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New data on the ostracode genera *Laocoonella* de Vos & Stock, *Redekea* de Vos, and *Aspidoconcha* de Vos; with a key to the family Xestoleberididae and a resume of symbiosis in Ostracoda

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ABSTRACT

Investigation of the commensal genus *Aspidoconcha* de Vos indicates that it belongs in the family Xestoleberididae. Relationships of the commensal *Redekea* de Vos are uncertain. The genus *Laocoonella* de Vos & Stock is referred tentatively to family Cytheruridae. Among Ostracoda, symbiosis is more common than was previously realised; the possible occurrence of intra-Ostracoda symbiosis is reported.

INTRODUCTION

Among the few papers on commensal ostracodes other than entocytherids (Hart & Hart, 1967; Hobbs & Hobbs, 1970) are those by de Vos (1953) and de Vos & Stock (1956) which dealt with their new genera *Aspidoconcha, Redekea* and *Laocoonella.* I was able to restudy these taxa recently thanks to a generous loan of the type materials from the Zoological Museum Amsterdam, and thank Prof. Dr. J. H. Stock and Drs. S. Pinkster for arranging this loan.

I am also grateful to Dr. L. S. Kornicker, Smithsonian Institution, for providing information on *Paradoxostoma* cf. *hypselum* Müller, 1908, from collections studied at the British Museum (Natural History) by Mrs. P. Barker (Lofthouse, 1967).

SYSTEMATICS

Family Xestoleberididae Sars, 1928

Genus **Aspidoconcha** de Vos, 1953
(Pl. I, Figs. 1—8; Pl. II, Figs. 1—4)

Type species **Aspidoconcha limnoriae** de Vos, 1953

Diagnosis. The shell bears the characteristic elongate-arcuate eye scar of

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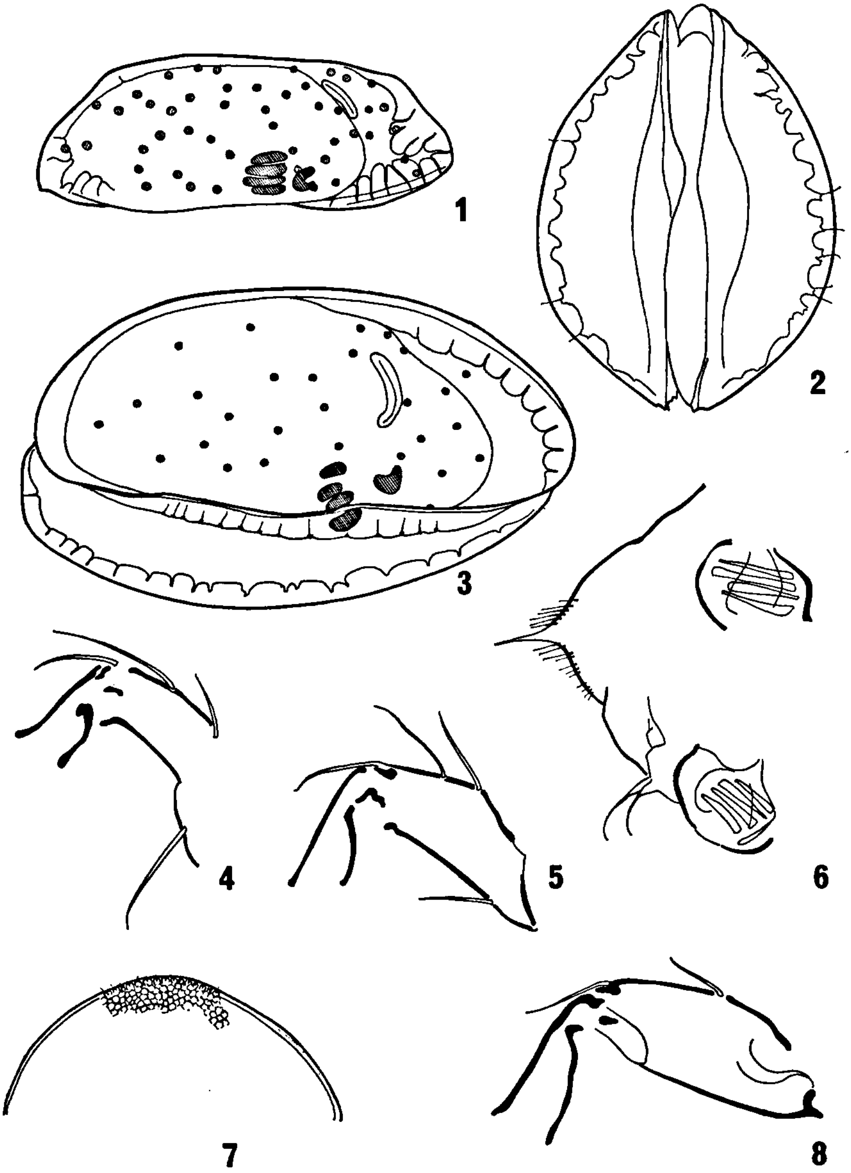

Plate I. *Aspidoconcha limnoriae* de Vos, 1953

Figure 1. Internal lateral view left valve (LV); × 312.5; Zandvoort-Bloemendaal; 16.i.1954; Z.M.A. Ost. 105—304. Figure 2. Ventral view of carapace; paratype; × 312.5; Katwijk; 20.ii.1949; Z.M.A. Ost. 105—048. Figure 3. Internal oblique view LV; × 312.5; Roscoff; 3.viii.1953 Z.M.A. Ost. 105—373. Figure 6. Ventral view, posterior of body, ♀; Roscoff; × 1250; 3.viii.1953; Z.M.A. Ost. 105—303. Figure 5. P1 protopod; × 1250; San Diego Harbour, California; 11.ix.1953; Z.M.A. Ost 105—307. Figure 4. P2 protopod; × 1250; San Diego Harbour, California; 11.ix.1953; Z.M.A. Ost. 105—307. Figure 7. Dorsal view of front of head, showing photosensitive (?) region; × 1250; Roscoff: 3.viii.1953; Z.M.A. Ost. 105—303. Figure 8. P3 protopod; × 1250; San Diego Harbour, California; 11.ix.1953; Z.M.A. Ost. 105—307.

the family Xestoleberididae even though the soft body lacks normal eyes. This taxon also has a xestoleberidid muscle scar pattern which includes four large elongate subvertical adductors and a large U- or V- shaped frontal scar; further, it has sieve-type normal pore canals as do other xestoleberidids.

The soft anatomy was figured by de Vos (1953, figs. 1—3). Attention is drawn to the antennule which has two basal and three distal segments with the penultimate segment weakly sutured. This is unlike other xestoleberidids in which the antennules consist of two basal and four distal segments. The setation (chaetotaxy) of the *Aspidoconcha* antennule, however, is very similar to that of other species in the family (cf. Sars, 1928, pl. 111). Other features also indicate the xestoleberidid connection. They include; a single aberrant (downwards-directed) seta on the maxillule epipod (fide de Vos, 1953: 25); a bisetose furca and posterior body spine; well developed mandibles; thoracic leg protopods which bear mediodorsal as well as posteroventral bristles (the latter not confirmed by me on the P3 of *Aspidoconcha limnoriae* although it is likely to be present — certainly it occurs on the P3 of *Xestoleberis* and *Microxestoleberis*); prominent lobate antennal glands; hemipenes of generally similar organisation to those of *Xestoleberis* (compare de Vos & Stock 1956, fig. 6, with Sars 1928, plate III).

Although *Aspidoconcha* lacks eyes it does have what is probably a photosensitive region on the anterodorsal region of its head in a position homologous with that of the two-three celled median eyes of *Xestoleberis* and other podocopid ostracodes. This presumably photosensitive region in *Aspidoconcha* consists of numerous polygonal cells(?) each with a small fine central hair.

Discussion — It is necessary to compare *Aspidoconcha* with *Microxestoleberis* Müller (1894 : 339—340, pl. 39, figs. 1, 6, 7, 40—48) to which it appears very similar in both carapace and soft anatomy. For example, both genera lack normal eyes although an eye scar is present on the valves (Pl. 1 figs. 1, 3; Müller, 1894, pl. 39, fig. 7).

A significant difference is in the antennules, which comprise one less segment in *Aspidoconcha* than in *Microxestoleberis*, although the penultimate segment in *Aspidoconcha* is weakly sutured (de Vos, 1953, fig. 3a). Another difference is in the P3 protopod. Müller (1894: 339, pl. 39, fig. 41) states that in *Microxestoleberis* the P3 protopod is without a mediodorsal bristle but one is present on the P3 protopod in *Aspidoconcha*. I have noted earlier that I could not confirm a posteroventral P3 protopod bristle in *Aspidoconcha*. Thirdly, the antennal exopod (flagellum) is illustrated with three joints in *Aspidoconcha* whereas the figure for *Microxestoleberis* suggests that the same organ is single-jointed (de Vos & Stock, 1956, figs. 4, 5; Müller, 1894, pl. 39, fig. 46).

Müller (1894 : 340), does not record a commensal habit for *Microxestoleberis* which he found only once, at 60 m depth, amongst sand and living *Posidonia* in the Secca della Gajola of the Bay of Naples. The pronounced ventral flattening of the shell in *Microxestoleberis* and *Aspidoconcha* is certainly an adaptation favourable to commensalism — but it also favours an interstitial habit of life.

In summary, there appear to be sufficient differences between *Aspidoconcha* and *Microxestoleberis* to retain both generic names. The intraspecific variation in each of the two type species, however, is not known and needs to be studied since the ranges of the characters which have been referred to above may well overlap and a synonymisation then prove to be justified.

In the existing state of knowledge, the following key suffices to distinguish Cainozoic xestoleberidids.

1. Shell with cauda 2
   Shell without cauda 3
2. Shell with merodont hinge . . . . *Uroleberis* Triebel, 1958
   Shell with adont hinge . . . . *Microxestoleberis* Müller, 1894
3. Hinge lophodont or merodont 4
   Hinge adont . . . . *Aspidoconcha* de Vos, 1953
4. Hinge merodont 5
   Hinge lophodont . . . . *Semixestoleberis* Hartmann, 1962
5. P3 normal . . . . *Xestoleberis* Sars, 1866
   P3 much attenuated, terminal claw threadlike . *Linocheles* Brady, 1907

Dr. J. P. Harding pointed out to me that Cannon (1957) had recorded the occurrence of *Cytheropteron humile* in burrows of *Limnoria* and *Chelura*. The holotype of *Cytheropteron humile* Brady & Norman, 1889, is in the British Museum (Natural History), as part of the Norman Collection, with the register number 1911.11.8, M 3720. It was collected from the Clyde, near Greenock, by T. Scott in July 1884. This species is a *Aspidoconcha*. Further record for the species in the British Museum (Natural History) collections include: near Bass Rocks, collected by T. Scott in 1895 (B.M.(N.H.), Norman Collection, 1911.11.8, 35842—35851); and Plymouth, collected by H. G. Cannon and S. M. Manton (Mrs. J. P. Harding) in 1937 (B.M.(N.H.), 1948.3.3.18—29). The synonymy of *Aspidoconcha* thus includes *Cytheropteron* (partim) sensu Brady & Norman, 1889.

PLATE II. *Aspidoconcha limnoriae* de Vos, 1953
Figure 1. Antennule, 2nd to 5th segments; paratype; × 1250; Katwijk; 20.ii.1949; Z.M.A. Ost. 105—048. The figures give the number of setae at the sites indicated. Figure 2. Maxillule epipod, downwards-directed seta not shown; paratype; × 1250; Zandvoort; 30.v.1952; Z.M.A. Ost. 105—047. Figure 3. Mandible coxale and palp, epipod not shown; paratype; × 1250; Zandvoort; 30.v.1952; Z.M.A. Ost. 105—047. Figure 4. Maxillule palp and lobes, ♂; paratype; × 1250; Katwijk; 20.ii.1949; Z.M.A. Ost. 105—040. *Laocoonella commensalis* (de Vos, 1953); paratype; Annabaai, Curaçao; 1923; Z.M.A. Ost. 105—052. Figure 5. Anterior half of broken right valve (RV), showing anteroventral denticles and some muscle scars; × 312.5. Figure 6. Posterior half of broken RV, showing hinge elements; × 312.5. Figure 7. Median hinge element of LV; × 312.5. Figure 8. Surface ornament of carapace; × 1250. Figure 10. Antenna, with lobate antennal gland; × 1250. Figure 9. Maxillule epipod, indicating presence of at least 7 setae (four shown complete, sites of others indicated); × 1250. Figure 11. Maxillule palp and lobes; × 1250. Figure 12. Antennule; × 1250.

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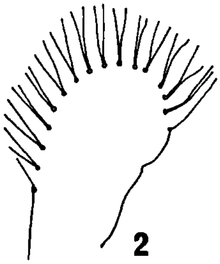

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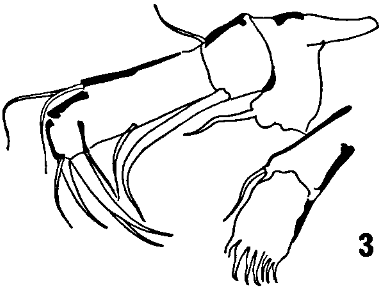

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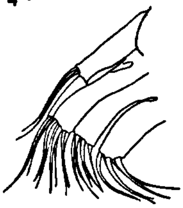

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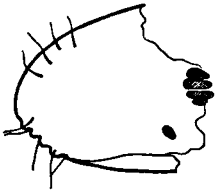

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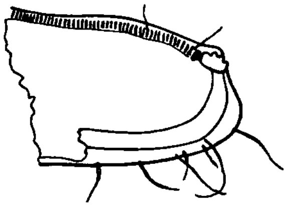

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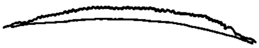

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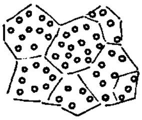

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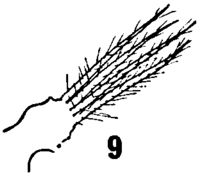

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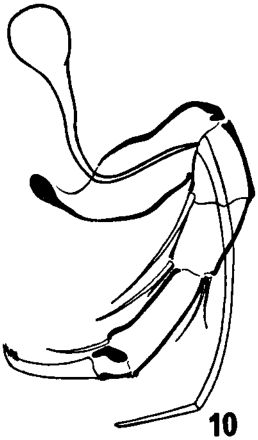

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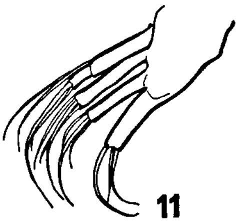

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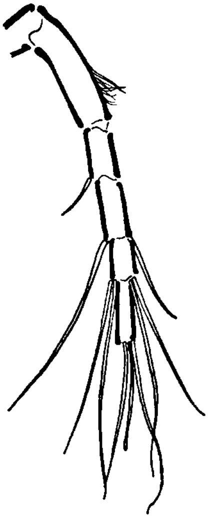

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Family (?) Cytheruridae G. W. Müller, 1894

Genus **Laocoonella** de Vos & Stock, 1956
(Pl. II, Figs. 5—12; Pl. III, Figs. 1—3, 6)

Synonymy: *Laocoon* de Vos, 1953, not *Laocoon* Nierstrasz & Entz, 1922 (de Vos & Stock, 1956 : 138).

Type Species: **Laocoonella commensalis** (de Vos, 1953).

Diagnosis — Shell small, with a holomerodont hinge (Scott, in Moore (ed.) 1961) and other features which often characterise members of the family Cytheruridae. These include: anteroventral denticulation on each valve; a reticulate surface ornament; relatively few radial pore canals some of which correlate positionally with the anteroventral denticules (by inference, cf. pl. II, fig. 5). I was unable to determine definitely the type of normal pore canals, because I found it difficult to orient the very fragile shells of the type material, but believe that small simple normal pore canals may occur.

The soft anatomy includes a slender antennule; a moderately elongate antenna associated with which is a lobate antennal gland; a mandible coxale without a projecting tooth; a maxillule epipod with at least 7 setae but apparently without any downwards-directed setae, and an elongate maxillule palp and lobes; plus thoracic leg protopods which have mediodorsal bristles but which lack posteroventral bristles.

Discussion — Some characters of *Laocoonella* are reminiscent of, but others show significant differences from, those in cytherurids. Thus, when *Laocoonella* is compared against *Microcytherura* Müller, 1894 they appear similar in general shape and in several shell characters although *Microcytherura nigrescens* Müller, 1894, the type species of *Microcytherura*, is about twice as long as *Laocoonella*. There are obvious differences between *Laocoonella* and *Microcytherura*, however, in the soft anatomy. For example, *Microcytherura* is distinguished by a very powerful anterior tooth on the mandible coxale; and by posteroventral setae on each of the three thoracic leg protopods. None of these characters occur in *Laocoonella*. It is possible that there are posteroventral setae on the *Laocoonella* thoracic leg protopods and that they were missed during my examination or were torn off in dissection of the generally fragile and very small (0.22 mm) body. This argument cannot apply to the mandible coxale which, as in usual in Ostracoda, is relatively more strongly chitinised than other parts of the body and dissects off easily. Other differences between the two genera occur in the antennular and antennal chaetotaxy. Thus, two terminal claws occur on the antennae of *Microcytherura* but only one on the same limbs in *Laocoonella*.

Another genus with which *Laocoonella* might bear comparison is *Nannocythere* Schäfer, 1953, which is of a similar size and, like *Laocoonella*, is flattened ventrally. But *Nannocythere* has a different hinge to *Laocoonella* and sieve type normal pore canals as well as differing significantly in some soft parts characters — for example, there are only 5 antennular segments in *Nannocythere* but 6 in *Laocoonella* (Schäfer, 1953: 353—360).

The habitat of *Microcytherura* in the Bay of Naples was described as being among coarse sand at about 10 m depth, near *Amphioxus* (Müller, 1894 : 384) and *Nannocythere* also was collected from an *Amphioxus* sand, but at Helgoland and by Professor Remane in 1934 (Schäfer, 1953 : 358). The ventral flattening in both these genera is an adaptation favourable to their life in an interstitial habitat. In *Laocoonella*, however, ventral flattening favours commensalism.

TABLE I. Symbiotic marine ostracode genera, excluding entocytherids, with their family and host affinities. The symbiosis of *Cytherois* is questioned because although possessing a partial suctorial disc it does not have a styliform mandible coxale.

Genus	Family	Symbiotix with	Author and Date
Aspidoconcha	Xestoleberididae	Isopods, Amphipods	de Vos, 1953, 1957; Cannon, 1957
Redekea	Incertae Sedis	Isopods	de Vos, 1953 1957
Laocoonella	?Cytheruridae	Isopods	de Vos, 1953; de Vos & Stock, 1956
Cylindroleberis	Cylindroleberididae	Sponges	Pearse, *fide* Harding, 1966
Vargula	Cypridinidae	Sharks, other fishes	Wilson, *fide* Harding, 1966
Sheina	Cypridinidae	Sharks, Rays	Harding, 1966
Pontocypria	Pontocyprididae	Starfish	Maddocks, 1968
Acetabulastoma	Paradoxostomatidae	Amphipods	Schornikov, 1970
Paradoxostoma	Paradoxostomatidae	Plants, ?Myodocopid Ostracods	various authors, this paper
Paracytherois	Paradoxostomatidae	Plants	various authors
Cytherois	Paradoxostomatidae	?Plants	various authors
Machaerina	Paradoxostomatidae	Plants	various authors

Incertae Sedis

Genus **Redekea** de Vos, 1953

(Pl. III, Figs. 4, 5, 7—15)

Type species **Redekea perpusilla** de Vos, 1953.

Diagnosis — A genus with a very small (length of male 0.23 mm), relatively compressed shell, characterised by a smooth surface interrupted by large normal pore canal pits, a subreniform shape with rounded extremities in lateral view; prominent vestibules; relatively few (about 20 or less) radial pore canals; sieve like normal pore canals; a muscle scar pattern which includes 4 subvertical adductors and an elongate frontal scar; and an adont hinge (pl. III, fig. 4). The soft parts include a slender antennule with 6 segments; antenna with a single well developed terminal claw and a lobate antennal gland; a well developed mandible coxale and a three-segmented palp with a single epipodial seta; a maxillule with at least two downwards-directed setae; and thoracic leg protopods with mediodorsal setae but apparently lacking posteroventral setae. The oral cone is well developed, bidentate terminally, and embraces paired rakelike organs each with four teeth.

Discussion — The diagnosis given above compares fairly well with the original diagnosis and figures differing mainly in that I found the mandible palp to be well divided and was able to add some details to the shell and maxillule descriptions. *Redekea* has earlier been referred to a separate tribe Redekeini and, following de Vos (1953, p. 21), associated with *Laocoonella* (McKenzie, 1969, fig. 5). Comparison of the two type materials shows that they differ strikingly in shell characters although illustrations of the soft parts show several resemblances. I believe that at least some of these resemblances reflect the common commensal habit of life of the two genera rather than a phylogenetic connection and that Redekeini should be restricted at present to genus *Redekea* which is not, in my opinion, at all like a cytherurid and

PLATE III. *Laocoonella commensalis* (de Vos, 1953); paratype; Annabaai, Curaçao; 1923; Z.M.A. Ost. 105—052.

Figure 1. P1; × 1250. Figure 2. P2; × 1250. Figure 3. Mandible: × 1250. Figure 6. P3; × 1250.

Redekea perpusilla de Vos, 1953; holotype; Zandvoort; 30.v.1952; Z.M.A. Ost. 105—049.

Figure 4. Internal lateral view RV; × 312.5. Figure 5. Mandible coxale; × 1250. Figure 7. Antennule, 3rd to 6th segments; × 1250. The figures give the number of setae at the sites indicated.

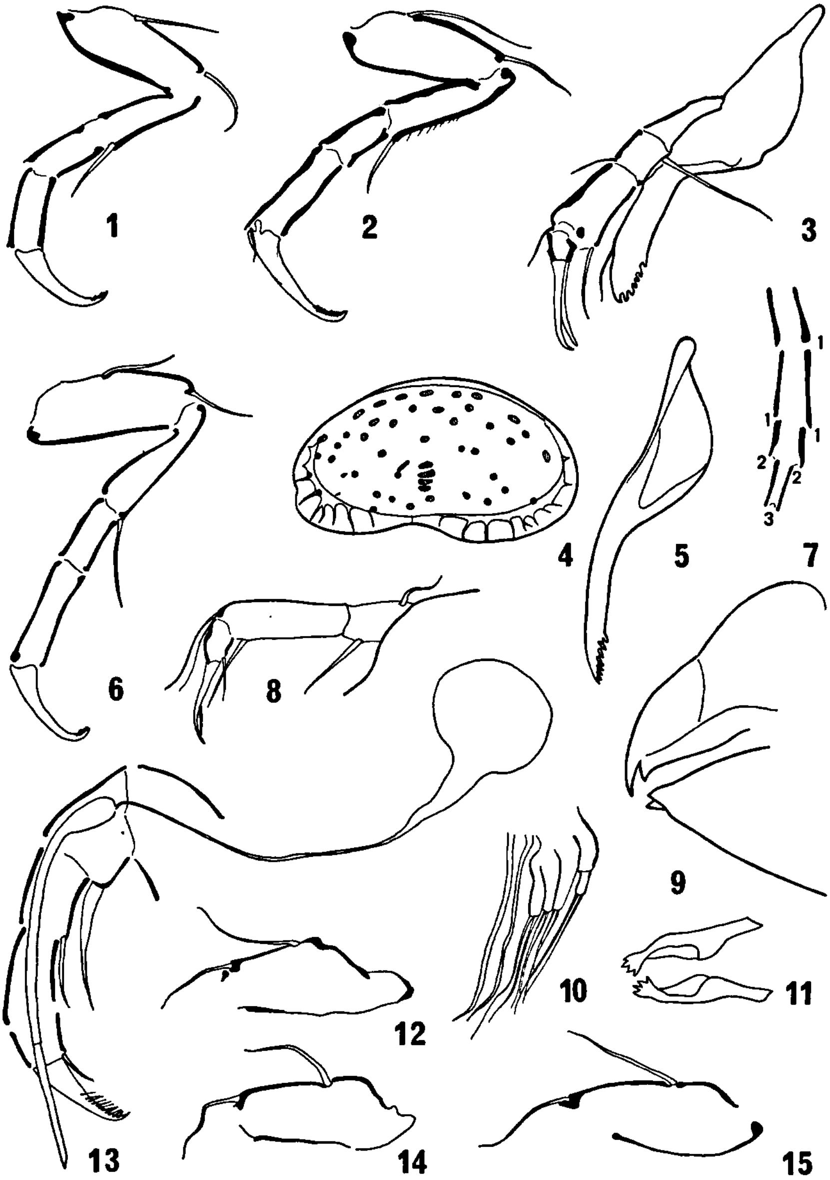
Redekea perpusilla de Vos, 1953; paratype, ♂; Zandvoort; 30.v.1952; Z.M.A. Ost, 105—050.

Figure 9. Oral cone; × 1250. Figure 12. P1 protopod; × 1250. Figure 13. Antenna, with lobate antennal gland; × 1250. Figure 14. P2 protopod; × 1250. Figure 15. P3 protopod; × 1250.

Redekea perpusilla de Vos, 1953; Roscoff; 3.viii.1953; Z.M.A. Ost. 105—310. Figure 11. Rake-like organs; × 1250.

Redekea californica de Vos & Stock, 1956; paratype; San Diego Harbour, California; 11.ix. and 14.xii.1953; Z.M.A. Ost. 105—309.

Figure 8. Mandible palp; × 1250. Figure 10. Maxillule pulp and lobes; × 1250.



should no longer be associated systematically with *Laocoonella.* The only genus with which a comparison may be warranted is *Paracythere* Müller (1894 : 285—286, pl. 16, figs. 6, 37—41). *Paracythere* resembles *Redekea* in some shell characters, for instance its shape in lateral view is very similar, but differs markedly in some soft part characters. These notably include the two terminal antennular segments which are very short in *Paracythere*; the occurrence of two antennal claws in *Paracythere* against one in *Redekea*; the complete absence of a maxillular palp and lobes in *Paracythere*; the occurrence of posteroventral bristles on the thoracic leg protopods of *Paracythere*. I conclude that, in spite of some degree of homeomorphy in shell characters, these two genera are not very closely related.

SYMBIOSIS IN OSTRACODA

There is a vast literature upon parasitic copepods, which exhibit an intriguing diversity of adaptations for their parasitic habits of life. Equally well known, although less diverse, are branchiurans which are common parasites of some fishes, and rhizocephalans which parasitize crabs. But symbiosis in Ostracoda has until lately been very little studied with the notable exception of the family Entocytheridae, taxa in which are known to be symbiotic on freshwater crayfishes, freshwater and marine isopods and marine amphipods (Hart, 1962; Hart & Hart, 1967; Hart, Nair & Hart, 1967). Recent work, however, has shown that symbiosis is more common in Ostracoda than was realised and is also more widespread in the group as a whole than the concentration of research into entocytherids would indicate. Table I lists some recent publications upon this aspect of ostracode biology and shows the diversity not only of symbiotic ostracodes but also of the hosts which they are now known to favour. It is expected that future work will greatly expand this list.

All symbiotic ostracodes have some structural modifications which favour the symbiotic habit of life. These include: small size; ventrally flattened or compressed shells sometimes with specially modified anteroventral margins; modifications for suctorial feeding such as attenuated oral cones, suctorial discs and styliform (piercing) mandible coxales; modifications for attachment such as hook-like claws on the antennae and thoracic legs; and, possibly, adventitious stabilisers such as the long antennal 'natatory' setae of some species of commensal *Pontocypria* (Maddocks, 1968).

Symbiosis is often a specialisation adopted by only some taxa in dominantly free-living groups, but Entocytheridae are an exception. There appears to be only one record of free-living entocytherids which is considered reliable by entocytherid specialists (Hart & Hart, 1969, p. 167), otherwise the group is known to be commensal even during ontogeny. The entocytherids are characterised above all by high morphologic diversity in reproductive mechanisms, indeed their taxonomy is based almost entirely upon copulatory apparatus characters (Hobbs & Hobbs, 1970). It is thus possible that the unique entocytherid copulatory mechanism reflects a long evolutionary history, as commensals, for the group.

Of the new data on *Aspidoconcha*, *Laocoonella* and *Redekea*, only that pertaining to *Aspidoconcha* seems to have evolutionary significance. It indicates, in my opinion, that some xestoleberidids from interstitial habitats have adapted to the commensal habit with rather few structural changes. The latter observation suggests that this adaptation has occurred rather recently.

Ostracode workers generally have been conservative in advocating a parasitic type of symbiosis for the animals which they have studied, but recently this inhibition has been shed (e.g. Harding, 1966) and a new paradoxostomatid genus, *Acetabulastoma*, has been described as an ectoparasite of marine amphipods (Schornikov, 1970).

There is as yet no definite evidence in favour of intra-Ostracoda symbiosis but it seems at least a possibility and I was recently sent a paradoxostomatid with a damaged shell which had been removed from inside the shell of an Antarctic myodocopid ostracode near, "..... the area of muscle of the protopodite of the 2nd antenna....." (L. S. Kornicker, pers. comm., December 16th 1970). I have determined this paradoxostomatid as *Paradoxostoma* cf. *hypselum* Müller, 1908, and observed what appeared to be a piece of tissue attached near the suctorial mouth of the animal with the styliform mandible coxales both oriented correctly for suctorial feeding, i.e. aligned near the mouth. If my interpretation is correct, then this record suggests that some paradoxostomatid ostracodes may parasitize epibenthic myodocopids. This is not a startling hypothesis in view of the fact that the genus *Paradoxostoma* is adapted for suctorial feeding anyway and that at the depth at which the myodocopid was collected there may be little plant material available for paradoxostomatids to feed on. Obviously, further and more careful work with freshly-trawled living material is necessary before any firm statement can be made on this interesting possibility. It should be noted that the ectoparasite *Acetabulastoma*, mentioned earlier, includes a species formerly assigned to *Paradoxostoma rostratum* Sars, 1866 (cf. Baker & Wong, 1968).

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