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### Biting mechanism of the amphipod *Anonyx* (Crustacea: Amphipoda: Lysianassoidea)

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## **Biting mechanism of the amphipod *Anonyx* (Crustacea: Amphipoda: Lysianassoidea)**

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*Anonyx* amphipods feed extensively on dead or weakened animals, often of large size. They cut off strips of food using the wide incisor processes of their mandibles like a pair of shears. The mandibles and associated mouthparts are specialized for this shearing action. The strips of food are coiled and packed into their proventriculi.

KEYWORDS: Amphipoda, Lysianassoidea, *Anonyx*, biting mechanism, functional morphology.

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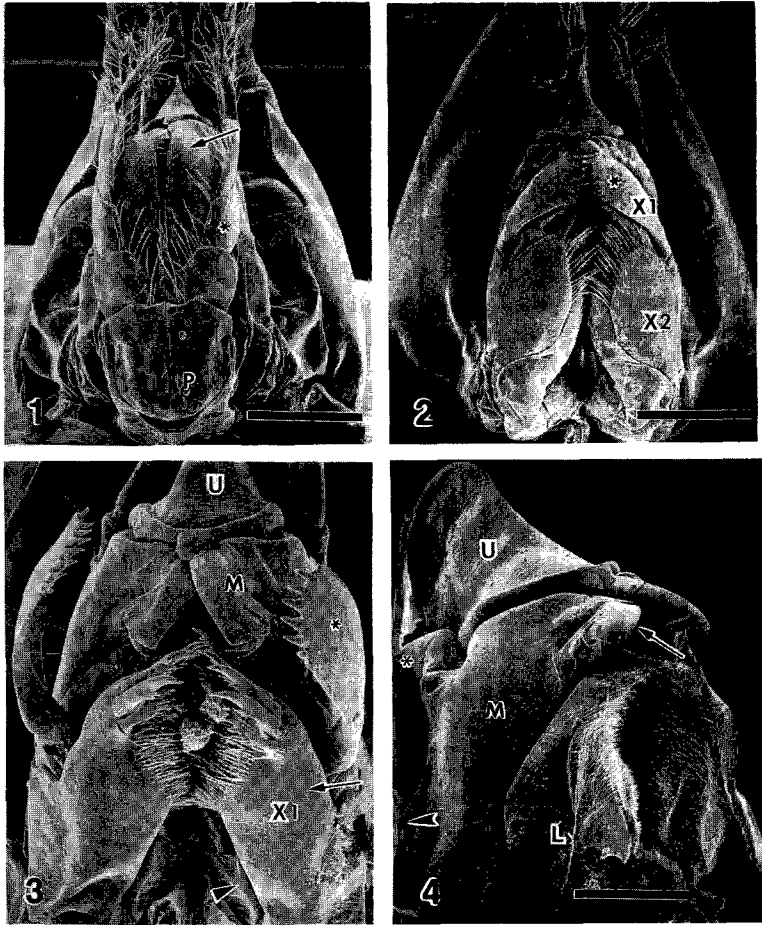
### **Introduction**

Forty-four species of the genus *Anonyx* have been described from northern seas. They feed on dead and weakened animals of all kinds (Sainte-Marie and Lamarche, 1985) and their ability to clean the flesh from a large carcass is legendary (Parry, 1824). They can be caught in large numbers in baited traps. The present study considers the biting mechanism of *Anonyx*, with particular reference to the functional morphology of the mandible.

### **Methods**

The detailed structure and orientation of the mouthparts were determined by scanning electron microscopy. *Anonyx lilljeborgi*, *A. makarovi* and *A. nugax* specimens were collected in baited traps by R. Hooper and placed whole in Karnovsky's glutaraldehyde–paraformaldehyde fixative containing 0.2 M cacodylate buffer, pH 7.4. After fixing for  $\geq 24$  h and six buffer rinses, the animals were postfixed in 2% buffered osmium tetroxide for 6 h, rinsed in six buffer changes, dehydrated in an ethanol series, and critical-point-dried in liquid carbon dioxide. Dried specimens were attached to aluminium stubs with silver paste (SPI), gold-coated in an Edwards S150A sputter coater, and viewed with a Hitachi S570 scanning electron microscope operated at an accelerating voltage of 20 kV. *Gammarellus angulosus*, used for comparison, were collected at Logy Bay, Newfoundland and treated in the same manner. *Gammaracanthus loricatus* from the Arctic had been preserved in 7% formalin before treatment.

Specimens of *Anonyx* preserved in 7% formalin and cleared in 3N KOH were also dissected, and their mouthparts manipulated to observe their plane of action. The shapes and sizes of ingested food particles were determined by dissecting the



FIGS 1–4. *Anonyx lilljeborgi*: 1, ventral view of mouthparts with thoracopods 2 and 3 (peraeopods 1 and 2) removed. Maxilliped (thoracopod 1) (P) with its anteriorly directed palp (\*) and large lateral plates (arrow); 2, ventral view of the mouthparts with the maxilliped removed. Maxilla 2 (X2) and maxilla 1 (X1) with its palp (\*) extend anteriorly; 3, ventral view of the mouthparts with maxilla 2 removed and with the palps (\*) of maxilla 1 (X1) displaced. Inner lobe of maxilla (arrowhead) with its medially directed pappose setae are visible. Upper lip (U) and open mandibles (M) are anterior; 4, ventrolateral view of the mouthparts with maxilla removed. Upper lip (U), mandible (M), lower lip (L), mandibular pulp (\*), incisor process (arrow) and the horizontal hinge line of the mandible (arrowhead). Scale bars ( $\mu\text{m}$ ): 1, 550; 2, 480; 3 and 4, 270.

proventriculus of *Anonyx nugax* caught in traps baited with squid mantle. The contents of the stomach were teased apart and the width and length of the particles measured with an eyepiece micrometer.

## Results

The mouthparts of *Anonyx* are concealed by the anterior coxal plates and covered ventrally by thoracopods 2 and 3 (peraeopods 1 and 2). With these parts removed, the maxillipeds (thoracopod 1) can be observed extending forward, and their lateral plates

cover the other mouthparts ventrally (Fig. 1). The coxal segments of the maxillipeds are completely fused, whereas the bases meet in the midline but are not fused in *Anonyx* at any point (Fig. 1).

With the maxillipeds removed, the maxillae are visible (Fig. 2). The palps of the first maxillae, with their apical blunt spine-teeth extend towards each other and cover the cutting edge of the mandibles. Anterior to the mandibles, the helmet-shaped upper lip forms the lower margin of the head.

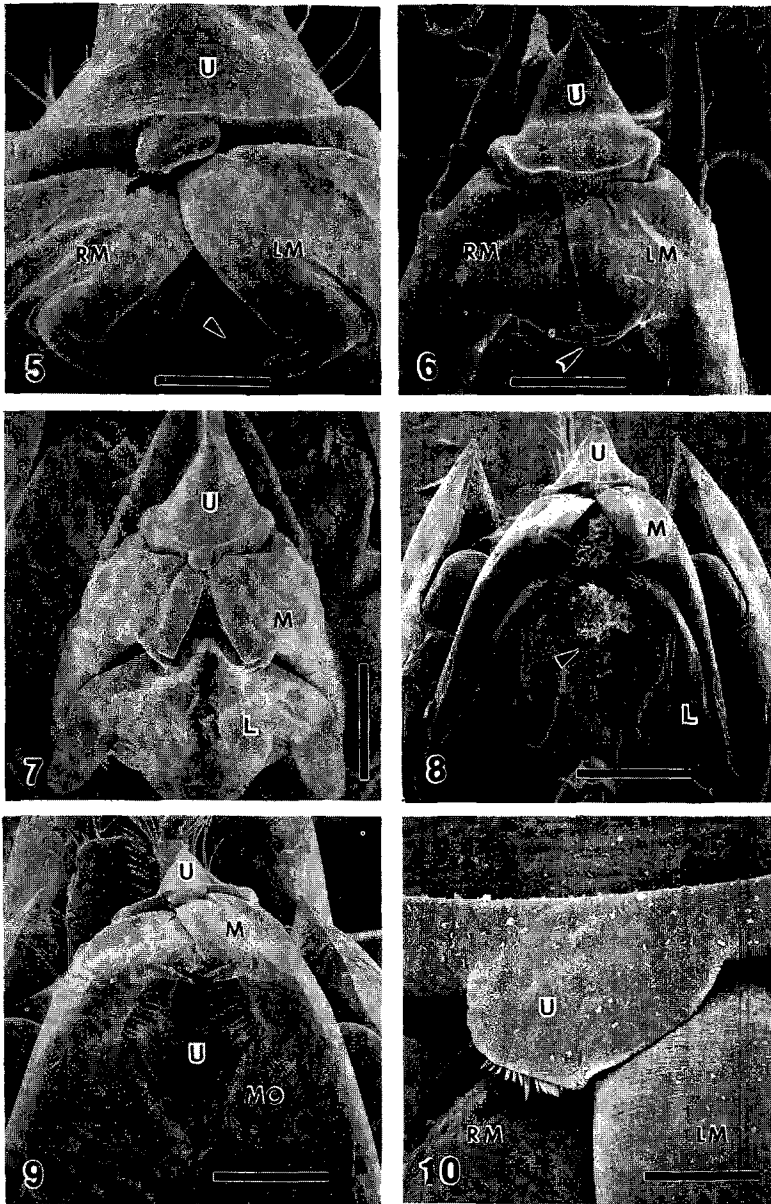
After removal of the second maxillae and the palps of the first maxillae, the lateral plates of the first maxillae are visible (Fig. 3). The apical, spinulate setae of the opposing lateral plates mesh together in the midline. Above the plates, the lower lip is visible.

With removal of the first maxillae, the densely setose, flat, lower lip can be seen forming the posterior margin of the oral cavity (Figs 4 and 5). The mouth, or stomodeum, which opens ventrally, is at the anterior end of the mouthparts. The mandible fits precisely between the lower and upper lips. The mandibular palp extends anteriorly on either side of the upper lip and epistome (Fig. 4). The hinge line is transverse and located towards the posterior end of the mandible, with the cutting edge (incisor process) directed anteriorly (Fig. 4).

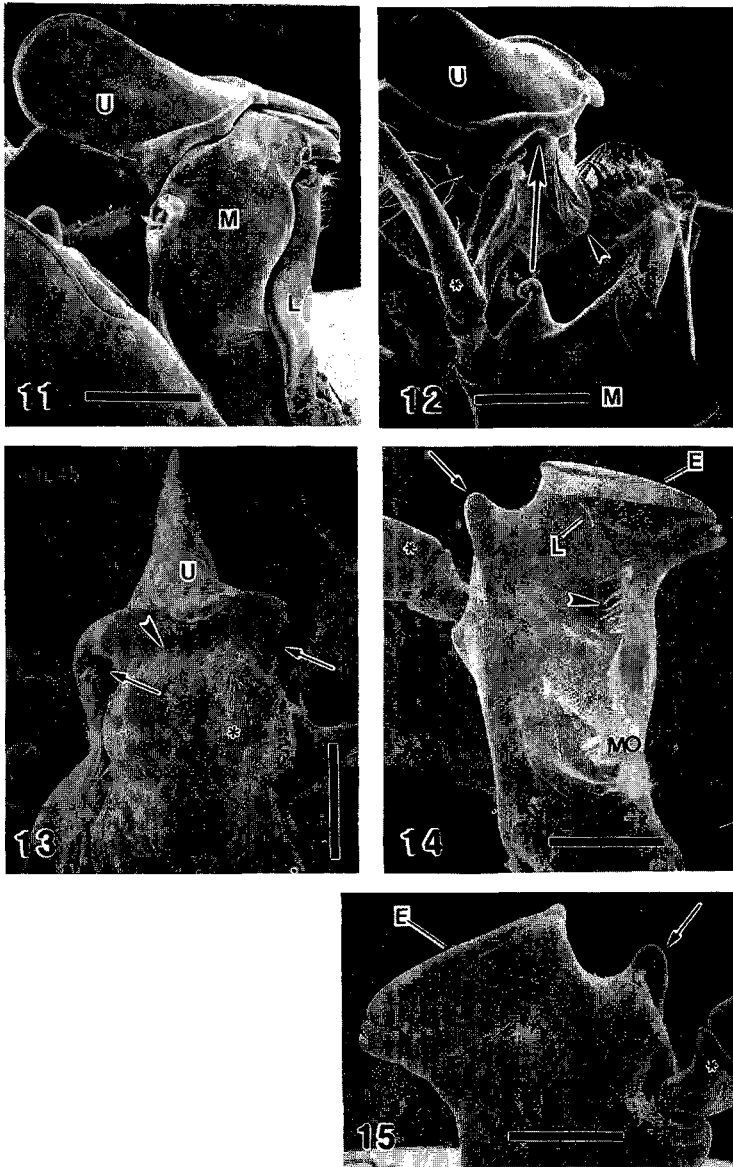
The cutting edges of the mandible are widened, with the left overlapping the right (Figs 5–7 and 10). When closed, the single tooth on the left mandible fits between the two teeth of the right (Fig. 6). A lacinia mobilis is found only on the left mandible and is reduced to an untoothed peg (Fig. 14). The outlines of the upper lip, mandible and lower lip fit precisely together (Figs 5 and 11), and the free space between the mandibles is limited.

The mouthparts of *Anonyx* are formed and arranged so that pieces of food can be cut off using a shearing action (Figs 7 and 8). Setae have been reduced in number (outer plate of the maxilliped, inner plate of maxilla 1) and size (palp of maxilla 2) or modified into strong spiniform setae (outer plate of maxilla 1 and on the mandible). These spiniform setae, which mesh in the midline, presumably serve to prevent the food from moving while it is being cut.

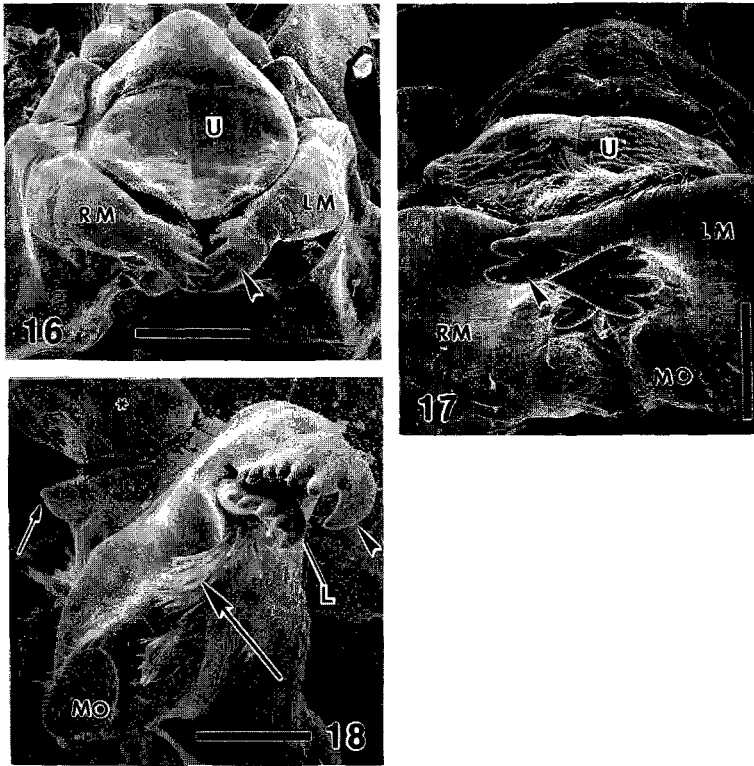
The mandibles shear the food and are highly modified for this purpose. They are elongated and narrow, with their incisor processes directed anteriorly. The incisor processes are widened to form cutting edges (Figs 5 and 6). Adduction of the mandible is by two large muscles (dorsal adductors) which originate at the side of the head and are inserted on two small projections on the medial side of the mandible. Only a single dorsal adductor muscle has been found in talitroid and gammaroid amphipods (Snodgrass, 1950; personal observations). The significance of these differences in muscle structure is unknown. Contraction of these muscles causes the cutting surfaces to slide past each other from anterior to posterior (Figs 6 and 10). The cutting edges function like long-handled garden shears, except that the mandibles are not crossed. The rounded knob on the anterior surface distal to the palp (Figs 12, 14 and 15) fits precisely into a corresponding socket on the posterior side of the upper lip (Figs 11–13). Together they form an articulation for the movement of the mandible, which provides the shearing action. The medial portion of the upper lip is thickened and densely setose (Figs 9, 12 and 13). The dorsal surface of the mandible fits neatly around the upper lip so that the thickened portion of the upper lip fills the space between the two mandibles (Figs 9 and 12). The anterior margin of the mandible between the knob and the cutting edge fits into a groove in the upper lip (Fig. 13).



FIGS 5–10. *Anonyx lilljeborgi* (Figs 5, 7, 10) and *A. makarovi* (Figs 6, 8, 9): 5, ventral view of open incisor processes of the mandibles. Left mandible (LM), right mandible (RM), mandibular, spiniform seta (arrowhead) with the setose upper lip (U) behind; 6, ventral view of closed incisor processes of the mandibles. Left mandible (LM), right mandible (RM), upper lip (U) and the incisor teeth (arrowhead) meeting in the midline; 7, ventral view of the mouthparts without food (maxilla 1 removed). Upper lip (U), mandible (M), lower lip (L); 8, ventral view of the mouthparts with food (maxilla 1 removed). Upper lip (U), mandible (M), lower lip (L) and food (arrowhead); 9, ventral view of the mandibles with the lower lip removed. Mandible (M), mandibular molar (MO) and upper lip (U) above the mandible; 10, upper lip with setae (U), right mandible (RM) and left mandible (LM). Scale bars ( $\mu\text{m}$ ): 5, 110; 6 and 9, 480; 7, 320; 8, 550; 10, 40.



FIGS 11–15. *Anonyx lilljeborgi* (Figs 11 and 13), *A. makarovi* (Fig. 12) and *A. nugax* (Figs 14 and 15): 11, lateral view of upper lip (U), right mandible (M) with palp removed and lower lip (L); 12, lateral view of upper lip (U) and displaced right mandible (M) with palp (\*) and the thickened portion of the upper lip (arrowhead). The arrow indicates where the knob of the middle fits into the socket on the posterior margin of the upper lip; 13, ventral view of the upper lip (U) with the setose thickened portion (\*) and the anterior groove (arrowhead) into which the mandibles fit. The posterior sockets for the mandibular articulations are indicated by arrows; 14, medial view of the left mandible with molar (MO), incisor process (E), lacinia mobilis (L), knob (arrow) and three simple spiniform-setae (arrowhead) between the molar and the incisor process; 15, lateral view of the left mandible with the incisor process (E), palp (\*) and knob (arrow). Scale bars ( $\mu\text{m}$ ): 11, 320; 12, 550; 13, 190; 14, 480; 15, 380.

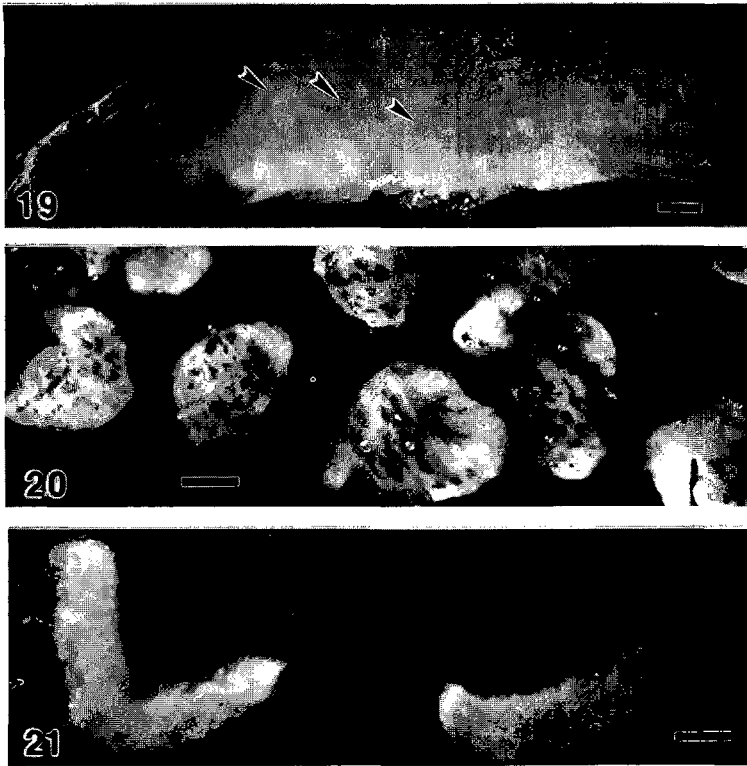


FIGS 16–18. *Gammaracanthus loricatus* (Fig. 16) and *G. angulosus* (Figs 17 and 18): 16, ventral view of the mandibles (RM, LM) and upper lip (U). Note the horizontal position of the upper lip and the posteriorly directed short mandibles with toothed incisor processes (arrowhead); 17, ventral view of the mandibles (RM, LM) and upper lip (U). Note the vertical position of the upper lip and the vertical short mandibles with overlapping toothed incisor processes (arrowhead) and molars (MO) that meet in the midline; 18, medial view of mandible with palp (\*), pointed knob (small arrow) near the palp, toothed incisor process (arrowhead), movable lacinia mobilis (L), molar (MO) with triturating surface and pappose setae (large arrow) between the molar and the lacinia mobilis. Scale bars ( $\mu\text{m}$ ): 16, 550; 17, 95; 18, 110.

The precise fit of the mandibles between the upper and lower lips, the teeth at the ventral end of the cutting edges, and the articulation of the mandibles with the upper lip all enable the mandibles to slice off pieces of food.

The conical molars of the mandibles are densely setose, do not meet in the midline (Fig. 9) and do not have any grinding surfaces. Instead they are in a position to push pieces of food into stomodeum when the mandible is adducted (Fig. 9).

Pieces of food are sheared off in the form of a ribbon and packed into the proventriculus, where they are coiled up side by side (Fig. 19). The individual food pieces (Fig. 20) have a uniform diameter when stretched out (Fig. 21) (coefficient of variation = 11.5%) but vary more in length (CoV = 33.9%). The mean diameter of the strips from each animal varies directly with body size (Fig. 22).



FIGS 19–21. *Anonyx nugax*: 19, proventriculus containing squid bait. Individual coiled pieces of food are packed side by side (arrowheads); 20, coiled strips of squid removed from the proventriculus that are viewed end on; 21, pieces of squid bait that have been unravelled and pressed flat. All scale bars 1 mm.

### Discussion

Although the morphology of the mouthparts has been the basis of amphipod systematics since the time of Boeck (1871), and the foraging of amphipods, including *Anonyx* spp. has been studied intensively (Thurston, 1979; Ingram and Hessler, 1983; Sainte-Marie, 1987) the functional morphology of the mouthparts has been little studied (Dahl, 1979; McGrouther, 1983) and is poorly understood (Coleman, 1991).

Snodgrass (1950) and Manton (1977) have discussed the evolution of the mandible of arthropods. Amphipod mandibles are similar to those of *Anaspides* (Syncarida) as described by Manton (1977). The mandibles of *Anaspides* are short with toothed incisor processes that meet in the midline behind the upper lip and bite into their food when the mandible swings on its oblique hinge line. Snodgrass (1950) and Watling (1983) showed that the mandibles of amphipods typically have horizontal hinge lines, with the toothed incisor processes meeting ventrally (e.g. Fig. 17) behind the transverse upper lip, as is also true of the tanaids and isopods. The left incisor invariably overlaps the right (Figs 6 and 17; Dahl and Hessler, 1982). However, at least some amphipods, such as *Gammaracanthus*, have an oblique hinge line with the toothed incisor processes directed posteriorly above a horizontal upper lip (Fig. 16). In the plesiomorphic state a toothed lacinia mobilis (Figs 17 and 18) is found on each mandible, and both are used to guide the incisor processes when they come together,



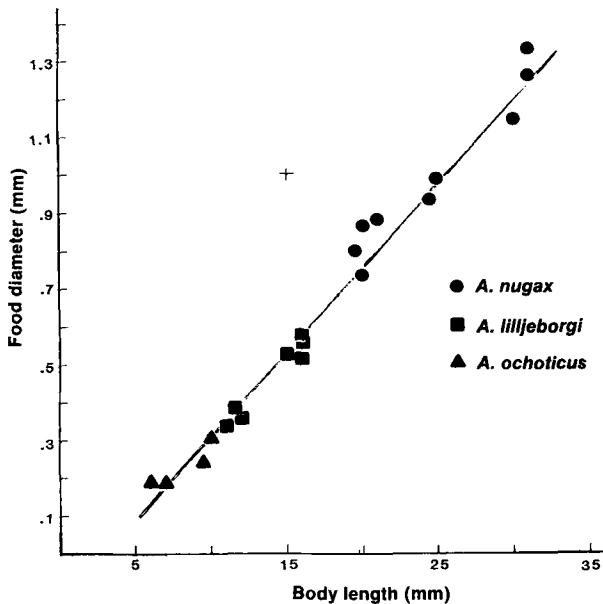


FIG. 22. Mean diameter of strips of squid from individuals of *Anonyx* spp. of varying body lengths. The least-squares regression equation is Food diameter =  $-0.1276 + 0.443$  (Body length) ( $r^2 = 0.96$ ). *Paralicella caperasca* food diameter indicated by +.

as well as for biting (Dahl and Hessler, 1982). The knob of the mandible is typically pointed and situated next to the hinge line and the palp (Fig. 18) in most amphipods. Snodgrass (1950) next to the knob to provide a second articulation for the mandible, which it does in *Anonyx* and talitroids where it is oriented anteriorly. However, its pointed shape and medial orientation in other amphipods indicate that it would allow little rotation when the mandibles close. It is concluded that in these amphipods it serves to fix the mandible in place when the toothed incisors and laciniae come together.

While the incisors are biting, the molars also meet and rotate so as to grind up food on their triturating surfaces before it enters the mouth (Oleröd, 1975; Oshel and Steele, 1985; Coleman, 1989). The rotation of the molars also pushes food into the mouth. Therefore the mandible may have as many as three separate functions—cutting, grinding and ingestion.

Amphipod mandibles show many variations on the basic structure (Figs 16–18), and the lysianassoids are one of the most specialized groups. All typical lysianassoid amphipods lack teeth on their incisor processes. *Valettropsis* and related genera have incisor teeth as well as other primitive characters (Lincoln and Thurston, 1983), and probably should be removed to another superfamily. The teeth on the incisor process of *Anonyx* mandibles represent specialized characters that can be used to define the genus. In addition, lysianassoid mandibles are elongate with a simple lacinia mobilis distant from the cutting edge and widened incisors directed anteriorly.

Lysianassoid amphipods have many large species in the cold-water environments of high latitudes and the deep sea (Steele, 1983). Species of the genera *Anonyx*, *Tmetonyx*, *Tryphosa*, *Orchomenella*, *Orchomenopsis*, *Scopelocheirus*, *Onisimus*, *Eurythenes*, *Hirondellea*, *Alicella*, *Paralicella* have become specialized scavengers

(necrophages) of dead or wounded animals, often of large size. They are attracted to carcasses and can be collected in large numbers in traps. This behaviour would seem to be due to convergence rather than phylogeny, since in some genera only some of the species have developed the habit. At shallow depths of mid-latitudes where decapod crustaceans (lobsters, crabs and shrimp) and fish are the dominant scavengers, only small lysianassoid amphipods occur, and they are not scavengers. Few scavenging amphipods are known in the other superfamilies that can be caught in traps. They include some eusiroids such as *Halirages fulvocinctus* (personal observations), *Leptamphopus sarsii* (see Vader, 1972) and *Dolobrotus mardeni* (see Bowman, 1974). However, many amphipod species, such as *Gammarus* spp., are generalists and will thrive on animal food if it is made available to them (Vassallo and Steele, 1980).

The shearing action of *Anonyx* mandibles, whereby long ribbons of tissue can be cut from large animals and packed into the proventriculus, is probably found in other necrophagous lysianassoids, judging from the size and shape of the food particles found in their proventriculi (Thurston, 1979; De Broyer and Thurston, 1987) and SEM illustrations on mouthparts (Dahl, 1979). Dahl (1979) and Sainte-Marie (1984) evidently envisaged the animals biting out chunks of food that would fill the space between the cutting surface of the incisors and the molars. However, the space between the two mandibles is filled by the thickened portion of the upper lip, and therefore cannot be used to accommodate food. Moreover, the ribbon shape of the food particles that are ingested does not indicate that they bite out pieces of food.

Although other genera have not been studied in detail, *Anonyx* appears to be the amphipod genus which is most specialized for shearing off large pieces of food (Dahl, 1979; Sainte-Marie, 1984). The precise fit of the mandibles, together with the unique teeth on their ventral corners, which guide the two surfaces together when the mandibles close, are adaptations for shearing. Even recently released young and individuals of small species can feed on large food items (Fig. 22). The diameter of the ingested food particles is positively correlated with body size within the genus *Anonyx*, but differs significantly from that observed in *Paralicella* (Thurston, 1979) or extrapolated to in *Alicella* (De Broyer and Thurston, 1987).

The relative positions of the molar and the palp have been used extensively in lysianassoid systematics to distinguish genera. This character has little functional significance since it is related to the length of the mandible. The knob on the mandible between the incisor process and the palp, on the other hand, is developed to varying degrees and occurs in various orientations on the mandible (Fig. 18) but has not been mentioned as a taxonomic character. However, it is functionally important, as discussed above, and should be described so that its significance for systematics can be assessed.

### Acknowledgements

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### References

- BOECK, A., 1871, Crustacea amphipoda borealia et arctica. *Saerskilt Aftryk af Forhandlinger i Videnskabs-Selskabet i Christiania Aar 1870*, 81–280.

- BOWMAN, T., 1974, The 'sea flea' *Dolobrotus mardeni* n. gen. n. sp., a deep-water American lobster bait scavenger (Amphipoda: Eusiridae), *Proceedings of the Biological Society of Washington*, **87**, 129–138.
- COLEMAN, C. O., 1989, On the nutrition of two Antarctic Acanthonotozomatidae (Crustacea: Amphipoda). Gut contents and functional morphology of mouthparts, *Polar Biology*, **9**, 287–294.
- COLEMAN, C. O., 1991, Redescription of *Anchiphimedia dorsalis* (Crustacea, Amphipoda, Iphimediidae) from the Antarctic, and functional morphology of mouthparts, *Zoologica Scripta*, **20**, 367–374.
- DAHL, E., 1979, Deep-sea carrion feeding amphipods: evolutionary pattern in niche adaptation, *Oikos*, **33**, 167–175.
- DAHL, E. and HESSLER, R. R., 1982, The crustacean lacinia mobilis: a reconsideration of its origin, function and phylogenetic implications, *Zoological Journal of the Linnean Society*, **74**, 133–146.
- DEBROYER, C. and THURSTON, M. H., 1987, New Atlantic material and redescription of the type specimens of the giant abyssal amphipod *Alicella gigantea* Chevreux (Crustacea), *Zoological Scripta*, **16**, 335–350.
- INGRAM, C. L. and HESSLER, R. R., 1983, Distribution and behavior of scavenging amphipods from the central North Pacific, *Deep-Sea Research*, **30**, 683–706.
- LINCOLN, R. J. and THURSTON, M. H., 1983, *Valettieta*, a new genus of deep-sea amphipod (Gammaridea: Lysianassidae) with descriptions of two new species from the North Atlantic Ocean, *Bulletin of the British Museum of Natural History (Zoology)*, **44**, 85–101.
- MANTON, S. M., 1977, *The Arthropoda. Habits, Functional Morphology and Evolution* (Oxford: Clarendon Press), 527 pp.
- MCGROUTHER, M. A., 1983, Comparison of feeding mechanisms in two intertidal gammarideans, *Hyale rupicola* (Haswell) and *Paracalliope australis* (Haswell) (Crustacea: Amphipoda), *Australian Journal of Marine and Freshwater Research*, **34**, 717–726.
- OLERÖD, R., 1975, The mouthparts in some North Atlantic species of the genus *Orchomene* Boeck (Crustacea, Amphipoda), *Zoologica Scripta*, **4**, 205–216.
- OSHEL, P. E. and STEELE, D. H., 1985, Amphipod *Paramphithoe hystrix*: a micropredator on the sponge *Haliclona ventilabrum*, *Marine Ecology-Progress Series*, **23**, 307–309.
- PARRY, W. E., 1824, *Journal of a second voyage for the discovery of a north-west passage from the Atlantic to the Pacific; performed in the years 1821–22–23, in his Majesty's ships Fury and Hecla, under the orders of Captain William Edward Parry, R.N., F.R.S. and Commander of the expedition* (London, J. Murray), 571 pp.
- SAINTE-MARIE, B., 1984, Morphological adaptation for carrion feeding in four species of littoral or circalittoral lysianassid amphipods, *Canadian Journal of Zoology*, **65**, 1668–1674.
- SAINTE-MARIE, B., 1987, Meal size and feeding rate of the shallow water lysianassid *Anonyx sarsi* Steele and Brunel (Crustacea: Amphipoda), *Marine Ecology-Progress Series*, **40**, 209–219.
- SAINTE-MARIE, B. and LAMARCHE, G., 1985, The diets of six species of the carrion-feeding lysianassid amphipod genus *Anonyx* and their relation with morphology and swimming behavior, *Sarsia*, **70**, 119–126.
- SNODGRASS, R. E., 1950, Comparative studies on the jaws of mandibulate arthropods, *Smithsonian Miscellaneous Collections*, **116**, 1–85.
- STEELE, D. H., 1983, Size compositions of lysianassid amphipods in cold and warm water habitats, *Australian Museum Memoir*, **18**, 113–119.
- THURSTON, M. H., 1979, Scavenging abyssal amphipods from the north-east Atlantic Ocean, *Marine Biology*, **51**, 55–68.
- VADER, W., 1972, Notes on Norwegian marine Amphipoda. 5. New records of *Leptamphopus sarsii* (Calliopidae), *Sarsia*, **50**, 25–28.
- VADER, W. and ROMPPAINEN, K., 1985, Notes on Norwegian marine Amphipoda. 10. Scavengers and fish associates, *Fauna norvegica*, Ser. A, **6**, 3–8.
- VASSALLO, L. and STEELE, D. H., 1980, Survival and growth of young *Gammarus lawrencianus* Bousfield 1956, on different diets, *Crustaceana*, **6** (Suppl.), 118–125.
- WATLING, L., 1983, Percacaridan disunity and its bearing in eumalacostracan phylogeny with a redefinition of eumalacostracan superorders, in F. R. Schram (ed.), *Crustacean Phylogeny*, Crustacean Issues No. 1 (Rotterdam: A. A. Balkema), pp. 213–228.