Functional morphology of the amphipod mandible

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While several features of the amphipod body are used both to classify and estimate phylogenetic relationships of species, little is understood of the functional significance of most of these features. The amphipod mandible consists of a compact coxa bearing a toothed incisor orientated to cut in the transverse plane of the body, a row of lifting spines leading dorsally to a molar designed for crushing. The basic pattern is retained in those groups where microphagy is important. Modifications include reduction of the incisor, loss of the lifting spines, reduction or loss of the molar, or all of these. In several families the mandible is maintained unmodified; in others most genera possess mandibles of the basic pattern but one or two modifications can be seen in a small number of genera. In a few families the basic form is retained in only one or two genera, while several different modifications are seen in the majority of the others. Finally, several families have lost all vestige of the basic mandible pattern. In this latter group, however, the number of modifications is low. Most mandible modifications occur in response to predation and/or scavenging as a feeding strategy, although two independent pathways to this end are seen. In the first the reductions occur on a compact coxa, and seem designed for feeding on small prey, while in the second the mandible body (coxa) becomes elongate and the orientation of the incisor changes such that cutting is now in the vertical frontal plane of the animal's body. It is concluded that families with exclusively predatory/scavenging mandibles cannot be considered to be plesiomorphous.

KEYWORDS: Amphipoda, mandibles, functional morphology, phylogeny.

Introduction

> The significance of convergencies of arthropodan structure, whereby animals of different ancestries come to resemble one another, some in surprising detail, can often be understood on a functional and evolutionary basis (Manton 1977, p. 35).

Amphipod classification is based largely on the form of the mouthparts, gnathopods, coxal plates, and details of the urosome. For most of these features, as well as other aspects of the morphology of amphipods, little is understood about the functional significance of the range of sizes and shapes that these features can take. Additionally, the impact of an evolutionary change in one structure on other structures nearby or at some distance along the body has been intimated only recently (Watling, 1992).

There is a scattering of work detailing the functional importance (if any) of selected morphological features of the amphipod body. For example, Vader (1983a) examined the occurrence and function of prehensile pereopods. While they could be found in 14 amphipod families, in all cases prehensile pereopods seemed to be an

adaptation for clinging, and were present in species that were either pelagic predators or were associates of large Crustacea. In the latter case the development of prehensile pereopods appeared to be an adaptation to prevent dislodgement while the host was grooming itself. Thus, there is probably little phylogenetic significance to the possession of prehensile pereopods, the possibility being that this feature has arisen many times as congeneric species have developed biological associations.

Moore (1983), similarly, examined the shape and posterior ornamentation of the third epimeral plates. Medium-sized tubicolous or infaunal species tended to possess rounded, unadorned epimeral plates, whilst in large or small active epifaunal or free-swimming species these plates were acute or quadrate, and distally excavate. Here too, the shape of this feature could be directly related to the lifestyle of the species, suggesting that its phylogenetic importance would have to be examined carefully.

Oostegite morphology has been mentioned as a feature that might bear phyloge-netic information. Steele (1990, 1991) compared the shapes of oostegites from various amphipod families and investigated their relationship to aspects of the species' repro-ductive biology. In general, two main types of oostegites have been observed: broad with short marginal setae and narrow with long marginal setae. He found that amphipods with broad oostegites tended to carry smaller eggs than those with narrow oostegites. Very few amphipod families examined by Steele possessed both types of oostegites; however, he noted that oostegite shape did not seem to correlate with any other obvious morphological feature; he therefore concluded that oostegite shape was determined by reproductive strategy after the evolution of the major amphipod groups.

It is clear that, if one is to understand the phylogeny of a group such as the Amphipoda, it is necessary to determine for each morphological feature of interest whether the characters exhibited are adaptations to present living conditions or convey historical (phylogenetic) information. To do this it is necessary to understand fully the mechanism of operation and structural limitations of the feature. In my view, amphipod mandibles have been greatly misinterpreted in this regard. It is the purpose of the present paper to begin an examination of the functional morphology of the mandible with a view to understanding its relationship to the food sources used and determining how information about the mandible can be used for phylogenetic studies.

Basic form and function of the mandible

Fundamental aspects of the structure and function of crustacean mandibles have been described in detail by Manton (1977). For malacostracans the basic mandible is of the dual-purpose type and serves both for cutting and grinding (crushing) food. Mandibular motion is about an axis of swing defined by a hinge line, the orientation of which determines the plane in which the bite occurs.

The basic amphipod mandible (Watling, 1983; Watling and Thurston, 1989) (Fig. 1; see also fig. 17 of Steele and Steele, 1993) consists of the *mandible body* (coxa), which is generally compact and bears: the *incisor*, which is a toothed distal projection of the mandible body oriented such that it cuts in the horizontal transverse plane of the body and in a plane perpendicular to the long axis of the mandible; the *molar*, a columnar structure, projecting mediad from the mandible body such that it meets its companion in a rolling, crushing action during extreme mandibular remotor motion; the *lifting spines*, also referred to as the *seta row*, or 'raker setae' (the origin of the last term is unknown), comprising a row of strong, upwardly curved, coarsely serrate setae which probably function to prevent food particles obtained from the biting action of the incisors from falling away from the molars; the *lacinia mobilis*, an

Group I

Leptocheirus hisrsutimanus (Bate)

Group II

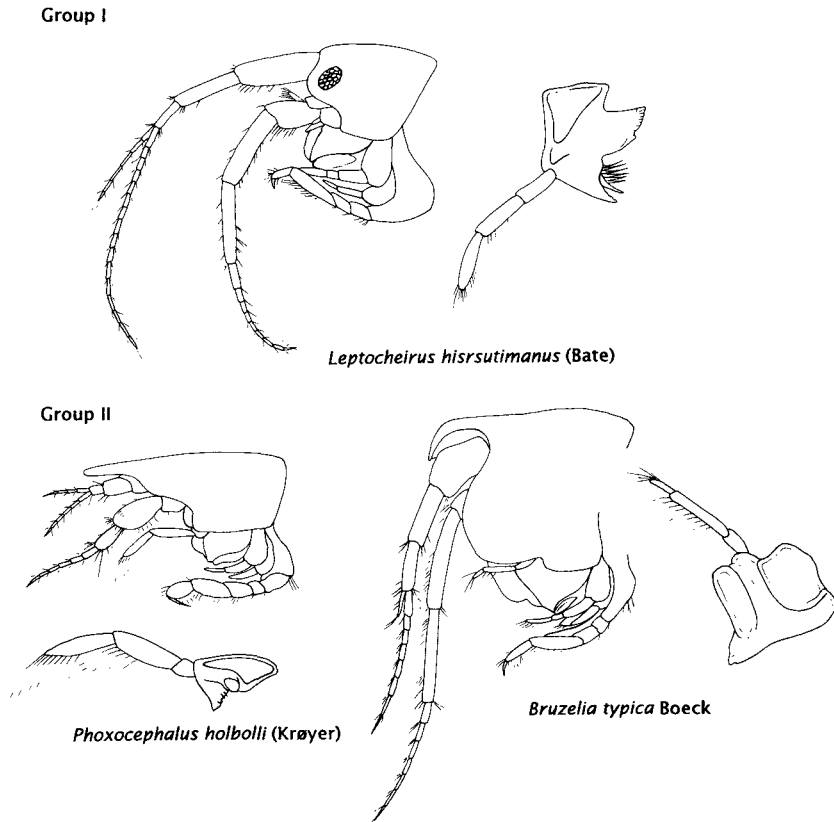*Phoxocephalus holbolli* (Krøyer)

Bruzelia typica Boeck

FIG. 1. Mandible and lateral views of the head of typical members of families with mandible types in groups I and II.

articulated, broad, flat, often toothed plate, designed to interdigitate with its companion, most likely to keep the mandible from twisting badly out of alignment during biting; and a *palp* of three articles which projects anterodorsally in front of the head and between the antennae. The mandible is attached to the outside of the head by an articular membrane which defines the *hinge line*. Movement about the hinge is effected by adductor and abductor muscles attached to *apodemes* arising from the interior dorsal surface of the mandible body.

The motion of the basic amphipod mandible is much as described by Manton for isopods (1977, fig. 3.5). In *Ligia* the dorsal end of the mandible hinge line has gradually moved posteriorly from its position in the more primitive syncarid, *Anaspides*, such that the hinge has come to lie horizontally on the side of the head. As a result, the promotor–remotor (forward–backward) motion generated by the abductor–adductor muscles now occurs in the transverse plane of the body. On abduction, the coxa of the mandible swings outward, the incisors part, and the molars open slightly ventrally but probably remain in slight contact dorsally. As adduction occurs, the molars increasingly come together ventrally until the material between them is thoroughly crushed by the interdigitating ridges, and the incisors gradually close on another piece of the food item. The form, and very likely the function, of the mandible as seen in the amphipod genus *Gammarus* is almost identical to that seen in *Ligia*. Since this mandibular design is so easily derivable from that of *Anaspides*, one

assumes that it, or something very close to it, must be the ancestral pattern for amphipods.

Modifications to the basic mandible

A wide range of modifications to this basic mandible plan can be seen. For the most part these involve changing the shape, generally through elongation, of the mandible body, changing the width, thickness, dentition and orientation of the incisor, reduction of the molar, and reduction (to complete loss ultimately) of the seta row. Most of the modifications discussed below represent a 'best-guess' interpretation of details from published taxonomic descriptions. Mandibles generally are not drawn in a form readily usable for a survey such as the present one. However, interpretations are based on the extensive survey of iphimediid mandible types conducted by Watling and Thurston (1989), wherein most mandibles were examined using preserved specimens. It should be noted, parenthetically, that early amphipod systematists, especially Stebbing (1888), Sars (1890–95), and Stephensen (1925) drew the mandible in relation to the head so that the orientation of the hinge and incisor can be seen for several families. In modern literature the mandible is removed from the head, put on a slide with coverslip, and drawn at whatever orientation to which it has settled.

The degree to which the mandible is modified differs among amphipod families. In Table 1 some of the larger families are arranged into four groups: I, where the basic form is maintained with only minor modifications in all genera; II, where most genera possess the basic mandible, but one or two have modified mandibles; III, where the basic design is retained in only one or two genera, but several different modifications are seen in the others; and IV, where the basic form can no longer be seen in any of the constituent genera.

In group I modifications of the basic mandible design are minor and include changes in the size and shape of palp articles, the number of lifting spines, and the strength of the lacinia mobilis on one of the mandibles (e.g. *Leptocheirus hirsutimanus* in Fig. 1). Species in group I families are primarily generalist microphage feeders whose food source is either organic particles in sediment, e.g. *Corophium* (Meadows and Read, 1966), *Corophium* and *Lembos* (Shillaker and Moore, 1987), or microalgal epiphytes, e.g. *Hyale* and *Paracalliope* (McGrouther, 1983), *Eogammarus* (Pomeroy and Levings, 1980). In these cases the incisor is used, usually in concert with the tips of maxilla 1 endites, to remove or capture 'clumps' of particles which are crushed when passed between the molars. Some instances of predation or scavenging have been documented in concert with microphagy, for example, in *Paraceradocus* (Coleman, 1989a; Klages and Gutt, 1990a), whilst *Eusirus perdentatus* may be exclusively a predator on polychaetes and small crustaceans (Klages and Gutt, 1990b).

Most genera in group II retain the basic mandible design for herbivorous or microphagous feeding. All modifications to the mandible body (i.e. incisor, lifting spines, and molar) are associated with changes in food source. Alterations in the palp seem unrelated to other mandibular changes, possibly because the palp often is used for grooming the antennal basal articles (Lincoln, 1979), though Nicolaisen and Kanneworff (1969) observed *Bathyporeia* spp. using the palp to manoeuvre sand grains toward the incisors. The functional relationship of the palp to the mandible body, however, is not well studied. In the Ampithoidae, two genera have lost the palp and in one of these the molar is also absent. The latter genus, *Amphitholina*, burrows into the stipes of kelp and, judging by the degree of reduction of the other mouth appendages, once there may feed on mucus and associated organic particles. The

Table 1.   Number of mandible types in selected amphipod families. Number of genera as listed for family by Barnard and Karaman (1991) unless otherwise noted.

Family	No. of mandible types		No. of genera
	Basic	Modified	
Group I			
Ampeliscidae	+	–	4
Corophioidea	+	–	102
Eusiridae	+	–	64
'Gammaridae'	+	–	50†
Ischyroceridae	+	–	9
Podoceridae	+	–	9
Group II			
Ampithoidae	+	2	12
Haustoriidae	+	1	8
Phoxocephalidae	+	2	68
Pleustidae	+	1	14
Synopiidae	+	2	15
Group III			
Iphimediidae†	+	10	30
Lysianassidae	+	6	152
Oedicerotidae	+	5	31
Dexaminidae	+	3	17
Group IV			
Eophliantidae	–	1	7
Hyalidae	–	1	6
Liljeborgiidae	–	1	5
Amphilochidae	–	3	11
Paradaliscidae	–	3	17
Phliantidae	–	2	7
Stegocephalidae	–	2	19
Stenothoidae	–	2	31
Stilipedidae	–	2	6

† After Barnard and Karaman (1991) by including the Paramphithoidae but not the Ochlesidae, but not Coleman and Barnard (1991), wherein the Iphimediidae is divided again into six families (no judgement is passed here on that revision).

modification of the haustoriid mandible has resulted in the reduction and/or loss of the incisor and lacinia in some genera. These reductions seem to be associated with the development of a predominantly filter-feeding habit in which only unattached micro-algal cells or interstitial meiofauna were ingested (Ivester and Coull, 1975). The opposite pattern is seen in the Phoxocephalidae (*Phoxocephalus holbolli*; Fig. 1) where the incisor remains toothed and a lacinia is present, but the lifting spines are reduced to a few, robust setae and the molar is a flabelliferous lobe capped with two to four setae, or is completely lost. Phoxocephalids are known to be active predators on meiofauna, but will also ingest detritus and small sediment grains (Oliver *et al.*, 1982; Oakden, 1984). Likewise, the only modification of the mandible in the Pleustidae involves a reduction of the molar, possibly also associated with a softer food source. In the Synopiidae at least one genus has lost the palp, but the other modification noted involves an enlargement of the molar (e.g. *Bruzelia typica*; Fig. 1), reflecting a change in function from crushing to a large, fuzzy (probably heavily microsetose), and likely

non-crushing structure along with a concomitant loss of lifting spines. The food source for this family is unknown.

The group III families are characterized by having one or a few genera possessing the basic mandible design, and the remaining genera showing a wide range of modifications. Since the range of modifications in this group is extensive, each family will be detailed separately.

Iphimediidae

Ten different apomorphic states of the mandible were detailed in a phylogenetic examination of this family by Watling and Thurston (1989) (although in that paper the iphimediids and paramphithoids were considered to be separate families; here they will be combined as suggested by Barnard and Karaman, 1991). Some of these were variants of a smaller set of fundamental design changes. In the first case (e.g. *Paramphithoe*, *Odius*), the mandibular body is compact to elongate, the incisor narrow, and the crushing molar, lifting spines, and palp retained. The reduction of the molar characterizes a second design (e.g. *Acanthonotozomella*), with subsequent loss of lifting spines representing another major change (e.g. *Nodotergum*). All other modifications follow from a fundamental change in the orientation of the incisor, from cutting in the horizontal transverse plane to cutting in the vertical frontal plane. The transitional state, with an oblique cutting plane, is seen in the genus *Anchiphimedia*. The now vertical incisor can be thick, and used for crushing in place of the molar which is absent (e.g. *Gnathiphimedia*, *Echiniphimedia*), or thin and either short or long and probably used for cutting in a scissors-like fashion (e.g. *Iphimedia*, *Acanthonotozoma*; Fig. 2). The molar in this last case may be absent but more often is a small fleshy lobe. The feeding habits of iphimediids have remained a mystery for some time, but some information is now available. *Paramphithoe hystrix* (Ross) has been found to be a micropredator on a sponge (Oshel and Steele, 1985), while members of the genus *Epimeria* may be either ambush predators (Klages and Gutt, 1990a) or grazers on colonial invertebrates (Coleman, 1990a). *Anchiphimedia dorsalis* K. H. Barnard, which has the mandible incisor orientated obliquely, was found to have only sediment detritus in its gut (Coleman, 1991). All the forms with vertically orientated incisors, however, were found to be predators, for example, on bryozoans (*Gnathiphimedia mandibularis* K. H. Barnard (Coleman, 1989b; Klages and Gutt, 1990a)), sponges (*Echiniphimedia hodgsoni* (Walker) (Coleman, 1989c)), and cnidarians, both antho-zoan and hydrozoan (*Maxilliphimedia longipes* (Walker) (Coleman, 1989c)). Many of the genera bearing apomorphic mandibles are found routinely in association with colonial animals, suggesting that the change in orientation of the mandible provided the means for exploiting this food resource.

Oedicerotidae

In this family five mandible designs can be seen. In the least modified case the molar is low and rounded, but the mandible is otherwise unchanged (e.g. *Oediceros*, *Paroediceros*). A further reduction of the molar to a small, subconical process with apical setae is seen in *Perioculodes* and *Synchelidium* (Fig. 2). The last modification along this line involves a weakening of the incisor (e.g. *Sinoediceros*). Retention of a strong molar with a reduction in lifting spines and thickening of the incisor is seen in *Westwoodilla* and *Bathymedon*, whilst *Machaironyx* shows a weakening of the incisor and loss of palp. In all cases it appears that the orientation of the incisor is unchanged. Little is known of feeding habits in this family, so the significance of these

Group III

Tmetonyx cicada (O. Fabricius)

Synchelidium haplocheles (Grube)
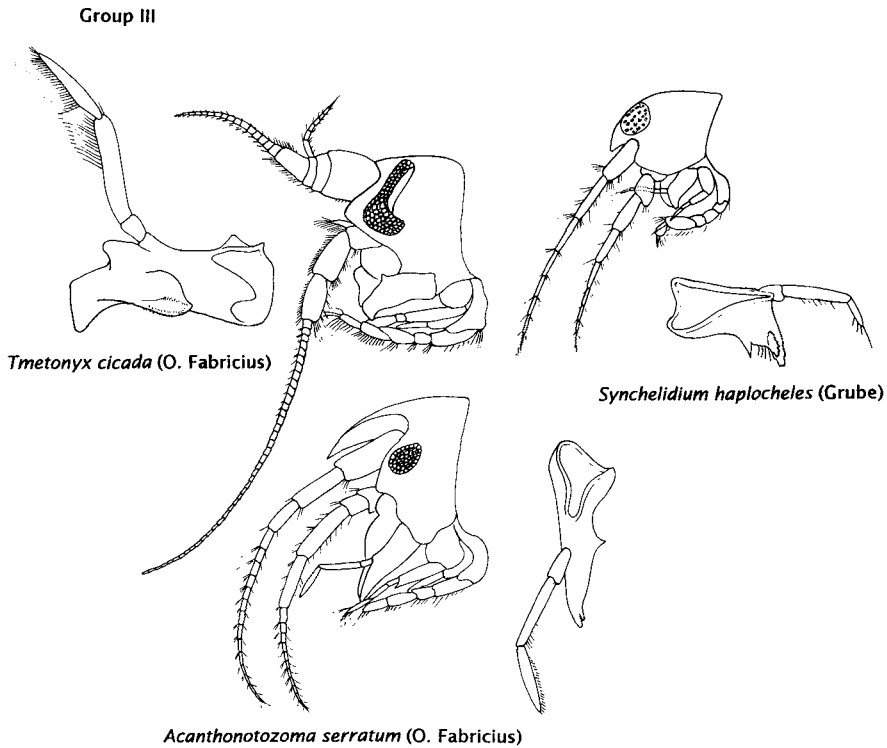
Acanthonotozoma serratum (O. Fabricius)

FIG. 2.   Mandible and lateral view of the head of typical members of families with mandible type in group III.

modifications is hard to judge. Enequist (1949) observed several species, with widely varying mandible designs, all of which readily buried themselves in the loose sediment of the aquaria in which they were kept, but he could not determine whether detritus particles or meiofaunal organisms, such as Foraminifera, were being fed upon.

Lysianassidae

This family is second only to the Iphimediidae in the changes that have been made to the form of the mandible. The first modification retains most of the basic features but the lifting spines are mostly lost (e.g. *Hippomedon*) and the orientation of the incisor now cuts obliquely, rather than in the horizontal transverse plane. The next change involves elongating the mandible body, reducing the molar to a flabelliferous process, and elongating the palp as seen in *Lepidepecreum*. From a phylogenetic point of view it seems that the major advance in this family is the shifting of the incisor process ever more forward, with the consequence that the incisor comes to cut in the vertical frontal plane just below the epistome and reduced upper lip. The incisor is conspicuously widened, with few teeth, being adapted for shearing-off large pieces of tissue (see figs 3 and 5 in Steele and Steele, 1993). The molar in this group is of varying size, flabelliferous or heavily setose (e.g. *Orchomene*; Oleröd, 1975) and the palp is normal (e.g. *Normanion, Opisa, Socarnes, Anonyx, Tmetonyx*; Fig. 2). The next change involves the loss of the molar altogether, as in *Acidostoma*. In *Trischizostoma* the mandible is the same as the previous design except that the incisor process is elongate vertically, creating a scissors-like motion and cutting with small

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Group IV

Idunella aequicornis (Sars)

Gitanopsis arctica Sars

Stenothoe megacheir (Boeck)

Stegocephalus inflatus Krøyer
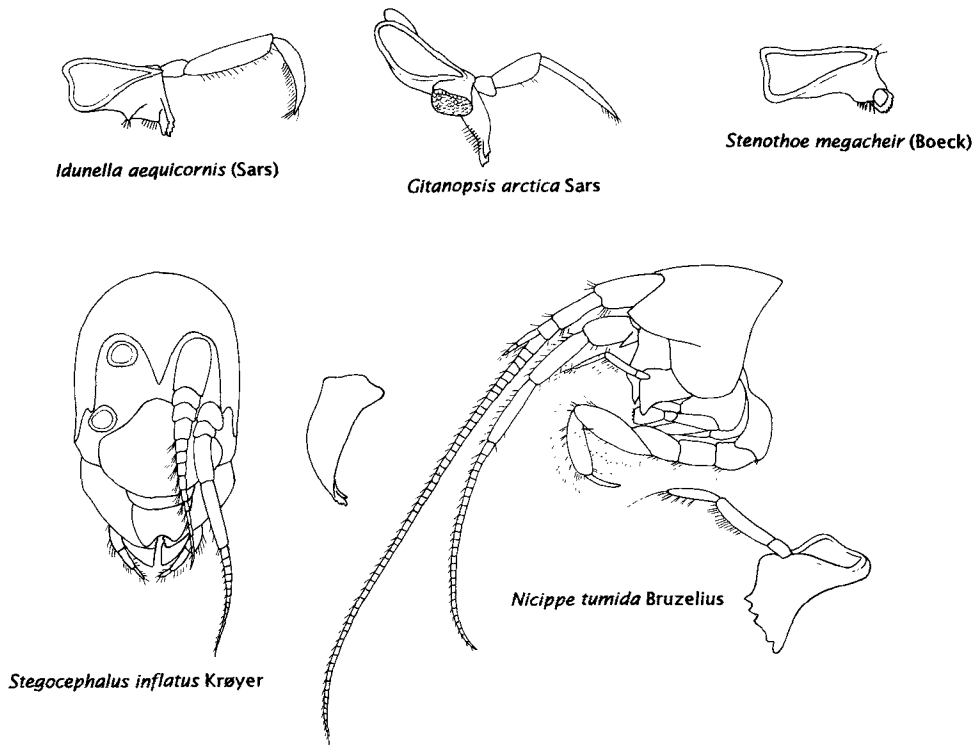
Nicippe tumida Bruzelius

FIG. 3.   Mandibles and lateral and enface views of the head of typical members of families with mandible of type IV.

vertical edges, much as is seen in some Iphimediidae. A highly aberrant pattern exhibited by *Kerguelenia* involves the complete loss of the incisor and molar processes, but retains the palp in its normal form. It is likely that several other mandibular types exist in this family, but a thorough investigation will have to wait the results of J. K. Lowry's forthcoming revision. Lysianassids appear to be broadly classifiable as meat-eaters, some being primarily predaceous but most are scavengers (Sainte-Marie, 1984; Sainte-Marie and Lamarche, 1985; Slattery and Oliver, 1986; J. K. Lowry, personal communication), though for some of the more specialized forms the specific nature of the food resource remains to be determined.

Dexaminidae

The simplest modification of the basic mandible type involves the loss of the lifting spines and the palp (e.g. *Dexamine*, *Tritaeta*). *Lepechellinoides* retains a small group of lifting spines on the left mandible, and has a large, non-crushing molar and a uniarticulate palp. The other common design has the mandibular body compact, the incisor reduced but vertical, lifting spines absent, molar fleshy and non-crushing, and palp absent (e.g. *Haustoriopsis*, *Guernea*, *Prophlias*).

The group IV families (Fig. 3) all have advanced beyond the basic mandible, but for the most part there are only a few designs in each family. In the Eophliantidae the

mandible body is compact, the molar is reduced to a nub or is absent, the incisor cuts in the horizontal transverse plane, a lacinia is present, the lifting spines are reduced or absent, and the palp uniarticulate or absent. All eophliantid mandibles are slight variations on this pattern. The Hyalidae mandible is of the basic pattern but without a palp. A single modification of the basic form occurs also in the Liljeborgiidae. Here the mandible body is compact, the incisor weak, but toothed, lifting spines are present, the molar is reduced to a nub with apical setae, and the palp is slender but of normal length. At least three types of mandible can be seen in the Amphilochidae. For the most part the mandible body is elongate and the incisor cuts in the horizontal transverse plane. The molar can be either columnar (e.g. *Gitana*), elongate and styliform (e.g. *Paramphilochoides*), or obsolescent (e.g. *Amphilochus*). Lifting spines are always present and the palp is of the normal three articles. In the Stenothoidae all mandible types are variations on the compact basic design. In *Cressa*, for example, the incisor is widened, toothed, with a large lacinia, lifting spines are present, the molar is a low nub, and the palp is normal. A second type involves loss of the molar and a reduction of the palp, e.g. *Metopa*, *Proboloides*, and the third type the subsequent complete loss of the palp, e.g. *Stenothoe* and several other genera. Little is known about the feeding habits of these families, although Vader (1983b) has suggested that stenothoids living on sea anemones may be consuming mucus and trapped debris.

In three group IV families the mandible is extensively modified, with the incisor vertical and cutting in the frontal plane. In the Pardaliscidae the mandible body extends slightly forward, lifting spines and molar are absent, and a normal palp is present. In some genera the mandibles are symmetrical, whereas in others they may be asymmetrical, with the left incisor being weaker than the right. In *Rhynohalicella* the fundamental structure is similar but the palp has been lost. The mandible body extends below the head in the Stegocephalidae (see, for example, Moore and Rainbow, 1992, fig. 3). Here the incisor may be of varying dimension but is always oriented vertically, lifting spines and molar are absent, the lacinia is present as a fixed guiding tooth, and the palp is absent. One type has the incisor appearing as a transitional form, being toothed along a relatively narrow tip, whereas in the other it is a broad flat blade. The mandible of the Stilipedidae is very much like that of the Stegocephalidae, but in one form the molar is present as a low lobe. Only a little is known about the feeding habits of any member of these families. Moore and Rainbow (1989) noted in laboratory culture that the stegocephalid, *Parandania boecki* (Stebbing), fed on the bell of a medusa, and Moore and Rainbow (1992) suggested that *Andaniexis abyssi* (Boeck) fed on benthic prey and *Andaniopsis nordlandica* (Boeck) was a specialist predator of cnidarians. Coleman (1990b) discovered that *Bathypanoploea schellenbergi* Holman and Watling (a stilipedid) eats holothurian body wall tissue, perhaps as a parasite.

Perhaps the most modified of the group IV families is the Phliantidae. In this family the mouthparts lie well posteriorly on the head, the mandible incisor has a few teeth, lifting spines are reduced to two or three, the molar is either absent or is replaced by a setose spike, and the palp is absent. Further reductions in the mandible and all mouthparts are seen in other small families. For example, in the Nihotungidae the mandible is reduced to a stylet-like structure with no lifting spines or molar and a slender non-setose palp.

Functional patterns and phylogenetic inferences

There seems to be strong evidence that the form of the mandible has become altered, and perhaps even should be considered as having become more specialized, as
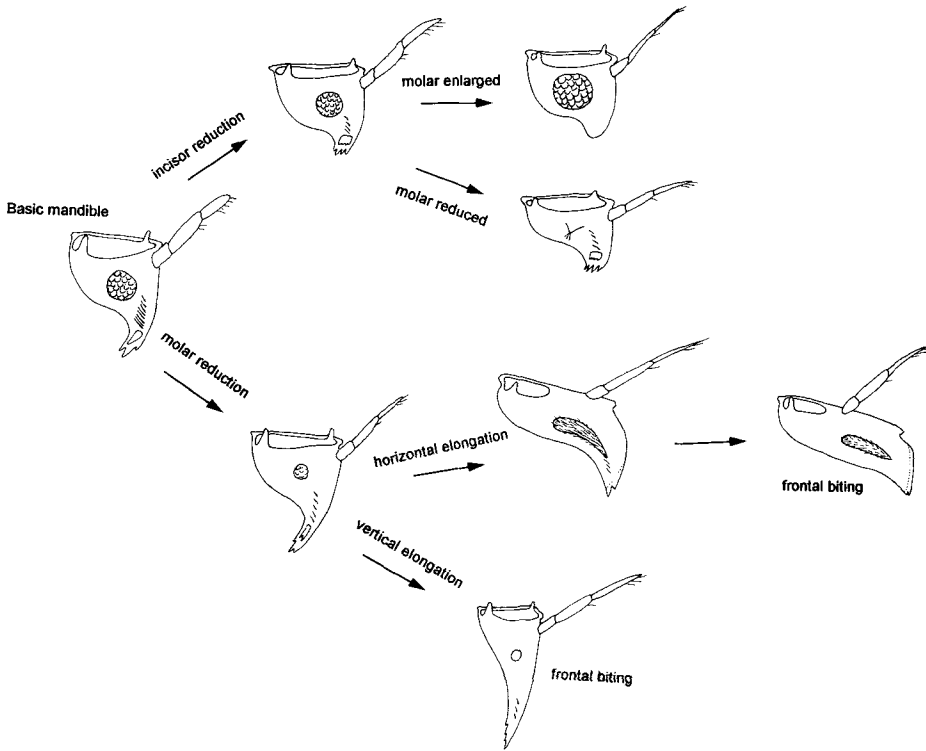
FIG. 4. Postulated pattern of modification of the basic mandible. Two independent pathways are proposed leading to carnivory; one involving shortening of the incisor process with subsequent reduction of the molar, and the other a lengthening of the incisor process before molar loss. In the latter path the incisor is lengthened either ventrally or anteriorly, but in both cases the cutting edge is in the vertical frontal plane.

new food resources have been exploited. Also evident is the likelihood that these design changes may have occurred more than once, but certain types are probably derivable only from particular precursors. Mandibles of the basic form are used predominantly for microphagy, but some instances of predation are known. Most, if not all, modifications are associated with the invasion of specialized habitats or for predation. Nearly complete reduction or loss of mandibles is seen only in those groups that have become adapted to a commensal existence.

The following hypothesis regarding the evolutionary changes in mandible form is, therefore, proposed. The initial modification of the basic pattern may involve either the reduction of the incisor or elongation of the mandible body (Fig. 4). When the incisor is reduced the mandible body remains compact and the molar becomes much enlarged, retaining its crushing function (e.g. some haustoriids and oedicerotids), or becomes reduced to a small lobe armed with one or two short, stiff setae (e.g. some oedicerotids and phoxocephalids). In a few, rare, cases the reduced incisor may change orientation such that whatever cutting function remains is completed in the vertical frontal plane (e.g. prophliantids). A greater degree of morphological change and functional capability is seen when the molar loses its crushing capability concomitant with an elongation of the mandible body. Two major patterns are seen. In one instance the elongation of the mandible body results in a stretching of the, by now, flabelliferous

molar followed by a gradual movement of the incisor anteriorly until it is cutting in the vertical frontal plane (e.g. lysianassids). In the other case the molar fades to a small nub, the mandible body becomes elongate below the head, and the incisor gradually comes to cut in the vertical frontal plane, but below, rather than in front of, the head (e.g. iphimediids).

There are therefore two independent and unrelated types of modifications associated with predation. The first involves reduction of the molar on a compact mandible body. This type is seen, for example, in the phoxocephalids and oedicerotids, and seems to be related to predation on infaunal macrofauna and meiofauna. In these two families there is a notable correspondence of the body bearing fossorial appendages designed for rapid burrowing into sediment with the mandible designed for predation on small infaunal organisms. The second predaceous mandible type is more elaborate and widespread. It involves elongation of the mandible body, gradual change in orientation of the incisor, and is seen, for example, in the iphimediids, lysianassids, stegocephalids, and stilipedids. Such mandibles are used either for taking large bites from large prey, scavenging, or for snipping off parts of colonial or large solitary epifaunal organisms. Many members of these families are excellent swimmers and spend much of their time in the water column. One can conclude, then, that because of the great degree of modification involved in the form of exclusively predatory mandibles, such as is seen in the stegocephalids, pardaliscids, or stilipedids, families bearing this mandible type cannot be considered to be the most plesiomorphic of amphipods.

This examination of mandible form and function is necessarily somewhat cursory. It is hoped that this study will stimulate a more thorough examination of feeding habits in some of the amphipod families that exhibit unusual mandible morphologies. Also critically needed are studies involving detailed views of the mandible and associated mouthparts by scanning electron microscopy, so that some of the statements regarding incisor orientation made above can be verified. Finally, it is hoped that when mandibles are described in taxonomic works an attempt will be made to represent these structures in all their three-dimensional complexity.

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