## Chapter 12

# Scenarios, selection and the ecology of early vertebrates

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## ABSTRACT

Hypotheses that provide explanations of major transitions in early vertebrate evolution can be tested by analysis of fossils. In this chapter I consider two widely held views of early vertebrate evolution: firstly, the hypothesis that jawless vertebrates were driven to almost complete extinction by competition with gnathostomes during the late Palaeozoic; and secondly, scenarios that link the origin of vertebrates and the origin of gnathostomes to a long-term ecological trend towards increasingly active and predatory lifestyles.

Analysis of familial diversity suggests that there is no simple relationship between the decline of agnathans and the rise of gnathostomes. Rates of family extinctions in jawless vertebrates were highest in the Early Devonian, but gnathostome diversity peaked in the Late Devonian. Also, the ecology of many early vertebrates is poorly constrained. The hypothesis that the pattern of early vertebrate diversity reflects competition between agnathans and gnathostomes or between specific clades of jawless and jawed fish must be regarded as untested, and at present untestable, speculation.

Evidence from conodonts supports the hypothesis that a shift to predation occurred at the origin of vertebrates, but data concerning feeding in other groups of fossil agnathans, exemplified here by heterostracans, are currently inconclusive. If rigorous analysis demonstrates that any of the major clades of fossil agnathans were non-predatory, hypotheses that early vertebrate evolution was driven by a long-term trend towards increasing levels of activity and predacity may be overturned.

## 12.1 The fossil record, stem gnathostomes, and the significance of functional morphology

Two major transitions in the evolution of life form the subject of this chapter: the origin of vertebrates, and the origin of gnathostomes. Specifically, I wish to consider hypotheses that have sought to explain the acquisition of certain key vertebrate characters, and the pattern of vertebrate diversity, particularly during the evolution of stem gnathostomes. As major transitions these events are among the most obvious targets for the integrated approach that has come to be known as evolutionary developmental biology (e.g., Hall 1998), and several hypotheses (e.g., Gans and Northcutt 1983; Northcutt and Gans 1983; Mallatt 1996; 1997) have attempted to integrate disparate developmental, anatomical and ecological

evidence from extant organisms and from fossils into broad explanatory scenarios. Analyses of fossil jawless vertebrates, their functional morphology and their feeding mechanisms are important in testing these hypotheses and understanding these events.

Without the fossil record of early vertebrates our view of vertebrate evolution would be seriously distorted. Figure 12.1 illustrates this point by contrasting two representations of vertebrate relationships. One illustrates vertebrate diversity today, and the other shows diversity at the end of the Silurian Period. The extant vertebrate fauna (Figure 12.1a) is dominated by gnathostomes, with jawless vertebrates limited to two groups, hagfish and lampreys. At the end of the Silurian (Figure 12.1b), gnathostomes are represented by only five groups, placoderms and acanthodians (both now extinct), chondrichthyans, actinopterygians and sarcopterygians, but it is the jawless vertebrates that are dominant. This example provides a good illustration of the value of fossils. They provide a very different picture of morphological and taxonomic diversity (i.e., evidence of unique combinations of characters which do not occur in the living fauna), but they also preserve the only direct evidence for the timing and sequence of acquisition of characters. This is of particular importance in the context of stem groups of major extant clades, because the key features of the living members of the clade are accumulated sequentially through the evolution of the less derived, extinct members of the clade (see e.g., Budd 1998 and Jefferies 1979 for further discussion of the significance of stem groups). In the case of vertebrates, where the living fauna is made up almost entirely of gnathostomes, the paraphyletic group traditionally referred to as extinct agnathans (in Figure 12.1b Anaspida, Astraspida, Arandaspida, Heterostraci, Galeaspida, Thelodonta, and Osteostraci, together with Conodonta) comprise the bulk of the gnathostome stem group. It is through the evolution of this stem group that many key gnathostome characters, including paired appendages, phosphatic skeletal tissues, and jaws, were acquired. Thus, only the stem taxa (i.e., the extinct agnathans) can provide evidence for the sequence and timing of acquisition of these characters.

But an integrated approach to understanding early vertebrate evolution requires more than just evidence of character distributions and combinations. If we are to attempt to understand the causal basis of character distributions in cladograms, and general principles in the evolution of form, then functional data are critical (Lauder 1990). Consequently, many of the most influential and widely cited hypotheses or

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*Figure 12.1* Vertebrate diversity expressed in terms of hypotheses of relationship. (a) Living vertebrates, dominated by gnathostomes. (b) Vertebrates alive at the end of the Silurian Period, dominated by vertebrates without jaws. This figure shows just two of several possible hypotheses of relationship (see e.g., Janvier 1996a, b for others), but for the purposes of this figure the precise details are not important. The paraphyletic group traditionally referred to as fossil agnathans (Anaspida, Astraspida, Arandaspida, Heterostraci, Galeaspida, Thelodonta, and Osteostraci together with Conodonta) represent stem gnathostomes, and it is through the evolution of the stem group that many key gnathostome characters were acquired. Only the fossil record provides evidence for the sequence and timing of acquisition of these characters. Note that although there is no unequivocal pre-Carboniferous fossil record of lampreys or hagfishes, their existence in the Silurian can be inferred from hypotheses of relationship. **N.B. A small error in (b) has been corrected from the original**

scenarios of vertebrate evolution have attempted to interpret the functional and ecological setting, and the selection pressures that were operating during the acquisition of key vertebrate characters (e.g., Gans and Northcutt 1983; Northcutt and Gans 1983; Gans 1989; Mallatt 1996, 1997). Again, the fossils represent a vital source of ecological and functional data for the construction and testing of such scenarios.
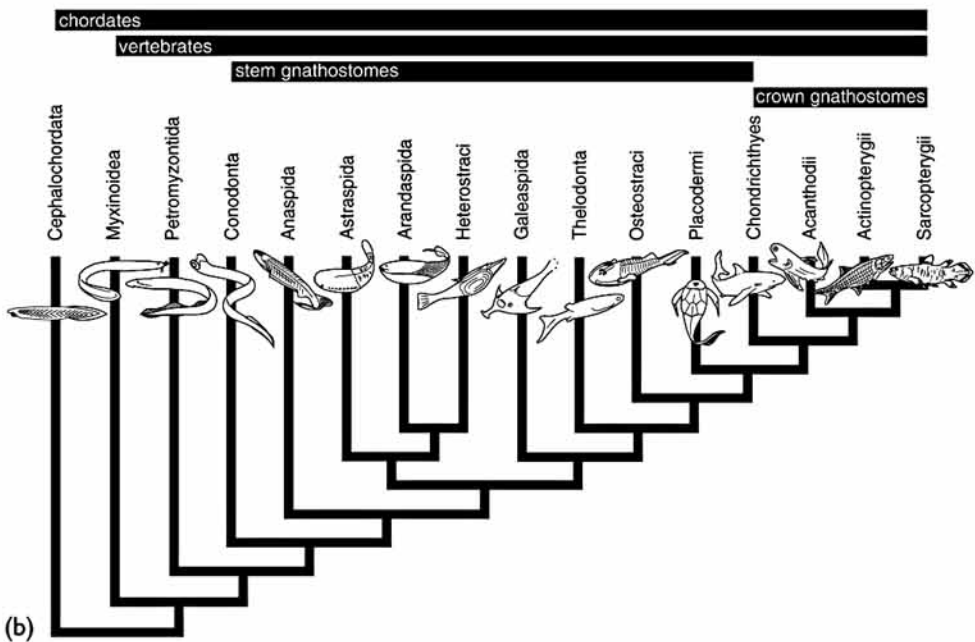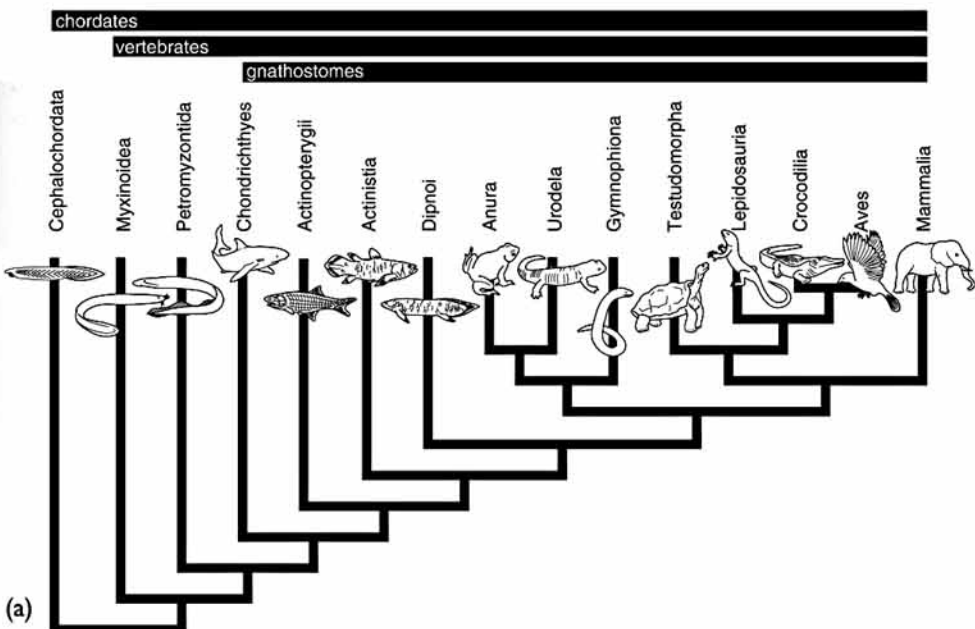
It is perhaps worth emphasizing at this point that, to avoid circularity and improve testability, phylogenetic hypotheses underpinning evolutionary scenarios should not draw directly on ecological or functional data. The relationship between phylogeny and 'functional evolution' has recently been discussed in detail by Lee and Doughty (1997), who emphasized that if cladograms and evolutionary principles (including hypotheses of function) are examined independently, then the results of phylogenetic analysis can be used to test hypotheses of function, and vice versa.

Functional analysis of extinct jawless vertebrates may also pay dividends in investigating the possibility of correlated progression in early vertebrate evolution (for discussion of correlated progression see, for example, Thomson 1966; Lee and Doughty 1997; Budd 1998). The current emphasis on applying phylogenetic systematics to early vertebrates is directing the attention of many researchers towards the reduction of fossil taxa to a series of discrete independent characters for phylogenetic analysis. But early vertebrates were clearly sophisticated organisms in which many anatomical characters formed integrated functional complexes. Thus, some characters must have been more constrained by their interactions than others, and during evolution some characters may have varied together because of their functional interdependence (see e.g., Galis 1996, for discussion and examples). This is the essence of correlated progression, and the possibility that correlated progression was a significant factor in early vertebrate evolution can only be investigated if sound functional data are available. A related point concerns the significance of functional interpretations in the selection and coding of characters in phylogenetic analysis. As noted above, it is important that hypotheses of phylogeny are not derived from hypotheses of function, and vice versa, but in the absence of functional data characters may be considered independent which are in reality interdependent components of functional integrated structural complexes. In some cases it may be best to treat all characters as independent, as recommended by Smith (1994), for example. However, this assumption seems unjustifiable if there is good evidence for certain characters being closely integrated. This is a challenging problem, but coding interdependent characters as if they were independent can have the same effect as weighting the correlated characters, and this may lead to significant bias in the results of phylogenetic analyses (see, for example, Felsenstein 1982; Lee 1998).

## 12.2 Agnathans and gnathostomes, competition and progress

### 12.2.1 The fossil record and hypotheses of competition

As Figure 12.1 shows, sometime between the Early Palaeozoic and today there has been a significant turnover in the vertebrate fauna. Almost all the agnathans became extinct and gnathostomes now dominate. Probably the most widely held view of this turnover explains these changes in relative diversity in terms of competitive replacement. For example, Pough *et al.* (1996, p. 115) stated that 'The great majority of agnathan fishes succumbed to what is generally thought to have been competition from jawed vertebrates'. Similarly, Long (1995, p. 63) suggested that 'The reason for the rapid decline in agnathan diversity is probably the rapid increase in the diversity of jawed fishes', and more specifically that 'long-shielded heterostracans were

probably outcompeted by the long-shielded early placoderms' and that 'detrital bottom-feeding agnathans may have been put out of business by the many new forms of bottom-feeding placoderms'. Osteostracans may have been outcompeted by the antiarchs (Janvier 1996b, p. 115). Competitive replacement is also clearly implicated in Gans' view (1989, p. 260) that in the origin and early evolution of vertebrates, 'present descendants of their early ancestral stages survived because they occupied and successfully maintained themselves in favourable niches. Here they outperformed members of later radiations that replaced the early groupings.' Raff (1996, p. 342) makes a similar point, but his interpretation, that 'The precipitous and almost entire replacement of the agnathans by the enormous Palaeozoic radiation of jawed vertebrates' was brought about because 'Once jaws and teeth evolved, they opened up niches for large carnivorous fishes and other specialists' also incorporates a component of ecological expansion, and not simple competitive displacement.

Some authors (e.g., Janvier 1996b) have noted that evidence for competition is in fact hard to find, and that other factors may have been responsible for significant phases of extinction. Janvier (1985; 1996a, b) suggested that the extinctions of jawless vertebrates at the beginning of the Middle Devonian were probably caused by a reduction in their preferred habitats brought about by mid-Devonian transgression. He also advocated a hypothesis previously proposed by Long (1993), that the decline in diversity during the Givetian to Frasnian (Middle to Late Devonian) was probably due to a period of global biotic interchange which brought widespread taxa into new areas where they caused extinctions in long-standing endemic communities (Janvier 1996b, p. 291). However, Long (1993) invoked competition between the immigrants and the endemics as the cause of the extinctions.

In similar vein, Maisey (1996) noted that competition from jawed vertebrates has been invoked as the cause of the disappearance of many 'ostracoderms' in the Early Devonian. However, he went on to suggest that 'another, more profound extinction took place toward the end of the Devonian' and that there 'is no evidence that competition from new kinds of fishes was a factor in that extinction; ostracoderms did not become extinct through any inherent inferiority in their anatomy' (Maisey 1996, p. 57). Although, according to Maisey, new fishes were not the culprits, competition for suitable shallow water habitats may have been to blame. This was brought about as a result of a decline in global sea levels after a lengthy period of gradual rising, and lower sea levels may have resulted in the destruction of many shallow marine shelf habitats. The habitats of many non-marine ostracoderms may have simply dried up as continental climates became increasingly arid (Maisey 1996).

So what is the evidence for competitive interactions between jawless vertebrates and gnathostomes, and between different groups of jawless vertebrates? Is it even possible to formulate and test hypotheses of competition? I will deal with these questions separately.

### 12.2.2 Evidence for extinctions resulting from competition

Although rarely discussed other than in the most general terms, the hypothesis that competition between gnathostomes and agnathans led to the extinction of the latter seems to be based on the coincidence in timing of the decline of one group and the

rise of the other. Figure 12.2 illustrates the pattern that might be expected to result from such competitive replacement (type A). Also shown are a range of other hypothetical patterns expected from alternative models of biotic replacement against which actual patterns in the fossil record can be compared.

The agnathan–gnathostome turnover, based on family level data from *The Fossil Record 2* (Halstead 1993), is shown in Figure 12.3a. Analyses of patterns in early vertebrate evolution derived from ranges and numbers of fossil taxa have been criticized as over-simplistic and biased by inadequate data (e.g., Halstead 1987; Janvier 1996b). Furthermore, *The Fossil Record 2* (Benton 1993) has been considered to be so flawed as a database that it is almost useless, and certainly less useful than other compilations (Conway Morris 1994). Such criticisms have some validity, and the data for early vertebrates were compiled before the recognition of thelodonts and possible gnathostomes in the Caradoc Harding Sandstone (Sansom *et al.* 1996, and this volume), for example. *The Fossil Record 2* is certainly less than perfect, but it is considerably better than the databases from which previous analyses of early vertebrate diversity were derived. More generally, Janvier (1996b) voiced reservations
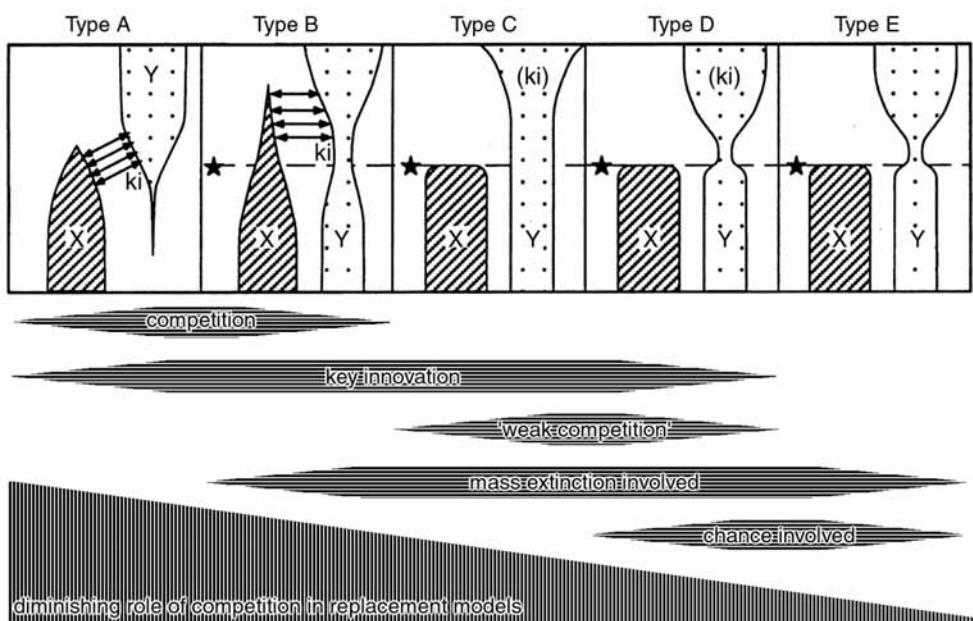


*Figure 12.2* Alternative models of biotic replacement in which competition and mass extinction play variable roles. The role of competition diminishes from left to right, from fully competitive replacement (a), through post-extinction competitive replacement (incumbent replacement) (b), extinction resistance (c), and non-competitive adaptive radiation (d), to non-competitive radiation, (stochastic broom). All except (e) involve some level of competition. KI refers to a key innovation which confers competitive superiority on the clade which possesses it; in the traditional scenario of agnathan–gnathostome interaction, jaws are generally considered to be just such a key innovation. Parentheses indicate that possession of KI is not an essential component of the model of replacement. Stars indicate an extinction event caused by something other than interaction between the clades in question (Modified from Benton 1991; 1996a).
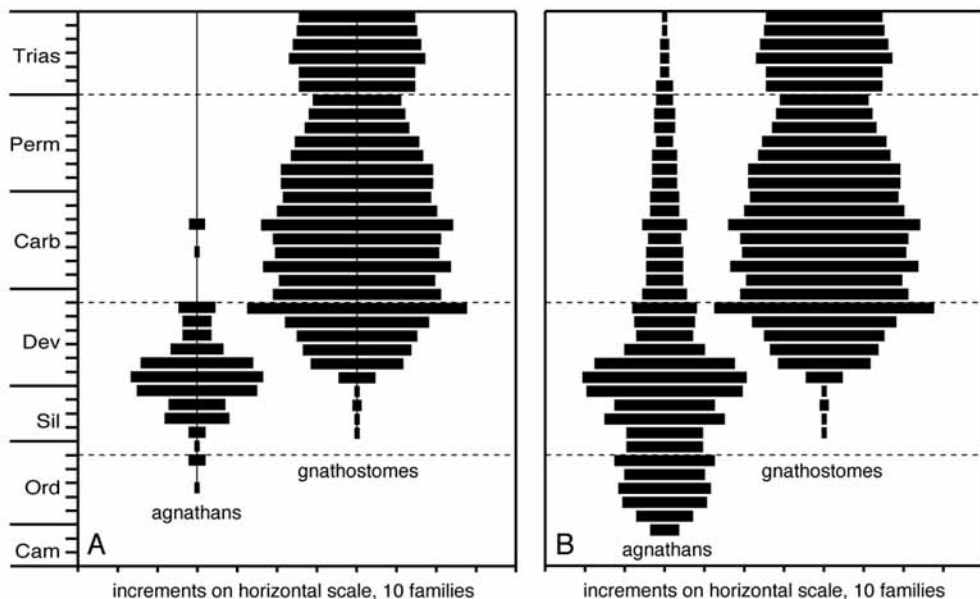
*Figure 12.3* Diversity plots of agnathans versus gnathostomes through the Palaeozoic and Triassic. (a) Families traditionally considered to be agnathans versus gnathostome families. (b) Agnathans, including conodonts, versus gnathostomes. Data taken from *The Fossil Record 2* (Cappetta *et al.* 1993; Gardiner 1993a; Halstead 1993; Patterson 1993; Schultze 1993; Zidek 1993) with some modification (addition of fossil myxinoid from Mazon Creek (Bardack 1991); inclusion of astraspids within heterostracans (= Pteraspidomorphi *sensu*, e.g., Janvier 1996b). Dashed lines indicate recognized mass extinction events.

about the taxonomic underpinning of compilations of data, and although these concerns may be well founded, when it comes to documenting patterns of diversity in the fossil record traditional taxonomic groupings, even if they are paraphyletic, have been shown to be at least as reliable as cladistically defined, monophyletic taxa (Sepkoski and Kendrick 1993). More detailed discussion of the value of compiled taxonomic databases is beyond the scope of this contribution; my purpose here is simply to evaluate whether the pattern of early vertebrate diversity, based on the best available data, supports a hypothesis that the extinction of agnathans could have been caused by the rise of gnathostomes.

The pattern shown in Figure 12.3a is broadly similar to that presented by Long (1993, based primarily on pre-1981 data). Declines in agnathan diversity parallel increases in gnathostome diversity, and in this respect the pattern resembles the double-wedge that might be expected to result from competition between the two groups (Benton 1987; 1991; Figure 12.2, type a). However, this is a drastically oversimplified picture of agnathan diversity. Conodonts are now generally accepted to be jawless vertebrates (see Aldridge and Purnell 1996, and Donoghue *et al.* 1998 for recent reviews), and any plot of agnathans versus gnathostomes cannot simply ignore them. When conodonts are included in agnathans (Figure 12.3b), the simple double-wedge disappears, and a picture emerges which, perhaps, more closely

resembles what might be expected from incumbent replacement (Figure 12.2, type B; see Rosenzweig and McCord 1991 and Benton 1996a for more detailed discussion of incumbent replacement).

There are further problems. Agnathans do not constitute a clade; they are an arbitrary grouping of divergent clades united by little other than their lack of jaws. Thus it makes little sense to talk of competition between 'the agnathans' and 'the gnathostomes' (Janvier 1996a, b). This lumping of agnathans and gnathostomes into two all-embracing groups also masks a great deal of information, and if the diversity through time of what are generally recognized as major groupings of jawless fish are plotted, a much more complex picture emerges (Figure 12.4). These data rather undermine the traditional picture based on simple plots of agnathans versus gnathostomes: there is no simple relationship between the decline of agnathans and the rise of gnathostomes. Compared with previous analyses, the data also reveal a different pattern of the timing of the most significant extinctions, with highest levels of family extinctions in jawless vertebrates, particularly heterostracans and osteostracans, occurring in the Lower Devonian, not the Middle to Upper Devonian (contra Long 1993). These plots also confirm the point made by Halstead (1987), among others, that the time of last appearance of a higher level taxon does not provide a reliable indicator of times of extinction. Changes in diversity through time of separate clades of jawless vertebrates provide a more detailed and probably more realistic picture of extinctions.
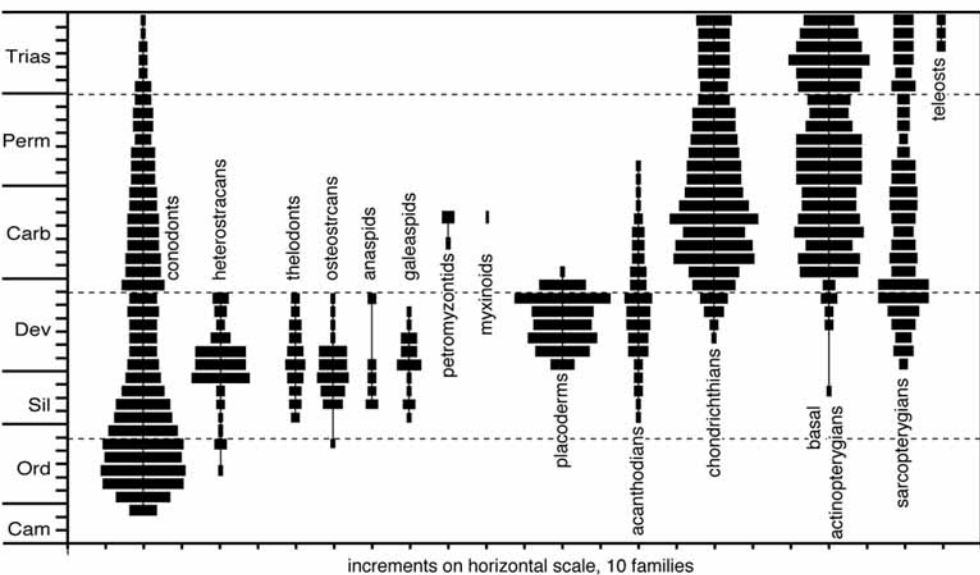


*Figure 12.4* Diversity of different clades of vertebrates through the Palaeozoic and Triassic. Most of the agnathan groups were considered to be subclasses by Halstead (1993); all, with the exception of the thelodonts (Janvier 1996a, b, contra Turner 1991), are generally thought to be monophyletic. Dashed lines indicate recognized mass extinction events. Data sources as in Figure 12.3.

### 12.2.3 Tests of competitive interaction and clade replacement

That the pattern of extinction to emerge from a closer look at the data does not match the double-wedge (Figure 12.2, type a), however, does not rule out the possibility that competition was a factor in controlling early vertebrate diversity. But, more rigorous analysis is required if this hypothesis is to be tested. In order to have been competitors, the distributions of two species must at least have overlapped in time and space, otherwise individuals could never have met. And they must also have shared some limiting resource or enemy (see e.g., Benton 1996a; Sepkoski 1996). From these basic prerequisites, Benton (1996a, b) has derived a set of minimum criteria which must be fulfilled in order to test the hypothesis of competitive replacement of one clade by another. Sepkoski (1996) has pointed out some of the difficulties in investigating such competitive displacements, but it does seem reasonable that taxa must meet simple criteria of the sort laid out by Benton if they are at least to have been *potential* competitors. That is to say, unless two taxa have overlapping stratigraphic ranges, were of roughly similar size, had broadly similar diets (Benton used categories such as carnivory, omnivory, and herbivory for tetrapods), had similar habitat (terrestrial, freshwater, marine, etc.), and occupied broadly the same geographic area, they probably could not have been competitors. Diet seems particularly significant here, simply because food is one of the most important limiting resources for heterotrophic metazoans and among extant fishes feeding mode is a major factor in determining ecological niches (e.g., Schluter and McPhail 1992).

Unfortunately, at the present time it is not possible to test the possibility of competition between early vertebrates based on these criteria. The best available database (*The Fossil Record 2*) allows families to be assessed according to stratigraphic range but little else. In terms of habitat, the database only differentiates between freshwater and marine, and for some groups this is still not known with certainty, even after analysis of stable isotopes in skeletal remains (Schmitz *et al.* 1991). Neither does the database contain any palaeogeographic information. These data could probably be compiled from various published sources (e.g., Young 1993), but this has yet to be accomplished. Finally, as I will discuss in more detail below, the functional morphology of fossil jawless fish is so poorly constrained, especially with respect to feeding, that very few taxa can be assigned even to very broad trophic categories such as macrophagy or microphagy. In conclusion to this section, it seems that we are not in a position where we can test the hypothesis of competitive interaction between early vertebrates. The view that early vertebrate diversity and the extinction of most clades of jawless fish was the result of competition between agnathans and gnathostomes or between specific clades of jawless and jawed fish, must be regarded as untested, and at present untestable, speculation. Competitive interactions are just one of a number of possible explanations.

## 12.3 Hypotheses of feeding in jawless vertebrates and scenarios of early vertebrate evolution

### 12.3.1 The new head and the new mouth

The scenario that has come to be known as 'the new head hypothesis' (Gans and Northcutt 1983; Northcutt and Gans 1983; Gans 1989) is among the most

influential and widely cited of recent ideas concerning the origin and early evolution of vertebrates. In essence, the hypothesis links the acquisition of a number of key vertebrate synapomorphies, such as the head and anterior parts of the brain, with the possession of neural crest and epidermal placodes. The hypothesis draws on evidence from developmental biology, neurobiology, functional morphology, and systematics, and combines this evidence, together with data from fossils, to produce a scenario which seeks to explain the sequence of events and the selective pressures involved in the origin and early evolution of vertebrates. The modifications in development involved in early vertebrate evolution are linked to shifts in feeding, and in several papers Gans and Northcutt (e.g., Gans and Northcutt 1983; Northcutt and Gans 1983; Gans 1989) have outlined the ecological setting within which, according to their scenario, vertebrate characters were sequentially acquired. Thus the acquisition of key vertebrate characters was correlated with a long-term ecological trend – from suspension feeding, in a lancelet-like prevertebrate, towards increasingly active and predatory habits. It is worth noting that recent work on gene expression patterns suggests that the 'new head' was differentiated and elaborated from a preexisting rostral region and was not a completely novel addition to the body, but these results are otherwise compatible with the new head hypothesis (e.g., Holland 1996; Williams and Holland 1996).

Mallatt (1996; 1997) has proposed a comparable scenario to explain the origin of gnathostomes, i.e., the acquisition of jaws. He argued that most of the changes leading to the evolution of the grasping jaws of gnathostomes were adaptations for improved ventilation and that the evolution of gnathostomes was driven by selection for increasing activity and predacity (see Figure 12.5), a similar trend to that
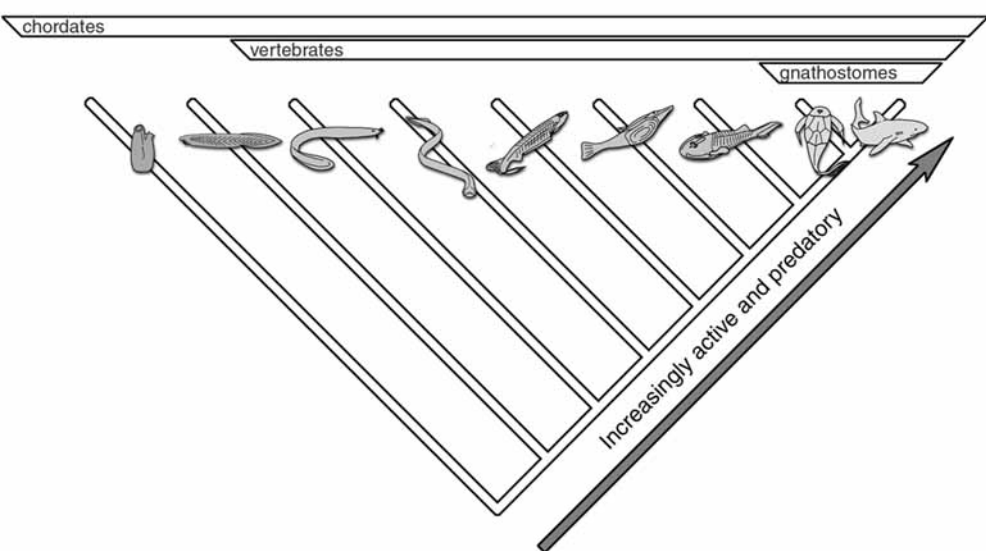


*Figure 12.5* Trend towards increasingly active and predatory habits in scenarios of vertebrate evolution (Gans and Northcutt 1983; Northcutt and Gans 1983; Gans 1989; Mallatt 1996; 1997). The hypothesis of vertebrate relationships is diagrammatic, but the branching order of the clades agrees with recent analyses (e.g., Donoghue *et al.* 2000). This hypothesis of relationship differs in significant details from that presented by Mallatt (1996; 1997), but this does not affect the validity of the test outlined in this chapter.

invoked by Gans and Northcutt (1983; Northcutt and Gans 1983; Gans 1989). These hypotheses also echo Denison's (1961) stages in the evolution of vertebrate feeding mechanisms: a microphagous suspension feeding 'ancestral stage', a 'jawless stage' in which feeding was limited to deposit feeding, scavenging and parasitism, and a 'gnathostome stage' where jaws permitted an expansion into previously unavailable trophic niches such as predation.

This view of a long-term trend towards increasing activity in the evolution of chordates is widespread, and the innovations 'in the nervous system, jaws, and appendages [which] transformed meek filter feeders into fearsome predators' have even been linked to gene duplication events (Postlethwait *et al.* 1998, p. 345). However, to many people ecological explanations of evolutionary events are suspect, and Janvier (1996b, p. 281), for example, warns that 'One step further removed from reality, we enter here the realm of evolutionary processes and life history, ... whence, how and why early vertebrates evolved, how they lived, on what they preyed, etc. These stories are often amusing, sometimes plausible, but generally untestable as theories.' Nevertheless, the scenarios concerning the early evolution of vertebrates and the acquisition of key characters of the crown group vertebrates outlined above (Gans and Northcutt 1983; Northcutt and Gans 1983; Gans 1989; Mallatt 1996; 1997) make specific interpretations of how fossil jawless vertebrates fed, and invoke functional trends that are potentially testable using fossil data. Thus rigorous analysis of feeding in early vertebrates may provide a test of the ecological hypotheses which are an integral component of these scenarios.

### 12.3.2 Hypotheses of feeding in fossil jawless vertebrates

It is not possible in this short contribution to consider feeding in each of the major clades of jawless vertebrate. Thus, I have limited discussion to just two groups: the conodonts and heterostracans. These clades provide a good illustration of some of the problems involved in analysis of feeding (and other aspects of the palaeoecology of fossils) that may lie behind misgivings such as those expressed by Janvier (1996b, quoted above).

#### 12.3.2.1 Feeding in conodonts

Until quite recently, feeding in conodonts was probably less well understood than in any other group of fossil agnathans, but the evidence of the few specimens that preserve remains of conodont soft tissues clearly show that the elements were located in the oropharyngeal region of the head. Natural assemblages preserving elements in their original but flattened arrangement indicate that they formed a complex bilaterally symmetrical array (Aldridge *et al.* 1987; Purnell and Donoghue 1998; cf. Nicoll 1987; 1995), and there is no longer any dispute that this array was involved in feeding. What has been more contentious, however, is whether conodonts were microphagous, the apparatus forming a suspension feeding array, or macrophagous, with elements functioning as teeth. Both these hypotheses are supported by analogies with living organisms, but the elements lack homologues among extant taxa, and the decades of debate regarding function were not ended by the discovery of soft tissue remains of conodonts (for a recent review, see Purnell 1999).

This impasse in functional analysis was largely the result of the difficulties of

testing functional hypotheses derived from direct analogies with extant taxa (see Purnell 1999). In order to get around this, attempts have been made to derive testable predictions of apparatus growth rates from competing hypotheses of function (Purnell 1993; 1994). If the conodont apparatus formed a filtering device, the food intake of the animal would have been dependent on the surface area of the filtering array formed by the anterior elements of the apparatus, and in an isometrically growing animal this would have increased in proportion to body mass to the power 0.67. Food requirements, however, are linked to metabolic rate, which increases in proportion to body mass to the power 0.75 (for more detailed discussion, see Purnell 1999). Thus, the increasing metabolic demands of a growing conodont would require positive allometry of the elements involved in filtering. These theoretical predictions are supported by data for feeding in *Branchiostoma* (Azariah 1969) and by positive allometry in the filter feeding structures of ammocoetes (Lewis and Potter 1975; see Purnell 1994 for discussion). No conodont taxa for which apparatus growth rates have been analysed quantitatively exhibit positive allometric growth (Purnell 1993; 1994; 1999). This provides strong evidence against the hypothesis that conodonts were suspension feeders.

This test may be quantitative, but it is nonetheless inferential, and relies on a number of assumptions regarding conodont growth (Purnell 1999). Analysis of wear and surface damage on conodont elements, however, has revealed direct evidence of feeding in conodonts. In fossils, direct observation of function is obviously not possible, but damage to feeding structures produced during normal use provides a fundamentally different type of evidence to that obtained from functional analysis of morphology; such damage represents the closest possible approximation of direct observation of function (Purnell 1999). Of particular significance in conodonts is the development of microwear textures within wear facets on functional surfaces (Figure 12.6). These are comparable to the microwear textures developed on the teeth of mammals which take the form of distinctive polished, scratched, or pitted textures produced *in vivo* by the action of abrasives in food and by the compressive and shearing forces that act on enamel during feeding (Teaford 1988; Maas 1991; 1994). The presence of microwear on conodont elements thus allows precise characterization of feeding. Smooth, polished areas indicate either contact with the opposed element without intervening food, or more likely that a species ate food that was not abrasive; pitted microwear indicates that food was crushed between opposed elements, but the lack of associated scratches indicates that they did not grind; parallel scratching is diagnostic of shearing (Purnell 1995). The broader significance of shearing for hypotheses of feeding lies in the fact that it represents a method of food breakdown that is incompatible with microphagy, thus providing unequivocal evidence for macrophagy in conodonts (Purnell 1995).

Food acquisition in conodonts is not yet known in the same detail as food processing, but modelling of skeletal architecture has provided new physical constraints derived from the spatial arrangement of the elements (Purnell and Donoghue 1997). The comb-like elements at the anterior of the many conodont apparatuses may have been attached to a pair of cartilaginous dental plates, similar to those of extant agnathans. According to this hypothesis, these plates were pulled forwards and pivoted over the anterior edge of an underlying ventral cartilage, resulting in anterior and ventral motions which opened the apparatus. The reverse action brought about grasping by producing a net posterior and inward rotation of the elements (Purnell and Donoghue 1997).
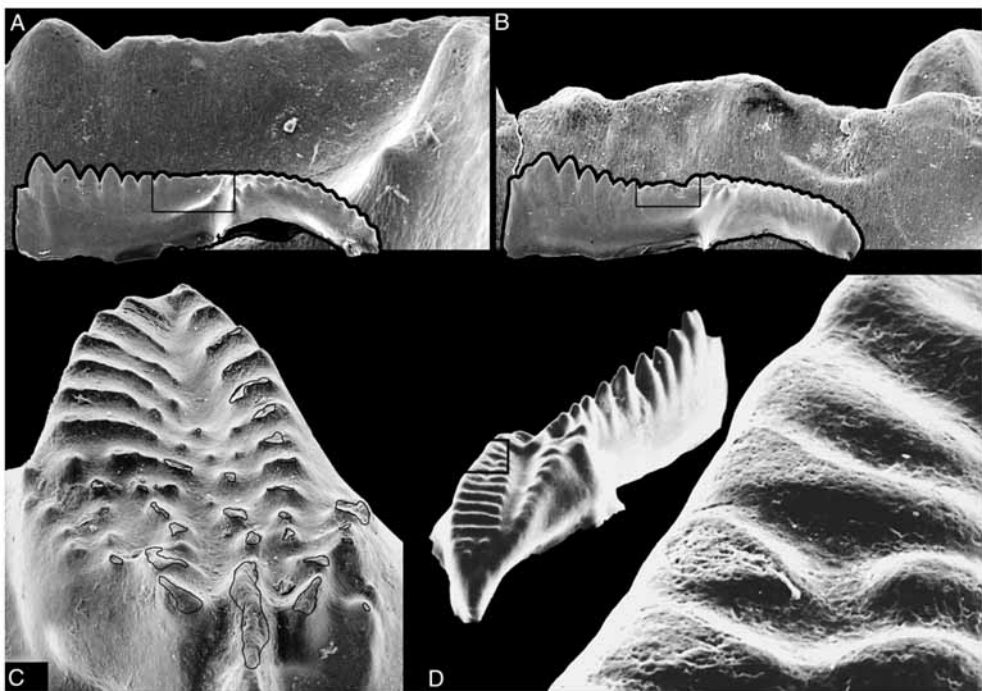
*Figure 12.6* Patterns of recurrent damage and surface wear in conodonts, all P$_1$ elements of *Idiognathodus*. (A) and (B) Recurrent damage on dorsal blades resulting from occlusion and use in feeding during life; (A) Repeated damage has reduced the denticulate area at the occlusal (dorsal) end of the blade to a flat ridge, surface damage is evident; specimen ROM 49779; whole element × 17, close-up × 178. (B) Occlusal (dorsal) end of the blade is reduced to an undulating ridge, surface damage is evident; specimen ROM 49780; whole element × 29, close-up × 178. (C) Oblique view of damage on an element platform resulting from contact with the opposed element during occlusion. This element was dissected from a partially articulated skeletal array (natural assemblage) and the surface damage cannot be the result of *post-mortem* abrasion; specimen BU 2683b, × 130. (D) The crests of the platform ridges in this element are blunted and flattened to form triangular wear facets with pitted microfeatures. Such features are not developed elsewhere on the element and are most unlikely to be *post mortem* artefacts; specimen ROM 50699, whole element ~× 35, close up ~× 378. (A,) (B) and (D) Royal Ontario Museum specimens from Upper Carboniferous, Elk County, Kansas, USA; (C) Birmingham University specimen from Upper Carboniferous, Bailey Falls, Illinois, USA. Modified from Donoghue and Purnell (1999a, b) and Purnell (1995); reproduced by permission of Geology (A and B), The Paleontological Society (C), and *Nature*, Copyright (1995) Macmillan Magazines Ltd. (D). Terms for orientation and conodont element notation follow Purnell *et al.* (2000). High resolution images are available on the www at http://www.le.ac.uk/geology/map2/conowear/

### 12.3.2.2  Feeding in heterostracans

Because of their well-developed exoskeletal 'armour', fossils preserving whole articulated heterostracans considerably outnumber those of conodonts. These articulated specimens have also been known and studied for a longer period of time, but this seems simply to have increased the range and variability of interpretations of how
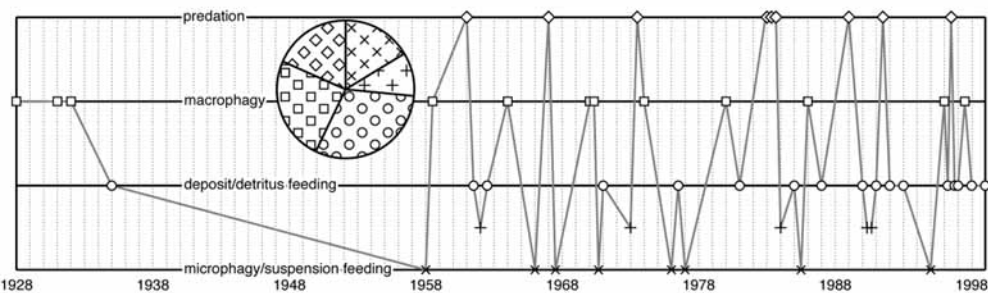
*Figure 12.7* Published hypotheses of feeding in heterostracans through time (from 1928 to 1999). Most of the data are specific hypotheses of feeding in heterostracans, but some are general hypotheses of feeding in 'ostracoderms'. Hypotheses of feeding in arandaspids are included (e.g., Elliott *et al.* 1991). Some categories, especially 'macrophagy' include a range of interpretations (see text for details). In years when more than one opinion or hypothesis concerning feeding was published, data points are placed in alphabetical order of authors. Points which lie between deposit/detritus feeding and microphagy/suspension feeding did not clearly distinguish between the two, or suggested that heterostracans fed by either or both methods (e.g., Heintz 1962; Soehn and Wilson 1990). The grey line connects successive interpretations and serves only as a crude indicator of the variability in interpretation, the absence of a trend through time, and the clear lack of consensus or trend towards consensus. The pie diagram indicates the relative 'popularity' of the alternative interpretations. Note that opinions concerning feeding in heterostracans are widely dispersed throughout the specialist and non-specialist literature and the database from which this plot is compiled (spanning 70 years and including 50 published hypotheses of feeding) will inevitably be somewhat incomplete.

they fed (see Figure 12.7). The evidence from conodonts, myxinoids and lampreys indicates that a bilaterally operating feeding apparatus is a synapomorphy of verte-brates (Janvier 1981; 1996a; Purnell and Donoghue 1997), but there is no evidence that any other extinct agnathans, including heterostracans, possessed such a feeding apparatus (cf. Mallatt 1997). Nevertheless, comparisons between the arrangement and function of the tooth plates of myxinoids and the oral plates of heterostracans (Figure 12.8) have been made several times (e.g. Stensiö 1932; 1958; 1964; Janvier 1974; Jarvik 1980), but as long ago as 1935 (p. 409) White dismissed this hypothe-sis as 'wholly fictitious' (see also Janvier 1981). The problem with interpreting feeding in heterostracans is similar to that encountered with conodonts: the oral structures lack homologues among extant vertebrates and hypotheses of function are generally poorly constrained and speculative because of an over-reliance on analogy.

Interpretations of heterostracan feeding can be assigned to three or four broad trophic categories (Figure 12.7). These form a continuum between suspension feeding and predation, embracing deposit or detritus feeding, and less specific hypotheses of macrophagy. As Figure 12.7 makes clear, there is not at present (and there seems never to have been) much agreement about how heterostracans (or other fossil agnathans) fed.

A detailed review is beyond the scope of this chapter, but many authorities have advocated suspension feeding as the primary trophic mode of heterostracans (e.g., Romer 1959; 1966; 1970; Mallatt 1985; Mark-Kurik 1995). Similarly, interpreta-
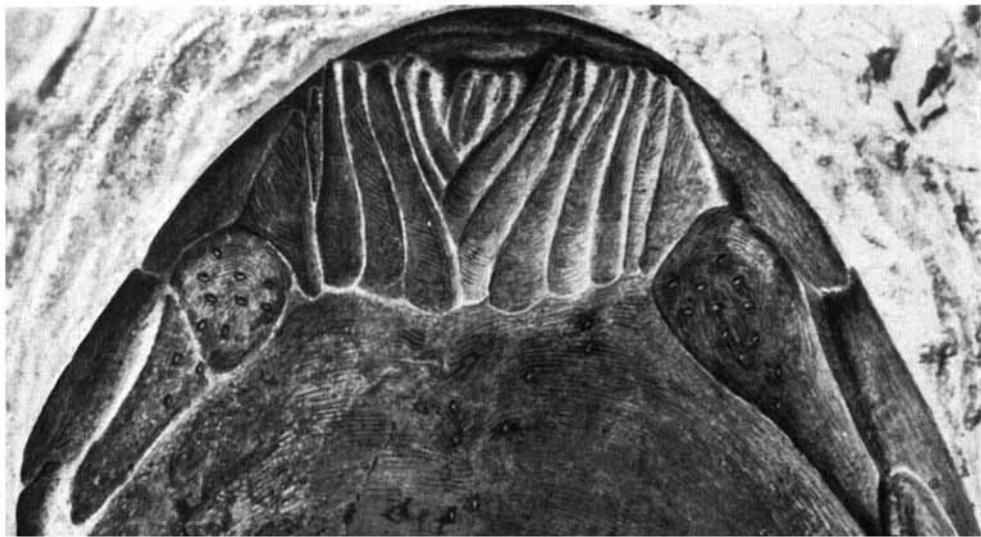
*Figure 12.8* The heterostracan *Protopteraspis* (ventral surface, rostral end) showing the oral plates; × 4.7. Modified from Kiaer (1928).

tions that they obtained their food by filtration of either water or sediment are common (e.g., Heinz 1962; Halstead 1973; Mallatt 1984). These views are based on the hypothesis that without jaws, heterostracans could not have done much else: 'The absence of jaws and teeth denied [heterostracans] a life of predation. Hence they were restricted to the pacific existence of microphagous feeders, sucking up microscopic organisms or ingesting sediment in order to extract the nutrients' (Halstead 1973, p. 279). The possibility that the oral plates may together have formed a scoop-like structure has influenced several advocates of such hypotheses. White (1935) was the first to suggest this, specifically linking the idea of an oral scoop with deposit feeding, but many subsequent authors have expressed similar opinions (e.g., Moy-Thomas and Miles 1971; Dineley and Loeffler 1976; Soehn and Wilson 1990). Opinions favouring macrophagy of some sort are also common, with oral plates interpreted as biting, crushing, grasping or shearing structures (e.g., Kiaer 1928; Stetson 1931) analogous to the upper and lower jaws of gnathostomes (Kiaer 1928), or as hagfish-like rasping 'teeth' (Stensiö 1932) or dorso-ventrally chewing teeth (Stensiö 1958; 1964). Similar views have also been voiced subsequently (Patten in Robertson 1970; Janvier 1974; Jarvik 1980), with several authors specifying scavenging macrophagy as the most probable mode of existence for heterostracans. The intriguing suggestion that cyathaspid heterostracans were herbivorous macrophages, with the adjacent oral plates shearing against one another to snip fragments from strands of algae (Bendix-Almgreen 1986) is supported by little more than comparisons between the body shape and trunk squamation of heterostracans and extant catfish.

Heterostracans may also have been predatory, selectively scooping or otherwise ingesting slow moving inactive prey (e.g., Denison 1961; Northcutt and Gans 1983; Gans 1989; Mallatt 1996). The possibility that suction played a significant role in

food acquisition has been suggested (e.g., Moy-Thomas and Miles 1971; Halstead 1973; Radinski 1987; Elliott *et al.* 1991), but the view that it has at any time represented the most widely held opinion (Robertson 1970) is not supported by the literature.

Unfortunately, evidence to support these hypotheses is scant, and some are contradicted by what is now known of the biology of agnathans. Suction feeding, for example, is difficult to reconcile with evidence that, without jaws, agnathans were unable to generate strong suction (Mallatt 1984; 1996). The functional constraint imposed by the lack of jaws seems to be the most frequently cited support for interpretations of non-predaceous modes of feeding such as suspension or deposit feeding (e.g., Romer 1959; 1966; 1970; Halstead 1973), but hagfish, certain lampreys and conodonts falsify the view that jaws are a prerequisite for macrophagy in vertebrates. That hagfish demonstrate the possibility of macrophagy without jaws was pointed out by Gans and Northcutt (1983), who also questioned the anatomical and ecological basis for interpretations of deposit feeding in early vertebrates. However, their preferred hypothesis, that fossil agnathans including heterostracans were predatory, is supported only by their conclusion that they had dismissed the alternative hypotheses.

As noted above, many interpretations of feeding in heterostracans focus on the reconstruction of the oral plates as a scoop-like structure with a role in either deposit feeding or macrophagy. Little detailed work has been done to reconstruct the three-dimensional geometry of the oral plates from their flattened arrangement in fossils, but a scoop-like arrangement seems quite plausible. In itself, however, this does little to constrain hypotheses of function. It is possible that such an oral structure was involved in ploughing or scooping sediment (e.g., White 1935; Soehn and Wilson 1990) or scavenging (e.g., Patten in Robertson 1970; Tarrant 1991) or predation (e.g., Denison 1961; Northcutt and Gans 1983; Tarrant 1991; Mallatt 1996), but it may also have served simply as a flexible cover to close the mouth of a suspension feeder. The view that the oral plates could not have functioned in strong dorsoventral biting or crushing is supported by the evidence that muscles could attach only on the posterior part of their inner surface (White 1935; Mallatt 1996). Janvier (1993; 1996b) has noted 'that the mouth of a hagfish, when retracted, displays ventral skin folds that match exactly the pattern of the oral plates in arandaspids and heterostracans' (1996b, p. 95). Taking this pattern as evidence that heterostracans and hagfish had similar feeding mechanisms is, however, somewhat speculative, and it is not at all clear how the oral plates could be protracted without either muscle or cartilage attachment to their ventral surface.

### 12.3.3.3 Feeding and scenarios of early vertebrate evolution

What, then, are the implications for scenarios of early vertebrate evolution? The evidence that conodont elements functioned as the teeth of a primitive macrophagous vertebrate supports hypotheses (Gans and Northcutt 1983; Northcutt and Gans 1983; Gans 1989) that the first vertebrates were predators (Purnell 1995). In the absence of convincing evidence for any of the alternative hypotheses of feeding in heterostracans, however, consensus remains elusive. Nevertheless the resolution of questions concerning how heterostracans fed has important implications for understanding early vertebrate evolution. With the present state of knowledge

regarding feeding it is not possible to test the hypothesis that extinctions in heterostracans were linked with competition from gnathostomes, and the same applies to other groups of extinct agnathans. Thus, hypotheses which link the evolutionary history of the early jawless vertebrates to changes in feeding mechanism or to competition from gnathostomes must, for the time being, be viewed as rather speculative. In terms of long-term trends and selective pressures, if the debate concerning heterostracan feeding is resolved in favour of non-predatory habits, this will effectively falsify the hypothesis that a long-term trend towards increasingly active and predatory habits in the stem gnathostomes was a significant selective pressure in early vertebrate evolution.

## 12.4 Conclusions

When constrained by phylogenetic hypotheses, evolutionary scenarios that incorporate interpretations of the functional attributes of extinct taxa are open to testing by independent investigation of the functional morphology of fossils. In the context of early vertebrate evolution, evidence from conodonts (Purnell 1995) supports the hypothesis that an ecological shift to predation occurred at the origin of vertebrates (Gans and Northcutt 1983; Northcutt and Gans 1983; Gans 1989). Data concerning feeding in other groups of fossil agnathans are currently inconclusive, but if the outcome of rigorous analysis demonstrates that any of the major clades of fossil agnathans were non-predatory, this may overturn hypotheses that early vertebrate evolution was, to a large extent, driven by a long-term trend towards increasing levels of activity and predation (Gans and Northcutt 1983; Northcutt and Gans 1983; Gans 1989; Mallatt 1996; 1997). Alternatively, this result could indicate that the evolutionary scenario is correct but that current hypotheses of vertebrate phylogeny are wrong. However, this would require a radical reinterpretation of relationships, some of which are robustly supported in recent analyses (e.g., Donoghue *et al.* 2000), and arguments of parsimony therefore suggest that this possibility is not likely.

Another consequence of the limited understanding and the lack of consensus regarding the functional morphology of fossil jawless vertebrates is that the possibility that correlated progression was a significant factor in early vertebrate evolution simply cannot be investigated at present.

Concerning broader hypotheses of early vertebrate diversity, the view that diversity patterns and the extinction of most clades of jawless fish reflect competition between agnathans and gnathostomes or between specific clades of jawless and jawed fish, although widely held, must be regarded as untested, and at present untestable, speculation. The available data for feeding habits, palaeogeographic distribution, and habitats are inadequate for this purpose, and the possibility that members of two contemporary clades were potential competitors can be neither confirmed nor refuted. Competitive interactions are just one of a number of possible explanations of the pattern of early vertebrate diversity.

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