

A Scanning Electron Microscope Study of the Mandibular Morphology of Boreal Copepods

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Abstract

Morphological details of the mandibular blades of 11 species of copepods were examined with scanning electron microscopy. The micrographs improved our understanding of the complex toothed edge of the mandibular blade, which in turn aids in identification of the copepod prey of chaetognaths by gut-content analysis. Beklemishev's discovery of siliceous tooth crowns in calanoid copepods was confirmed for most of the species examined. Long, sharp projections on the crowns of herbivorous species, and the deep grooves into which they fit on the teeth of the opposite mandible, suggest a cracking rather than a grinding function for these teeth.

Introduction

Giesbrecht (1892) discussed the specific distinctness of the mandibular blade of copepods for a wide spectrum of species. However, the mandible is a complex 3-dimensional structure that can be difficult to interpret with the light microscope. Grice and Lawson (1971) have shown that scanning electron microscopy (SEM) greatly improves the accuracy of visualization of mandible structure and reveals some surprising details.

We present in this paper the results of a comparative study of the mandibles of 11 species of copepods using SEM. The information contained in the micrographs should be of value to taxonomic studies and to the investigation of mandible structure and function. We have sought this morphologic information in order to identify copepod species from their mandibles alone using light microscopy. This is useful to the study of copepod prey found in the guts of chaetognaths. Frequently, the only parts which remain identifiable are the mandibles. This technique was also suggested for the copepod prey of shrimp by Judkins and Fleminger (1972).

Crustaceans have paired, opposed mandibles. In copepods the toothed edges of the individual blades are oriented dorso-ventrally (Fig. 1), and

are curved. The concave surface faces anteriorly and apposes a bump on the posterior surface of the labrum. Giesbrecht (1892, p. 105, freely translated) says the following about the blade in the genus *Calanus*: "The chewing edge is almost linearly truncated, and bears eight transparent teeth on knobs which are separated from one another by flat gaps.... Each tooth, with the exception of the most dorsal, bears several prongs." Giesbrecht treats this tooth list as a graded series: the teeth become progressively smaller toward the dorsal end of the blade. In general, it seems more convenient to treat the tooth list as being composed of 3 groups of teeth, following Beklemishev (1954) (see Figs. 2A and 3A of present paper). The ventral end of the mandible bears 1 or 2 large teeth, termed the ventral group. This is separated by a diastema from a central group of 3 or 4 teeth. The dorsal end bears a group of small teeth called the dorsal group. A setulose seta is situated at the dorsal end of the mandible.

The individual teeth have been shown by Beklemishev (1954, 1959) to be mineral elements set in sockets in the surface of the exoskeleton. He demonstrated that the teeth are not dissolved by concentrated sulfuric acid, which dissolves the chitinous mandible blade. He also showed that they are not

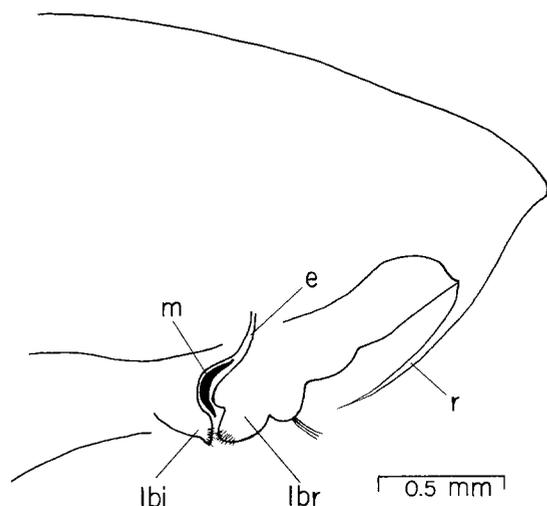


Fig. 1. *Calanus cristatus*. Diagrammatic sagittal section of mouth. e: Esophagus; lbi: left labial palp; lbr: labrum; m: toothed end of left mandibular blade; r: rostrum

birefringent in polarized light. The only reasonable substance which would give these results is opaline silica. Possession of glass teeth for eating food in glass cases is surely one of the lyrical symmetries of nature.

A number of investigators have tried to relate mouthpart structure and the type of food eaten in the copepods. Anraku and Omori (1963) found 3 basic structural types: mandibles of herbivorous species have grinding teeth; predators have elongate and sharp teeth; omnivores have mandibles intermediate in structure between the other two. Arashkevich (1969) describes these same general categories. Itoh (1970) proposed an index derived from the number of cutting edges on the mandible blade and the height of these edges. The value of the index was thought to reflect the food preference of the species.

Materials and Methods

The mandibles examined were dissected from specimens stored in buffered 8% formaldehyde in seawater. Each was air-dried and mounted on a mica disc directly or on a chip of metallic tape. Mounted samples were glued to aluminum support stubs with electrically conductive paint and coated with 100 Å of 60:40 gold:palladium applied by vacuum evaporation. Examination was made in an ISI Mini-SEM. Photographs of each mandible were taken from a number of angles of incidence until it was felt that the 3-dimensional aspects were correctly

understood. The species examined are among the dominant forms in two ocean regions: the subarctic Pacific and the boreal temperate neritic zone of Oregon's coast (USA). They were collected at Ocean Station P (50°N; 145°W), and at 44°40'N; 124°10'W. The following species were included:

Subarctic Pacific

Calanus cristatus Kroyer
C. plumchrus Muruwaka
Eucalanus bungii Giesbrecht
Oithona similis Claus
Metridia pacifica Browskii
Scolecithricella minor Brady

Neritic

Calanus marshallae Frost, 1974
Pseudocalanus sp.
Acartia longiremis Lilljeborg
A. clausi Giesbrecht
Centropages abdominalis Sato

Adult females were used except where adults of the species have reduced mouthparts (*Calanus cristatus* and *C. plumchrus*), in which case Stage V copepodites were examined.

To test for the presence of silica in teeth, we treated mandibles of all 11 species with concentrated hydrofluoric acid for 5 min and reexamined them under the light microscope for erosion of the tooth crowns. A polarizing microscope was used to examine teeth for birefringence (Beklemishev, 1954, 1959), to establish the opaline character of the teeth. Tests with acid and the polarizing scope are not effective in detecting silica in very small teeth, however. A microprobe could be used to refine the analysis for silica.

Results

The SEM micrographs (Figs. 2 to 6) show the toothlike structures that line the edge of the mandibular blade very clearly. The same mandible may bear teeth that are structurally complex modifications of the chitinous surface and others that are relatively simple projections of chitin. Some of the teeth are crowns set in sockets in the chitinous surface. Our tests with hydrofluoric acid confirmed Beklemishev's (1954, 1959) determination of the presence of silica in these crowns. In Fig. 3B a broken crown reveals that the material is brittle and probably of mineral character.

Morphological details for the species studied are described below using the groups of teeth proposed by Beklemishev

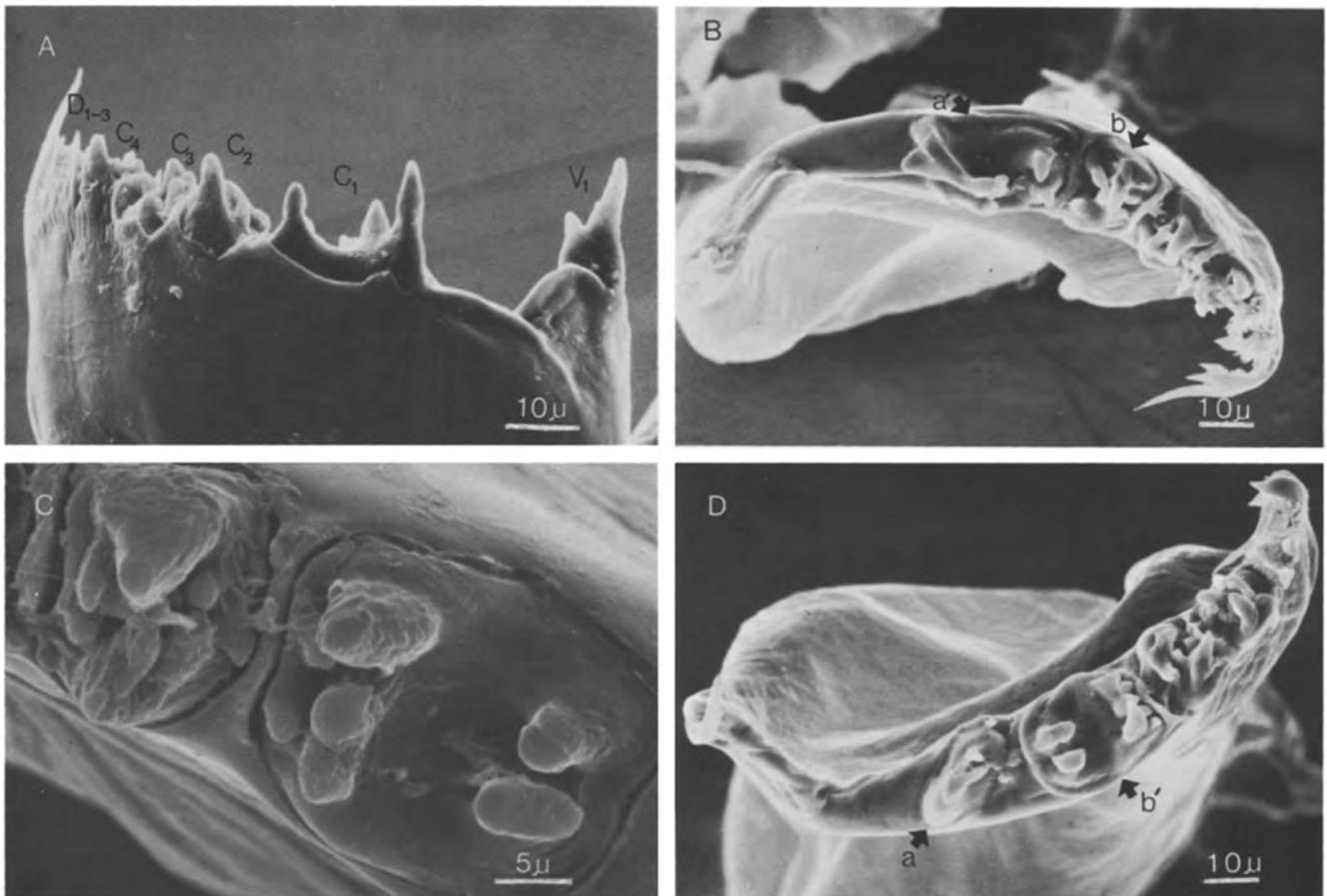


Fig. 2. *Calanus plumchrus*. Scanning electron micrographs of mandibular blade. (A) Left mandible, posterior surface of distal or chewing end; V₁: ventral tooth; C₁-C₄: central teeth; D₁₋₃: dorsal teeth. (B) Left mandible, distal or chewing edge. (C) Right mandible, detail of central tooth group. (D) Right mandible, chewing surface. (B) and (D) are a pair from same copepod; the teeth match so that a fits into a' and b fits into b'

(1954, 1959). As examples of the application of these groupings, teeth on the mandibles in Figs. 2A and 3A are labeled ventral, central, or dorsal depending on the group to which they belong.

The central group of teeth is somewhat similar in the *Calanus* species, *Pseudocalanus* sp., and *Eucalanus bungii*. Micrographs of these species are presented in Figs. 2 to 4. The crowns have nearly square bases, like molars, but bear high cusps and deep grooves. We have examined both the right and left mandibles from *C. cristatus*, *C. plumchrus*, and *E. bungii*, and they are complementary in structure (see Fig. 2B, D): each projection on a crown either matches a socket on the opposing crown of the other mandible, or fits between two crowns. Fig. 2B, D shows this most clearly. The region marked a fits into a', and b fits into b'. Because of their length, these projections appear to be suited to cracking diatoms,

rather than grinding them. The *Acartia* species bear a single extremely large crown in the central position (Fig. 4C, D). In *Metridia pacifica* and *Centropages abdominalis* (Fig. 5), there are no separate teeth in sockets, and there is no central group distinct from a dorsal group. A continuous thickened ridge of apparently hard material is elaborated into 7 bicuspid teeth. Our tests show that this ridge is not siliceous, but appears to be chitinous in its entirety.

The dorsal end of the mandibles of the *Calanus* species, *Pseudocalanus* sp., and *Eucalanus bungii* bears 3 teeth of a complex shape that has not been described before. They are steep-sided wedges that bear rows of conical projections (Fig. 4A, B). These correspond to the dorsal group described by Beklemishev (1954, 1959). We do not know the function of these teeth but they might serve to tightly grip food of a softer nature. The *Acartia* species

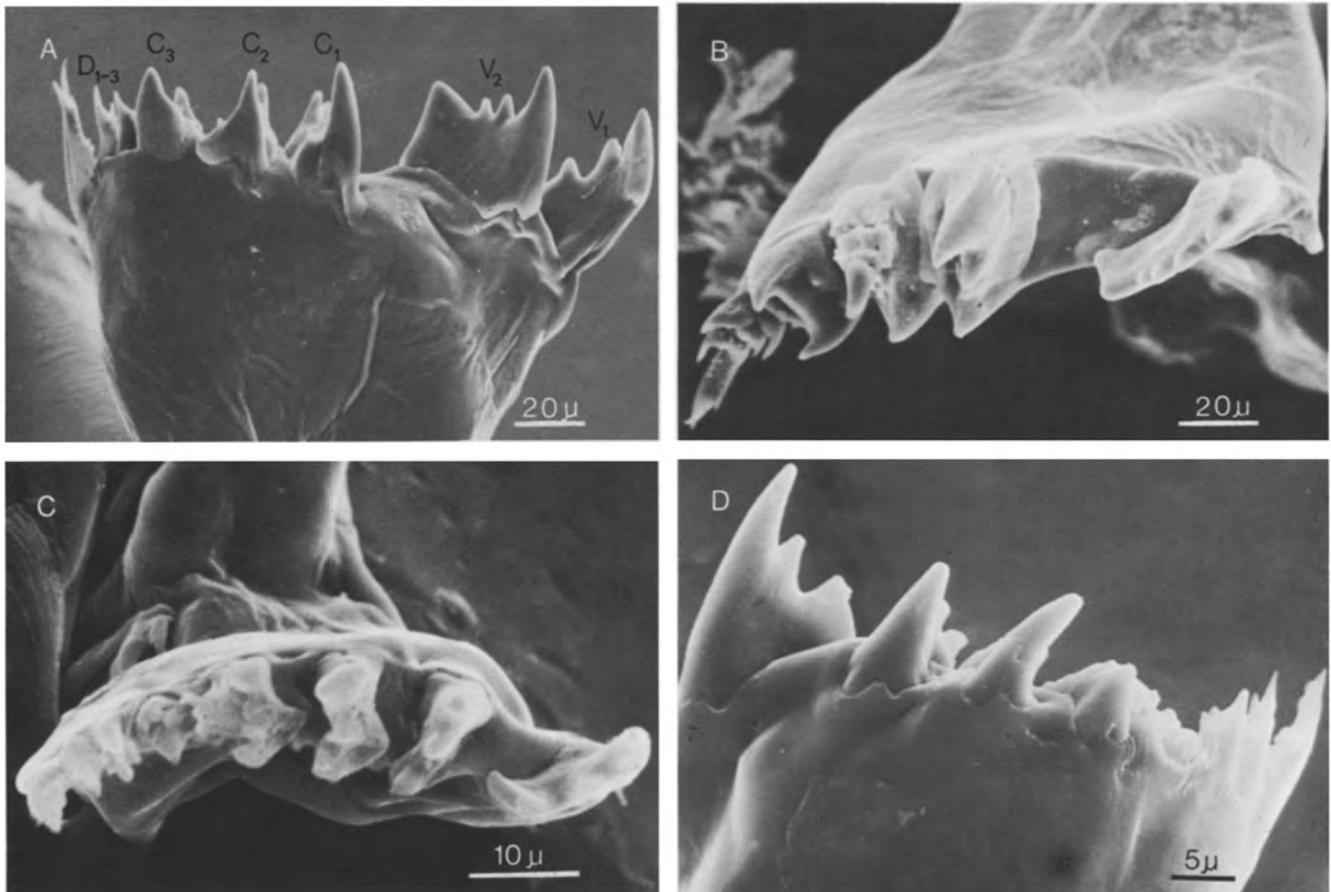


Fig. 3. *Eucalanus bungii* and *Pseudocalanus* sp. SEM micrographs of mandibles. (A) *E. bungii*; posterior surface of left mandible; V_1 and V_2 : ventral teeth; C_1 - C_3 : central teeth; D_{1-3} : dorsal teeth. (B) *E. bungii*; cutting edge of right mandible. (C) *Pseudocalanus* sp.; right mandible, chewing surface. (D) *Pseudocalanus* sp.; right mandible, posterior surface

have fingerlike projections of chitin in the dorsal position (Fig. 4D) which could perform a similar function. We speculate that in all these species, soft food gripped between the mandibles is abraded against the file-like teeth on the bump on the oral surface of the labrum. A setose bristle is usually the last projection on the dorsal edge of the mandible.

All the species examined have at least one ventral projection or tooth separated by a diastema from the rest of the tooth list. In *Pseudocalanus* sp. and *Eucalanus bungii*, the ventral group consists of cockscomb-shaped silicious teeth (Fig. 3). In *E. bungii* there is one such tooth on the right mandible and two on the left. We have not studied the left jaw of *Pseudocalanus* sp. In the *Calanus* species there is a single ventral tooth that is elongate rather than comb-like. The chitinous projection which bears this tooth usually has a shoulder next to the diastema (Fig. 2A). *Metridia pacifica* and *Centropages abdominalis* each

have a flattened conical projection in the ventral position which is separated from the central group by a smooth, deep diastema (Fig. 5A). Tests with acid show that this single ventral point has a siliceous cap. *Acartia* species have a single, extremely pointed ventral projection of great length which is heavily mineralized (Fig. 4C, D).

All the species studied were found to have small setules arrayed on the posterior surface of the mandible just proximal to the toothed edge. *Metridia pacifica* and *Centropages abdominalis* have them on both surfaces. Additional patches of hair-like sencillae can be seen in various positions on the mandibles of many of the species. Setules of this sort were described and illustrated by Giesbrecht (1892).

The teeth of *Scolecithricella minor* do not seem to group conveniently in the categories used by Beklemishev (1954, 1959). There are 3 teeth on the ventral end of the left mandible which have a long silicious shaft terminating

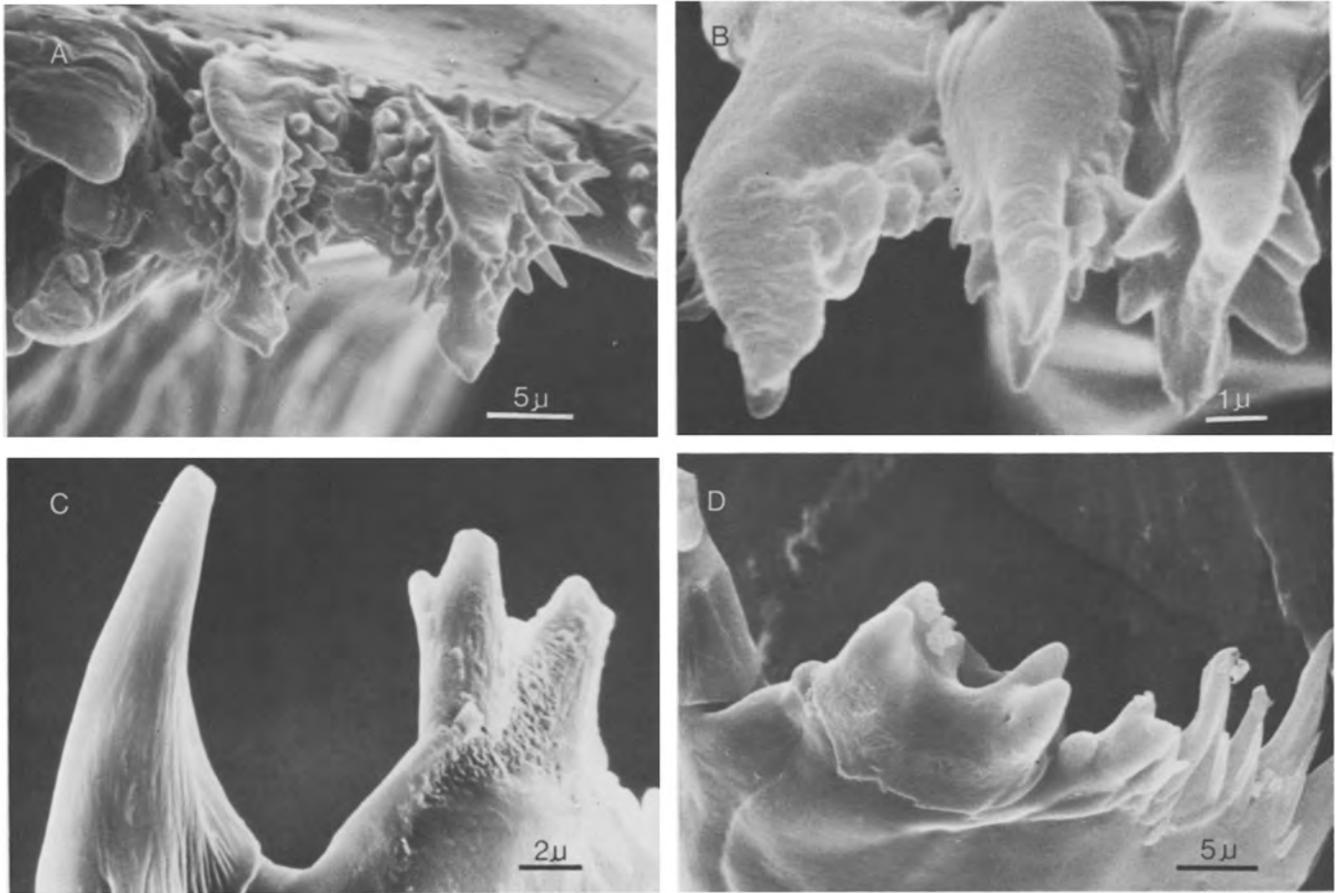


Fig. 4. SEM micrographs of mandibles of 4 copepod species. (A) *Calanus plumchrus*; detail of 2 dorsal teeth of left mandible. (B) *Pseudocalanus* sp.; detail of dorsal tooth group of right mandible. (C) *Acartia longiremis*; right mandible, detail of the ventral end. (D) *Acartia clausii*; right mandible, posterior surface

in an expanded dentate blade. The dorsal end of the mandible bears a complex cluster of spines arising from the chitinous surface. Some spines arise on the anterior surface proximal to the edge of the mandible (Fig. 6A, B).

Oithona similis has such small jaws that adequate mounts for SEM are exceedingly difficult to prepare. Fig. 6C and D are the best we could obtain. They show a single blunt projection on the ventral end separated by a v-shaped diastema from a cluster of heavy spines. There are no crown-like structures or grinding surfaces.

In addition to the characteristic features of the mandibles just described for each species, some variability of the structure of the crowns was observed among individuals of the same species. For example, Fig. 7 shows two right mandibles from *Calanus plumchrus*. The teeth of one mandible appear to be more worn than those of the other. Wearing down of the pointed crowns may be a real feature of copepod biology. Some of the

variability observed may also be an artifact of the preparation technique used (air drying) to mount the samples for SEM. We have not been able to quantify the range of variability in form. However, we feel that it is not sufficient to impair species recognition.

Discussion

The SEM study has shown that the mandibles of different copepod genera and species are quite distinct. The shape and arrangement of the ventral tooth group appears to be the best character for separating closely related species. Beklemishev (1959) has already described variation of the ventral teeth among geographical varieties of *Calanus finmarchicus*. The warmer the sea, the smaller the size of tooth V₂. Characteristics of the ventral group useful for distinguishing the *Calanus* species included in the present study are as

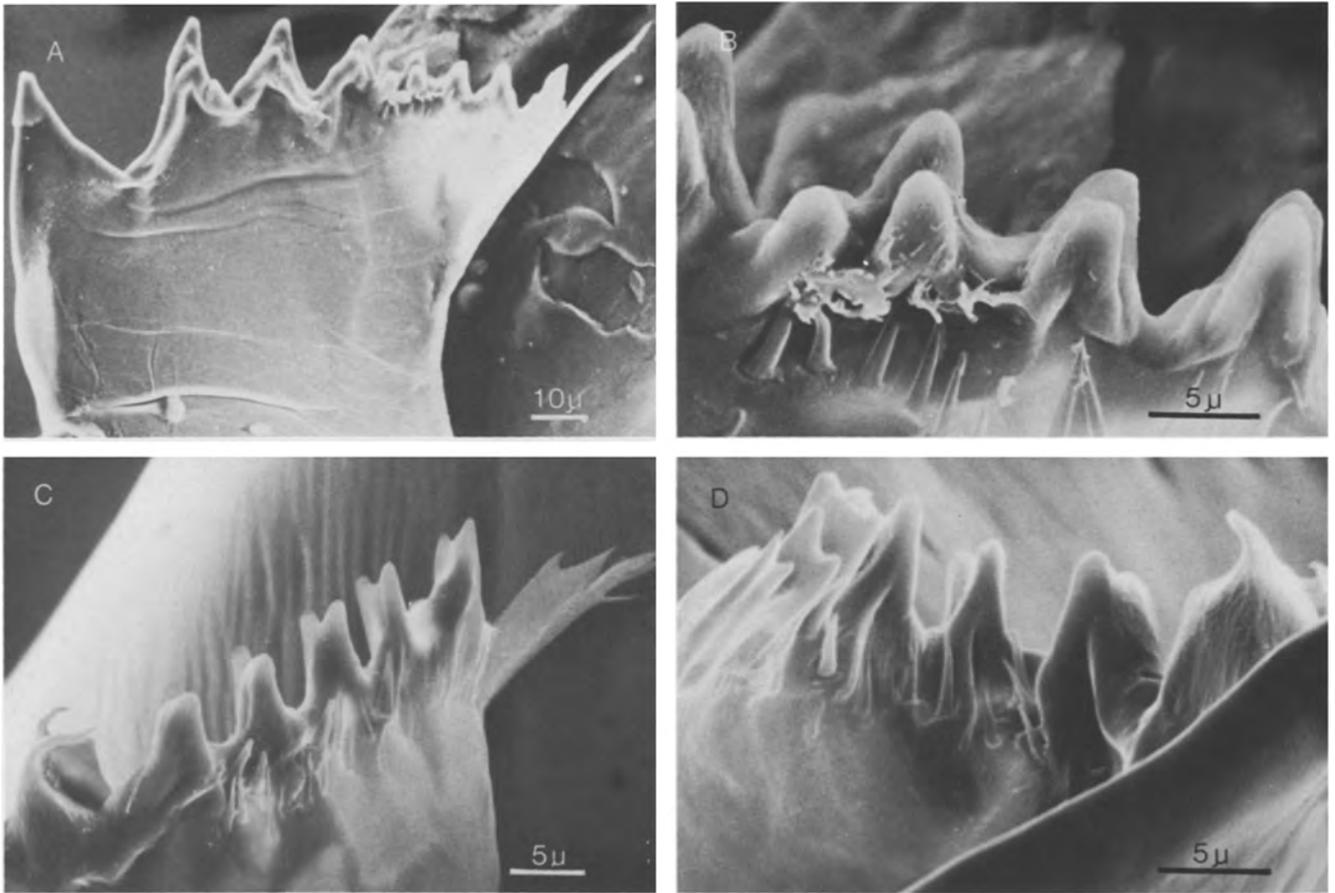


Fig. 5. *Metridia pacifica* and *Centropages abdominalis*. Micrographs of mandibles. (A) *M. pacifica*; right mandible, posterior surface. (B) *M. pacifica*; detail of dorsal end. (C) *C. abdominalis*; right mandible, posterior surface. (D) *C. abdominalis*; right mandible, anterior surface. Detail of dorsal end

follows: *C. plumchrus* has only 1 ventral tooth and a smoothly sloping shoulder at the diastema. Mandibles of *C. marshallae* have a sharp projection of chitin on this shoulder which may bear a silica crown. *C. cristatus* mandibles bear a smooth round knob on the surface of the diastema.

In addition to specific differences, different copepod families have distinct and characteristic general mandible types. However, we have not studied a wide enough spectrum of taxa to indulge in many generalizations about feeding types such as those of Anraku and Omori (1963), Arashkevich (1969), and Itoh (1970). All of the forms considered are in the filter-feeding group (Calanidae, Eucalanidae, Paracalanidae, and Pseudocalanidae) or in the mixed mode of feeding group (immature Euchaetidae, Centropagidae, Temoridae, Lucicutiidae, Acartiidae, and Metridiidae). The predatory feeders (Heterorhabdidae, Augaptilidae, Candaciidae, Pontellidae, Tortanidae and adult Euchaetidae) are

not represented because they are not numerical or biomass dominants in the two regions in which we are studying chaetognath feeding. The jaws of the two species of *Acartia* (Fig. 4C, D) and of *Centropages abdominalis* (Fig. 5) are so different in kind that the mixed mode of feeding group (Itoh's Group II) cannot be considered a structurally uniform assemblage. Jaws of the *Acartia* species are also unlike those of *Metridia pacifica* [Fig. 5A, B, another copepod classed as a mixed feeder by Arashkevich, (1969)]. In fact, comparison of the SEM photos would lead to doubt that the mandibles of members of this group could be functionally similar. However, Arashkevich also identified this same group on the basis of a more general study of the mouth parts. Further study of the relation of mandible structure and function is needed. On the other hand, the representatives we have studied from the "filter-feeding" group are so similar structurally, that functional similarity seems assured.

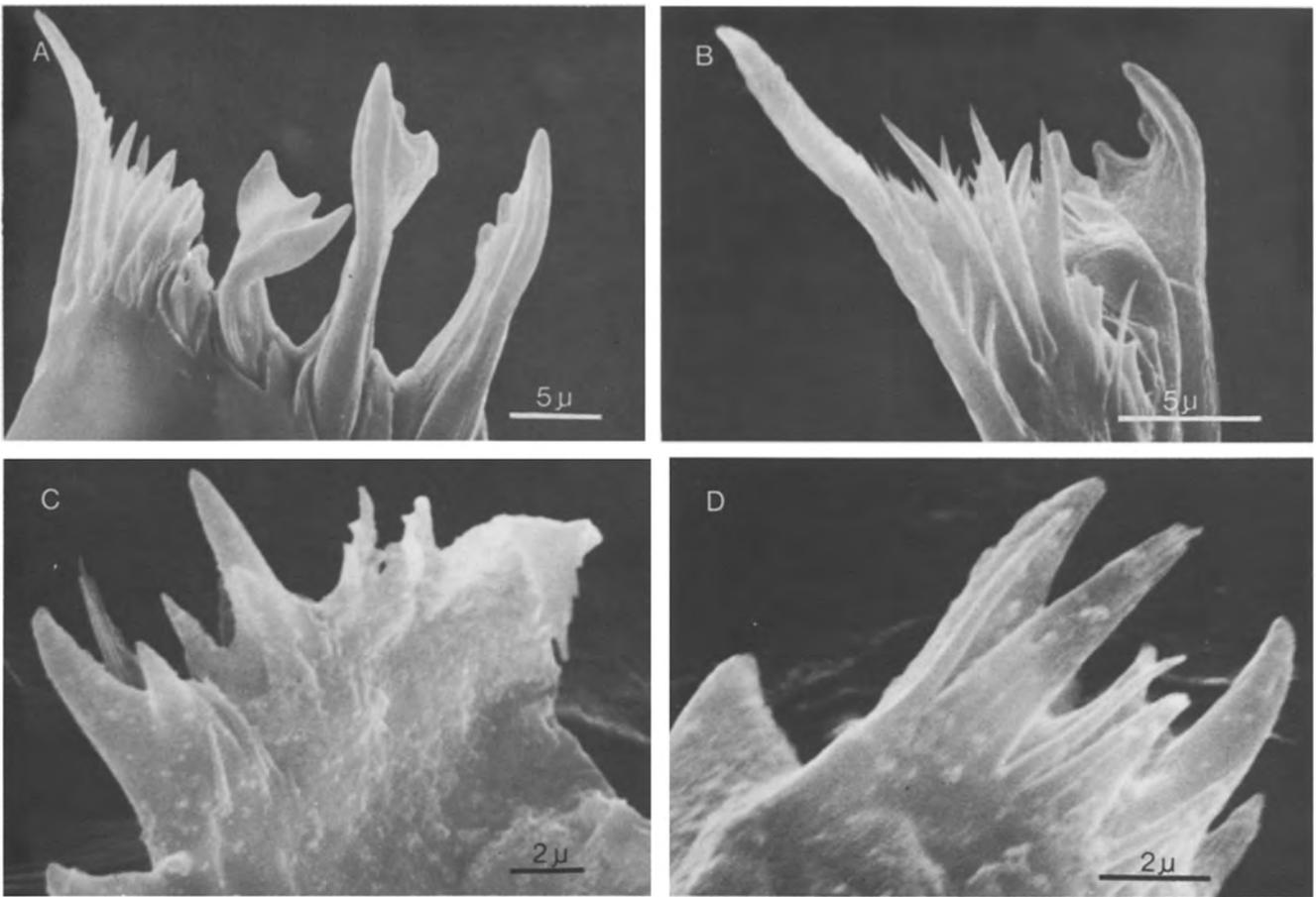


Fig. 6. *Scolecithricella minor* and *Oithona similis*. Micrographs of mandibles. (A) *S. minor*; posterior surface of left mandible. (B) *S. minor*; left mandible, detail of dorsal end. (C) and (D) Two mandibles of *O. similis*

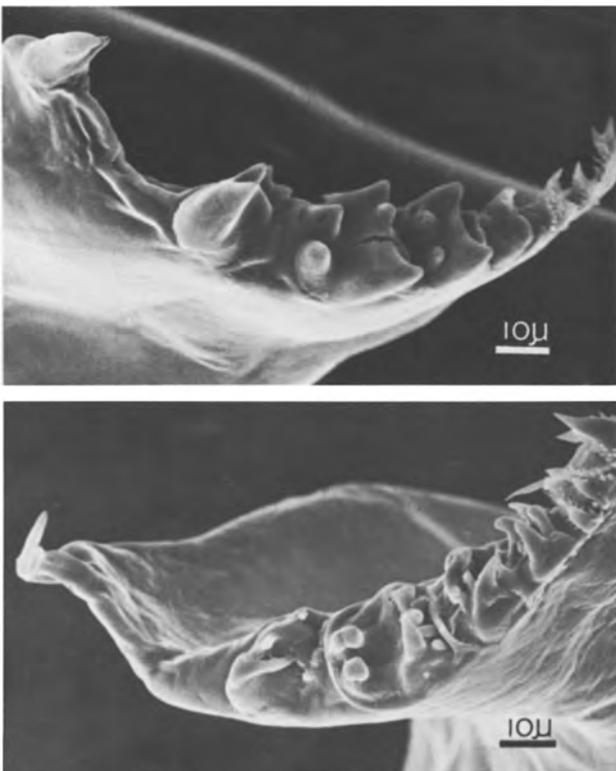


Fig. 7. *Calanus plumchrus*. Comparison of right mandibles from 2 different specimens, showing marked differences in degree of tooth wear

The presence of siliceous teeth in the copepods has not been widely recognized in the English-language literature (it is mentioned by Marshall, 1973), although it has been recognized in the USSR for 20 years. So far as we can determine, siliceous teeth do not occur in other crustaceans. It is very general among the marine calanoids, including all three feeding types. Light microscope studies of female *Euchaeta japonica* Marukawa show very elongate blades of glass deposited over cone-shaped projections of the exoskeleton (see also Arashkevich, 1969).

The teeth imply a silicate requirement for copepods. This could be met either from the diet (diatoms or other copepods) or by direct uptake from seawater. Because many copepods, like *Acartia clausi*, can be reared on flagellates alone, this should be amenable to experimental analysis. Tracer studies employing Si^{32} should also be possible. Studies of silicon metabolism in copepods can be performed similar to studies already made for other organisms (diatoms: Lewin, 1966; Darley and Volcani, 1969; sponges: Elvin, 1972).

It seems likely that the crowns of copepod teeth will eventually be iden-

tified in siliceous sediments. Preparations of opal fossils we have examined so far have not contained them.

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