the cyclostomes are monophyletic or not, the relationships of hagfishes and lampreys to the fossil jawless vertebrate taxa remain largely an enigma. In the mid-nineteenth century, the armored jawless vertebrates, now informally referred to as "ostracoderms," were first regarded as bony fishes (e.g., Lankester, 1868–1870; Fig. 2.5A), until it was proven that they are jawless and that

some of their anatomical features (e.g., the lack of horizontal semi-circular canal) also occur in extant cyclostomes, notably lampreys. However, apart from their being jawless, "ostracoderms" could not easily be related to either hagfishes or lampreys. Stensiö (1927) assumed that hagfish were the closest relatives of heterostracans, whereas lampreys were that of anaspids, and that the latter two groups were in turn the sister-group of osteostracans. Contrary to the classical definition of the cyclostomes, Stensiö's one was thus stem based (Fig. 2.5B). This theory, referred to as the "diphyletism of the cyclostomes" (i.e., independent appearance of the characters that are regarded unique to hagfishes and lampreys, within a clade Agnatha), has been the subject of debates until the 1970s, mainly regarding Stensiö's assumption that hagfishes were related to heterostracans (Stensiö, 1927, 1932, 1958, 1964, 1968; see review in Janvier and Blicek, 1993). Yet nobody rejected his theory, outlined by Kiaer (1924), that lampreys were the closest relatives of anaspids and osteostracans, all three groups forming the clade Cephalaspidomorphi, characterized by a dorsal nasohypophysial opening. It was thus assumed, except by Stensiö, that hagfishes were more closely related to lampreys than to any extinct vertebrate taxon, and thus that hagfish morphology was derived from a cephalaspidomorph, and most probably a lamprey-like one. Some "ostracoderms" were thus stem cyclostomes, whereas others (namely heterostracans) were possibly stem gnathostomes because of their paired olfactory capsules (Fig. 2.5C). Only Moy-Thomas and Miles (1971) removed hagfishes from the cephalaspidomorphs (in Stensiö's sense), but they nevertheless regarded them as the sister-group of the latter because of their monorhinal condition (i.e., single median nostril). Then, after the rise of the theory of cyclostome paraphyly (Løvtrup, 1977), only lampreys and gnathostomes were thought to be derived from "ostracoderms" through loss of a calcified skeleton, but cephalaspidomorph monophyly remained the received wisdom (Janvier, 1978; Fig. 2.5D). Cephalaspidomorph monophyly was questioned much later (Forey, 1984; Janvier, 1984), and more clearly so after the first computer-assisted parsimony analysis of vertebrate interrelationships by Gagnier (1993b), as well as by subsequent analyses (Forey and Janvier, 1993; Janvier, 1996b; Donoghue et al., 2000, 2003; Donoghue and Smith, 2001), all of which showed hagfishes and lampreys as more inclusive than all vertebrates with a mineralized skeleton (i.e., euconodonts, "ostracoderms," and gnathostomes; Fig. 2.5E,F).

Hagfishes and lampreys are almost unknown as fossils, and there is no hint for knowing how much derived or generalized they may be relative to the early Paleozoic "ostracoderms." All the fossils referred to hagfishes and lampreys are Carboniferous in age and preserved as imprints. The two fossils referred to lampreys, *Hardistiella* and *Mayomyzon* (Fig. 2.6A,B), both look like a small present-day lamprey, except for their lack of separate anterior and posterior dorsal fins and their shorter branchial apparatus (gp, Fig. 2.6A2; Bardack and Zangerl, 1968, 1971; Janvier and Lund, 1983; Janvier et al., 2004b). The head of *Mayomyzon* displays imprints



of cartilages that somewhat match the shape and position of the characteristic piston, tectal and annular cartilages, and the small olfactory capsule of adult lampreys (pc, tc, anc, olf, Fig. 2.6A2). There is thus little doubt that these two Carboniferous forms actually represent lampreys and are adults, despite their small size.

The fossil record of hagfishes is less clear. Of the two presumed fossil hagfish, *Myxinikela* and *Myxineides*, the former displays the characteristic tentacles at the tip of its snout (tcl, Fig. 2.6C2), but its body is much stouter than that of extant hagfishes (Bardack, 1991; Fig. 2.6C). The few imprints of internal structures in *Myxinikela* only provide some indication of a hagfish-like cartilaginous nasal basket (corbiculum nasale) and prenasal sinus (olf, Fig. 2.6C2). In contrast, *Myxineides* shows no clear evidence for tenta-

cles nor for a nasal basket, but it has the characteristic eel-like body shape of modern hagfishes and shows indications of two V-shaped rows of horny teeth (ht, Fig. 2.6D) in the form of impressions in the natural cast of the oral cavity (dt, Fig. 2.6D3; Poplin et al., 2001). None of these specimens, provided that they are correctly identified as lampreys and hagfish, respectively, shows character combinations such as, for example, an annular cartilage in a hagfish or large tentacles in a lamprey, which would suggest that one taxon is nested in the other. Only *Myxinikela* suggests that the branchial apparatus was primitively closer to the braincase than in modern hagfishes, as was also inferred earlier from hagfish development (e.g., Holmgren, 1946). In addition, these fossils provide no indication of any character loss, at least since the Carboniferous, in hagfishes and lampreys, such as the long-presumed loss of exoskeleton or paired fins implied by the traditional “degeneracy” theory of cyclostome evolution. Only *Mayomyzon*, which displays no separate dorsal fins, suggests that the two dorsal fins of present-day lampreys and gnathostomes could be homoplastic.

#### *The Question of the Cephalaspidomorphs*

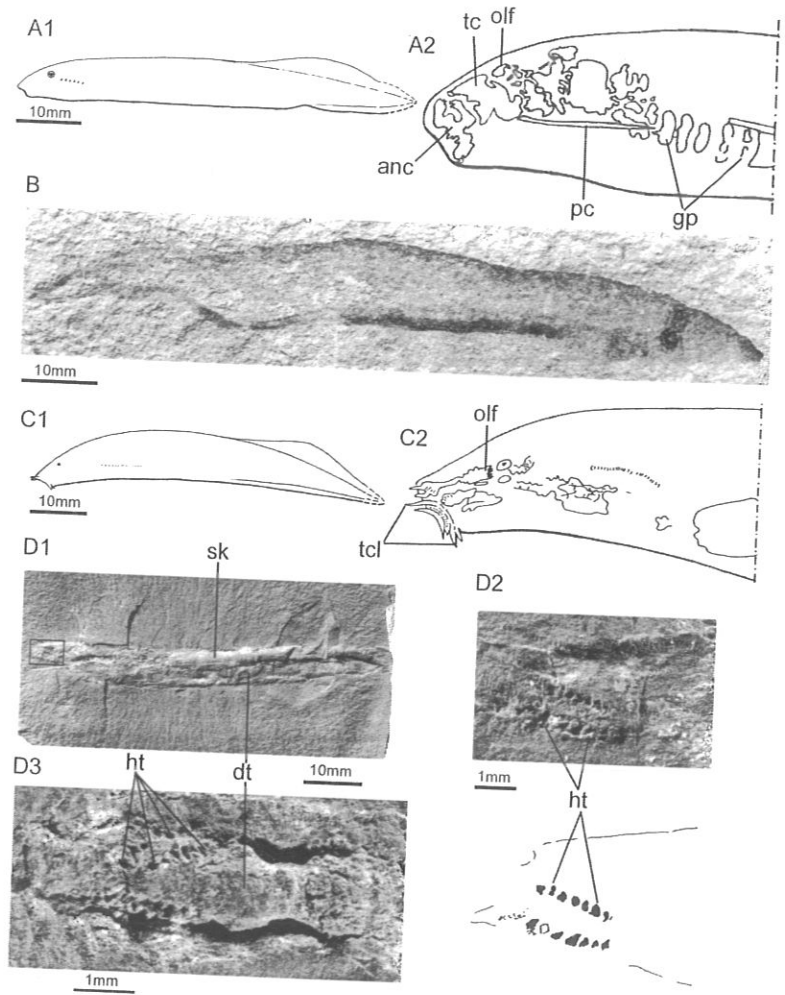
Hagfishes and lampreys display very few characters that are uniquely shared with any particular group of the fossil jawless vertebrates referred to as “ostracoderms.” The presence of a common external branchial opening in some hagfishes, the Myxinidae, and heterostracans, long invoked by Stensiö (1964, 1968) in support to his theory of hagfish-heterostracan relationships, is regarded as homoplastic (Janvier, 1996a,b). Only lampreys and osteostracans (and possibly anaspids) share some uniquely derived characters, which have been highlighted by Stensiö (1964) and others (e.g., Jarvik, 1980; Janvier, 1981a, 1984) and long recognized as robust support for the monophyly of the clade Cephalaspidomorphi. Most of these characters (e.g., enlarged right habenular ganglion; shift of the dorsal aorta to the right side, dorsally to the heart; ventricle and atrium of the heart closely set and lying side by side; lateral and dorsal expansions of the membranous labyrinth) have often been dismissed as either highly variable in vertebrates, ambiguous, or shared also with either some hagfishes or some gnathostomes (Janvier, 1984, 1996b; Janvier et al., 1991; see below). However, the presence of a dorsal nasohypophysial opening in osteostracans, lampreys, and possibly anaspids remains an intriguing character, which, in current vertebrate phylogenies, is assumed to have evolved separately in lampreys and osteostracans.

In lampreys, the olfactory organ is much reduced and housed in a small cartilaginous capsule that is independent from the braincase proper (olf, Fig. 2.7B1). In ontogeny, it is derived from an anterior median olfactory placode, which is situated immediately rostral to the hypophysial tube, long presumed to be the homologue of the Rathke’s pouch in gnathostomes. For recent reviews of the question, see Kuratani et al. (2001) and Ushida (2003). During early embryonic development, the two structures remain closely united as the na-

Figure 2.5. (opposite page)

Simplified history of the conceptions about the relationships of “ostracoderms.” The areas in gray indicate the extent of all possible relationships for taxa referred to as “ostracoderms.” A, Lankester’s (1868–1870) theory that “ostracoderms” were primitive osteichthyans; B, Stensiö’s (1927) theory of “cyclostome diphyletism,” where “ostracoderms” are paraphyletic and subgroups ancestral to hagfishes and lampreys, respectively; C, theory defended by various opponents to Stensiö, assuming that some “ostracoderms” are either ancestral to or the closest relatives of the cyclostomes, whereas others (generally heterostracans) are either ancestral to or the closest relatives of the gnathostomes; D, Janvier’s (1978) theory, incorporating Løvtrup’s (1977) theory of cyclostome paraphyly, and assuming “ostracoderm” paraphyly; E, current morphology-based theory, assuming that “ostracoderms” are paraphyletic stem gnathostomes; F, current consensus, incorporating the conflicting results from morphology- and molecular sequence-based analyses of crown-group vertebrate relationships.

Figure 2.6. Presumed fossil hagfish and fossil lampreys. A, *Mayomyzon pieckoensis* Bardack and Zangerl (1968), Upper Carboniferous of Illinois; A1, overall shape; A2, details of the cartilage imprints in the head (based on Bardack and Zangerl, 1968, and Janvier, 1993). B, *Hardistiella montanensis* Janvier and Lund (1983), Upper Carboniferous of Montana (from Janvier and Lund, 1983). C, *Myxinikela siroka* Bardack, 1991, Upper Carboniferous of Illinois; C1, overall shape; C2, details of the cartilage imprints in the head (from Bardack, 1991). D, *Myxineides gononorum* Poplin, Sotty and Janvier (2001), Upper Carboniferous of Allier, France; D1, D2, head and anterior part of the body (D1) and detail of the internal cast of the oral cavity of the same specimen (D2, framed in D1), showing impressions of the horny teeth; D3, internal cast of the oral cavity of the holotype, showing impressions of two pairs of rows of horny teeth (from Poplin et al., 2001). Abbreviations as in Figure 2.4.



sohypophysial placode, but their common external opening, the nasohypophysial opening, migrates dorsally, as a result of the development of the "upper lip," or oral hood (Gorbman and Tamarin, 1985). In the larval lamprey, the nasohypophysial opening is slit-shaped (nho, Fig. 2.7A), and in the adult lamprey, it is rounded (nho, Fig. 2.7B2) but continued internally by a short duct, which ends ventrally with a valve, the nasohypophysial valve (nhv, Fig. 2.7B), that surrounds a keyhole-shaped opening and marks the entrance to both the olfactory organ and the posteriorly closed hypophysial tube (olf, hyp, Fig. 2.7; Janvier, 1975b). The ontogeny of osteostracans is, of course, unknown, but adult osteostracans display, anteriorly to the orbits, a keyhole-shaped opening (nho, Fig. 2.7C3), which strikingly resembles the nasohypophysial valve of lampreys (Fig. 2.7B3). Because the endoskeleton is perichondrally ossified, it can be shown that the posterior division of this opening is prolonged internally by a small pear-shaped cavity (nac, Fig. 2.7C1), which is confluent with the telencephalic division of the brain cavity and supposed to have

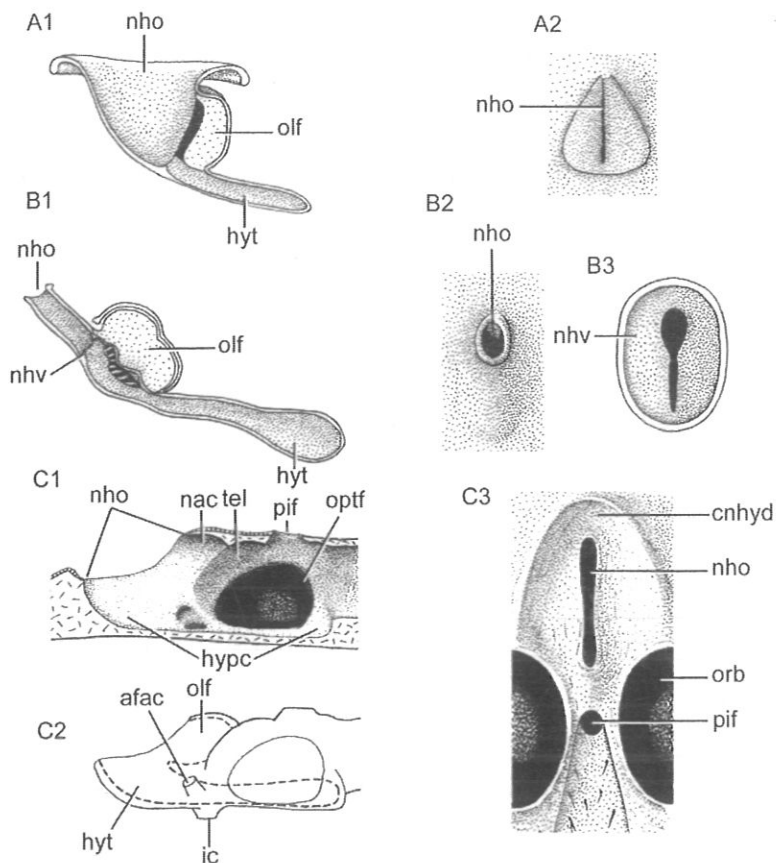


Figure 2.7. Nasohypophysial complex in lampreys and osteostracans (not to scale). A, nasohypophysial complex of a larval lamprey; A1, sagittal section; A2, nasohypophysial opening in dorsal view. B, nasohypophysial complex of an adult lamprey; B1, sagittal section; B2, nasohypophysial opening in dorsal view; B3, nasohypophysial valve in dorsal view. C, nasohypophysial complex in the Early Devonian osteostracan *Belonaspis*; C1, sagittal section through the ethmoid and anterior brain cavity of the head shield; C2, attempted reconstruction of the olfactory organ and hypophysial tube (dashed line); C3, dorsal view of the nasohypophysial opening. (A, B, after Janvier, 1975b; C, after Janvier, 1985a.) Abbreviations as in Figure 2.4.

housed the olfactory organ (olf, Fig. 2.7C1). The anterior division of the nasohypophysial opening is prolonged internally by an elongated cavity (hypc, Fig. 2.7C1), which is confluent dorsally with the ventral part of the diencephalic division of the brain cavity and the cavity for the olfactory organ, and is considered to have housed the hypophysial tube (hyt, Fig. 2.7C2). As already shown by Stensiö (1927), the structure of the nasohypophysial complex (Janvier, 1974) in lampreys and osteostracans is strikingly similar, and this is further emphasized by the quite similar distribution of the surrounding arteries derived from the internal carotids in this area (Janvier, 1975b: fig. 4). Nevertheless, the late Colin Patterson (London) once asked me, "How do you know that osteostracans have a nasohypophysial opening? Can you see the hypophysis?" Admittedly, we cannot see the hypophysis of osteostracans, nor can we see any recess of the brain cavity of the braincase where it could possibly be housed, because of the coalescence between the brain cavity and the lodge for the hypophysial tube. Thus, in common with many fossil data, this interpretation of osteostracan anatomy remains only a strong probability that is based on striking resemblance.

Kiaer (1924) and Stensiö (1927) argued that the same condition of the nasohypophysial complex also occurred in anaspids on

account of the median, keyhole-shaped opening, which is situated between two dermal plates, anterior to the orbits. However, anaspids lack a calcified endoskeleton, and the actual shape of the nasohypophysial complex is unknown in this taxon.

The question of the significance of this remarkable resemblance in the structure of the nasohypophysial complex between lampreys and osteostracans is no longer at the core of current debates about vertebrate phylogeny, but it has long been the cornerstone of cephalaspidomorph monophyly and the theory of lamprey "degeneracy" (relative to "ostracoderms"). In the 1960s, the reliability of this character to paleontologists, as a signature (i.e., an indisputable synapomorphy), was comparable to that of, for example, the choana of *Eusthenopteron* and tetrapods.

Although Gross (1964) already hinted at the possibility of the dorsal nasohypophysial opening of lampreys and osteostracans being independently derived, I feel somewhat responsible for the way this character is currently regarded as being inconsequential, and even overlooked, as an obvious homoplasy. In fact, early cladistic analyses of fossil and extant vertebrates did not clearly break through the "cephalaspidomorph barrier," although they supported both cyclostome and "ostracoderm" paraphyly (Fig. 2.5D; Janvier, 1978, 1981a; Janvier and Blicek, 1979). The idea that cephalaspidomorphs (at any rate lampreys and osteostracans) might not be a group has developed progressively, in the wake of computerized cladistic analyses, and as characters were given equal weight. The unique structure of the nasohypophysial complex shared by lampreys and osteostracans was thus outnumbered by characters that are uniquely shared by the latter and gnathostomes (e.g., Forey, 1984, 1995; Janvier, 1984, 1986, 1996a; Gagnier, 1993b; Fig. 2.5E). Osteostracans admittedly do share a larger number of characters with gnathostomes (e.g., true pectoral fins, well-developed, perichondrally ossified endoskeleton, cellular bone, and epicercal tail) that Stensiö (1927) considered as general vertebrate characters, lost in lampreys, whereas other paleontologists regarded them as convergences between osteostracans and gnathostomes.

The discovery of the galeaspids and pituriaspids (L, M, Fig. 2.3), two groups that, like osteostracans, possess an exo- and endoskeletal head shield, and the elucidation of part of their internal anatomy have also cast doubts on cephalaspidomorph monophyly (Wang, 1991; Young, 1991). Galeaspids lack paired fins and possess a median, dorsally opening "nostril," as in lampreys and osteostracans, but their "nostril" is in fact the external opening of a duct, which communicates ventrally with the oralbranchial (or orobranchial) cavity (more or less like the nasopharyngeal duct of hagfishes), and into which open distinctly paired olfactory organs (Janvier, 1996b). Remarkably, this dorsal opening is slit-shaped in some galeaspids, thereby mimicking the nasohypophysial opening of osteostracans, but this condition is currently regarded as derived within galeaspids (Janvier, 1984, 1996b). Pituriaspids possess pectoral fins, like osteostracans, but seem to lack any dorsal nasohy-



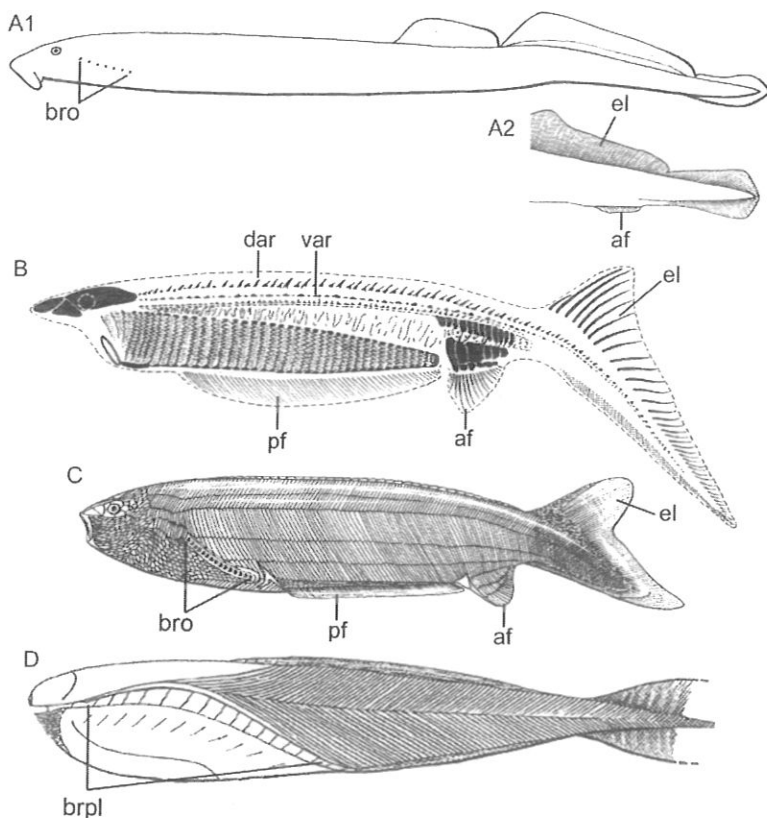
pophysial or nasopharyngeal opening (the olfactory organs may have opened ventrally, anterior to the mouth; Young, 1991). Galeaspids suggested that a dorsally opening nasohypophysial complex that retains an incurrent function could coexist with a massive, osteostracan-like, endoskeletal head shield, and thus that a convergence between lampreys and osteostracans was plausible. Moreover, pituriaspids showed that an osteostracan-like head shield structure could possibly coexist without any dorsal nasal or nasohypophysial opening, and thus that a head shield-shaped skull was not necessarily linked to a dorsal “nostril,” be it incurrent or not. In sum, the nasohypophysial complex of fossil “agnathans” seemed to have had a greater morphological plasticity than was believed 50 years ago.

All computerized cladistic analyses of extant and extinct vertebrate taxa published during the past decade show all “ostracoderms” (i.e., pteraspidomorphs, galeaspids, pituriaspids, thelodonts, osteostracans, and anaspids) and even euconodonts as more closely related to the gnathostomes than to either lampreys and hagfishes (Figs. 2.3, 2.5E,F; Gagnier, 1993b; Forey, 1995; Janvier, 1996a; Donoghue et al., 2000; Donoghue and Smith, 2001; Donoghue and Sansom, 2002). In all these analyses, cephalaspidomorphs are non-monophyletic, with osteostracans being almost always the sister-group to the gnathostomes. Only one of the analyses performed by Donoghue et al. (2000: fig. 17, “preferred phylogeny”) shows osteostracans, galeaspids, and pituriaspids (i.e., all taxa with an endoskeletal head shield) as a clade that, in turn, is the sister-group to gnathostomes and the poorly known Ordovician genus *Eriptychius* (not considered here), and this would lend further support to the theory that the lamprey-osteostracan type of nasohypophysial complex is homoplastic. Yet this clade including galeaspids, pituriaspids, and osteostracans is no longer considered as supported by Donoghue and Smith (2001), Donoghue and Sansom (2002), and Donoghue et al. (2003). As a whole, the current phylogenies yielded by standard parsimony, in which “ostracoderms” are stem-group gnathostomes, display a character distribution from the more particular to the more general, but, frustratingly, the most diverse character complex in these taxa—that is, the nasohypophysial complex—displays incongruent distributions. Some scenarios have been proposed to account for the convergence in the structure of the nasohypophysial complex of lampreys and osteostracans (Schaeffer and Thomson, 1980; Janvier, 2001), but none of them is fully satisfactory.

#### *Lampreys, Euphaneropids, and Anaspids*

Assuming that the monophyly of cephalaspidomorphs is refuted, this leaves us with very few hints as to the relationships of lampreys with any particular fossil vertebrate taxon, and even less so as to the relationships of hagfishes. Nevertheless, recent investigations on the Late Devonian naked anaspid, *Euphanerops*, possibly throw new light on the old hypothesis of a sister-group relationship between lampreys and anaspids. The anaspids, like osteostracans, have long

Figure 2.8. Lampreys, euphaneropids, anaspids, and arandaspid (not to scale). A, extant lamprey *Petromyzon marinus*; A1, lateral aspect; A2, tail of an abnormal female individual showing fin radials in the position of an anal fin (drawn after Vladikov, 1973). B, *Euphanerops longaevus*, Upper Devonian of Canada, reconstruction of the calcified endoskeleton (black) in lateral view (based on personal observations by P. Janvier and M. Arsenault). C, *Pharyngolepis oblongus*, Lower Silurian of Norway, reconstruction in lateral view (after Ritchie, 1964). D, *Sacabambaspis janvieri*, Ordovician of Bolivia, reconstruction in lateral view (after Gagnier, 1993a). Abbreviations as in Figure 2.4.



been regarded as cephalaspidomorphs, but are currently regarded as stem gnathostomes alongside other “ostracoderms” (Fig. 2.3G).

The overall structure of lampreys compares best with that of anaspids (slender body shape, small gill openings arranged in a slanting line behind the eyes, hypocercal tail, body musculature—inferred from the squamation—extending dorsally and ventrally to the branchial apparatus, and possibly a similar dorsal nasohypophysial opening; Fig. 2.8A,C). However, contrary to anaspids, lampreys lack paired and anal fins, although an anal fin-like structure supported by radials sometimes occurs as an abnormality in extant lampreys (af, Fig. 2.8A2; Vladikov, 1973). Conversely, anaspids lack an anterior dorsal fin, but their epichordal lobe is regarded as homologous to the posterior dorsal fin of lampreys. Unfortunately, no anaspid displays any trace of endoskeletal structures, but an extensively calcified endoskeleton can be observed in large individuals of the anaspid-like form *Euphanerops longaevus* (Janvier and Arsenault, 2002). Although it is uncertain whether this calcification is biogenic or the result of early diagenesis, it does provide information about the morphology of some endoskeletal structures (Arsenault and Janvier, 1991; P. Janvier and M. Arsenault, pers. obs.). *Euphanerops* shares with anaspids a markedly hypocercal tail, an anal fin, and elongated ventrolateral paired fins, but seems to lack a

dermal skeleton (Fig. 2.8B), and thus cannot reliably be proven to belong to the clade Anaspida, which is diagnosed on the basis of dermoskeletal characters.

In contrast, its endoskeleton is somewhat suggestive of that of lampreys, with a large branchial basket, although the latter is composed of more than 30 sinuous branchial arches (Figs. 2.2B, 2.8B). Some other endoskeletal elements recall certain lamprey characters, such as a ring-shaped structure and a median ventral rod, which vaguely recall the annular and piston cartilages, respectively. In addition, the calcification of its endoskeleton forms a thin lining around very large, bubble-like spaces, which were presumably occupied by chondrocytes and are grouped into cell nests, quite comparable in size and arrangement to the chondrocytes of lamprey cartilage (Langille and Hall, 1993; Janvier and Arsenault, 2002). Yet this still unexplained structure is at odds with the spherulitic calcified cartilage of "ostracoderms" (such as *Eriptychius*, galeaspids, and osteostracans) and gnathostomes. As a whole, the head endoskeleton of *Euphanerops*, whatever the nature of its calcification, is more similar to that of lampreys than to the massive endoskeletal head shield of galeaspids and osteostracans, but we know virtually nothing of the endoskeleton of the pteraspidomorphs (Fig. 2.3H–J; i.e., astraspids, arandaspids, and heterostracans), and it cannot be ruled out that they possessed a lightly built, lamprey- or *Euphanerops*-like endoskeleton, housed in an elongated dermal armor.

Other early Paleozoic "naked agnathans," namely *Achanarella* and *Cornovichtys*, closely resemble *Euphanerops* and could readily be lumped in the family Euphaneropidae Woodward, 1900, which would thus range in time at least from the early Middle to the Late Devonian (Newman, 2002; Newman and Trewin, 2001). It is also possible that the Early Silurian "naked agnathan," *Jamoytius* (Ritchie, 1968), also belongs to this clade.

*Euphanerops* thus displays an anaspid-like overall structure and some lamprey-like features (Fig. 2.8). These shared characters could be regarded as supporting the once classical theory that lampreys are derived from anaspids, and that *Euphanerops* would illustrate an intermediate form, which has lost the dermal skeleton (assuming that the number of gill arches in lampreys have been reduced and the paired fins lost). Other possible relationships can be inferred either among these three taxa, or among each of them and the other vertebrate taxa, but these are strongly dependent on how much one can rely on their interpretation based on such material, with radically different character quality (i.e., an extant taxon and a fossil taxon essentially preserved as imprints, both lacking a dermal skeleton, and a fossil taxon known exclusively from its dermal skeleton). Moreover, the homology of most of the characters observed in *Euphanerops* remains putative and depends on how one interprets such flattened structures. Very few of these characters can be readily homologized with a structure found in either lampreys or other vertebrates. Therefore, attempts at including *Euphanerops* in a data matrix of all major extant and extinct vertebrate taxa show that it groups with

lampreys and anaspids, generally as the sister-group to anaspids, because of its paired fin morphology and more strongly hypocercal tail.

I shall not discuss further here the possible interpretations of this topology, but it may be worth raising the question of the overall resemblance of these three taxa, which contrasts to that of most other fossil and extant vertebrates, notably "ostracoderms" and gnathostomes. In previously published phylogenies, anaspids and *Euphanerops* appear more closely related to the gnathostomes than to lampreys, with various positions within the "ostracoderms." Anaspids appear as the sister-group to all "ostracoderms" and gnathostomes, except for either euconodonts (Donoghue and Smith, 2001; Donoghue and Sansom, 2002), or euconodonts and pteraspidomorphs (Donoghue et al., 2000). It is nevertheless possible that the lamprey-like aspect of anaspids and *Euphanerops* (i.e., slender body shape, hypocercal tail, branchial basket extending far behind the eyes, and possibly dorsal nasohypophysial opening) is, in fact, general for the clade that includes lampreys, "ostracoderms," and gnathostomes. Interestingly (or coincidentally), this structure somewhat recalls that of the Ordovician arandaspids, the earliest completely known vertebrates (Fig. 2.8D). Notably, anaspids share with arandaspids numerous external branchial openings (or compartments) arranged in slanting line (bro, brpl, Fig. 2.8), a strongly oblique head/trunk limit, rod-shaped body scales arranged in chevrons, and open sensory-line grooves.

The presence of a lamprey-like branchial basket in *Euphanerops*, as well as some other endoskeletal structures that vaguely resemble lamprey characters, are tenuous hints at a close relationship between the two taxa because they could well be more general characters, also present in anaspids and even arandaspids, astraspids, and heterostracans, for which we still lack direct information about the endoskeleton. The presence of ventral arcualia in the axial skeleton of *Euphanerops* and gnathostomes (var, Fig. 2.8B), but not in lampreys, may also suggest that *Euphanerops* is a stem gnathostome, more inclusive than anaspids and still lacking an extensive dermal skeleton. The intuitive theory that lampreys are derived from anaspids through a loss of the dermal skeleton and paired fins is thus barely better supported by the new data on *Euphanerops*, however lamprey-like they may be, as long as endoskeletal data remain virtually unknown in euconodonts, anaspids, and pteraspidomorphs.

Nevertheless, apart perhaps from euphaneropids, no fossil provides information about any evolutionary transition between non-lampreys and lampreys, non-hagfishes and hagfishes, and even non-cyclostomes and cyclostomes, if the latter are a clade.

### "Ostracoderms" and the "Agnathan"- Gnathostome Transition

Despite the uncertainty over the phylogenetic position of the lampreys and hagfishes, or the cyclostomes as a whole, relative to the fossil vertebrate taxa, there is currently a consensus on the pa-

raphy of the "ostracoderms," with certain taxa, such as the osteostracans or galeaspids, being more closely related to the gnathostomes than to the two cyclostome taxa and other "ostracoderm" taxa (Figs. 2.3L–N, 2.5E,F; Forey and Janvier, 1993; Gagnier, 1993b; Forey, 1995; Janvier, 1996a; Donoghue et al., 2000, 2003; Donoghue and Smith, 2001; Donoghue and Sansom, 2002). This hypothesis of phylogenetic relationships provides interesting insights as to the degree of generality and the relative dates of appearance for certain gnathostome characters among extant vertebrates, such as dermal bone, perichondral bone, paired fins, epicerca tail, cerebellum, open endolymphatic ducts, or cellular bone (Forey, 1995; Janvier, 1996a, 2001; Donoghue and Sansom, 2002). However, one must not forget that the distribution of these characters is essentially that which gives structure to the current trees. These trees tell us that such primary homologies as the pectoral fins of osteostracans and crown-group gnathostomes are not overturned by optimizations.

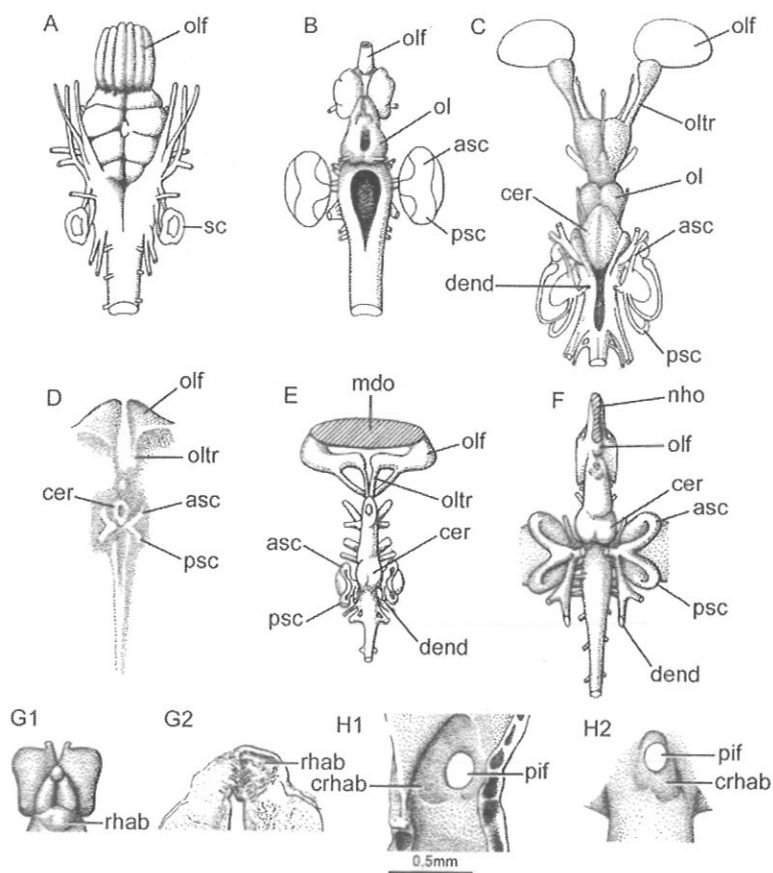
The theory that "ostracoderms" are paraphyletic is not new, and many opponents to Stensiö's theory of "agnathan" monophyly considered that, among "ostracoderms," heterostracans were possibly the closest relatives of the gnathostomes (Fig. 2.5C), essentially because of their paired olfactory organ (unknown in galeaspids until the mid-1980s; Fig. 2.9D; Kiaer, 1924; Romer, 1945; Obruchev, 1964; Halstead, 1973; Novitskaya, 1983). However, after 1927, no author ever thought of osteostracans as gnathostome relatives, this taxon being then well established as a cephalaspidomorph, alongside lampreys and anaspids. The current vertebrate phylogenies that place the paraphyletic "ostracoderms" as stem gnathostomes may be regarded as somehow illustrating an evolutionary transition between jawless and jawed vertebrates (Fig. 2.3G–R).

One of the best supported of these nodes is generally the sister-group relationship between osteostracans (and possibly pituriaspids) and gnathostomes (6, Fig. 2.3). It is based on homology relationships, which are briefly outlined below, with particular references to problematic interpretations of some of them. Illustrations of the characters currently regarded as synapomorphies shared by the gnathostomes, and a variable number of "ostracoderms" have been repeatedly published or cited during the last decade (e.g., Janvier, 1984, 1996a,b, 2001; Forey and Janvier, 1993; Donoghue et al., 2000, 2003; Donoghue and Smith, 2001; Donoghue and Sansom, 2002). This time, I shall play the devil's advocate by emphasizing the characters whose distribution is incongruent with the current trees, however these may be interpreted. Three of these characters have been discussed earlier (Janvier, 1984; and see above), but others are considered here.

### *Brain*

The brain cavity of osteostracans is supposed to provide a relatively accurate cast of the brain (Fig. 2.9F). Its overall structure is rather similar to that of the brain cavity in galeaspids (Fig. 2.9E),

Figure 2.9. Brain, olfactory, and otic capsules (dorsal view) in extant hagfishes (A), lampreys (B), and crown-group gnathostomes (C, elasmobranch). D, impression of the brain, olfactory and otic capsules in the internal surface of the dorsal head armor of a heterostracan (not to scale). E, F, internal cast of the cavity for the brain, olfactory capsules, and labyrinth (dorsal view) in a galeaspid (E) and an osteostracan (F). G, habenulopineal region of the brain of a lamprey in dorsal view (G1) and vertical section (G2), showing the enlarged habenular ganglion of the right side. H, roof of the habenulopineal region of the brain cavity in ventral view (H1) and internal cast of the same region (H2) of an Early Devonian osteostracan (*Belonaspis*), showing the enlarged recess for the habenular ganglion of the right side. (A–D, F, after Janvier, 1996b; E, after Wang, 1991; G, H, after Janvier, 1984.) Abbreviations as in Figure 2.4.



and its dorsal surface also matches the brain impression in the internal surface of the dorsal exoskeleton of heterostracans (Fig. 2.9D). In many respects, it also resembles the shape of the brain of lampreys (Fig. 2.9B), but it lacks the strong dorsal flexure of the adult lamprey brain. One of the most conspicuous features of the osteostracan brain cavity is the paired dorsal recess, regarded by Stensiö (1927) as housing a paired cerebellum (cer, Fig. 2.9F). The cerebellum is lacking in lampreys, but the optic lobes form a pair of prominent dorsal swellings (ol, Fig. 2.9B). Therefore, it has been suggested that the recess reconstructed by Stensiö (1927) as having housed the cerebellum perhaps in fact housed the optic lobes (Halstead Tarlo and Whiting, 1965; Janvier, 1975c). Nevertheless, this interpretation is now regarded as unlikely, because such a posterior position of the optic lobes would not agree with the position of the canals for the cranial nerve roots, notably that of the trochlear nerve (Janvier, 1985a; Janvier and Blicek, 1993). The elongated and straight brain of larval lampreys, galeaspids, osteostracans, and possibly heterostracans seems to be a general feature for vertebrates (except perhaps for hagfishes; Fig. 2.9A), but there is no evidence that the cerebellum is secondarily reduced in hagfishes and lampreys. The large paired cerebellum of osteostracans, galeaspids,

gnathostomes, and possibly heterostracans is thus likely to be a homology (cer, Fig. 2.9C–F).

The brain cavity of osteostracans displays a single character that was regarded by Stensiö (1927) as uniquely shared with the brain of lampreys: the enlarged habenular ganglion of the right side (rhab, crhab, Fig. 2.9G,H). This character was later dismissed because of its variability, notably in extant gnathostomes (Janvier, 1984), where the size of the habenular ganglia depends largely on the relative development of the pineal and parapineal organ. This asymmetry has been observed in a number of osteostracans belonging to widely different taxa (Stensiö, 1927, Janvier, 1985a), which admittedly all have a pineal foramen. It would be interesting to check its presence in the few osteostracans that lack a pineal foramen, such as the Acrotomaspidae. Moreover, this character should also be looked for in galeaspids. To date, the limited available information on the galeaspid brain cavity does not show evidence for such an asymmetrical habenular recess (Fig. 2.9E; Wang, 1991: fig. 4).

#### *Cranial Nerves*

Osteostracans are the only fossil “agnathans” in which the path of the cranial nerves within the endoskeletal head shield has been described in detail. Their pattern is, however, somewhat difficult to compare with that of either lampreys or gnathostomes, because of the unique forward shifting of the entire branchial apparatus in this group, which makes the postotic nerves (IX, X) bend rostrally and pass through the cavity for the otic capsule. Nevertheless their arrangement is globally similar to that of the cranial nerves in certain placoderms (e.g., acanthothoracids, petalichthyids), in which the branchial apparatus lies well beneath the braincase (Janvier, 1996a). What is known of the cranial nerves in galeaspids generally agrees with the condition in osteostracans, apart from the lack of forward shifting of the branchial nerves. In contrast to osteostracans, lampreys, and hagfishes, galeaspids resemble gnathostomes in having a pair of long olfactory tracts (which are probably also present in heterostracans; oltr, Fig. 2.9C–E). The condition of the visceromotor nerves in lampreys (and hagfishes) is relatively different from that in osteostracans, notably as to the path of the trigeminal, glossopharyngeal, and vagal nerves (although this is probably linked to the unique development of the lingual apparatus in hagfishes and lampreys). In addition, osteostracans and galeaspids resemble gnathostomes in possessing an occipital region to the endoskeleton that encloses the glossopharyngeal and vagal nerve roots.

#### *Olfactory Capsule and Nasohypophysial Complex*

As mentioned above, the olfactory capsule of osteostracans was enclosed in a small median cavity, and thus bears no resemblance to the paired olfactory capsules of the gnathostomes, but it is strikingly similar to the condition in lampreys (olf, Figs. 2.7, 2.10B,F). In addition, the anatomical relations between the olfactory organ and the proximally closed hypophysial tube are likely

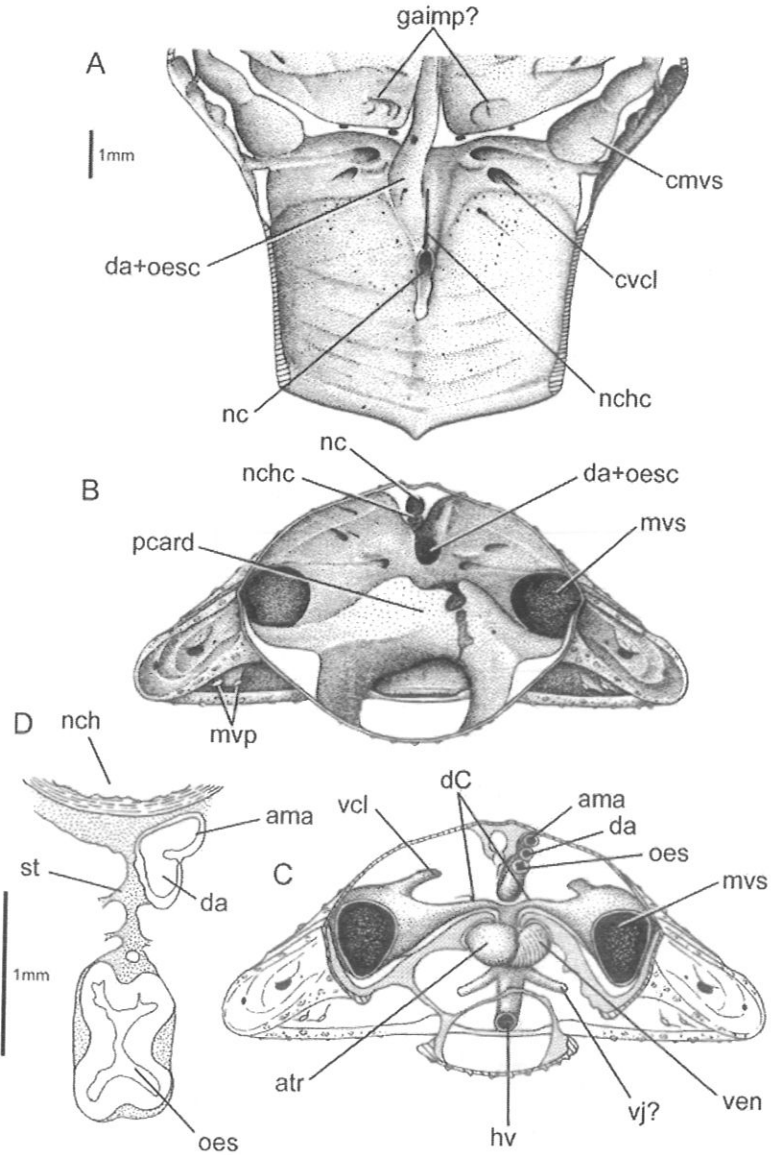


Figure 2.10. Heart and associated blood vessels in the lampreys and osteostracans. A–C, abdominal division and postbranchial wall of the head shield of the Early Devonian osteostracan *Norselaspis* in ventral (A) and posterior (B) views; C, attempted reconstruction of the heart and major blood vessels, showing the shift of the dorsal aorta, the esophagus, and probably the anterior mesenteric artery to the right. D, transverse section of the notochord, esophagus, dorsal aorta, and anterior mesenteric artery of a larval lamprey at the level of the heart, showing the shift of the dorsal aorta and anterior mesenteric artery to the right side. (A–C, after Janvier, 1985a, and Janvier et al., 1991, modified; D, drawn after Percy and Potter, 1991.) Abbreviations as in Figure 2.4.

to be the same as in lampreys (hyt, Fig. 2.7C). Remarkably, the position of the endocranial division for the hypophysial tube in osteostracans relative to the internal carotid arteries and the facial arteries is virtually the same as in lampreys (afac, ci, Fig. 2.7C2; Janvier, 1975c). In contrast, the paired olfactory capsules of galeaspids (olf, Fig. 2.10E) strikingly resemble the gnathostome condition (olf, Fig. 2.9C), differing from the latter only by the fact that they open into a large median, supposedly incurrent duct (mdo, Fig. 2.9E), instead of opening separately to the exterior by means



of external nostrils. The little we know of the paired olfactory organ in heterostracans would agree with the condition in galeaspids (olf, Fig. 2.9D), except that there is no material evidence for a separate incurrent duct (Purnell, 2002). The osteostracan-lamprey homology relationship of the nasohypophysial complex thus remains, after nearly a century, a major problem of vertebrate morphology, currently solved by an appeal to homoplasy.

### *Optic Capsule*

Osteostracans are the only "agnathans" for which we have reliable information about the anatomy of the optic capsule and the extrinsic eye muscles. Galeaspids only provide a possible indication of a posterior ventral myodome for the insertion of the recti muscles.

Osteostracans and gnathostomes (notably placoderms; Goujet, 1984; Goujet and Young, 2004) share a perichondrally ossified sclera, which is attached to the sclerotic ring. Nevertheless, there remains the question of the possible presence of a sclerotic ring and calcified sclera in arandaspids (Gagnier, 1993a), which are only observed in three distorted specimens. Recent reexamination of the material confirms the presence of a sclerotic ring (P. Janvier, pers. obs.). To date, there is no way to know whether osteostracans possessed an intrinsic eye musculature, like gnathostomes. However, no paraxial musculature could extend anteriorly to the occipital region, and this precludes the presence of a corneal muscle of lamprey type, supposedly derived in development from the foremost myomeres (Janvier, 1975a; yet the postotic derivation of the corneal muscle remains debatable; Nicol, 1989). The accommodation of the eye lens in osteostracans, if any, was thus most likely effected by an intrinsic eye musculature, as in extant gnathostomes. Some indications about the arrangement of the extrinsic eye muscles in osteostracans are provided by the myodomes in the wall of the orbital cavity. At least two large myodomes are clearly visible: a posterodorsal one, into which opens the canal for the trochlear nerve and thus is inferred to have housed the superior oblique muscle; and a large, ventral one, for either all or part of the recti muscles (Stensiö, 1964). The posterodorsal insertion of the trochlear-innervated superior oblique muscle is comparable to the condition in lampreys (Stensiö, 1964), but a similar condition is also inferred from the myodomes of placoderms (Young, 1986; Goujet and Young, 2004). It is thus likely to be a general condition, relative to the anterodorsal insertion of the superior oblique muscle in chondrichthyans and osteichthyans (Goujet and Young, 2004).

### *Labyrinth*

Among fossil "agnathans," only galeaspids and osteostracans can be proven to have only two vertical semicircular canals, with respective ampullae, like lampreys (asc, psc, Fig. 2.9E,F). Heterostracans only display imprints of two vertical canals (asc, psc, Fig. 2.9E,F), but the medial extension of a branchial compartment between them renders unlikely the presence of a horizontal canal, as

once advocated by Halstead (1973). The semicircular canals of osteostracans and galeaspids (and probably heterostracans) differ from those of lampreys in forming distinct loops, widely separated from the saccular division of the labyrinth, whereas those of lampreys are closely appressed against the utricular wall (asc, psc, Fig. 2.9B; Janvier, 1996a; Mazan et al., 2000). Again, it is unclear whether this condition in lampreys is general or unique because hagfishes only have a single semicircular canal with two ampullae (sc, Fig. 2.9A), the homology of which is still debated.

Jarvik's (1965) suggestion of a homology between the large ciliated recesses in the utricular wall of lampreys and the "sel" canals that connect the labyrinth cavity to the lateral and dorsal cephalic fields of osteostracans has been discarded on the basis that the only resemblance between the two structures was in their number (Janvier, 1985a). It is nevertheless not clearly refuted because we still ignore what passed through the "sel" canals (nerves or endolymphatic expansions of the labyrinth). Jarvik's interpretation was aimed at providing yet another character supporting the sister-group relationship between lampreys and osteostracans. We know that galeaspids, which lack cephalic fields, have a small utricular division of the labyrinth, which shows neither "sel" canals nor utricular recesses that could suggest the presence of ciliated recesses (Fig. 2.9E).

Like placoderms, some chondrichthyans, and possibly acanthodians among gnathostomes, all osteostracans have an externally open endolymphatic duct (dend, Fig. 2.9C,F). This is unknown in all other fossil "agnathans," except in the primitive galeaspid *Xiushuiaspis* (dend, Fig. 2.9E; Wang, 1991). However, it is possible that the presumed paired pineal foramina of arandaspids (Gagnier, 1993a) are, in fact, external endolymphatic openings, as suggested by their funnel-like shape, and this character could be either more general or more variable than currently believed. Lampreys and hagfishes have a possible homologue of the endolymphatic duct, but the latter never opens to the exterior, and this has long been regarded as a secondary condition. Sahney and Wilson (2001) showed that exogenous sand grains could penetrate through the endolymphatic duct into the labyrinth of osteostracans and acanthodians, as in some extant chondrichthyans, and serve as statoliths. This is an additional shared trait shared by osteostracans and gnathostomes, hitherto unknown in other vertebrate taxa.

#### *Blood Vessels*

The blood vascular system of galeaspids and osteostracans seems to have been quite similar, with the exception of the large marginal arteries and veins (a possible homologue of the anterior cardinal veins; Janvier et al., 1991), which are lacking in the former. The most striking resemblance between galeaspids and osteostracans in the anatomy of the blood vascular system is the very large lateral head vein that drains the blood from the anterior part of the head (and possibly part the branchial region in galeaspids). It was regarded by Stensiö (1927) as the homologue of the lateral

head vein of larval lampreys, although in the latter it is far thinner and much reduced in the adult. In contrast, it compares fairly well with the large but more laterally situated dorsal jugular vein of placoderms and other gnathostomes (Forey and Janvier, 1993: fig. 3).

The blood vascular system of osteostracans displays a character that can be regarded as uniquely shared with lampreys: the canal for the dorsal aorta and the groove that prolongs it posteriorly are displaced to the right side (da + oesc, Fig. 2.10A,B). Stensiö (1927) considered that the anterior cardinal veins flanked the dorsal aorta in osteostracans, and that this asymmetry was evidence for the lack of the left duct of Cuvier, as in adult lampreys, with both anterior cardinal veins emptying into the right duct of Cuvier. A reinterpretation of this peculiar asymmetry has been suggested in the light of larval lamprey anatomy (Janvier et al., 1991). In larval lampreys, the dorsal aorta and anterior mesenteric artery (ama, da, Fig. 2.10D) have to pass to the right side above the heart because of the median wall of connective tissues that suspend the esophagus from the notochord at this level (st, Fig. 2.10D). Although this could also apply to osteostracans, there remains a difference in the position of the esophagus that, in osteostracans, had to pass through the post-branchial wall through the same asymmetrical canal as the dorsal aorta (oes, Fig. 2.10C). Consequently, the median connective tissues that in lampreys connect the esophagus dorsally to the heart were probably lacking in osteostracans—or at any rate, they played no role in shifting the dorsal aorta to the right side. This asymmetry, to date unique to lampreys and osteostracans (we ignore the condition in other “ostracoderms”), may thus be homoplastic, the condition in osteostracans being possibly a consequence of the dorsoventral flattening of the head shield, which leaves little space for the esophagus for passing dorsally to the heart (Fig. 2.10C). Moreover, the symmetry of the marginal vein sinuses and posterior end of the lateral head vein canals in osteostracans (mvs, Fig. 2.10B,C), as well as the large dorsal opening of the pericardial cavity (pcard, Fig. 2.10B), rather suggest that both ducts of Cuvier were retained, leaving even less space for the esophagus (dC, Fig. 2.10C; Janvier et al., 1991).

The organization of the heart in osteostracans is known from the internal shape of the pericardial cavity, which shows that the atrium and ventricle were lying side by side and closely set, exactly as in lampreys (atr, ven, Fig. 2.10C; Janvier et al., 1991). Although the condition in other “ostracoderms” and in placoderms remains unknown, current phylogenies with a paraphyletic group, Cephalaspidomorpha, imply that this condition is intermediate between that of hagfishes (atrium and ventricle side by side, but well apart) and that of extant gnathostomes (atrium and ventricle closely set, but with the atrium expanding dorsally to the ventricle). Lamprey heart structure displays a unique character, with the venous network lining the wall of the pericardium and involved in the lubrication of the heart (Percy and Potter, 1991). The grooves on the internal surface of the pericardial cavity, described by Stensiö (1927: fig. 35) from horizontal grinding sections of the osteostracan *Mimetaspis*

(then interpreted as impressions of the pronephric tubules), could either be impressions of this venous network or a mere artifact of preservation. Vertical grinding sections through *Norselaspis* and direct observation of the pericardial wall in *Axinaspis* (Wängsjö, 1952: pl. 99:2) failed to yield similar grooves (Janvier, 1985a).

### *Gills*

Much has been written about the organization of the gills and gill arches in fossil jawless vertebrates, sometimes in connection with the question of the origin of jaws (e.g., Stensiö, 1927, 1964; Wängsjö, 1952; Damas, 1954; Watson, 1954; Halstead, 1973; Whiting, 1977; Novitskaya, 1983; Janvier, 1985a, 1996a,b). However, there is very little evidence of detailed gill structure, apart from the path of branchial nerves and some vague imprints of the gill filaments. Strangely, even in the extensively ossified head shields of osteostracans and galeaspids, the gill arches seem to vanish beyond the medial ventral processes of the oralbranchial cavity (mvp, Fig. 2.10B) on which they are supposed to be attached. Janvier's (1985a, 1996b) default option was to consider that the gills in osteostracans were organized in much the same way as in larval lampreys, the cartilaginous branchial skeleton as a whole being housed in the oralbranchial cavity, the roof of which did not incorporate dorsal gill-arch components (contra Stensiö, 1927), and that the same condition could be generalized to galeaspids. There are some hints suggesting that the gills of "ostracoderms" were supported by sinuous cartilaginous arches of lamprey type, notably some sinuous imprints in the roof of the oralbranchial cavity of osteostracans (gaimp?, Fig. 2.10A; Janvier, 1981b: fig. 4).

The external gill openings of most osteostracans (except for some tremataspidids) somewhat resemble those of elasmobranchs in being slit-shaped (gs, Fig. 2.11B), in contrast to those of the extant and most fossil "agnathans" (e.g., anaspids, astrapidids, galeaspids), which are smaller and rounded in shape.

The anatomy of osteostracans implies that the posteriormost gill compartments (or gill pouches) were connected to the pharynx by means of a pharyngobranchial duct, as in adult lampreys (Janvier, 1984: fig. 2.5C,D). It is probable that the same condition also prevailed in galeaspids, anaspids, and euphaneropids (Janvier, 2004).

### *Shoulder Girdle and Paired Fins*

The shoulder girdle and paired fins of osteostracans bear a striking resemblance to those of the gnathostomes, in particular placoderms (Janvier, 1978, 1984, 1985a; Goujet, 1984, 2001). In both taxa, the girdle is a massive endoskeletal structure, on which the fin endoskeleton articulates by means of a small articular facet. The foramina for the brachial artery and brachial veins occupy exactly the same position in both groups, relative to the articular surface. Additionally, the surface of the fin insertion area displays a number of depressions for muscle insertions, which indicate a relatively complex musculature. The paired fin endoskeleton of osteostracans

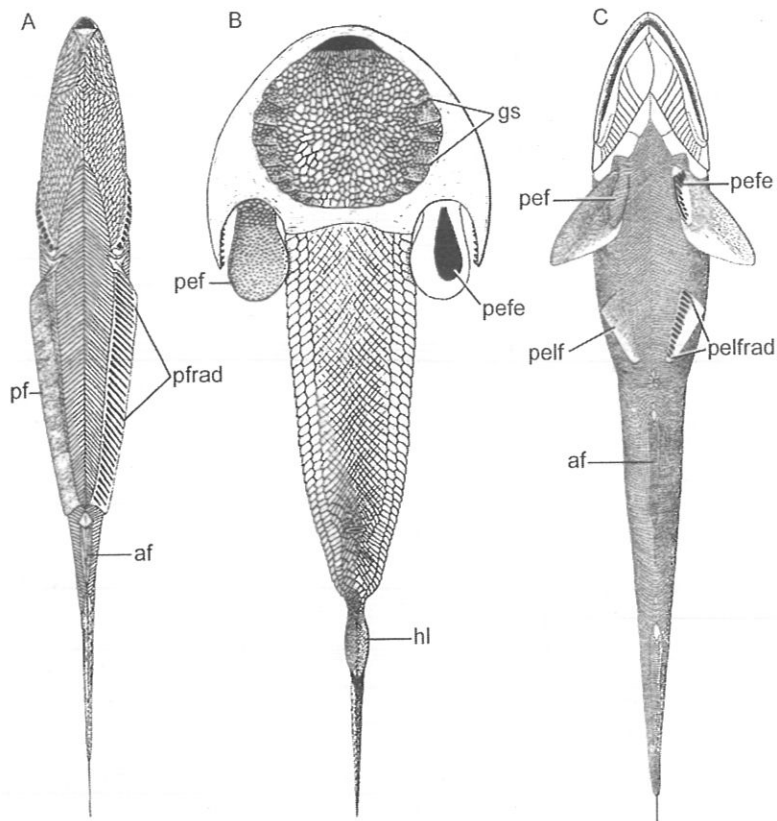


Figure 2.11. Comparative organization of the paired fins in an anaspid (A, *Pharyngolepis*, Early Silurian), an osteostracan (B, *Zenaspis*, Early Devonian), and a gnathostome (C, *Cheirolepis*, Late Devonian) in ventral view (not to scale). Endoskeleton (in black) of the paired fins reconstructed on the right side (inferred from the conditions in *Euphanerops* in A, *Escuminaspis* in B, and *Mimia* for the pelvic fin in C). (A, after Ritchie, 1964; B, based on Heintz, 1967, Janvier, 1996b, and Janvier et al., 2004a; C, after Pearson and Westoll, 1979.) Abbreviations as in Figure 2.4.

has been reconstructed on the basis of a single specimen of *Escuminaspis laticeps*, where it is partially preserved in the form of patches of calcified cartilage (Janvier et al., 2004a), and the recent discovery of a second specimen of the same species showing similar structures suggests that it is unlikely to be a fabric due to diagenesis. The paired fin endoskeleton was probably a leaf-shaped cartilage plate (pefe, Fig. 2.11B) that recalls the one or two radials of most placoderms, and more so the cartilaginous disk of the embryonic pectoral fins of most extant fishes (Grandel and Schulte-Merkel, 1998; Cohn et al., 2002; Coates, 2003). The main difference between osteostracans and gnathostomes is that the endoskeletal shoulder girdle is continuous with the braincase (i.e., it is part of the endoskeletal head shield) in osteostracans, whereas it is always separate from the latter in the gnathostomes. It is assumed that pituriaspids possessed much the same kind of paired fins as osteostracans, yet this is merely a guess based on the similar aspect of the fin insertion area.

The presence of endoskeletal radials in the ribbon-shaped paired fins of *Euphanerops* suggests that similar radials were also present in the similarly shaped paired fins of anaspids (pfrad, Fig. 2.11A; P. Janvier and M. Arsenault, pers. obs., 2004). Thus, if true paired fins (i.e., with endoskeletal supports), as a whole, are regarded as homologous, their absence in all pteraspidomorphs,

galeaspids, and presumably thelodonts (at least *Turinia*; Donoghue and Smith, 2001; but see Wilson et al., Chapter 3) poses a problem in the framework of most current phylogenetic hypotheses because this would imply that paired fins were lost independently in several "ostracoderm" groups (pteraspidomorphs, galeaspids, and probably most thelodonts). In fact, there are important differences between the paired fins of *Euphanerops* and anaspids on the one hand, and the osteostracan and early gnathostome pectorals on the other. The former are ribbon-shaped webs (pf, Fig. 2.11A) extending from the anus to the branchial region and supported by numerous thin, parallel radials, lacking any fin support or girdle (pfrad, Fig. 2.12A), whereas the latter are stout, paddle-shaped structures concentrated behind the branchial apparatus and supported by a few large endoskeletal elements that articulate with a massive girdle (pef, Fig. 2.11B,C).

The paired fins of *Euphanerops* and anaspids, with their more ventral position and their numerous parallel radials, rather resemble the pelvic fins of such early gnathostomes, as acanthodians and generalized actinopterygians (pelf, Fig. 2.11C; yet the pelvics of the latter do not extend as far anteriorly, and their radials articulate on a pelvic girdle; see Wilson et al., Chapter 3), whereas the paired fins of osteostracans and the pectorals of the gnathostomes are basically similar. This also relates to the difference between the pelvic and pectoral fins of the gnathostomes as to their early embryonic development: the radials of the pelvics arise from the beginning as separate cartilage rods, whereas those of the pectorals appear later, by subdivision of a single cartilage disk (Grandel and Schulte-Merkel, 1998; Cohn et al., 2002; Coates, 2003; Davis et al., 2004). Apart from some indications of possible pelvic fins in a thelodont in the form of scaled skin flaps in addition to pectoral fin folds (Märss and Ritchie, 1998; Wilson et al., Chapter 3), no fossil "agnathan" displays both pectoral and pelvic fins with indisputable endoskeletal radials. Maisey (1986, 1988) invoked this resemblance between the anaspid paired fins and the gnathostome pelvics as support for a sister-group relationship between anaspids and gnathostomes. However, this would pose the problem of the characters shared by osteostracans and gnathostomes, but lacking in anaspids. Thus, apart from the pectoral fins of gnathostomes and osteostracans (and possibly pituriaspids), for which a hypothesis of primary homology is acceptable and which is congruent with other uniquely shared characters, the distribution of the paired fins in extant and fossil vertebrates raises problems of either homoplasy or loss, as in the case of the nasohypophysial complex.

#### *Axial Skeleton*

Curiously, and contrary to what is observed in decay experiments (Briggs and Kear, 1994), the notochord, which is made up by relatively tough tissues, rarely leaves any imprint in fossil vertebrates, even when preserved under conditions that allow soft-tissue

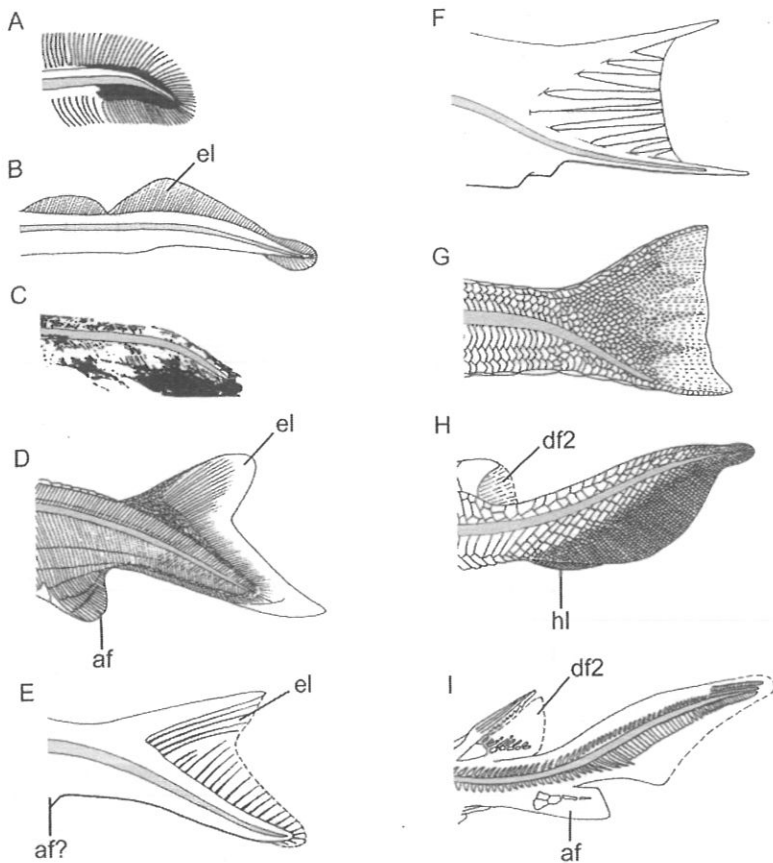


Figure 2.12. Tail in crown-group vertebrates, in lateral view (not to scale). The position of the notochord (gray) is hypothetical, except in A–C and I. A, hagfish (endoskeleton in black); B, lamprey; C, euconodont; D, anaspid; E, thelodont (*Loganellia*); F, thelodont (furcaudiform); G, heterostracan; H, osteostracan; I, crown-group gnathostome (hybodontiform chondrichthyan). (A, after Janvier, 1997; B, after Janvier, 1996b; C, after Aldridge et al., 1986; D, after Ritchie, 1964; E, based on specimen GBP 367, Muséum National d'Histoire Naturelle, Paris; F, after Wilson and Caldwell, 1993; G, after Gross, 1963; H, after Heintz, 1967; I, after Maisey, 1989.) Abbreviations as in Figure 2.4.

preservation. The position of the notochord in the various fossil “agnathans” reconstructed in Figure 2.13 (gray) is entirely hypothetical and is only inferred from the overall shape of the tail, except possibly in euconodonts. However, the path of the notochord can be reconstructed with some confidence only when the arcualia bordering it are visible (Figs. 2.8B, 2.13I).

Lampreys and gnathostomes are the only extant vertebrates that possess vertebral components, in addition to the notochord. They both have dorsal arcualia (basidorsals and interdorsals), and gnathostomes have, in addition, ventral arcualia (basiventrals and interventrals; Fig. 2.2B,C). *Euphanerops* is the only fossil “agnathan” in which the arcualia can actually be observed, forming complete series of dorsal and ventral arcualia, as in gnathostomes (dar, var, Fig. 2.8B; P. Janvier and M. Arsenault, pers. obs.), suggesting that euphaneropids (and possibly anaspids) are more closely related to gnathostomes than to lampreys. The very elongated occipital region of galeaspids and certain osteostracans suggests that it incorporates vertebral elements, at any rate dorsal arcualia, but provides no information as to their posterior extension. Only an enigmatic series of five calcified elements in the trunk of the osteostracan *Ateleaspis* (Ritchie, 1967: pl. 4, fig. 1) is suggestive of an axial skele-

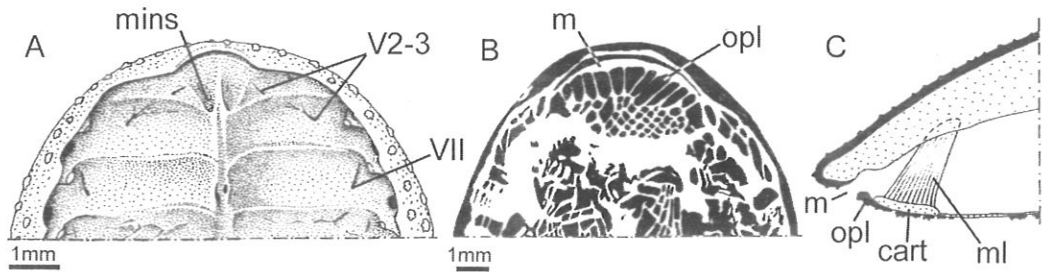


Figure 2.13. Organization of the oral region in osteostracans. A, *Norselaspis* (Early Devonian), anterior part of the roof of the oralobranchial cavity in ventral view, showing a pair of probable muscle insertions in the oral roof; B, *Hirella* (Early Silurian), dermal covering of the oralobranchial membrane in ventral view, showing the oral plates bordering the mouth; C, reconstructed sagittal section of the oral region of an osteostracan head, showing the possible position of the hypothetical cartilage plate bearing the oral plates and its associated musculature. Abbreviations as in Figure 2.4.

ton. Nevertheless, these elements do not resemble the arcualia of *Euphanerops*.

#### *Median Fins and Tail*

Osteostracans and gnathostomes are the only vertebrates in which the tail is unambiguously epicercal (Fig. 2.12H,I). In fact, the only difference between the tail of an osteostracan and that of a gnathostome is the small horizontal ventral lobe that underlies the hypochordal web of the osteostracan tail (hl, Figs. 2.11B, 2.12H), and which is an autapomorphy of this group, although possibly representing a modified anal fin. The evolutionary transformations that can be inferred from the various tail structures in extant and fossil vertebrates (Fig. 2.12) seem relatively simple in the framework of current phylogenies, assuming that the apparently homocercal tail in heterostracans and furcicaudiform thelodonts (Fig. 2.12F,G) is merely a particular case of the hypocercal condition (Fig. 2.12A–E), much in the same way as the homocercal tail of teleosts is a particular case of the epicercal condition of gnathostomes. Nevertheless, the transition from a generalized hypocercal tail (as exemplified by the thelodont *Loganellia* or anaspids; Fig. 2.12D,E) to the epicercal tail of osteostracans and gnathostomes (Fig. 2.12H,I) remains undocumented by transitional states.

The primitive number of dorsal fins in gnathostomes remains debatable. It is generally assumed that two dorsal fins is the general condition for gnathostomes. This may be true for crown-group gnathostomes, but placoderms seem to have a single dorsal fin, except perhaps for ptyctodonts. The most generalized osteostracans have two dorsal fins, but the anterior one lacks evidence for a fin web and appears as a mere hump that becomes reduced to a large median scute in cornuates, and finally disappears. Wängsjö (1952:110, 234) showed that the vascular canals in the endoskeletal dorsal spine (or hump) of osteostracans are arranged segmentally and suggested that it was originally a real fin supported by radials. In contrast, the second dorsal fin of osteostracans clearly displays a fin web with lepidotrich-like series of scales (df2, Fig. 2.12H), and may well be the homologue of the anterior part of the epichordal lobe of anaspids, thelodonts, and lampreys (el, Fig. 2.12B,D,E). In “agnathans” that display an anal fin (euphaneropids, anaspids, and probably some thelodonts; af, Fig. 2.12D,E), the latter is situated well in front of the



level of the epichordal lobe. Assuming that the anterior part of the epichordal lobe is the homologue of the second dorsal fin of osteostracans and gnathostomes, this suggests that the modular development of anal and posterior dorsal fin invoked by Mabee et al. (2002) for the actinopterygian unpaired fins did not apply to "ostracoderms."

#### *Organization of the Exoskeleton*

Apart from the pineal plate and sclerotic ring, none of the dermal bones of the osteostracan head shield displays any plausible homology with the dermal head and shoulder girdle skeleton of the macro- or mesomeric gnathostomes. The long-presumed homology between the cornual processes of osteostracans and the pectoral fin spines or spinal plates of gnathostome does not hold because the most plesiomorphic osteostracans are all noncornuates. Whether the structure and organization of the body scales have any significance remains debated. Admittedly, the macrosquamose, diamond-shaped body scales of osteostracans bear some superficial resemblance to those of placoderms and osteichthyans, but the most striking resemblance is perhaps between their closely set dermal rays of their median fins and the osteichthyan lepidotrichs. Unfortunately, there is to date no consensus as to the general condition for the gnathostome exoskeleton; yet the primitiveness of the microsquamose or micromeric elasmobranch condition remains a widespread assumption—essentially for historical reasons—and because thelodonts, among "agnathans," also have a microsquamose exoskeleton (Janvier, 1981a; for an extensive review see Donoghue, 2002). The macro- or mesomeric condition of placoderms and generalized osteichthyans, as to both scales and dermal bones, would rather support the theory that this condition is general for the gnathostomes, and therefore somewhat similar to that in osteostracans.

#### *Histology*

Histological characters are generally difficult to assess because of their considerable variability in certain taxa and, in some cases, uncertainties as to their definition and characterization. Certain hard tissues, however, can be regarded as unique to particular taxa, or are empirically known to display little homoplasy, such as the semidentine of placoderms. Osteostracans and gnathostomes are the only vertebrates in which the exoskeleton and endoskeleton show bone cell lacunae. Admittedly, some acanthodians and chondrichthyans have an acellular exoskeleton, and some acanthomorph teleosts have an entirely acellular skeleton, but this is currently regarded as a particular condition relative to cellular bone. Similarly, the Late Devonian cornuate osteostracans *Escuminaspis* shows no evidence for bone cell lacunae, and this is also assumed to be a derived condition because the exo- and endoskeleton of all other osteostracans, including the generalized noncornuate taxa, show the same cellular structure as those of the placoderms and generalized osteichthyans.

The presence of perichondral bone seems restricted to osteostracans.

cans and gnathostomes, but perichondral calcification, lacking cell lacunae, occurs in galeaspids. The nature of the possible perichondral calcification described in arandaspids (Gagnier, 1993a), notably in the sclera, remains debated. It is far from being as extensive as in galeaspids, osteostracans, and gnathostomes.

Spherulitic (globular) calcified cartilage has long been regarded as a widespread and structurally monotonous type of hard tissue in "ostracoderms" (in fact, known only in *Eriptychius*, galeaspids, and osteostracans) and gnathostomes. The unusual type of calcified cartilage of *Euphanerops*, with very large chondrocyte spaces lined with a thin calcified shell (Janvier and Arsenault, 2002) and a spherulitic matrix, is still a matter of debate; it may either be of diagenetic origin or may represent a mode of calcification that occasionally occurs in vivo in lampreys (Bardack and Zangerl, 1971) but is still undescribed in detail.

#### *Homology Relationships of the Characters in Crown-Group Vertebrates*

As a whole, and except for the vexing question of the nasophypophysial complex, most of the characters that can be observed in osteostracans have their sister character in the gnathostomes, rather than in either lampreys, hagfishes, or other "ostracoderms." However, the problem lies in the fact that most of the latter characters are less clear-cut than those of the nasohypophysial complex, and according to a paleontological tradition, regarded as adaptive or subject to variability. The nasohypophysial complex of osteostracans is always present with the same structure. Admittedly, the presence of cellular bone, epicercal tail, and complex pectoral fin musculature and endoskeleton seem generally unique to osteostracans and gnathostomes, but there are some exceptions (e.g., the acellular bone of *Escuminaspis* and certain gnathostome taxa, the lack of paired fins in tremataspidid osteostracans, and the variable state of the caudal fin in gnathostomes), which may raise questions about the distribution of these characters. Tail structure is often regarded as a typically adaptive character because of its diversity in extant gnathostomes, although neither the latter nor osteostracans display any instance of a hypocercal tail. Moreover, if one assumes a loss of the paired fins in tremataspidids or a loss of bone cells in *Escuminaspis*, then why not assume the same for the acellular dermal bone and lack of paired fins of more inclusive "ostracoderms," such as arandaspids or heterostracans? The only reason for not doing this is perhaps that in contrast to osteostracans, all members of these clades share this lack of cellular bone and pectoral fins.

When considering the distribution of the morphological and histological characters that can be readily observed in fossil and extant vertebrates (e.g., the character-taxon matrices provided by Janvier, 1996a; Donoghue et al., 2000; Donoghue and Smith, 2001), one can notice that they fall into three classes: (1) those that have a broadly congruent distribution and largely define the shape of the current trees, in which either some, or all, "ostracoderms" are more

closely related to the gnathostomes than to either lampreys or hagfishes (e.g., large paired cerebellum, dermal bone, perichondral bone, pectoral fins); (2) those that have a poorly informative, or disjunct, distribution, but can nevertheless be accommodated by the preceding character distribution (e.g., orthodontine), by an appeal to plausible processes of loss (or autapomorphic modification) rather than to homoplasy; and (3) those whose distribution shows no congruence with the majority of other homologies and are thus currently regarded as homoplastic (e.g., nasohypophysial complex of the lamprey and osteostracan type). These differences in data congruence tell us that the current view of "agnathan"-gnathostome transition is far from being as remarkably illustrated as other evolutionary transitions in vertebrate history, and much imagination is still required to make a narrative from the current trees. For example, current trees generally imply that the shield-shaped head endoskeleton of galeaspids, osteostracans, and pituriaspids is a general condition, relative to the narrower braincase and independent shoulder girdle of the gnathostomes. The "agnathan"-gnathostome transition would thus involve a general reduction of the head and pectoral endoskeleton. No character state clearly documents such a process of reduction, except perhaps for the broad expansion of the placoderm braincase over the branchial region, which could represent a transitional condition between that of galeaspids or osteostracans and that of crown-group gnathostomes (Janvier, 2001).

If osteostracans, and probably the other "ostracoderms," best fill the morphological gap between extant "agnathans" and gnathostomes and provide some examples of evolutionary transitions at the level of particular characters or character complexes, the transition from a jawless to a jawed mouth remains virtually undocumented by fossils. The situation is somewhat comparable to that of the question of the fin-limb transition before the discovery of the Devonian tetrapods and elpistostegalians. The scenarios about the origin of jaws thus must rest essentially on developmental data. To some extent, this could also apply to the origin of paired fins, although thelodonts possess structures referred to as paired fin folds, which cannot be clearly proven to be actual fins with endoskeletal radials, but are at least potential precursors to fins (see Wilson et al., Chapter 3).

### Question of the Origin of Jaws

What we know of the organization of the oral region in fossil "agnathans" (apart perhaps from fossil hagfishes and lampreys, and euconodonts) suggests that none of them possessed the highly specialized lingual apparatus of extant cyclostomes. They may nevertheless have possessed a protraction and retraction device, the basic function of which was somehow similar, and possibly general to all vertebrates, but lost in the gnathostomes (Janvier, 1981a). The mouth of arandaspid, heterostracans, galeaspids, and osteostracans is generally bordered ventrally by a series of dermal oral plates

(opl, Fig. 2.13B; a single plate in galeaspid), which, one may imagine, could be slightly expanded as the mouth opened (Kiaer, 1928; Janvier, 1996b; Purnell, 2002; Elliott et al., 2004). The presence of large muscle insertion pits in the supraoral field of osteostracans (mins, Fig. 2.13A) and the fact that the oral plates of osteostracans sometimes remain articulated when displaced (e.g., in *Hirella*; Heintz, 1939: pl. 24, fig. 3, pl. 25, fig. 2) suggest the presence of some still unknown endoskeletal structure involved in the movements of the oral region (cart, Fig. 2.13C; Janvier, 1985a:49), which was moved up and down by means of muscles (ml, Fig. 2.13C). Possibly, this hypothetical element was articulated laterally to the foremost endoskeletal medial ventral process of the oralbranchial cavity, which is sometimes much developed (e.g., in tremataspids; Janvier, 1985b: figs. 11, 26a). The median part of the oral roof is covered with dermal denticles in some osteostracans, which, together with certain thelodonts (such as *Loganellia*) and gnathostomes, are the only vertebrates in which oral or pharyngeal denticles can be seen. The question of the presence of a velum in fossil "agnathans" remains debated, although the prebranchial fossae of osteostracans are best interpreted as having housed a velum of larval lamprey type (Janvier, 1985a, 1996b). In contrast, Mallatt (1996) followed Stensiö's (1927, 1964) interpretation and considered that osteostracans possessed a respiratory spiracular pouch, with a posterior mandibular hemibranch and an anterior hyoidean hemibranch, but no velum. In sum, none of the fossil "agnathans" displays any structure that would possibly foreshadow a mandibular arch of gnathostome type—that is, with a palatoquadrate and a Meckelian cartilage.

Theories about the origin of jaws are thus entirely based on either an imaginary transformation series based on presumed homologies in the oral apparatus of extant vertebrates (e.g., Romer, 1945; Jollie, 1962; Mallatt, 1996; Janvier, 1996b), or, more recently, inferences based on data from developmental genetics (see reviews in Kuratani et al., 2001; Kuratani, 2004; Shigetani et al., 2005). In a key article on this question, Kimmel et al. (2001:116) refer to the origin of jaws as a "wonderful problem, long debated in the literature." It is indeed, and studies on this subject have become a small industry among developmental biologists. Since the nineteenth century, jaws have been regarded as serial homologues of the more posterior visceral arches ("repeated parts" of Schmitt, 2004), but the debates about their origin began with the question of the homology between the visceral arches (as a whole) of the extant "agnathans" and gnathostomes. To make a long story short, Goette (1901) discovered that lampreys differ from gnathostomes by the fact that their gill filaments are of endodermal origin, and, alongside the branchial nerves and blood vessels, are medial to the skeletal gill arches (bra1, Fig. 2.14A). In the gnathostomes, they are lateral to the skeletal gill arches (bra1, Fig. 2.14B) and can be shown to be of ectodermal origin, at any rate in osteichthyans. This later became a key argument for Stensiö (1927) and others for arguing that vertebrates fell into two sister clades, the Agnatha

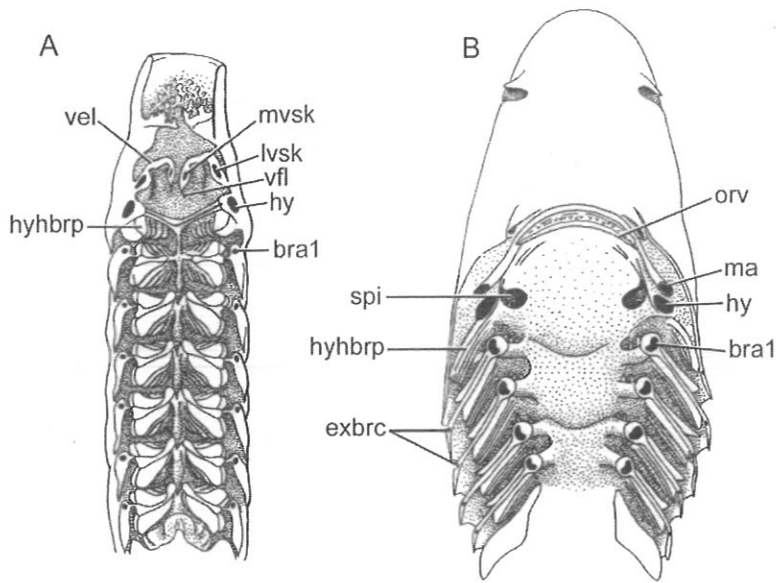


Figure 2.14. Horizontally sectioned heads of a larval lamprey (A) and a crown-group gnathostome (B, elasmobranch), in ventral view, showing the relative position of the endoskeletal branchial arches and gill filaments. Not to scale. (After Mallatt, 1984, modified.) Abbreviations as in Figure 2.4.

and Gnathostomata (or Entobranchiata and Ectobranchiata), precluding any evolutionary transition from one group to the other. After a century-long debate about which of these two gill conditions could possibly be primitive relative to the other, Jarvik (1980, 1981) finally concluded that the gill arches of lampreys and gnathostomes were homologous, but not the gill filaments and their associated musculature and vessels, whereas others (e.g., Mallatt, 1984; Janvier, 1981a, 1996a,b) considered that the gills, musculature, and blood vessels were homologous, but the arches were not.

Because the jaws of the gnathostomes were unanimously regarded as serially homologous to the more posterior gill arches, they had to be organized according to the same pattern; that is, they should be medial relative to their nerves and blood vessels, which they essentially are in extant gnathostomes. Only placoderms possess mandibular arch elements that are reconstructed as being situated laterally to the adductor jaw musculature, but it is still undecided whether this represents a general gnathostome condition, or an autapomorphy of this particular extinct group. Because “agnathans” have no jaws but share gill arches with the gnathostomes, the received view used to be that gill arches have preceded jaws in evolutionary history, and it was thus necessary to have fossil evidence for a gill-bearing mandibular arch and, of course, to assume homology between the “agnathan” and gnathostome visceral arches. This was basically the aim of Stensiö’s (1927) interpretation of osteostracans. This evidence is now discarded, and the homology of the lamprey and gnathostome visceral arches is still debated, despite much detailed investigations by developmental biologists. Nevertheless, most textbooks, and even more so

popular books, about vertebrate evolution still propagate the classical and naive idea that the first (i.e., mandibular) or first two (i.e., mandibular and premandibular) respiratory branchial arch or arches of some unknown extinct jawless vertebrate once turned into jaws.

The foremost visceral arch (or arch 1, in current terminology) of embryonic lampreys is now almost unanimously regarded as the homologue of the mandibular arch of the gnathostomes, and therefore also termed the *mandibular arch*. In neither of these two groups does it develop into a respiratory gill arch (leaving aside the complex question of the pseudobranch of the gnathostomes; Mallatt, 1996), and none of the anatomically well-known extant and extinct "agnathans," notably osteostracans, can be proven to have possessed a mandibular gill (for details, see Janvier, 1981b, 1985b, 1996b). Instead, the mandibular arch of lampreys is connected to a complex skeleton, which supports a special water-pumping and antireflux organ, referred to as the *velum* (hagfish development remains almost undocumented, and it is difficult to clearly know which parts of the adult hagfish skull are mandibular arch derivatives).

Two morphology-based scenarios about the origin of jaws have been proposed during the past decade. Mallatt (1996) considered that the common ancestor to all vertebrates possessed both the lateral (lamprey-like) and medial (gnathostome-like) visceral arches, and that the former progressively disappeared in the gnathostomes, whereas the latter disappeared in lampreys (and hagfishes), except perhaps at the level of the velum. In larval lampreys, the velar skeleton actually displays two components: a lateral one, level with the more posterior arches, and a medial one, closer to the pharynx (lvsk, mvsk, Fig. 2.14A). Janvier (1993, 1996b) argued that the medial visceral arches of the gnathostomes were a neomorph, resulting from the invasion of the medial part of the interbranchial septa by neural crest-derived skeletogenous tissues, which started in the mandibular arch, as suggested by the medial component of the lamprey velar skeleton. Then this process was continued by the development of the medial, respiratory, hyoid, and gill arches. The joint between the dorsal and ventral portions of the visceral arches in general, which is absent in lampreys, arose first in the mandibular arch and, for functional reasons, progressively extended to the hyoid and gill arches. Subsequently, the lateral gill arches disappeared, unless they remain in elasmobranchs in the form of the extrabranchial cartilages (exbrc, Fig. 2.14B), which, however, are apparently not neural crest-derived (this remains to be checked by means of current marking techniques). Both Mallatt (1996) and Janvier (1996a,b) considered that at least part of the velar skeleton and the jaws could be homologous, but Mallatt rejected Janvier's (1993) hypothesis that jaws could be derived from any velum-like structure.

Kimmel et al. (2001) showed that the difference in the embryonic branchiomeres (the precursors of the mandibular, hyoid, and gill arches) of lampreys and gnathostomes can be traced as early as

the neural crest cells have migrated ventrally into them. These authors considered that in lampreys, the neural crest cells, which will give rise to the visceral arch cartilages, lie lateral to the mesoderm bars of the branchiomeres, whereas in gnathostomes, they surround them, forming a cylinder. Subsequently, the gnathostome arches form from the cells that are in the medial part of this cylinder. Kimmel et al. (2001) therefore concluded that the lamprey and gnathostome arches are homogenic, forming from the same embryonic tissue, but that the chondrogenic cells have migrated medially in the gnathostomes to form medially placed arches, a process that these authors depict as the outside-in theory. Thus, visceral arch homology in lampreys and gnathostomes remains undecided, depending on whether homogeneity is or is not evidence for homology ("causes of homologues are neither causes for homology nor homology itself" [Nelson, 1994:123]; see also discussion in Patterson, 1982). Kimmel et al. (2001) pointed out the fact that at an early stage, the lateral component of the velar cartilage of lampreys was described by Damas (1944) as showing a cylinder of neural crest-derived cells, surrounding a core of mesodermal cells, as in a gnathostome arch. However, subsequently, Meulemans and Bronner-Fraser (2002) and McCauley and Bronner-Fraser (2003) showed that even in lampreys, the neural crest cells surround the mesodermal components of all arches, after having migrated simultaneously along both lateral (subjacent to the ectoderm) and medial (between the mesoderm and endoderm) routes. This seemed to refute the promising outside-in theory by Kimmel et al. (2001) as an explanation for the origin of the gnathostomes, but Cerny et al. (2004b:266) did not regard the question as settled. They concluded that "still more precise cell tracing experiments are needed in both vertebrate groups to understand how developmental pathways were changed during the agnathan transition." In particular, they pointed out that in gnathostomes (at any rate, in the axolotl), only the neural crest cells that lie medial to the mesoderm and close to the endodermal wall of the pharynx condense into cartilage. Thus the outside-in theory would only concern the chondrogenic potentiality of the neural crest cells. McCauley and Bronner-Fraser (2003:2321) tentatively concluded that the difference in the position of the branchial arches in the lampreys and gnathostomes may "depend on a mechanism that is independent of neural crest migration." This is also favored by Kimmel et al. (2003) in the wake of the discovery by Couly et al. (2002) of the role of endoderm-ectomesenchyme induction in the patterning of the visceral arches. In sum, the position (lateral or medial) of the endoskeletal visceral arches would not so much be determined by the position of the neural crest cells, but rather by the proximity of the endoderm to the latter.

To sum up what we currently know of the early development of the gill arches in lampreys and gnathostomes, it seems that: (1) in lampreys, early neural crest cell migration simultaneously follows both lateral and medial routes in all arches, but only the lateral neural crest populations become chondrogenic and form

arches, except perhaps in the medial component of the velar skeleton; (2) in gnathostomes, neural crest cells fail to migrate along the medial route from the beginning, but progressively surround (outside-in) the mesodermal bars of the arches; (3) in gnathostomes, only the medially placed neural crest cells of the cylinder surrounding the mesodermal bars become chondrogenic and form visceral arches, the position and structure of which is induced by the endoderm. As to the lateral arches of lampreys, it cannot be ruled out that a similar induction, but from the ectoderm, may also occur (G. Crump, pers. comm., 2004). Cerny et al. (2004b:266) thus considered that the “the failure of cranial neural crest cells to migrate along the medial migratory pathway in gnathostomes was the first step in the modification of the gnathostome body plan away from their agnathan forerunners.”

This seems quite a different scenario than those proposed by morphologists (e.g., Janvier, 1996b; Mallatt, 1996). Yet despite the complexity of the arguments now involved in this debate, it seems that we are coming closer and closer to a solution, and that the signaling from the endoderm or ectoderm to the neural crest cells at an early stage of their migration is a crucial factor in determining the lateral or medial position of the pharyngeal arches. The only contribution of paleontology to this debate has been to provide some evidence that the transition from the “agnathan” to the gnathostome condition of the mandibular arch has occurred later than the acquisition of other features, such as the exoskeleton, pectoral fins, and epicercal tail, and was a comparatively sudden event in vertebrate evolution. In a sense, the rise of jaws appears as sudden as (and coeval with) that of the horizontal semicircular canal (Mazan et al., 2000).

In a somewhat different field than the mere lamprey-gnathostome visceral arch homology, fundamental data have been recently published by S. Kuratani and his collaborators on the developmental genetics of the lamprey head, with particular reference to the origin of jaws (Kuratani, 2003; Kuratani et al., 2004, Shigetani et al., 2002; see also reviews in Kuratani, 2004; Shigetani et al., 2005). Although these authors agreed with others on the fact that the early development of the pharyngeal arches of lampreys and gnathostomes is basically similar, with homologous mandibular-arch primordia in both taxa, they point out a number of fundamental differences as to the extension of the ectomesenchyme in the oral and rostral regions of the vertebrate head. Notably, these authors demonstrated that the neural crest-derived tissues of the lamprey “upper lip” (i.e., the oral hood) are entirely premandibular in origin (pm, Fig. 2.15A1). Here, of course, they did not mean that they are derived from a once-existing premandibular arch, but only from the ectomesenchyme that extends anteriorly to the mandibular arch proper and gives rise to the trabeculae cranii in the gnathostomes (pm, Fig. 2.15A2). They thus inferred that the so-called trabeculae cranii of lampreys are not homologous to those of the gnathostomes, but rather are a mere prolongation of the mesoderm-derived



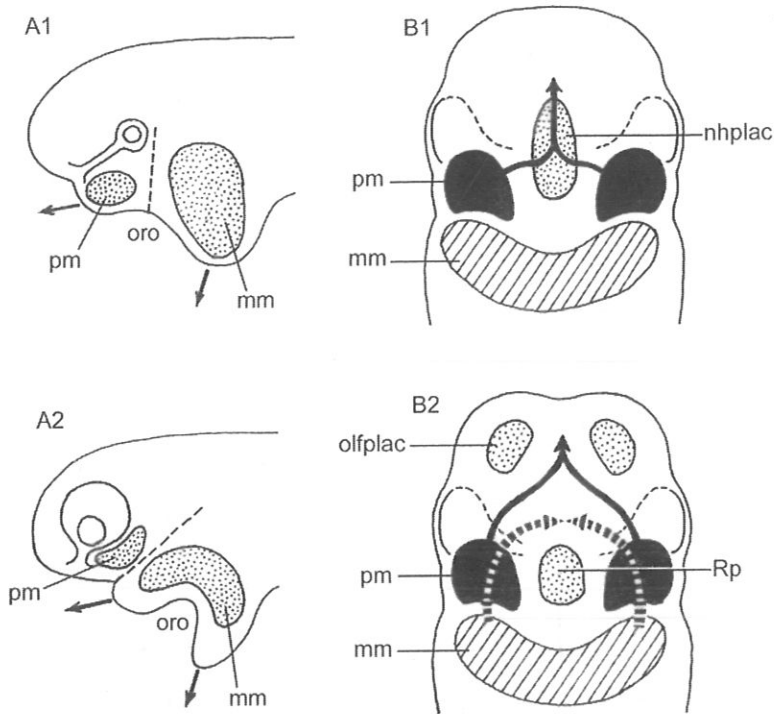


Figure 2.15. A, distribution of the ectomesenchyme surrounding the premandibular and mandibular mesoderm (dotted) in the embryonic head of a lamprey (A1) and a gnathostome (A2); the arrows indicate the direction of the growth of the upper and lower lips. B, schematic distribution of the premandibular (black) and mandibular (hatched) ectomesenchyme in a lamprey (B1) and a gnathostome (B2), as well as the nasohypophysial placode, the olfactory placodes, and the Rathke's pouch (dotted). The arrows indicate the direction of the extension of the premandibular (black arrow) and mandibular (dashed arrow) ectomesenchyme. (A, after Kuratani et al., 2004; B, after Kuratani et al., 2001.) Abbreviations as in Figure 2.4.

parachordals. Consequently, the oral apparatus (which, as Kuratani [2004] correctly noted, has much more diverse derivations than the mandibular arch alone) of lampreys and gnathostomes would be radically different in this respect because the ectomesenchyme extends much farther anteriorly in lampreys (Fig. 2.15A1).

The heterotopy theory of jaw evolution proposed by Shigetani et al. (2002) and Kuratani (2004) suggests that the premandibular ectomesenchyme, which in gnathostomes forms the prechordal plate and anterior braincase floor, underwent a heterotopic shift in ectoderm-ectomesenchyme interactions and differentiated into a large upper lip (pm, Fig. 2.15A1) that somehow parallels the anterodorsal expansion of the more posterior mandibular arch of gnathostomes (mm, Fig. 2.15A2). Kuratani et al. (2004) and Kuratani (2004) thus concluded that the oral hood of lampreys is in no way homologous to the dorsal part of the gnathostome jaw. However, it should be pointed out that most early anatomists and embryologists never envisaged such a homology because all of them regarded that the lamprey oral hood as being derived from the posthypophysial region of the head. Kuratani et al. (2004:459) stated that heterotopy leads to a "loss of homology" between the mandibular arches of lampreys and gnathostomes. In other words, heterotopy implies that changes in the position of gene expressions and tissue inductions make two anatomical structures be no longer homologous. Again, such homology concepts based on causes and aimed at justifying one particular theory of character relationship

or, more frequently, of character transformation, have been reviewed and criticized by Nelson (1994). There was once a belief that the knowledge of the processes (the causes or pathways) involved in developmental genetics would solve the homology problem (Gilbert and Bolker, 2001), but it only provides yet another subset of homology relationships (assuming that gene-expression patterns can be regarded as homologues), sometimes congruent with the previously proposed ones, and sometimes not.

What this evidence tells us is perhaps not that the oral apparatus of lampreys and gnathostomes displays no homology, but rather that the oral opening is not exactly in the same position in the two groups, relative to the distribution of the mandibular and premandibular ectomesenchyme (oro, Fig. 2.15A). Which of these two conditions can be regarded as general for the vertebrates or as ancestral to the other remains undecided, for lack of a third set of characters, which could perhaps be provided by hagfish development. It thus seems that heterotopy is not just displacing gene expressions and tissue interactions; it also results in displacing the homology problem to a different level of organization. These debates about heterotopy are, I think, the result of the long-lived confusion of homology relationships and ancestor-descendant character relationships (or character transformations). This is reflected in such sentences as this: "the velum would be homologous with the jaws only as a derivative of the mandibular arch, but neither of them would represent an ancestral condition to the other" (Kuratani et al., 2001:1629). Again, the question is not whether there has been a transformation, but whether two structures are related characters (or character states) relative to a third one.

Now, this question of the lamprey-gnathostome homologies as to the oral apparatus may turn out to be considered in a different way, following the recent suggestion by Cerny et al. (2004a) that the palatoquadrate of the gnathostomes is in fact a composite structure formed by an anterior portion, which is derived from the same "premandibular" ectomesenchyme as the trabeculae cranii, and a posterior (pterygoquadrate) portion, which is derived, like the Meckelian cartilage, from the mandibular ectomesenchyme that accumulates in the ventral (mandibular) prominence of the mandibular arch. Surprisingly, this new interpretation of the palatoquadrate is almost identical to Jarvik's (1981: fig. 48) fossil-based theory of a composite palatoquadrate derived from both the premandibular and mandibular arches, a theory long dismissed as mere "anatomical philosophy" (see Janvier, 1996b). In this way, the mandibular arch proper of the gnathostomes, lacking an anterior expansion, would be more similar to that of lampreys. However, the interpretation offered by Cerny et al. (2004a) is based on a tetrapod (axolotl), and one may wonder whether this reduction of the mandibular ectomesenchyme-derived portion of the palatoquadrate is not a consequence of the reduction of the palatoquadrate as a whole in tetrapods. The same reduction process of the palatoquadrate in lungfishes had also led Bjerring (1977:164,

fig. 31D) to a similar conclusion concerning the nature of the dipnoan upper jaw.

Another important result provided by Kuratani's team is the evidence for a motor innervation of the lamprey upper lip musculature (derived from premandibular ectomesenchyme) by fibers from the maxillary branch (V2) of the trigeminal nerve (Kuratani et al., 2004). Back in the 1920s, this was a hotly debated question in connection with the premandibular arch theory, and the finding of Kuratani et al. (2004) may lead us to revisit Stensiö's (1927) old interpretation of osteostracan cranial nerves (with a visceromotor maxillary branch). The foremost nerve canal opening in the orolobranchial cavity of osteostracans (V2-3, Fig. 13A) was first regarded by Stensiö (1927) as having transmitted a visceromotor profundus nerve, then a visceromotor maxillary branch of the trigeminal (Wängsjö, 1952; Damas, 1954; Janvier, 1981a), and, finally, both the maxillary and mandibular branches of the trigeminal nerve (Whiting, 1977; Janvier, 1985b, 1996a,b), the former being exclusively viscerosensory. Now, it is no longer ruled out that the maxillary branch actually was also visceromotor and involved in the innervation of a premandibular ectomesenchyme-derived oral musculature, as in lampreys.

Janvier (1996a, 2001) pointed out that a major event in the "agnathan"-gnathostome transition was the disconnection of the olfactory placode (or placodes) from the hypophysial tube, resulting in the separate opening of the two nasal capsules to the exterior. Kuratani et al. (2001) and Ushida et al. (2003) also regarded this disconnection of the nasal placodes from the hypophysial anlage as having had a decisive impact on the reorganization of the premandibular and mandibular ectomesenchyme in the gnathostome head, notably in allowing the premandibular ectomesenchyme (pm, Fig. 15B2) to form the internasal septum, and the mandibular ectomesenchyme (mm, Fig. 15B2) to extend laterally to the Rathke's pouch (Rp, Fig. 15B2). Instead, the premandibular ectomesenchyme (pm, Fig. 15B1) of lampreys has to expand ventrally to the nasohypophysial placode (nhplac, Fig. 15B1), forming the oral hood.

Finally, Cohn (2002) suggested a most promising process for the rise of jaws. The neural crest cells that migrate into the mandibular arch of the gnathostomes are *Hox*-free. In contrast, those in the same arch (giving rise to the velar skeleton) of the lamprey *Lamprolaima fluviatilis* were shown by Cohn (2002) to express a *Hox* gene, *HoxL6*, whose ortholog in the cephalochordates (*AmphiHox6*) also extends far anteriorly, beyond the expression domains of *AmphiHox2-4*. It seems thus that there has occurred at some time after the divergence of lampreys and in the lineage that ultimately led to the gnathostomes a posterior retraction of the expression domain of *Hox6*, which freed the mandibular arch from any *Hox* gene. Because *Hox6* is known for having a role in homogenizing the structure of the serially homologous structures and was thought to be involved in the similar shaping of the hyoid and gill arches, Cohn (2002) assumed that by becoming *Hox*-free, the mandibular arch

could expand ventrally and develop a Meckelian cartilage. This discovery would have lent some support to the theory that jaws have appeared first and preceded in time the “gnathostomization” of the more posterior arches. However, further investigations failed to corroborate Cohn’s finding (Takio et al., 2004), as neither *HoxL6* nor any other *Hox* gene expression occurs in the mandibular arch of the closely related lamprey *Lethenteron japonicum* (“*Lampetra japonica*”), which is thus similar to the gnathostome condition in this respect. Because it is unlikely that such a major difference could occur in such closely related taxa, one may conclude that Cohn’s theory remains controversial.

One may try and imagine the kind of fossil data that could provide a hint for determining at which node of the current vertebrate phylogeny could occur conditions that would somehow foreshadow the gnathostome jaws. The presence of an extensive denticle covering in the pharyngeal cavity of certain thelodonts (Van der Bruggen and Janvier, 1993; Smith and Coates, 2001) could be an indication for an early skeletogenic neural crest–pharyngeal endoderm induction process, and thus the presence of precursors of the medial arches, but this awaits precise knowledge of the manner in which these denticles are organized in the thelodont pharynx. Mallatt’s (1996) suggestion of a homology between the oral valve of gnathostomes (orv, Fig. 2.14B) and the medial flap of the “agnathan” velum (vfl, Fig. 2.14A) seems an interesting hint (see, however, reservations expressed by Kuratani et al., 2001:1629). This antireflux valve attached to inner side of the mandibular arch of the gnathostomes has virtually the same anatomical relationships and function as the velum of larval lampreys and, when denticle covered, could be potentially preserved in stem gnathostomes. How much such a discovery would help in explaining the origin of jaws or provide evidence for evolutionary transition is uncertain, but it could provide an interesting character that is functionally related to the presumed early role of jaws—that is, increased ventilation and ultimately suction feeding (Mallatt, 1996).

## Conclusions

Certain fossil vertebrates, be they stem- or crown-group vertebrates, provide examples of character combinations that may support scenarios of evolutionary transition in early vertebrate history, notably as to the rise of the gnathostomes. Possible stem vertebrates, such as the Early Cambrian myllokunmingiids, represent a proxy for the kind of organism from which crown-group vertebrates may have derived. However, they already display most of the characters of the latter, and they thus barely fill the reputedly major morphological gap that still separates cephalochordates from vertebrates. The interpretation of the Early Cambrian yunnanozoans remains controversial, but they do bear some resemblance to the myllokunmingiids and crown-group vertebrates, notably in the organization of their gills. Whether this resemblance is a particular vertebrate or a general

deuterostome character is still debated. The absence to date of any fossil cephalochordates precludes any assessment of the derivedness of the extant representatives of this group relative to the common ancestor they are supposed to have shared with vertebrates.

However, the structure of the myllokunmingiids and yunnanozoans, which combines general euchochordate characters, hitherto reputedly unique cephalochordate characters, and some unique vertebrate characters, does not suggest a very long evolutionary history from the cephalochordate-vertebrate divergence to the earliest fossil evidence for vertebrates. A cascade of developmental innovations, such as the neural crest and its derivatives, could have rapidly led to profound modifications of stem-vertebrate anatomy to such an extent that they would differ widely from cephalochordates. The history of vertebrate paleontology and phylogeny shows that many major gaps (e.g., "agnathan"-gnathostome, fish-tetrapod, reptile-mammal, reptile-bird, ape-human gaps) were once regarded as evidence for deep divergence times and slow transitional process, but new or previously unnoticed character combinations showed that these evolutionary transitions were in fact much more simple and rapid than previously thought. The same perhaps also applies to the gap between cephalochordates and vertebrates.

Whatever the relationships between hagfishes and lampreys may be, the various clades of fossil armored "agnathans," colloquially referred to as "ostracoderms" or stem gnathostomes (although lacking jaws), provide some examples of evolutionary transitions, at any rate at the level of certain characters or character complexes. In fact, these assumptions about evolutionary transitions are merely the consequence of the co-occurrence of the lack of jaws on the one hand, and some characters that are only known in gnathostomes among extant vertebrates on the other. This may indeed give the impression that the stem of the gnathostomes is documented by a more or less acceptable series of fossil transitional forms, leading from the naked hagfishes or lampreys to the bony gnathostomes, but there is a danger that this scenario becomes doctrine. Therefore, instead of considering relationships between taxa and inferring transformation scenarios from character optimizations at nodes, as most current computer programs for phylogenetic reconstruction do, it may be sometimes useful to return to a consideration of the homology relationships at the level of individual characters in the form of a three-item statement. By doing so, there would be admittedly a temptation to return to the key characters established as such by an authority, as in the time of Stensiö's "cephalaspidomorph" characters. However, this would also make incongruent patterns of homology relationships less readily overlooked or dismissed forever as homoplasies by virtue of optimization. The nasohypophysial complex of lampreys and osteostracans is such an example.

Admittedly, in classical adaptationist scenarios, evolutionary transitions are perhaps more readily illustrated by taxa than by characters, but this exclusive consideration of the end product of character analysis, i.e., a taxon tree supported by optimized charac-

ter transformations at nodes, may be abused to generate narratives, in particular in the mind of researchers to whom the unending quest of phylogenetics is not familiar. The current vertebrate phylogeny is merely one hypothesis, more parsimonious by a few steps than Stensiö's (1927) assumption of "agnathan" monophyly, and most narrative evolutionary scenarios that can be inferred from it are mere incarnations of an optimization procedure. Perhaps this is entirely wrong; perhaps "agnathans" actually do form a clade and are far more derived than the gnathostomes, relative to the common ancestor of the vertebrates, as suggested by Jarvik (1980). However, I doubt it. At present, the evolutionary transition from "agnathans" to gnathostomes remains best illustrated by some characters or character complexes, most of which gain significance in the light of fossil data. However, whether or not these homology relationships (and the character transformations that may be inferred from them) can be integrated in an adaptationist scenario based on taxa remains a matter of personal choice and imagination.

The future of this field of research, as to its paleontological aspect, lies essentially in the methods used for analyzing the data (Nelson, 1994:111), but also in the good and equal quality of the latter. The source of data on the structure and diversity of extinct jawless vertebrates has not dried up yet. The anatomy of galeaspids could technically be as well known as that of osteostracans. A better knowledge of pituriaspids only depends on further fieldwork (in admittedly difficult areas). Exceptionally well-preserved thelodonts are being found in Canada, Estonia, and Scotland, and a hitherto unsuspected diversity of Ordovician vertebrates is turning up in Australia, Canada, and the United States. Moreover, certain early Paleozoic Konservat-Lagerstätten, such as Miguasha (Canada), the Soom Shale (South Africa), or Chengjiang (China), provide more and more data on soft-bodied jawless vertebrates. Early fossil vertebrates may not be able to overturn theories of relationships based on morphological data of extant taxa, but they may call into question some character homology relationships, and thus radically change the way we imagine evolutionary transitions at the level of certain characters.

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