

Feeding in extinct jawless heterostracan fishes and testing scenarios of early vertebrate evolution

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How long-extinct jawless fishes fed is poorly understood, yet interpretations of feeding are an important component of many hypotheses concerning the origin and early evolution of vertebrates. Heterostracans were the most diverse clade of armoured jawless vertebrates (stem gnathostomes), and the structure of the mouth and its use in feeding are the subjects of long-standing and heated controversy. I present here evidence that heterostracan feeding structures exhibit recurrent patterns of *in vivo* wear, are covered internally by microscopic oral denticles, and that the mouth may have been less flexible than has been thought. These data, particularly the absence of wear at the tips of oral plates, and the evidence that the mouth was lined with delicate outwardly directed denticles, effectively falsify all but one hypothesis of feeding in heterostracans: heterostracans were microphagous suspension feeders. This has a direct bearing on hypotheses that address ecological aspects of early vertebrate diversity and evolution, contradicting the widespread view that the pattern of early vertebrate evolution reflects a long-term trend towards increasingly active and predatory habits.

Keywords: agnathan; filter-feeding; predation; pteraspid; trophic ecology

1. EARLY VERTEBRATE EVOLUTION: FROM MEEK FILTER FEEDER TO FEARSOME PREDATOR?

Today, jawless fishes constitute a minuscule proportion of vertebrate diversity, yet for more than 140 million years they were the dominant form of vertebrate life. Fossils from this interval preserve a diverse range of unfamiliar and sometimes bizarre-looking 'fishes' (figure 1), most of which were covered by external armour plating of dentine and bone. However, by the end of the Devonian Period (355 Myr ago) all these armoured jawless vertebrates were extinct, and aquatic environments were dominated, as now, by vertebrates with jaws (gnathostomes). The only direct evidence for these major transitions in chordate evolution—the diversification of early vertebrates, the origin of jawed vertebrates and the subsequent demise of jawless fishes—comes from the fossil record of these stem group gnathostomes.

Some of the most widely cited and provocative hypotheses concerning the early evolution of vertebrates have combined fossil data with evidence from comparative anatomy, and developmental biology, to construct complex evolutionary narratives or scenarios (Gans & Northcutt 1983; Northcutt & Gans 1983; Gans 1989; Mallatt 1996, 1997; Northcutt 1996). One of these scenarios, the 'new head hypothesis' (Gans & Northcutt 1983; Northcutt & Gans 1983; Gans 1989), linked 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 modifications in development involved in early vertebrate evolution were linked to shifts in feeding, and the sequential acquisition of vertebrate characters was correlated with a long-term ecological trend, from suspension feeding in a lancelet-like prevertebrate, towards increasingly active and predatory habits. Some aspects of the new head hypothesis have been re-evaluated or rejected in the light of subsequent work (Northcutt 1996), but the hypothesis is still considered to be among the most important contributions

to the questions of vertebrate origins (Zimmer 2000). More recently, Mallatt (1996, 1997) proposed a 'new mouth' scenario to explain the acquisition of jaws and the origin of gnathostomes. This hypothesis linked the evolution of the grasping jaws to adaptations for improved ventilation (Mallatt 1996, 1997), suggesting that the evolution of gnathostomes was driven by selection for increasing activity and predacity.

This view, that the evolution of chordates reflects a long-term trend towards increasing activity, is extremely widespread; 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). Similarly, most hypotheses concerning the Devonian extinction of armoured jawless vertebrates interpret their demise as the result of replacement by competitively superior gnathostomes. Feeding and competition for food is of particular relevance 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 & McPhail 1992). Thus, hypotheses that the pattern of early vertebrate diversity reflects competition must assume some knowledge of how jawless fishes fed (see Purnell (2001) for a review).

Interpretations of feeding may feature in many hypotheses of early vertebrate evolution, but ecological explanations of evolutionary events, and evolutionary scenarios in general, are not without their critics (e.g. Peterson 1994; Gee 2000). In the context of early vertebrates Janvier (1996), for example, warns that 'One step further removed from reality, we enter ... the realm of evolutionary processes and life history' and dismisses ecological interpretations as 'often amusing, sometimes plausible, but generally untestable'. Other authors have gone so far as to suggest that analysis of function in extinct organisms is not science and has no value except, possibly, as enter-

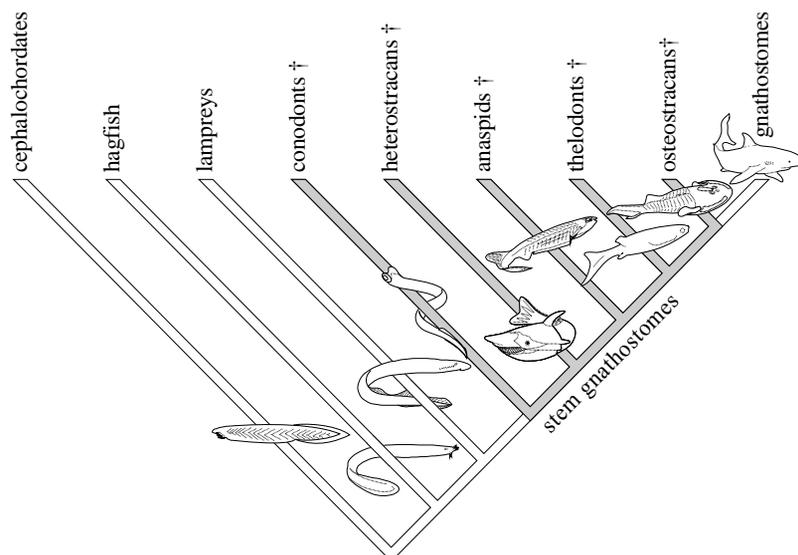


Figure 1. Diversity and relationships of jawless vertebrates and gnathostomes. Crosses indicate extinct clades. The paraphyletic group of extinct jawless vertebrates traditionally referred to as fossil agnathans (heterostracans, anaspids, thelodonts, and osteostracans together with conodonts (here used to refer to euconodonts)) 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. Most of the agnathan groups shown are considered to be subclasses (Halstead 1993); all, with the exception of the thelodonts (Janvier 1996; contra (Turner 1991)), are generally thought to be monophyletic. The cladogram is simplified from that of Donoghue *et al.* (2000). In their analysis, thelodonts were represented by *Loganellia*, heterostracans formed a clade with *Astraspis* and arandaspids, and osteostracans formed a clade with pituriaspis and galeaspids.

tainment (Gee 2000). However, the evolutionary scenarios outlined above make specific interpretations of how early vertebrates fed and invoke trends that are potentially testable using fossil data. I would contend that scientific analysis of function in fossils *is* possible and that analysis of feeding in early vertebrates provides a test of the ecological hypotheses that are an integral component of early vertebrate evolutionary scenarios.

2. THE HETEROSTRACAN MOUTH AND HYPOTHESES OF FEEDING

Heterostracans are the most diverse group of armoured jawless vertebrates and interpretations of how they fed are explicit in both the 'new head' and the 'new mouth' scenarios. Both scenarios interpret heterostracans as predatory, selectively scooping or otherwise ingesting slow-moving inactive prey (Northcutt & Gans 1983; Gans 1989; Mallatt 1996, 1997; Northcutt 1996). However, this view belies the fact that the structure of the heterostracan mouth and how it was used in feeding are the subject of long-standing and heated controversy (Janvier & Blicek 1993), with a range of alternative hypotheses of feeding that includes predation, suspension feeding, deposit feeding, scavenging and macrophagous herbivory (see Purnell (2001) for a review). In fact, there is no sign of consensus regarding feeding in heterostracans (Purnell 2001), primarily because evidence with which to test the alternative hypotheses has not been forthcoming.

(a) *Feeding, oral plates and wear patterns*

Hypotheses of feeding in heterostracans focus on the oral plates making up the lower margin of the mouth

(figure 2). These plates lack homologues among extant organisms but are generally interpreted as forming a scoop-like structure which, according to hypotheses of deposit feeding (e.g. Soehn & Wilson 1990) or macrophagy (e.g. Northcutt & Gans 1983), either ploughed through sediment, or picked up relatively large food particles or prey. Wear patterns on the oral plates provide a means of testing these hypotheses as either mode of feeding would result in wear on the anterior tips of the oral plates where they impinged on the sediment, the food or the upper margin of the mouth. White (1961) noted that the tips of well-preserved oral plates from the Devonian of the Welsh Borders seem to show no sign of wear, but he took this simply to indicate that they did not bite against an upper set of plates. I have re-examined these oral plates using scanning electron microscopy and this confirms that there is no evidence of wear on their tips resulting from their use *in vivo*. However, in all the specimens examined an area of wear occurs towards the posterior half of the plate on the ridged outer (ventral) surface (figure 2*c,d*). The position of this wear, on the ventral surface of the plate, and not along the edges, indicates that it is not post-mortem in origin. This pattern of wear, and that known to occur on the ventral shield of pteraspid and other heterostracans, supports interpretations that these organisms were nekto-benthic in habit, but it cannot be reconciled with the oral plates functioning as a sediment scoop. Further support comes from examination of the oral plates in articulated specimens of *Athenaegis chattertoni* Soehn and Wilson, a primitive heterostracan from the Northwest Territories of Canada (Soehn & Wilson 1990). These bear only a few indistinct scratches and this, again, is difficult to reconcile with a scoop-like function in deposit feeding.

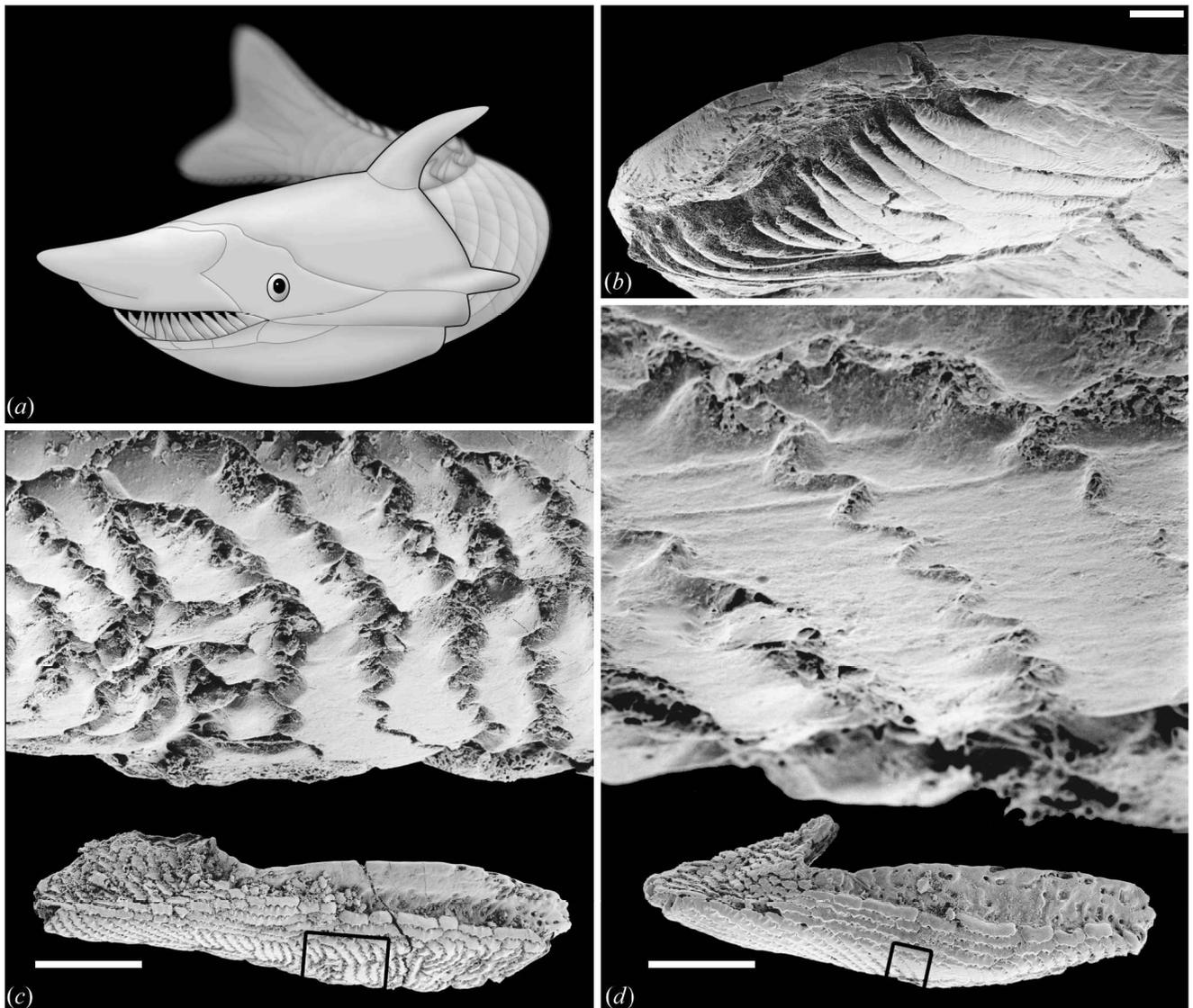


Figure 2. Oral plates of heterostracans. (a) Oblique anterior view of a pteraspid heterostracan showing the configuration of the oral plates forming the lower margin of the mouth. The illustration is based on a reconstruction of *Errivaspis waynensis* Blicek. (b) Oblique anterior view of the mouth of *Protopteraspis vogti* preserving oral plates *in situ*. The image is a montage of scanning electron micrographs of an epoxy replica of specimen A28720/2 (Paleontologisk Museum, Oslo; Devonian, Ben Nevis Formation, Spitzbergen). (c) Oblique view of isolated oral plate of *Loricopteraspis dairydinglensis* (White), specimen NHM P43713. (d) Oblique view of isolated oral plate of *L. dairydinglensis*, specimen NHM P43711. Both (c) and (d) show typical patterns of wear developed on the ventral surface of oral plates (anterior to left). The enlarged views of the areas outlined by the boxes show worn dentine ridges and parallel scratches (NHM P43711 and NHM P43713, Lower Devonian, Ditton Group, Dairy Dingle, near Neenton, Shropshire, UK). Scale bars, 1 mm.

More significantly, detailed examination of the plates surrounding the mouth in a range of heterostracans reveals new details of their surface structure that have broad implications for heterostracan anatomy, hypotheses of feeding and oral function, and models of skeletal evolution and the origins of teeth.

(b) *Feeding and oral denticles in heterostracans*

Characteristic ridges of dentine cover the exoskeleton of heterostracans, but examination by scanning electron microscopy reveals that on the inner and lateral surfaces of oral plates, and the inner surface of the ascending lamella (the structure which may form the upper margin of the mouth, but see Janvier & Blicek (1993) and Janvier (1996) for discussion), these ridges break up into a series of generally triangular or maple-leaf-shaped sharply

pointed denticles. Figure 3a–c illustrates oral denticles in *Loricopteraspis* Halstead, *Protopteraspis* Leriche and *Rhinopteraspis* Jaekel. These rather delicate microscopic features can be observed only in well-preserved material, but a survey of the literature and material in various collections suggests that they may be widespread among heterostracans. For example, as noted by Watson (1954), the ascending lamella of *Anglaspis* Jaekel is covered with small pointed denticles. Similarly, sections through the ascending lamella of *Poraspis* Kiaer (Kiaer & Heintz 1935, Pl. XXXVIII) show finely pointed structures that compare closely with those in sections through the ascending lamella and oral plates of *Protopteraspis vogti* (Kiaer) (Kiaer 1928); these structures are here revealed to be sharp, maple-leaf-shaped denticles (figure 3b). Significantly, *Loricopteraspis*, *Protopteraspis* and *Rhinopteraspis* are assigned

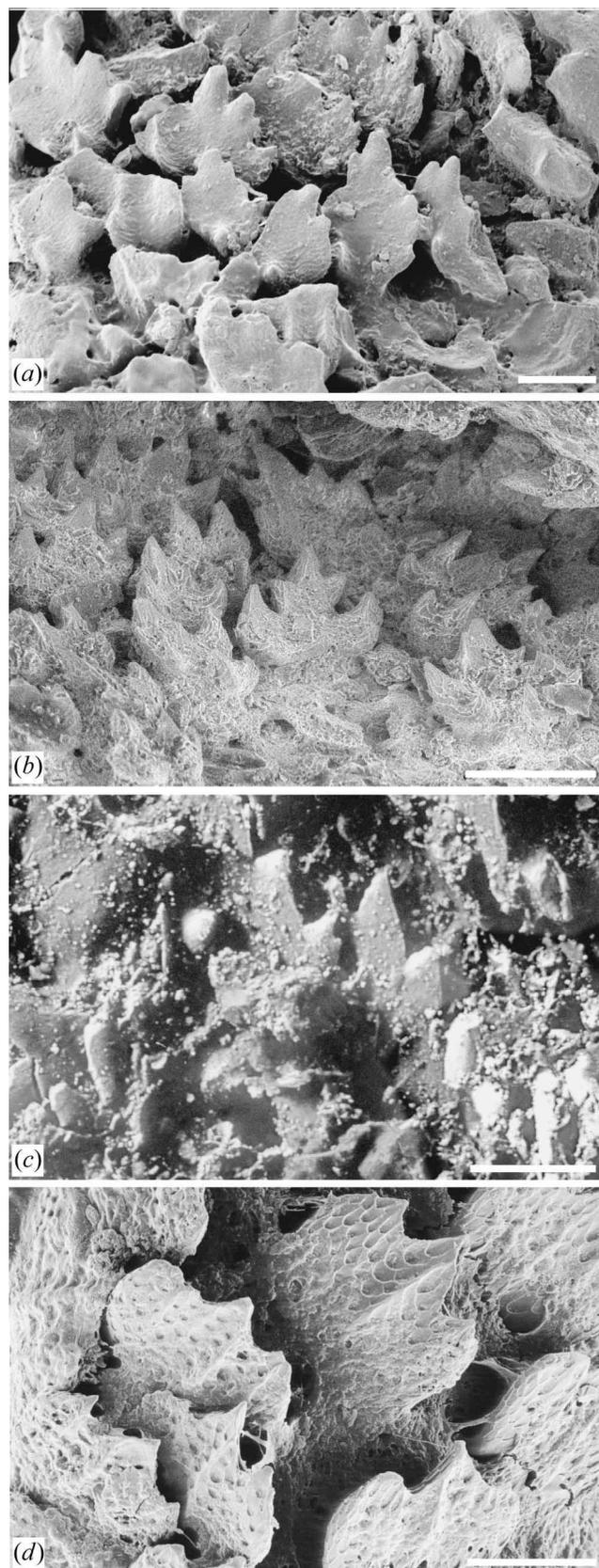


Figure 3. Outwardly directed oral denticles in heterostracans, and nasal denticles in a shark. (a) Oral plate of *Loricopteraspis dairydinglensis*, inner surface (specimen NHM P43710; Lower Devonian, Ditton Group, Dairy Dingle, near Neenton, Shropshire, UK). (b) Oral plate of *Protopteraspis vogti*, lateral surface (specimen A28720/1, Paleontologisk Museum, Oslo; Devonian, Ben Nevis Formation, Spitzbergen). (c) Ascending lamella of

to Pteraspidoformes whereas *Anglaspis* and *Poraspis* are assigned to Cyathaspidoformes. These two groups represent major clades that diverged fairly early in heterostracan evolution and together comprise the bulk of heterostracans (Janvier 1996); the presence of oral denticles in both these groups thus indicates a broad taxonomic distribution among heterostracans and is consistent with a hypothesis that the possession of oral denticles is plesiomorphic for the clade. The location and the consistent outward orientation of these denticles, including those on the inner and lateral faces of the oral plates and those on the ascending lamella, suggest that they are not a non-adaptive feature arising as a passive consequence of developmental, skeletogenic processes.

The functional significance of the denticles derives from the fact that their tips are consistently directed outwards, so that the entrance to the heterostracan mouth would have been lined with imbricate rows of anteriorly directed barbs. Although small, the size of the barbs is significant in relation to the oral plates and the mouth, and they would have prevented grasping, biting or any other form of macrophagy because contact between the barbs and large food particles would have prevented the food from moving into the mouth. Furthermore, biting and deposit feeding would have quickly resulted in breakage and loss of barbs. The barbs also falsify the hypothesis that heterostracans could have possessed a hagfish-like lingual feeding apparatus (Janvier 1996) as, being directed outwards, they would have prevented its retraction into the mouth. It is also worth noting that acid preparation of well-preserved material from Spitzbergen (Paleontologisk Museum, Oslo, specimens A28720/1 and A28720/2) provides new evidence that some of the oral plates became fused together during life, suggesting that the lower margin of the mouth may not have opened widely in a broad fan-like manner, as has been thought (M. A. Purnell, unpublished observation, cf. Janvier 1993, 1996).

So what was the function of the oral barbs in heterostracans? Unfortunately, this remains uncertain. They are strikingly similar in size and shape to oral denticles of some shark species (e.g. Reif 1985), and examination of the incurrent opening of the nasal passage in *Galeorhinus galeus* reveals that it too is lined with small denticles. These denticles are morphologically distinct from those that cover the body and are directed outwards, against the flow of water (figure 3d). Frustratingly, the function of such denticles in sharks, and similar denticles developed in actinopterygians, is not known (Nelson 1970; Patterson 1977; Raschi & Tabit 1992).

What is significant here, however, is not that we cannot be sure of the function of outwardly directed oral barbs in heterostracans, but that, when taken together with the wear patterns and fusion between plates, the barbs provide evidence that effectively falsifies all but one hypothesis of feeding in heterostracans: heterostracans were microphagous suspension feeders.

Rhinopteraspis crouchi (Lankester) (specimen NHM P19141; Lower Devonian, Ditton Group, Kilpeck, Herefordshire, UK). (d) Denticles lining inhalant nasal passage of *Galeorhinus galeus* (Linnaeus) (specimen LEIUG 121482, University of Leicester Department of Geology; Recent, Leicester Market, UK). Scale bars, 100 μ m.

(c) Oral denticles, teeth and nostrils

As noted above, the discovery of oral barbs in heterostracans may also have significance for understanding the evolution of the vertebrate skeleton and the origins of teeth. This arises from the recent hypothesis (Smith & Coates 1998, 2000) that the developmental controls for producing phosphatic skin denticles and oropharyngeal denticles diverged very early in vertebrate evolution, and that oral denticles and skin denticles are, in terms of their development, quite distinct. The barbs on the inner surfaces of the oral plates and the ascending lamella of heterostracans seem to fulfil several of Smith and Coates's criteria for recognizing oropharyngeal denticles in that the orientation of their cusps and gradients in denticle shape exhibit clear anterior–posterior polarity. If they are oral denticles (*sensu* Smith & Coates 1998, 2000), then heterostracans represent the most primitive group in which oral denticles have been found, but they raise a significant problem in that they intergrade with the ridges making up the external ornament. These ridges are homologous with skin denticles, and this intergradation does not support the hypothesis that oral denticles and skin denticles are developmentally distinct. If, on the other hand, these structures in heterostracans are not true oral denticles, but are simply elements of the dermal skeleton that have migrated into the oropharyngeal cavity, then the same may be true of the comparable internal denticles in thelodonts (as traditional views of vertebrate skeletal evolution would contend). If so, the internal denticles of thelodonts provide only equivocal support for an early divergence between oropharyngeal and dermal denticles.

The similarity between the anteriorly directed denticles of heterostracans and those of thelodonts also has interesting anatomical implications. By analogy with galeaspid (another group of extinct jawless fishes), the anteriorly directed denticles in the rostral region of thelodonts were used as evidence to infer the presence of a large terminal inhalant duct, separate from the mouth (Van der Bruggen & Janvier 1993; Janvier 1996). The presence of a similar structure has also been inferred in heterostracans (Janvier 1996), but this is controversial. The barbs on the oral plates of heterostracans, which were unequivocally part of the mouth, indicate that anteriorly facing denticles in the rostral area of jawless vertebrates cannot, in themselves, be taken as evidence of a separate terminal inhalant duct.

3. CONCLUSIONS

The evidence presented here indicates that heterostracans were microphagous. This has broad implications for various hypotheses and scenarios concerning the early evolution of vertebrates. In terms of the ecology of early vertebrate evolution, these results and analyses of feeding in conodonts (Purnell 1995) confirm the recent hypothesis that in vertebrates, as in other major metazoan clades, predation and microphagous suspension feeding are plesiomorphic relative to herbivory (Vermeij & Lindberg 2000) but suggest that predation is plesiomorphic relative to suspension feeding. Specifically, the evidence from extant jawless vertebrates and conodonts supports the hypothesis that the most primitive vertebrates were predatory and that a shift to predation occurred at the origin of the clade

(Gans & Northcutt 1983; Northcutt & Gans 1983; Gans 1989; Purnell 1995), but the heterostracans, a more derived group (figure 1), were not predatory. The implications of this are clear: the evidence from the fossils fails to support the hypothesis that early vertebrate evolution and the origin of jaws reflect a long-term ecological trend towards increasingly active and predatory habits.

For access to material, loans, discussion and reviews, the author thanks Dick Aldridge, Phil Donoghue, Dave Elliott, Peter Forey, Philippe Janvier, Franz-Josef Lindemann, Jon Mallatt, Giles Miller, Mark Wilson, Sally Young, and anonymous reviewers. Funded by Natural Environment Research Council Advanced Research Fellowship GT5/98/4/ES.

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