Biological Notes on the Copepod *Boeckella triarticulata.*

By E. W. Bennett, M.Sc., Canterbury College, Christchurch.

[*Read before the Philosophical Institute of Canterbury, 1st December, 1926; received by Editor, 31st December, 1926; issued separately, 10th August, 1927.*]

Although the animal which forms the subject of the present paper belongs to a family (Centropagiae) with numerous fresh-water as well as marine representatives, the family belongs to the Calanid group of Copepoda, which has very few other fresh-water representatives but is characteristically an open-sea group; in accordance with this mode of life, the animals are adapted in various ways for vigorous activity in the water. The anterior antennae for example, which are the chief swimming-organs, are extremely long and powerful, and the other appendages are well provided with muscles and setae. In these respects they contrast with other Copepoda, such as the littoral Harpacticoida, the fresh-water Cyclopids, and the parasitic forms. The fresh-water Centropagiae retain the chief characteristics of the Calanid group, the main tendency in the case of *Boeckella* and its relatives being a reduction in the number of joints and setae of the fifth feet of the male.

Boeckella triarticulata is the type species and genus of the Boeckellidae, the counterpart of *Diaptomus* of the northern hemisphere; over thirty species are known from New Zealand, Tasmania, the southern parts of Australia and South America, and from Kerguelen's Land. *Boeckella triarticulata* is known from New Zealand and the south-eastern corner of Australia; three other species of related genera have also been reported from New Zealand, but a more detailed account of these and some further recently-collected species is reserved for a later paper.

Boeckella triarticulata was originally described by the Hon. G. M. Thomson in 1882 from specimens collected by Dr. Chilton, and a fuller account was later given by Sars (*Videnskabs-Selskabets Skrifter.* 1-Mathem. Naturv. Klasse, 1894, No. 5). Brady, commenting on the collection of Copepoda from New Zealand Lakes made by Messrs. Hodgkin and Lucas (Proc. Zool. Soc., London, 1906, p. 696) says that *Boeckella* "seems to be the commonest of all the lacustrine Copepoda of New Zealand." This refers to the cold lakes of the mountainous regions; the present writer has also taken the species in abundance from many localities throughout the Canterbury Plains from Cheviot to beyond Waimate, and finds it equally abundant from those lower levels. It is absent from streams, except backwaters which are so filled with weeds as to be almost still; but it is nearly always to be found in stagnant pools, especially those which do not dry up during the summer. The writer has rarely taken it without *Cyclops*, and never without Ostracods; when found at all it is generally present in abundance. It is probably the commonest species of Copepod, though *Cyclops* is the commonest genus, and not infrequently taken without *Boeckella,* especially in slowly-running water; but in swifter water *Cyclops* also is absent, its place being taken by the Amphipod *Paracalliope fluviatilis.*

The aim of the present paper is to record some observations on the living animal, and especially the movements of the appendages, with an attempt to explain the significance of those movements and to point out some relations between structure and function. It is to be regretted that while among the Copepoda so much is known of the dead body, so little is known of the living animal; the difficulties in the way of such studies are lessened in the case of *Boeckella,* for the animal is common, comparatively large, frequently conspicuously coloured, easily cultivated, and docile under the microscope. Similar studies with other species and with *Diaptomus* would be of considerable interest.

The Colour.—Sars (l.c., pp. 50, 54, 56) says that the female is transparently bluish, with red markings, while the male is more pronouncedly red. The writer's observations show that while this is accurate as far as it goes, there is much variation in the colour; specimens from any one pond adhere fairly strictly to a definite colour-scheme, but there is a wide range of variability from different sources; this, however, probably does not imply that there are distinct strains, as the colour seems to depend on age and environmental circumstances, and the related genus *Diaptomus* is known to be very variable.

In some cases adult males and females of *Boeckella* are almost pure white as seen against a black background, the only colour being the red of the eye; but nearly always the genital area of the female is bright red, and the region around the mouth is usually red in both sexes. When the colour-scheme is more elaborate, a comparison of specimens of different sizes from the same locality indicates that the deposition of pigments is in the order named—eye, genitalia, mouth, and though other parts may become coloured these three regions always remain the most intensely pigmented. Sometimes the remaining coloration in the case of the female (possibly in semi-mature specimens only) is a diffused blue throughout the body; but usually the predominant colour is reddish-brown. This appears at an early stage in the dorsal parts of the second, third, and fourth body-segments, and in the posterior foot-jaws; most other parts of the body follow suit, especially the rest of the thorax, the remaining mouth-parts, anterior antennae, and anal furcae, the colour being faintest on the front part of the head, bases of the first antennae, the abdomen (except the furcae, and the genitalia of the female), and the setae. The deepest colour is finally found in the eye, female genitalia, mouth-region, and on the back, where it forms a distinct transverse band on each segment.

A very characteristic feature of the females from a good proportion of localities, especially from muddy water, is the intense inky blue over the ventral parts of the body-segments and on the bases of the legs, with more diffused shades of blue in other parts; the edges of the body-segments are also lined with blue behind each of the transverse brown bands already mentioned. The blending of the blue, brown, and white gives such specimens a particularly beautiful appearance.

Sars speaks of the males as "exhibiting in some places a faint bluish tinge." The writer has seen only very faint indications, and in comparatively few specimens, not nearly as deep as in Sars' figure. Indeed, in those cases where the female has the blue coloration, the colour constitutes a distinct secondary sex character by which the sexes may be readily distinguished, even with the naked eye; the males are brown, the females are brown with blue on the ventral parts. Other secondary sex differences are found in the smaller size of the male, the structure of the fifth pair of legs, the absence of projections on the last body-segment of the male, the number of joints in the abdomen, and the modification of the male right antenna. Females are about three times as numerous as males. Sars says that the maximum size of males and females respectively is 1.67 mm and 2.10 mm; the writer's measurements of 18 females and 8 males gave an average of 1.80 mm and 1.92 mm respectively, the maxima being 1.95 mm and 2.19 mm.

Further General Observations.—The animal is strongly attracted by light, though excited and repelled if the light is too intense. At night the eye, which is median and somewhat ventral, in a pellucid area between the antennae, appears as a conspicuously glistening red spot.

The heart is colourless; it is situated across the junction of the second and third body-segments, closely adjacent to the dorsal wall. The beat is rapid, generally 350-400 to the minute, though as many as 510 have been counted. The eye is in a state of continuous tremulation, and pulsations synchronous with the beat of the heart are noticeable at the base of each of the first antennae, and also backwards through the thorax, affecting the dorsal part of the intestine.

The intestine is yellowish. It performs regular lateral motions, which are not serpentine but extend simultaneously through the length of the animal. There is also a peristaltic contraction, giving a false appearance of constant ingestion. Between the intestine and the body-wall are a number of oil-globules, varying in number and size, but rarely exceeding twenty-four; they are found in young and old, except certain oviferous females. Although these globules might add to the food value of the animal for other organisms, it is difficult to imagine the rapid *Boeckella* being captured.

The spermatophore is pale yellowish, the sperms being contained in an inner sac which, by its variable size, suggests that the very abundant supply of sperms may be drawn upon from time to time. Occasionally it persists after a cluster of eggs has been laid, and extends from the side of the female genital opening to just beyond the ends of the caudal setae. The eggs, which though white in colour are so dense as to appear black under the microscope, are contained in a hyaline sac, and vary up to about twenty in number. The ovary is a double tube lying along the intestine on either side, the two parts approximating above it towards the head.

The projections on the last body-segment of the female are not long enough to protect the eggs, and the latter are not grasped by the fifth feet.

The General Habits and the Movements of the Appendages.— The general habits may be observed with a lens or dissecting microscope, and the finer details may be seen if the animal is mounted in water beneath a supported coverslip; if there is any difficulty in obtaining a lateral view the water should be drained off from some specimens in a watch-glass. As the animal commonly swims on its back in shallow water, views from all aspects may readily be obtained. Carmine is useful to show up the water-currents; chloroform is difficult to apply correctly, and unnecessary as the animal soon becomes sluggish in any case when mounted on a slide.

When a vessel of water containing *Boeckella* is agitated, the animals dart about with excessive rapidity. The flight is so sudden that little more than circumstantial evidence can be adduced to explain the means by which it is brought about; but there can be no doubt but that the anterior antennae are the organs of propulsion. Sars says that the movement is effected by a stroke of the swimming legs with a simultaneous bending forward of the abdomen, but this is the case only with another much less powerful type of progression. The bending forward of the abdomen could not drive the animal forwards, but in the opposite direction, this being the chief method of propulsion among certain higher Crustacea, notably the Macrura; and in the very rapid flights of *Boeckella* any extension of the legs would probably cause a frictional resistance greater than the propulsive action. The position of the legs is such that their use not only drives the animal forwards but tends to force the abdomen up and the head relatively down, and this tendency has to be corrected by the flection of the abdomen as mentioned by Sars. But in the more powerful flights there is no place for such a rudder, which is also necessarily a brake. The fan-like arrangement of the caudal setae furnishes an admirable rudder for turning in a lateral or vertical direction during less rapid flights, and is constantly used for that purpose.

It may be noted that the anterior antennae are so placed that their stroke, unlike that of the legs, drives the animal straight forwards; that their large muscles are such as to give the necessary powerful stroke; that their great length gives them a leverage far exceeding that of any other appendages; that the terminal setae serve to " grip " the water, as it were, in such a way that the fulcrum is the water at their extreme tips; and that the normal attitude of the antennae, which are held almost straight out from the body (except that they bend forwards and outwards for a short distance near the base, and thence slightly backwards), is exactly that which is best suited for a sudden dart at short notice—there is no need for preliminary adjustment. Indeed, they resume their outstretched position so rapidly after a flight that the movement of the animal is somewhat abruptly checked by the consequent friction.

Less powerful darts have already been partly described. The legs are usually held straight forward in a bunched position, and a simultaneous backward flection, with the necessary counter-flection of the abdomen, drives the animal forward for a short distance. Partly, no doubt, on account of the closeness of the legs to one another and the rich provision of setae, there is no continuous paddling such as occurs in the Callianassidae and other higher Crustacea, but by a repetition of the strokes the animal progresses by a series of jerks. The leverage is so small and the stroke so much less effectual than that of the antennae, that the legs actually move backwards through the water, so that they act as levers of the " first order," whereas the antennae are virtually of the " third order." The movement is sometimes and possibly always aided by a movement of the anterior antennae, but even these short darts appear so rapid under a lens, and the antennae regain their position so rapidly, that this is extremely difficult to verify. A slight movement of one antenna is sometimes used to change the direction of motion.

A backward kicking of the legs frequently occurs, without driving the animal appreciably forward; this is sometimes performed by the fifth pair only, or the first, or all together. In some cases at least the result is to free the legs or abdomen of small entangled particles of rubbish. The first pair of legs also sometimes poke food forwards towards the mouth. As will be explained below, the forward position of the legs has to do with the control of the food-carrying current; the fifth pair, however, are useless for such a function on account of their length and the deficiency of setae, and are not held forward in the bunch formed by the others, but are frequently in motion while the others are still. The outermost joints of the fifth pair are very flexible in a lateral direction, and frequently " comb" one another; the limbs may also bend inwards from the base, those of the female becoming momentarily interlocked by the curved hooks on the penultimate joints. The functions, if any, of these movements is not apparent, the special features of these limbs being no doubt concerned with copulation.

The rapid movements effected by the legs and antennae are much less constant than another type which may be described as a paddling movement. This was attributed by Sars to the posterior antennae, which are certainly the chief organs concerned; but the movement is really due to the concerted movement of various mouth-parts, and typically of all. The posterior antennae are remarkably long and muscular, and well provided with hairs and setae, and their consequent leverage and strength is sufficient to drive the animal slowly forwards; the antennae move with extraordinary rapidity, so that the forward movement is a continuous one. It is singularly persistent; the animal may be buffeted or almost deprived of water, but the paddling continues; so that the lack of response to teasing with a brush or other instrument is not a case of " shamming dead," as is commonly the case with *Cyclops,* but a placid refusal to be alarmed. In shallow water, several individuals may meet and paddle against one another; usually they do not trouble to change their course, and soon there may be a mass of paddling animals progressing not at all, or slowly in the direction of the majority, The arrival of a Cladocere makes no difference, the gentle and stately *Boeckella* being unperturbed even by such boisterous and clumsy interruptions.

As will be described more fully later on, the aim of the vibration of the mouth-parts is the creation of a water-current which carries food towards the mouth. The backwardly-directed parts of the mandibular and maxillary palps contribute by beating inwards, and the posterior foot-jaws beat forward in such a way as to deflect the current inwards and forwards again towards the mouth. The curvature of the setae in the direction of the stroke, and the curvature of the limbs themselves (see fig. 1) give power to the main stroke without counteracting its effect during the withdrawal of the appendage for the next stroke. The mouth-appendages move in unison at an exces-

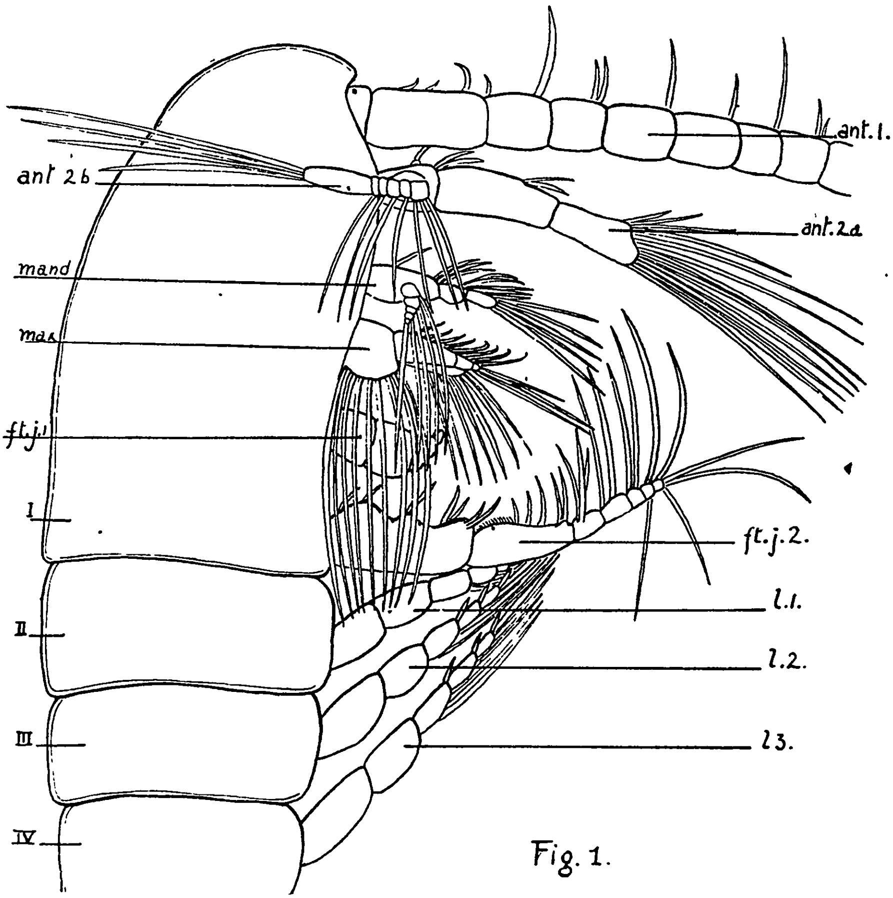

FIG. 1. *Boeckella triarticulata* G. M. Thomson. Lateral view of anterior part. X 100.
ant. 1.—basal part of anterior antenna.
ant. 2a. and *ant. 2b.* primary and secondary branches of posterior antennae, in their usual position.
mand.—mandible.
max.—maxilla.
ft. j. 1.—anterior foot-jaw. The setae are not shown.
ft. j. 2.—posterior foot-jaw, in forward position.
l. 1.-3.—legs.
I.-IV.—body segments.

sively fast rate; although such concerted action might be expected when the controlling nervous system is so simple, it is essential in the case of the posterior antennae and posterior foot-jaws, for the arcs through which they move overlap. The rhythm is transmitted vigorously through all parts of the body, the caudal setae for example showing the vibration, sometimes even to an exaggerated extent. The rate varies somewhat, and also the amplitude of the movements, which in the case of a sluggish animal are reduced to a feeble quivering at the tips.

Commonly the mandibles and maxillae cease action, and at times the second pair of foot-jaws; it rarely happens that the latter are in motion while the posterior antennae are at rest. In the latter case the animal moves slowly backwards; the combined action of these opposing appendages sends the animal slowly forwards; while the posterior antennae alone send it more rapidly forward. All movement periodically stops, as if for a rest, and this also happens when a solid particle becomes entangled in the appendages. The animal is somewhat heavier than water, so that when not paddling it sinks slowly. On account of the anterior position of the posterior antennae, their action supports the head region rather than the abdomen, and (as in the case of a swimmer who paddles on his back with his hands only) the action causes the body to assume a semi-erect position, and the animal rises or falls in the water instead of travelling horizontally, except when in contact with the bottom. To travel forward, the legs or anterior antennae are generally used. The semi-erect position when the animal is hanging in the water may be inclined either forwards or backwards; at the bottom the animal may rest or paddle quite horizontally on its back, or may assume the normal position with the ventral surface undermost and stir up the mud at the bottom with the posterior antennae. To some small degree at least therefore *Boeckella* is a bottom-feeder, though not characteristically so.

The posterior antennae can take up either of two positions. In the one, both branches are directed ventrally and beat backwards, the secondary branch being in front of the primary; both branches then contribute to the food-carrying current. In the other position, which is more frequent, the secondary branch extends upwards over the back, and beats backwards in that position, as indicated in figs. 1 and 2. The structure of these appendages is interesting in view of their function; the secondary branch is unusually long, and is well provided with joints, so that it can readily curve round and pass upwards towards the dorsal surface; it is also provided not only with a tuft of very long terminal setae, like the primary branch, but also with a fringe of strong setae at the "elbow" where the curvature is most pronounced, so that its "grip" of the water is considerably increased. Though the movement of the appendage in this position contributes only indirectly, if at all, to the food-carrying current, its significance is interesting, for whereas a wholly ventral movement tends to raise one end of the animal and thus tilt it up unduly, as in the case of the swimming-legs also, the distribution of the action on both sides of the body by the two branches corrects this tendency.

The steady forward movement may be of value in bringing the animal constantly forward into fresh grazing-areas without the loss of the advantage of the current already set up, as is the case after a rapid dart. The movement is the outcome of numerous factors—the resultant action of the mouth-parts, which partly oppose one another, and the frictional resistance of the anterior antennae, abdominal setae, and body generally. This frictional resistance must be considerable in the case of the anterior antennae especially, either when swimming forward or rising or sinking; this is well illustrated in the case of the male, for the expansion of the modified right antenna increases the friction to such an extent that the animal is deflected to the right. A specimen in which one antenna was accidentally amputated travelled round in narrow circles, the centre being the tip of the remaining antenna. Sars remarks that the anterior antennae serve "apparently as a sort of balancing apparatus." A stroke of the legs, a lateral or ventral flection of

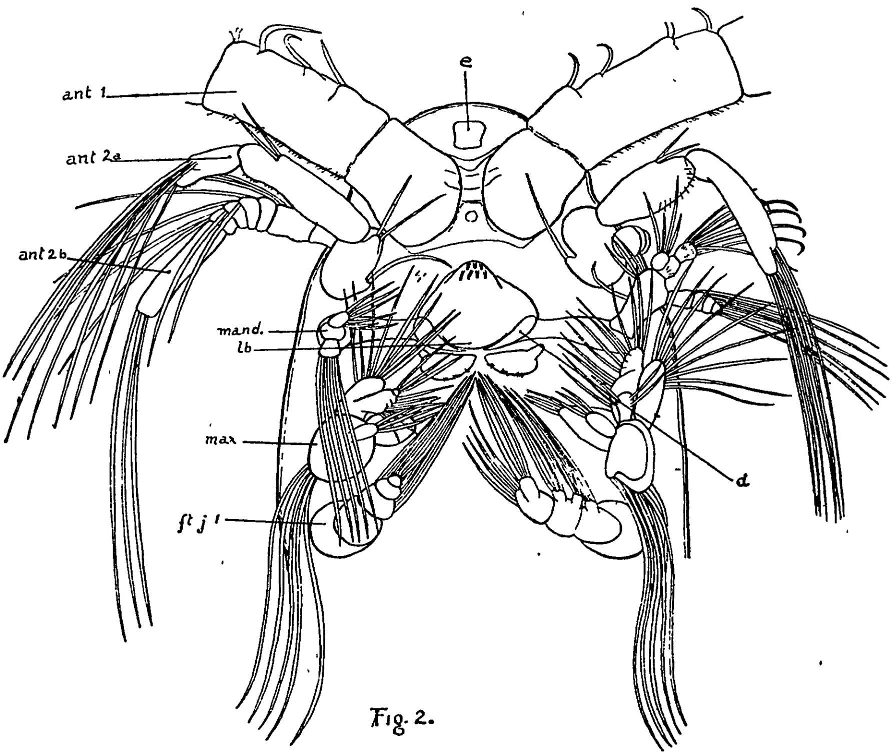

FIG. 2. *Boeckella triarticulata* G. M. Thomson. Ventral view of head region. Lettering as in Fig. 1, also: *e.*—eye. *lb.*—labrum. *d.*—cutting part of mandible. X 100.

The anterior antennae are represented as if cut off short. The left posterior antennae (right side of figure) shows the primary branch folded somewhat backwards, and the secondary branch bent round to the back; the right shows both branches. The posterior foot-jaws, which overlie the others, are not shown. The remaining mouth-parts are in their usual position on the left side of the figure, but show the structure more clearly on the right.

the abdomen, or a slight flick of one antenna, may be used to correct the direction of motion.

The process of food-capture remains to be described. Seen from the ventral surface, the mouth-parts are arranged in an almost continuous circle round the mouth (fig. 2), the only break being anterior to the mouth. The posterior antennae (or usually their primary branches) extend ventrally on either side from a forward position; the mandibles and maxillae arise at the side of the mouth, with branches directed backwards as well as towards the mouth; the anterior foot-jaws point inwards and forwards towards the mouth, and the posterior pair work above them, while in the median line is the bunch of swimming-legs. Part of the water-current which is swept backwards by the posterior antennae is caught by the posterior foot-jaws and deflected towards the body; it is met by the legs, and swirled forwards to the mouth. The length of the legs and their setae is sufficient to bring the tips of the setae to about the same level when held forward in the usual manner. The current is further prevented from passing backwards round the bases of the legs by the anterior foot-jaws and the maxillary palps, and though some does escape in that way, the organs mentioned remove any solid particles and retain them. The backwardly-directed branch of the maxillary palp is a broad disc-shaped expansion, from the margin of which arises a palisade of remarkably long and doubly-curved setae, which pass backwards beyond the foot-jaws. Seen laterally, these setae pass at right angles across the series on the posterior foot-jaws, and form an effective barrier to the escape of solid particles. When the maxillae come to rest, the water passes out somewhat freely through the grating, but not the particles; their effectiveness is illustrated when carmine is added to the water, for they speedily become clogged. The mandible-palps are longer and two-branched, with long and numerous setae. One branch guards the space between the mandibles and maxillae, the other extends towards the mouth, and a sparse fringe of setae stretches forward towards the posterior antennae.

The several functions of the mandibular and maxillary palps—the active beating in order to drive on the water-current, the poking of food to the mouth, and the retention of particles from the escaping water—are difficult to distinguish, especially as they are somewhat interfered with under the microscope. Those setae which point to the mouth, and especially those of the posterior foot-jaws, which extend to the opening of the funnel, are capable of directing the movement of solid particles to the mouth, whatever the course of the water or the action of the limbs themselves. The dental areas of the mandibles are held vertically between the labrum and the corresponding parts of the maxillae; the latter are triangular structures held horizontally, forming the funnel-like entrance to the mouth proper. The inner parts of the mandibles and maxillae do not move in unison with the palps and other mouth-parts, but more slowly, though they are capable of vigorous action when necesary.

Although there is a certain unavoidable waste of energy in that much of the water-current swirls past beyond reach, the mouth-parts are admirably constructed for the functions they fulfil. The legs are well provided with ciliated setae, probably beyond their requirements as propulsive organs, but effective in causing the necessary eddy in the water-current. The posterior foot-jaws, whose continuous action is essential for food-capture, are particularly strong, and are long enough to reach well out into the water-current; they are bent forward, and throughout their length have a row of cilia of which the outermost are directed outwardly into the current, while the more basal ones point downwards and forwards in the direction in which the current is to travel. The anterior foot-jaws, which are passive except for their poking-action, are smaller, but have numerous setae which extend inwards and forwards right into the funnel-aperture. The differentiation of the palps of the maxillae and mandibles into two parts—inwardly-directed and lateral respectively—has already been noted. The labrum rises like a wall at the inner end of the funnel, and beyond it is a median projection carrying a few short spines curved towards the mouth in such a way as to catch particles which may sweep across the labrum. On the basal joint of the posterior antennae is a long curved spine which may perhaps serve to force such particles back again within reach of the other mouth-parts.

Although there is always a danger of misconception in such interpretations as have been attempted in this paper, the investigation has shown, to the writer at least, that the appendages of such creatures as *Boeckella* have a further interest beyond their use in distinguishing new species.

While this article was in the press, I received, through the kindness of Dr. V. Brehm, of Eger, a copy of his account of the Copepoda (issued May 15th, 1927) in Vol. 3 of the "Handbuch der Zoologie," edited by Dr. W. Kükenthal. As if to anticipate my remark above, a brief statement of the feeding mechanism of *Diaptomus* sp. is therein given (pp. 467—8), and the illustrations (figs. 429 and 430) are very similar to those in the present paper. Dr. Brehm acknowledges as the source of his figures and information on this subject a paper by O. Storch and O. Pfisterer ("Der Fangapparat von *Diaptomus*," Zeitschr. f. wissensch. Biol., Abt. C, Bd. 3, 1925), and though I have not seen the original paper a few comparisons may be made.

For the most part, the account is similar to that given above in the case of *Boeckella*, but there are some differences, such as the rate of vibration of the mouth-parts. In *Diaptomus* the rate is "more than 300 per minute," while in *Boeckella* it is more than twice as great, and perhaps as much as 1,000 per minute.

The most striking point, however, is that although the footjaws are figured, no mention of them occurs in the text. If a forward beating movement occurred, as obvious and important as that in *Boeckella*, it could hardly be overlooked; the setate are very much shorter, and quite a different explanation is given for the forward diversion towards the mouth of the inner part of the backward water-current. In *Boeckella* I have attributed this to the bunch of swimming-legs and especially to the stroke of the posterior foot-jaws, but in the case of *Diaptomus* the only cause mentioned is the suction of the backward current as it streams along the sides past the mouth-parts; this suction withdraws water from the median region, and the replacement of this causes the steady forward flow towards the mouth. This forward current, which is distinguished from the general "Lokomotionsstrom" as the "Speisestrom" or food-current, passes forward within the median passage defined by the anterior footjaws, is drawn through the filtering setae of the latter, and is sucked backwards again as an "Aspirationsstrom" or exhalant current, through the "exhalant gap" between the maxillae and the anterior footjaws.

In *Boeckella* such a clearly-defined exhalant current was not observed, and this difference is reflected in the different arrangement of the mouth-parts. In *Diaptomus*, for example, the labrum is figured in lateral view as extending outwards as far as the end-segments of the mandibles and maxillae, whereas in *Boeckella* it is not even visible from that aspect. Such an enlargement would not only arrest the forward current at the level of the mouth, but also, if the exhalant current depends on suction, would be necessary to prevent a backward flow of unstrained water across the mouth. If there is a genuine suction in the case of *Diaptomus*, it must undoubtedly be present in *Boeckella* also; but in the latter the current is not dependent upon suction, but is forced forward by the stroke of the posterior footjaws. For this reason, no such expansion of the labrum is necessary to shield the mouth-region from the general backward current, and likewise the forward current is able to pass outwards at any point, even anterior to the mouth.

In the account and figures of *Diaptomus* it is insisted that while the posterior antennae, mandibles, and maxillae are situated forward in a group, there is a wide interval between them and the anterior footjaws, forming an exhalant gap. This is certainly not the case in *Boeckella* (see fig. 2), nor is there a clearly-defined channel leading to the small interstice that does exist. In *Diaptomus* the long backwardly-directed setae of the maxillae are much more strongly curved; they are not spoken of as assisting the anterior footjaws in straining the food from the current, but merely as aiding in the creation of the general backward current. To account fully for these differences, and especially to elucidate the mystery of the posterior footjaws in *Diaptomus*, the full text of Storch's paper would be necessary.