TRANSACTIONS
OF THE
ROYAL SOCIETY OF NEW ZEALAND

ZOOLOGY

VOL. 6 No. 8 APRIL 9, 1965.

The Biology of the Genus *Arthritica*

By W. F. PONDER,

Zoology Department, University of Auckland

[*Received by Editor, 23 March 1964.*]

Abstract

THE biology of three species of leptonid bivalve included in the genus *Arthritica* is discussed with particular reference to their mode of life. *A. crassiformis* lives on the large rock-boring pholad *Anchomasa similis*, in what appears to be a commensal relationship. External appearance and ciliation of the mantle cavity of *A. crassiformis* is described. *A. bifurca* is shown to be free living and closely similar to *A. crassiformis* in structure. A new species is described which lives commensally with the sea-mouse, *Aphrodite australis*, in deep water.

INTRODUCTION

THE superfamily Leptonacea consists of a large number of tiny bivalves whose habits and mode of life are still imperfectly known. Many of these species which have been studied in life have been found to live as commensals with larger burrowing invertebrates, including echinoderms, worms, and crustaceans. Within this assemblage the family Leptonidae is the most imperfectly known. The following account describes some aspects of the biology of the species belonging to the New Zealand leptonid genus *Arthritica*.

Arthritica (Finlay, 1927, p. 463) was originally proposed to cover *Kellia bifurca* and certain undescribed fossil species. Powell (1933a) discussed some aspects of classification, including the fact that so called characteristic limy patches on the inner side of the adductor scars are by no means always seen. This was the main character, according to Finlay (1927), that distinguished the genus. Powell, however, retained the generic name, presumably because the group is compact and distinctive, but no generic description has hitherto been provided. The main conchological features are:—

1. Quadrate shape with relatively short anterior and posterior ends.
2. Anterior end slightly longer than the posterior, produced and acutely rounded below.
3. Surface of shell with minute irregular linear wrinkles or smooth.

Published by the Royal Society of New Zealand, c/o Victoria University of Wellington, P.O. Box 196, Wellington.

4. One cardinal and two lateral teeth.
5. External and internal ligament present (Suter, 1913, states that there is no external ligament in *A. bifurca*).

Arthritica occurs first in the Miocene, there being six fossil species.

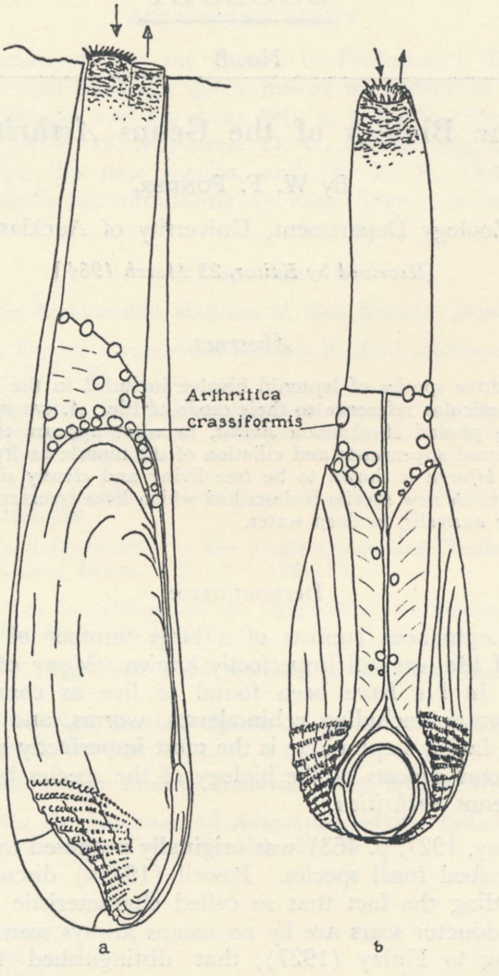

Fig. 1.—(a) Lateral view of *Anchomasa similis* (Gray) in its shaft with *Arthritica crassiformis* Powell attached. (b) The same in ventral view removed from shaft.

Arthritica crassiformis Powell, 1933

1933. *Arthritica crassiformis* Powell, *Proc. Malac. Soc. Lond.*, 20: p. 195, Pl. 16, figs. 2, 3.

A. crassiformis was originally described by Powell (1933a) without any indication of its habits or behaviour in life. I have recently found these bivalves living attached externally to the common rock-boring pholad bivalve *Anchomasa similis* (Gray), this being the first record of a Leptonacean associated with another lamellibranch. The host bivalve is shown *in situ* (Fig. 1a) in its bored shaft in low tidal soft sandstone or papa, with a group of *Arthritica* attached. Their characteristic position is between the narrowly gaping lower margins of the shell valves from the base of the siphon forward to a point just behind (i.e., above) the circular pedal gape (Fig. 1b). They form a very temporary attachment to the fused integument of the lower mantle edges by means of a few slender byssus threads. They obtain some protection from abrasion while the *Anchomasa* is burrowing by sheltering between the upstanding margins of the shell valves. About a dozen specimens are commonly found on an adult *Anchomasa,* but this number varies and juvenile *Anchomasa* rarely harbour the commensal at all. Wherever I have found *Anchomasa* boring, *Arthritica* has been present. The following localities are those at which *Arthritica* has been found attached to *Anchomasa*:—Kenepuru Sound, Marlborough (W.F.P.); Maheno Bay, Wellington (M. K. Mestayer (type locality)); Weymouth; Manukau Harbour; Auckland area (Takapuna and Narrow Neck) (W.F.P.).

Arthritica has never been observed on any other rock boring species such as *Pholadidea tridens* (Gray), *P. spathulata* (Sowerby), and *Zelithophaga truncata* (Gray) or on any of the quite numerous secondary invaders and nestling species occupying the rockborer's burrows.

External Appearance and Movement: Powell's conchological description (1933) needs little supplementing, the shell (Fig. 4e) being yellowish white, thick and solid in contrast with the other species of the genus and with the fragile shells of most leptonids, relatively compressed and lens-shaped in section. The largest specimen seen reached 4.55 (height) x 5.35 (length) mm, but the usual size is about 3.4(height) x 4.0 (length) mm. The sculpture is of well marked but widely spaced growth lines with prominent but minute, undulating wrinkles which run concentrically but do not always coincide with the growth lines. The umboes and central regions of the adult valves often show strong abrasions, which are usually accompanied by a thickening of the shell, and are probably caused by the movements of the host in its shaft. A few specimens have the shell stained brownish black, probably by leaching and depositing a ferric oxide in a way rather common among the Leptonacea and other small bivalves.

The shell fully covers the contracted animal, which, however, readily expands in a dish of seawater to expose the semi-transparent white foot and mantle edges (Fig. 2a). The foot, when extended, is as long as the shell, being deep but not very thick, pointed in front, with a well formed posterior heel. The byssus gland is prominent, appearing towards the posterior end of the foot as an opaque-white oval patch, its aperture just in front of the heel. A narrow ventral groove runs forward from the byssal gland about half way along the foot. Towards the tip of the foot is a pair of opaque white glands (" lateral organs ") with apertures facing slightly forward to open on to the side of the foot. The function of these organs is not known. Simple lateral glandular tracts on the foot have been described in *Lepton* and some galeommatids (Pelseener 1911) but no reference can be found to a structure of the type seen in *Arthritica*. The two other New Zealand species in this genus also have these lateral pores.

The animal begins to move by gliding forward the anterior part of the foot, while the shell remains stationary. The foot then appears to affix itself by its lower edge to the substratum and the shell is hauled forward upon it, the anterior end of the shell rocking up in the process. The anterior part of the foot is extended again, followed by the forward protraction of the shell. The shape of the foot remains rather constant during these movements, which are fairly rapid and give the appearance of regular gliding.

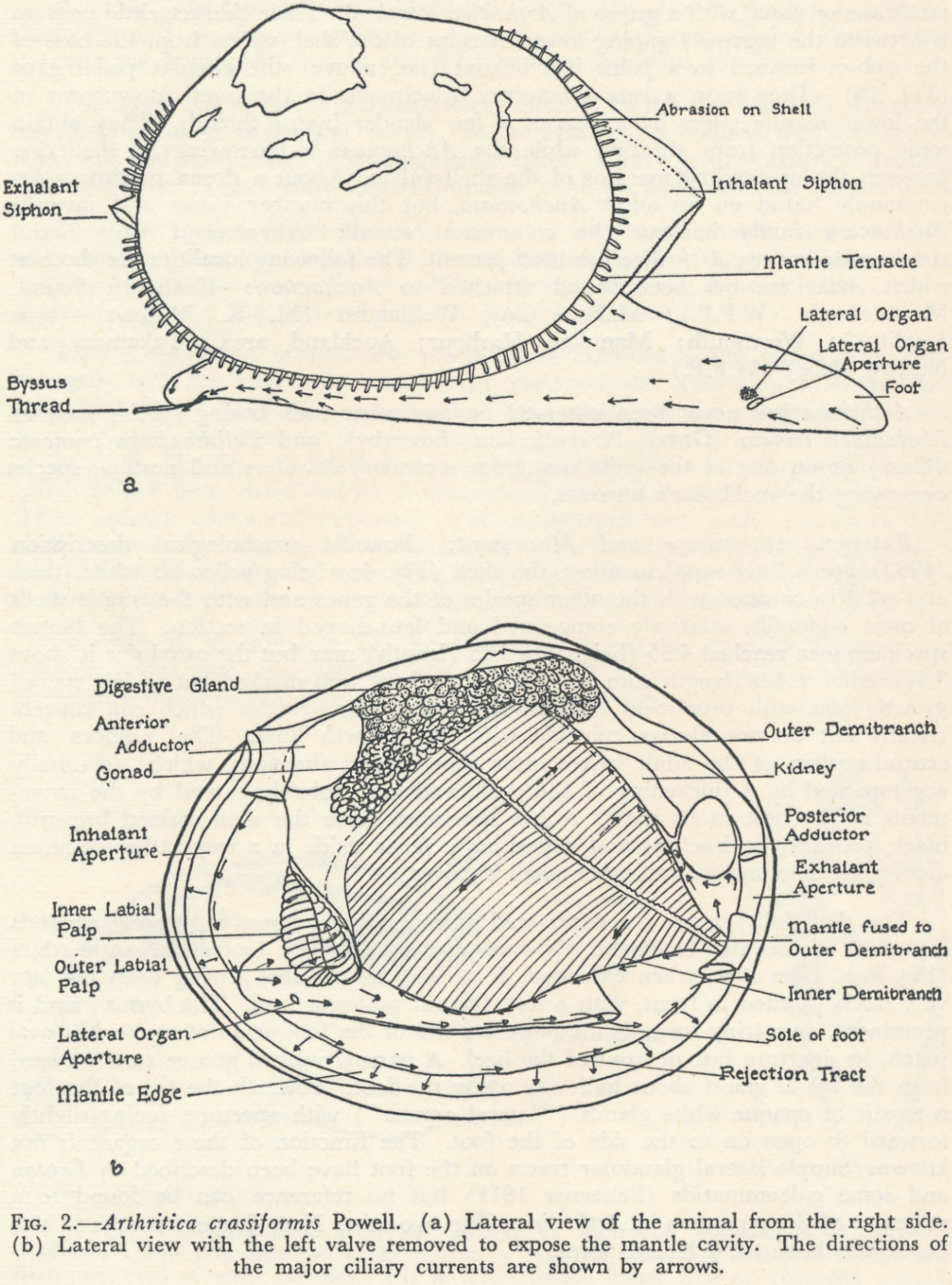

FIG. 2.—*Arthritica crassiformis* Powell. (a) Lateral view of the animal from the right side. (b) Lateral view with the left valve removed to expose the mantle cavity. The directions of the major ciliary currents are shown by arrows.

The mantle edges narrowly extend beyond the edge of the shell as the animal is moving, and just behind their naked margin a fringe of short, slender tentacles projects around the edge of the shell. Each of these bears a tuft of stationary cilia at its tip. The inhalant aperture, as is characteristic of the leptonids, is anteriorly placed, being overarched by a wide, hood-like projection of the free mantle margin, but openly continuous below with the long pedal gape. The exhalant siphon lies directly behind, being closed below by fusion of the mantle margins, these projecting above it to give the appearance of a large triangular tentacle.

The mantle cavity: The disposition of the organs of the mantle cavity (Fig. 2 b) was studied to ascertain the structure of the gill and the direction of the ctenidial and cleansing currents. A full description of the pallial organs and other structures will be given in a later paper, presenting an anatomical account of certain New Zealand leptonaceans.

The gill consists of two demibranchs of which the inner one is by far the larger, and has both ascending and descending lamellae, and the outer, no more than a third the size of the inner, having a descending lamella only, with its ventral edge fused to the inner surface of the mantle. Just below the exhalant aperture, both demibranchs narrow to a point and are fused to the mantle. The ascending lamella of the inner demibranch is fused along its whole length to the visceral mass. The free margin of the inner demibranch carries a food groove. The closed cavity, triangular in section, between the outer demibranch and mantle, and the space between the ascending and descending lamellae of the inner demibranch, are used as broad pouches. This is an arrangement commonly seen in the Leptonacea. The ciliation of the ctenidium is straightforward and follows the normal leptonid pattern (Popham, 1940). Guarding cilia occur along the food groove on the inner demibranch. Cilia sweep particles on the outer demibranch up its inner face into a dorsal groove between the two demibranches. It then passes to the palps along the anterior edge of the gill. On the inner demibranch particles are swept down both inner and outer faces to the ventral food groove. Tufts of guarding cilia on the edge of the descending lamella prevent the larger particles entering the groove. These very long cilia do not beat rapidly, the only movement being a slight vibration. The labial palps are conspicuously larger than those described by Popham (1940) for some other species in the Leptonacea. The sorting mechanism differs from the other species in certain details. It consists of two main series of cilia on each palp, one found on the crests of the numerous ridges and the other in the grooves between the ridges (Fig. 3). The outer palp has ridges on its inner face only, and particles are swept across these towards the mouth. The inner palp has orally directed cilia on the ridges on the outer face and, unusual among bivalves, posteriorly directed cilia on its inner ridges. On both faces cilia in the grooves sweep heavy particles to the outer palp, where they are passed down the grooves on that structure to its edge, and from there are rejected on to the mantle where they are passed posteriorly. Cilia on the lips carry food into the mouth. Large particles are sometimes dislodged from the palps by flicking motions which occur intermittently.

The cleaning cilia of the visceral mass are poorly developed and the mantle is hardly ciliated except in the groove inside the thickened marginal lobe (Fig. 2b and 3) where there is a strong rejection current running posteriorly carrying the mucus-bound waste from the palps to a point at the end of the pedal opening. Sometimes this well-developed rejection tract is marked by a ridge on the mantle edge. Weaker outward rejection occurs around the entire mantle edge bordering the inhalant pedal aperture. There does not seem to be any ciliation of the mantle edge at the exhalant aperture. Occasionally, when large particles become lodged in the inhalant siphon, the adductors contract forcing water back through this aperture and so removing the obstruction. Often mucus-bound waste is expelled in this manner from the posterior portion of the mantle cavity. The foot has a posteriorly directed cleansing current along the lower part of its lateral region. Cilia on the ventral anterior portion beat upwards to meet this tract.

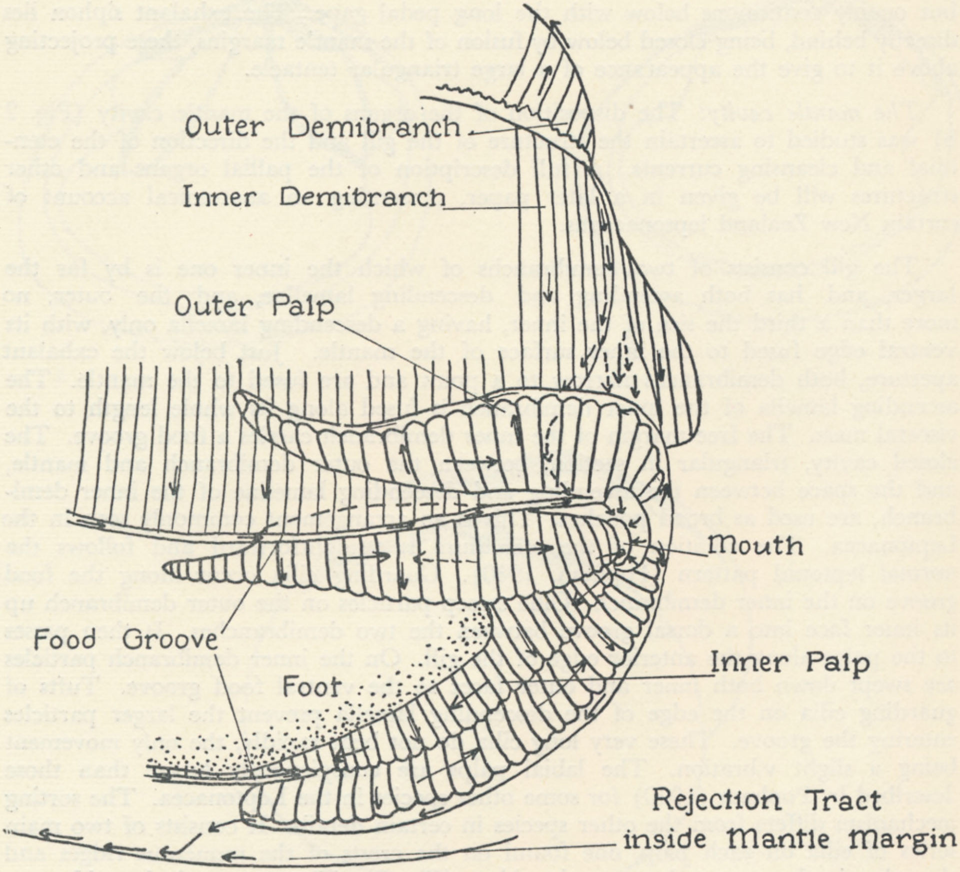

Fig. 3.—*Arthritica crassiformis* Powell. View of the anterior end of the animal showing the gills and the palps from the right side and ventrally. The ciliary tracts are shown by arrows. The dotted arrows represent currents beneath overlying structures.

Shelled larvae are incubated in the brood chambers described above. Many hundreds were extracted from specimens collected in late February and early March at St Leonard's Point, Takapuna, though the breeding season is probably a good deal longer than this. All the larvae were at about the same stage of development, the size being about 0.073mm high and 0.109mm long. The larvae had a velum, and on artificial liberation could swim well even at the earliest development of the shell. No specimens were observed incubating larvae past the prodissoconch stage. Though not yet taken in the plankton and never naturally liberated in the laboratory, there seems no reason—particularly from their large number and the small space available for growth—to doubt that they have a free swimming distributive phase of some duration.

Discussion

Arthritica crassiformis has never been found apart from *Anchomasa* and so far as I have found always accompanies some individuals of the larger borers in any population examined. The relationship between the two bivalves is presumed to be commensalism, with benefits conferred on *Arthritica* and with no apparent effects on the pholad. *Arthritica* apparently obtains a high degree of protection in the burrow and though there is no direct access to water currents drawn in by the pholad's inhalant siphon, it has indirect access to this through the water forced regularly out of the pedal openings. The main source of food for *Arthritica* would appear to be, however, the rich detritus naturally subsiding into the pholad burrow and settling around the base of the siphon. *Anchomasa* may receive a certain benefit by possible cleansing activities of the smaller bivalve.

Various problems are presented by this mode of life, notably the recruitment of the population in its special habitat. Possibly many young *Arthritica* remain within the burrow to take up attachment in the same population as their parent; but colonization of new burrows must be facilitated by the appreciable gap left between *Anchomasa* and its burrow wall. The large number of larvae produced suggest there is a high degree of hazard. Some may be caught by the inhalant current of the host, either leaving one burrow or entering another. Larvae removed from the parent show a strong negative geotropism swimming upwards in a long, narrow cylinder, regardless of the position at which a light is presented. In a cylinder laid horizontally they show, however, a weaker positive phototropism, moving towards a spot of light placed on the cylinder. Both of these reactions would allow the larvae to leave the parent burrow on release from the brood pouch. The adults show no clear cut reaction to either of the stimuli of light or gravity. At the settling stage the larval reaction would presumably be reversed and be combined with a reaction to a specific host stimulus. No such reaction has been described yet for the leptonacean larvae, but Morton (1962) has shown a positive chemotactic attraction by adults of *Montacuta ferruginosa* to its heart urchin host.

The larger pholad *Anchomasa* would seem to present certain physical advantages not found in the other species. First the shell is larger and the ventral gape between the valves is more spacious, allowing the commensal enough room to nestle and escape abrasion. In addition, *Anchomasa* has been found to fit considerably more loosely in its burrow than the other species. In *Pholadidea* moreover, the shell has a cup-like posterior extension, horny in *P. spathula* and calcareous in *P. tridens,* which effectively closes the opening around the siphons and precludes any possible entry of spat. The mode of boring by acid secretion in *Zelithophaga* and the formation of a cone of detritus, must make the tightly fitting burrow of the date mussel even more unhospitable.

The chemo-response to a specific host stimulus is suggested by the absence of *Arthritica* from burrows in which empty, but fresh, *Anchomasa* valves are found. Only a few dead valves have been found in such burrows which generally silt up rapidly, perhaps an additional reason for the exclusion of *Arthritica.*

Among the modifications of *Arthritica* for a commensal life with a borer in soft rock are the heavy compressed shell and the enlarged palps allowing for the efficient sorting of the large amount of detritus entering the mantle cavity. The efficiency of the palps may also be reflected in the reduction of the general cleansing ciliation of the mantle and visceral mass, and the concentration of waste rejection in the single mantle tract. Small size, efficient mobility, temporary byssus fixation, and larval incubation until they are freely mobile, as well as the anterior inhalant aperture are all pre-adaptations equipping leptonacean bivalves for a commensal mode of life with burrowing animals.

Arthritica bifurca (Webster, 1908)

1908. *Kellia bifurca* Webster, *Trans. N.Z. Inst.* XI: p. 257, Pl. 21, figs. 24–29.

1913. *Erycina bifurca* Suter, *Manual of the N.Z. Mollusca,* p. 921, Pl. 53, figs. 9, a.

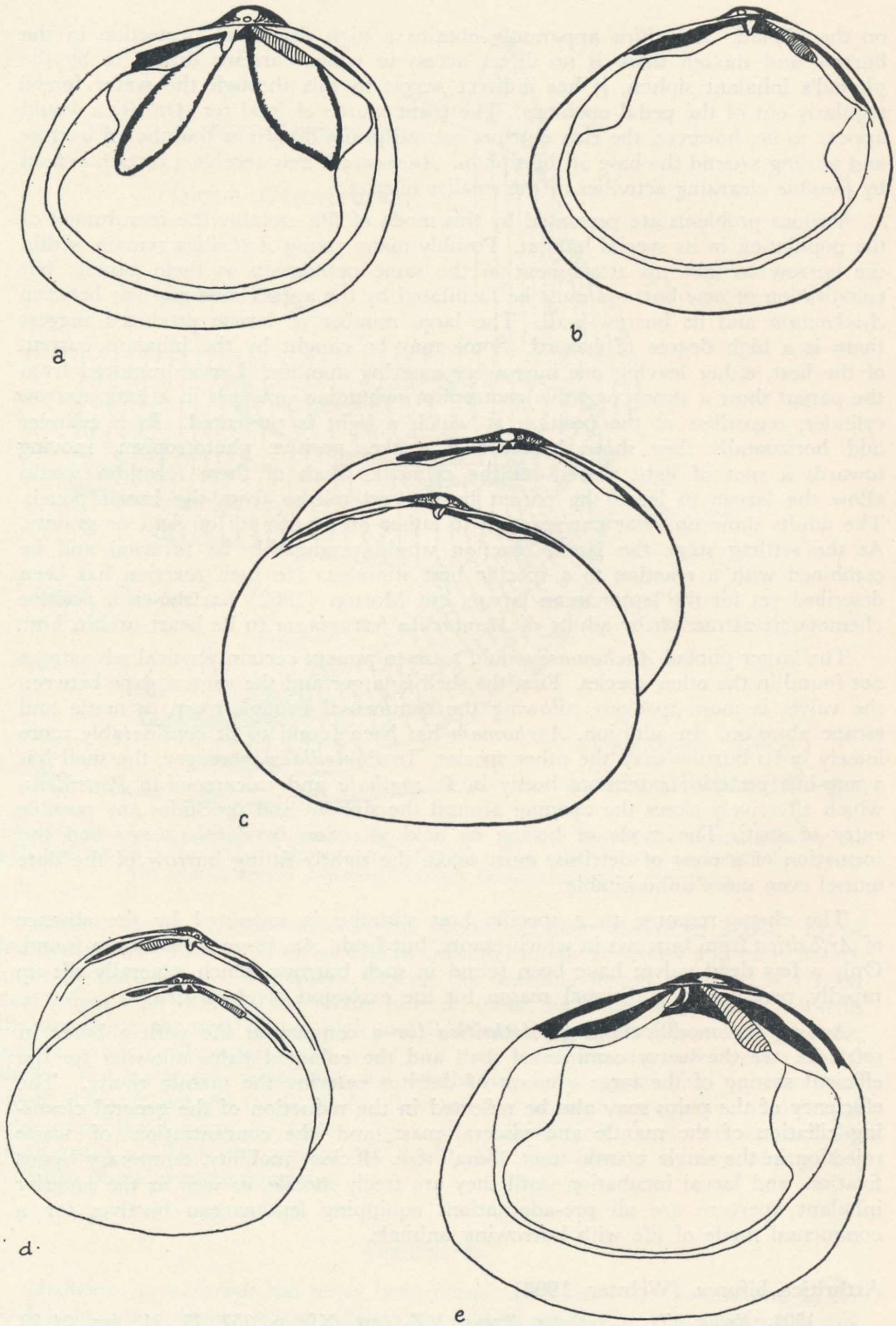

Fig. 4.—*Arthritica bifurca* Webster. (a) Right valve of the holotype (L.3.6mm). (b) Narrow Neck, Auckland. Under a stone. Right valve. (L.3.6mm). (c) Waikanae Beach near Wellington. Left and right valves. (L.4.1mm).

A. hulmei n.sp. (d) Holotype. Left valve. (L.3.3mm). Paratype. Right valve. (L.3.35mm). *A. crassiformis* Powell. (e) Manukau Weymouth, Manukau Harbour. Right valve. (L.3.48mm).

1913. *Lasaea neozelanica* Suter, *Manual of the N.Z. Mollusca,* p. 927, Pl. 54, fig. 1.

1926. *Arthritica bifurca* Finlay, *Trans. N.Z. Inst.,* Vol. 57; p. 463.

1933. *Arthritica bifurca* Powell, *Trans. N.Z. Inst.,* Vol. 63: p. 151.

A. bifurca is a free living species which usually occurs in mud or muddy sand from low tide to fairly deep water, though Dell (1956) does not record it among the "Archibenthal Molluscs" from over 100 fathoms. The shell is distinctive, Suter (1913) giving a good description. Webster's type is refigured here (Fig. 4a). It is thin and finely concentrically wrinkled like *A. crassiformis,* but the hinge line is much narrower than that species. The so-called characteristic limy patches on the adductor scars occur in a minority of specimens and these are usually from fine mud. The shape of the shell and the strength of the hinge and sculpture show some ecological and, perhaps, geographical variation. A specimen of the large, ovate, inflated shell usually found in sandy conditions is figured (Fig. 4c) for comparison with the typical form. An intermediate shell is also figured (Fig. 4b) which is similar to the type of the synonom *Lasaea neozelanica* Suter, (Powell 1933). However, full analysis of these variations should await more intensive collecting.

The morphology of the animal is very similar to that of *A. crassiformis* in external features, ciliation of the mantle cavity and gross internal anatomy, and will, therefore, not be discussed further.

Little is known of the mode of life of *A. bifurca* except that it can be obtained burrowing shallowly in mud and muddy sand. It does not seem to be associated with any " host " species* as are the other two members of the genus. Occasionally specimens are collected under stones at low tide (Narrow Neck, Auckland) being fixed by a few byssal threads. *A. bifurca* has been observed to completely bury itself in mud with no visible connection with the surface. It is thus probably a deposit feeder, and has large palps like those associated with deposit feeding in the Tellinacea (Yonge, 1950). If *A. crassiformis* arose from such a deposit feeding stock its large palps might be similarly explained.

Arthritica hulmei n.sp. (Fig. 4d)

Shell thin, smooth and shining, semi-transparent, subovate, fragile, slightly longer than high. Colour yellowish-white, imparted by a thin, glistening, iridescent, persistent periostracum. Beaks small but prominent, inclined forwards with a small, smooth prodissoconch. Anterior portion about a quarter as long again as posterior, its dorsal margin sloping to the anterior end, which is rather narrowly rounded. Posterior end more broadly rounded. Main sculpture of faint concentric growth lines of irregular strength, but with transmitted light, faint radial sculpture visible. Hinge typical of genus, but the hinge line narrower than in *A. bifurca.* Right valve with a short, stout anterior lateral tooth, the valve edge thickened above it. Immediately in front of beak is a peg-like cardinal tooth with a socket below beak, corresponding to left valve's cardinal. Behind beak is a moderately well developed internal ligament, a weak external ligament, and a long, thin lateral tooth, with dorsal edge of valve thickened above it. Left valve resembles right, but has cardinal tooth placed immediately below umbo, and corresponding socket for cardinal or right valve in front of it. Muscle scars not clearly distinguishable in the fresh shells.

Length 3.30mm. Height 2.725mm (holotype).

Length 3.35mm. Height 2.75mm (figured paratype).

---

* Mr R. G. Wear has recently obtained *A. bifurca* in what appears to be a commensal relationship with *Pectinaria australis,* a mud burrowing, tubicolous polychaete.

Locality: Dredged in Cook Strait off Island Bay (exact locality unknown). Holotype and the figured paratype in the Geological Survey, Lower Hutt. Paratypes in the Auckland Museum and the Dominion Museum, Wellington.

The specimens of the new species were collected by the late Mr S. G. Hulme of the New Zealand Geological Survey, Lower Hutt, who realised that the species was new, and the interest of its commensal habit. I have great pleasure in naming it as a tribute to his careful and enthusiastic work on Mollusca and Foraminifera.

The new species differs from *A. bifurca* in its proportionately larger anterior end and more rapidly descending dorsal margin, weaker hinge and absence of definite sculpture. *A. crassiformis* differs further in being heavier with a much thicker hinge (c.f. Fig. 4d with Figs. 4a, b and c, and 4e).

Fifteen specimens of the new species were obtained living, apparently commensally, with the large polychaete worm, the seamouse, *Aphrodita australis* Baird measuring 62 x 26mm. The specimen had been somewhat disarranged when it was received and several of the bivalves were displaced. Their probable arrangement is shown in Fig. 5b. A detailed anatomical investigation was not possible as the animals had been dried before I obtained them and consequently had shrunk. Those animals which still appeared to be undisturbed were under the elytra with their ventral edges uppermost and attached to the inner surface of the elytra by a few fine byssal threads. In most cases the position of an *Arthritica* was marked by a fairly deep depression in the underlying soft integument of the host (Fig. 5a).

Anatomical investigation of the animal revealed the essential features: an anterior pedal pore, two demibranchs, one double and one single, a well formed heel and a byssal groove in the foot and an anterior siphon.

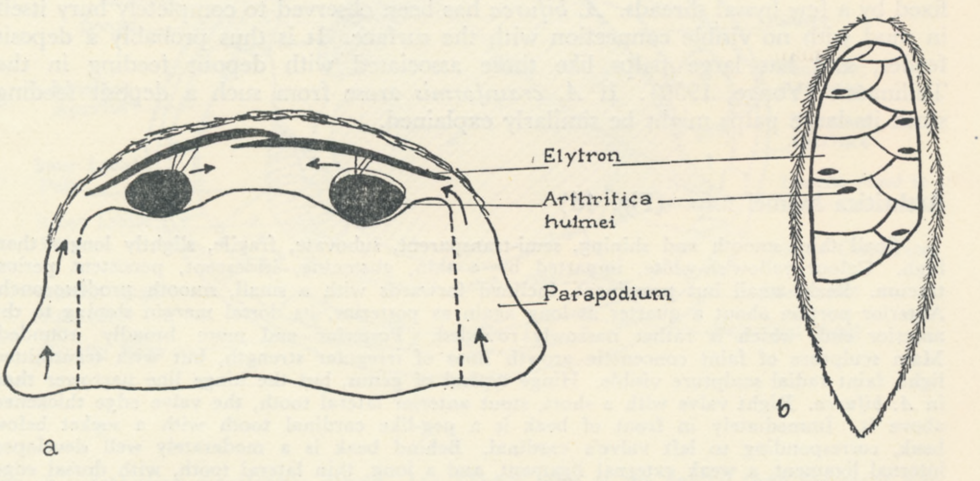

FIG. 5.—(a) A diagrammatic transverse section of *Aphrodita australis* Baird, showing *Arthritica hulmei* n.sp. attached to the elytron by byssal threads. The arrows show the most likely directions of water currents. (b) A diagrammatic dorsal view of *Aphrodita australis* Baird, with the felt cut away to show *Arthritica hulmei* in position under the elytra which are drawn as if transparent.

It is not difficult to see the advantages to the bivalve of such an association. *Arthritica* lies in the respiratory stream of the animal and thus obtains food and protection. Though it was not altogether certain how the bivalves were orientated in life they appeared to have their ends pointing to the sides of the *Aphrodita,* that is facing towards the water current. Body movements of the host drive water into the cavity between the elytra which are then depressed, expelling water at the posterior end of the worm. That the bivalves should be attached upside down can be explained by assuming that this position would allow the maximum freedom for entry of the inhalant current seeing that they lie in a relatively deep depression.

One specimen contained incubated larvae at the prodissoconch stage, and larvae, if liberated from the mantle cavity as swimming veligers, would probably pass out of the host with the respiratory stream. How the new host is located is unknown, but the young bivalves may possibly enter by chemotaxis in the inhalant stream. A juvenile measuring 1.05mm in length was amongst the specimens suggesting settlement at an early juvenile stage.

After the above was written two juveniles and two adults of this species were found attached to a specimen of *Aphrodita australis* from off Portland Island, Hawke's Bay, 39° 42.2′ S., 177° 28.8′ E., dredged in 42 fathoms by the New Zealand Oceanographic Institute (Station C826). One specimen showed ferric oxide staining.

DISCUSSION

The Leptonacea are a large group of conchologically rather featureless genera and species. Until satisfactory anatomical work is carried out the systematic position of many genera will remain in doubt. The genus *Arthritica* is clearly a member of the family Leptonidae as defined by Pelseener (1911). The tentaculate mantle margin, double ctenidium and lack of shell reduction when compared with most galeommatids, are characters shared by all the members of the family. The characteristic morphological features of the genus are as follows:—

1. The mantle tentacles are short and of equal length.
2. The mantle edges do not overlap the shells.
3. The foot is large but is not capable of great elongation, tending to remain spread along the whole ventral margin when the animal is crawling. It has a well formed posterior heel and long byssal groove.
4. The peculiar lateral pedal apertures leading to a glandular or sensory part of unknown function.
5. The anterior inhalant siphon is hood-like.
6. The labial palps are notably larger than those of other leptonacids.

Primitive features of the genus include the well developed hinge and completely closed shell, small mantle tentacles and absence of any reflection of the mantle over the shell. *Arthritica* also shows several specialised structures including the foot which has departed from the primitive digging " tongue " of " normal " lamellibranchs. The peculiar lateral pedal pores are undoubtedly specialized as is the well-developed anterior siphon.

The presence of free living and commensally associated species within the same genus showing very similar shells and with few (if any) noticeable morphological differences points to a relatively recent evolution of commensalism.

Incubation of larvae has been observed in *A. crassiformis* and *A. hulmei* and probably occurs in *A. bifurca* also. Incubation is a deep-seated feature of the Leptonacea enabling them to live in highly specialised habitats, because their young will not stray far away. One group, the Erycinidae have even developed a high tidal form, *Lasaea,* which incubates its young to a stage where they can crawl, thus elminating the need for a planktonic stage.

Commensalism is not a common mode of life for New Zealand leptonaceans, the galeommatid *Scintillona zelandica* (Odhner) (see Morton, 1957) being the only other known commensal bivalve. It is associated with the mud burrowing holothurian *Trochodota dendyi.* Further investigation, however, will undoubtably add to the list of New Zealand commensal bivalves.

ACKNOWLEDGMENTS

In particular I must express my thanks to Professor J. E. Morton for his inspiration, guidance and kindness given me as a student in his department at the University of Auckland, and his great help in preparing the manuscript. I am also very grateful to Dr A. W. B. Powell, Dr C. A. Fleming, the latter giving me permission to describe the new species, and Dr R. K. Dell, for reading the manuscript, but especially for stimulating my early interest in the Mollusca.

REFERENCES

DELL, R. K., 1956. The Archibenthal Mollusca of New Zealand. *Dom. Mus. Bull.,* 18.

FINLAY, H. J., 1927. A Further Commentary on New Zealand Molluscan Systematics. *Trans. N.Z. Inst.,* 57: 320–485.

LEYBORNE POPHAM, M., 1940. The Mantle Cavity of Some of the Erycinidae, Monticutidae and Galeommatidae with Special Reference to the Ciliary Mechanisms. *Journ. Mar. Biol. Ass. U.K.,* 24: 549–586.

MORTON, J. E., 1957. The Habits of *Scintillona zelandica* (Odhner) 1924. *Proc. Malac. Soc.,* 32(5): 185–128.

——— 1962. Habit and Orientation in the Small Commensal Bivalve Mollusc *Montacuta ferruginosa. Animal Behav.,* 10(1–2): 126–133.

PELSEENER, P., 1911. Les Lamellibranchs de l'Expedition du Siboga. Partie Anatomique. *Siboga Expeditie Mon.* 53a Leiden.

POWELL, A. W. B., 1933. The High Tidal Mollusca of Rangitoto Island. *Trans. N.Z. Inst.,* Vol. 63: 144–152.

——— 1933a. On Five New Zealand Species of Recent New Zealand Mollusca. *Proc. Malac Soc. Lond.,* 20: 194–206.

SUTER, H., 1913. *Manual of New Zealand Mollusca.* Govt. Printer, Wellington.

YONGE, C. M., 1949. On the Sructure and Adaptations of the Tellinacea, Deposit Feeding Eulamellibranchia. *Phil. Trans. B.,* 234: 29–76.

WINSTON F. PONDER,
Zoology Department,
University of Auckland.