CHECKLIST OF GASTROPOD SPECIES REFERRED TO THE ORDER COCCULINIFORMIA HASZPRUNAR, 1987 (GASTROPODA: COCCULINOIDEA ET LEPETELLOIDEA) WITH SOME REMARKS ON THEIR FOOD PREFERENCES

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ABSTRACT: Cocculiniform limpets live mostly in aphotic zones of deep-sea areas. In this environment, rather poor in organic nutrients, they have specialized in utilizing different odd food sources. The paper presents the list of all species included in the superfamilies Cocculinoidea Dall, 1882 and Lepetelloidea Dall, 1882. Data on their habitat, food preferences and distribution are also included. Adaptive features in cocculiniform limpets that permit them to assimilate organic nutrients of various origin are also discussed. It is suggested that some expanded parts in their alimentary tracts may be used as “fermentative chambers” in which symbiotic bacteria could change the unassimilable food particles into simple compounds absorbed by limpets.

KEY WORDS: limpet, food preferences, alimentary tract adaptations, Cocculiniformia, Cocculinoidea, Lepetelloidea, checklist

INTRODUCTION: COCCULINIFORM LIMPET FAMILIES

Sunlight does not reach bathyal and abyssal zones of seas and oceans, and photosynthesis cannot take place there. Thus, apart from the exceptional animal communities connected with chemoautotrophic primary production near hydrothermal vents and cold seeps (CHILDRESS & FISHER 1992, TUNNICLIFFE 1991), animal life at the sea bottom can be fuelled only by organic particles falling down from the euphotic zone (GOODAY & TURLEY 1990, STOCKTON & DELACA 1982). Such organic falls reaching the deep-sea floor are rather scarce, therefore deep-sea animals often specialize in consuming very odd food. Among such specialized consumers, there is a group of snails, most of them with limpet-shaped shells, which is especially noteworthy. They are included into two superfamilies: Cocculinoidea Dall, 1882(a) and Lepetelloidea Dall, 1882(a). Not long ago were they joined in the order Cocculiniformia Haszprunar, 1987(a), but recently only Cocculinoidea have been retained in Cocculiniformia (BIELER 1992, LINDBERG & PONDER 1991, PONDER & LINDBERG 1997). This superfamily includes the families Cocculinidae Dall, 1882(a) and Bathysciadiidae Dautzenberg et Fischer, 1899. Lepetelloidea (with 8 families: Lepetellidae Dall, 1882(a), Addisoniidae Dall, 1882(a), Bathyphytophilidae Moskalev, 1978, Choristellidae Bouchet et Warén, 1979, Cocculinellidae Moskalev, 1971, Osteopeltidae Marshall, 1987, Pseudococculinidae Hickman, 1983 and Pyropeltidae McLean et Haszprunar, 1987) have been shifted to Vetigastropoda Salvini-Plawen, 1980 (PONDER & LINDBERG 1997). This recent change in the taxonomic position of cocculinoid and lepetelloid limpets is recognized, however in this paper they all are called cocculiniform limpets according to the former classification.
FOOD PREFERENCES IN COCCULINIFORM LIMPETS

Cocculinidae and Pseudococculinidae feed on wood which has sunk to the ocean floor (HASZPRUNAR 1988ab, MARSHALL 1986, MOSKALEV 1976, WOLFF 1979). Although it is not excluded that they eat directly wood (maybe due to contamination with symbiotic bacteria which digest cellulose), probably their food consists of different microorganisms which decompose plant remains (MARSHALL 1986). Bathphytophilidae also eat plants, such as algal holdfasts and seagrass (MOSKALEV 1978, WOLFF 1976). Lepetelloididae are found on empty polychaete tubes (DALL 1882a, 1889a, MOSKALEV 1976, 1978, VERRILL 1880). It is again disputable whether the tubes themselves, or microorganisms living on them are the nutrition for lepetellids. Bathysciadiididae feed on chitinous beaks of microorganisms living on them are the nutrition for Tentaoculus lithodicola (MOSKALEV 1976) and addisoniid Helicopelta rostricola (MARSHALL 1996). Furthermore, Cocculinellidae derive their nutrition from decaying fish bones (HASZPRUNAR 1988c, MARSHALL 1983). On the other hand, whale skeletons have become food for Osteopeltidae (MARSHALL 1996, MCLEAN 1985, 1992b, VERRILL 1882, Villa 1985). Two other pseudococculinids of the genus Tentaoculus balantiophaga) have been found exclusively in empty egg cases of sharks and skates (MARSHALL 1996, MCLEAN 1985, 1992b, VERRILL 1882, Villa 1985). Two other pseudococculinids of the genus Tentaoculus (T. lithodicola and T. neolithodicola) live on carapaces of living deep-sea crabs of the family Lithodidae (MARSHALL 1986). A bathysciadiid-like limpet feeds on the periostracum of a gastropod of the genus Capsula (WAREN 1993). Pyropeleta bohlei was also found attached to the shell of Bathycnemaea jonassoni (BECK 1996).

The substrata used by cocculinoid and lepetelloid gastropods as sources of their nutrition are built of unassimilable substances. Wood is built of cellulose, cephalopod beaks are composed of chitin. Both are large, filamentous polysaccharides. Egg cases of elasmobranch fish comprise a fibrous protein, collagen. Gastropod periostracum is also built of fibrous proteins. Animals usually do not secrete their own enzymes which could digest such molecules. Only bacteria can produce appropriate enzymes. MARSHALL (1986) suggested that the cocculiniform limpets feed on bacteria which are associated with their biogenic substrata, rather than directly on the substrata. It is an open question if the cocculiniform limpets consume bacteria free living on the substrata or if they harbour symbiotic bacteria in their alimentary tracts. Although particular families specialize in characteristic nutrition sources, there are some exceptions. Teuthirostria cancellata feeds on cephalopod beaks (MOSKALEV 1976) (the other cocculinids feed on wood), so does Helicopelta rostricola (MARSHALL 1996) (the other addisoniid limpets prefer elasmobranch egg cases). Pyropeleta corymba and P. musasica probably feed on chemotrophic bacteria living on sulphide crust at hydrothermal vents (MCLEAN & HASZPRUNAR 1987) but they have also been collected from whale skulls (MCLEAN 1992a). Coccolpigya spinigera usually consumes wood, like the other cocculinid limpets, but it was found on a whale skull, too (WAREN 1991). Another cocculinid limpet, Pyrococculina cervae, was usually collected from deep-sunken wood or algal holdfasts (HASZPRUNAR 1987a, MARSHALL 1986) but MARSHALL (1994) noted its occurrence on whale bones. Such exceptional cases have led WAREN (1996b) to a conclusion that many deep-sea limpets can live on a “second choice” substratum when the first is not available. Such a conclusion would be in agreement with the hypothesis that these limpets feed on free living bacteria. However, it seems that the hypothesis of symbiotic bacteria in the alimentary tract of cocculiniform gastropods is more probable. Several authors noted substratum debris observed in the digestive tracts (HASZPRUNAR 1987ab, 1988b, HASZPRUNAR & MCLEAN 1996, SIMONE 1996). The actual consumption of the odd substrata may be also evidenced by the very diverse radular structures in particular families, suggesting adaptive differentiation (HICKMAN 1983) and by differences of the alimentary tract anatomy in these families (HASZPRUNAR 1987ab, 1988ab, 1992ab, HASZPRUNAR & MCLEAN 1996). HASZPRUNAR (1988a) suggested that the alimentary tract of the families feeding on wood, that is Cocculinidae and Pseudococculinidae, represents the most primitive organization. Strongly cuticularized epithelium of some stomach part, creating a so called gastric shield, may be used for mechanical crushing of hard food before it is digested by bacteria in the long intestine coiled in three loops (a long intestine is usually characteristic for plant consumers). The specialization of the other cocculiniform families to other food sources is reflected in serious modifications of their alimentary tracts. Polysaccharides (chitin) consumers, such as bathysciadiids, have a very large stomach but they have lost their midgut gland, which has been replaced with a greatly expanded oesophageal gland. A very large stomach is also characteristic for bathphytophilids (HASZPRUNAR & MCLEAN 1996). On the other
hand, fibrous protein diet resulted in progressive reduction of the stomach, observed in cocculinellids and addisoniids (members of the latter family have no stomach at all) (HASZPRUNAR 1987b, 1988ac). It appears that, instead of stomach, addisoniid limpets have an extremely large intestinal sac which occupies about two thirds of the animal’s body (HASZPRUNAR 1987b). Although Haszprunar initially reported a lack of stomach in choristellids and a similarity of their alimentary tract anatomy to that of addisoniids (HASZPRUNAR 1988a), later he described a very large, highly modified stomach for this family (HASZPRUNAR 1992ab). Nevertheless it may be said that in all cocculiniform gastropods there is some expanded chamber in their alimentary tracts. It is suggested here that such chambers may be used as “fermentative chambers” in which symbiotic bacteria could change the unassimilable food particles into simple compounds absorbed by limpets. However, further physiological studies are desperately needed to explain the details of digestive processes in cocculinoid and lepetelloid gastropods.

MARSHALL (1996) noticed that decaying beaks, egg cases, bones, wood and algal holdfasts are generally rare at the sea-floor. This raises a further unanswered question: how can the limpets find their food? The development of these gastropods is unknown. Their larvae are probably lecithotrophic and may be dispersed by bottom currents (MARSHALL 1986). The chemoreception-based recognition of the food substrata may be only speculated upon.

RECENT KNOWLEDGE OF COCCULINIFORM LIMPETS

During the last 25 years our knowledge of the snails of the superfamilies Cocculinoidea and Lepetelloidea has been seriously increased. Studies initiated by MOSKALEV in the seventies (1971, 1973, 1976, 1978) and continued in the eighties and nineties by HASZPRUNAR (1987ab, 1988ab, 1992ab, 1996), MARSHALL (1983, 1986, 1987, 1994, 1996), MCLEAN (1985, 1988, 1991, 1992ab) and WAREN (1989, 1991, 1993, 1996ab) have brought not only the discovery and description of several new species. As a result of the detailed comparative anatomical studies, they have revealed relationships between them. It has also been possible to revise descriptions of earlier discovered species as well as to improve the system introduced on the turn of the 19th century (DALL 1882ab, 1889ab, 1896, DAUTZENBERG 1886, 1889, THIELE 1908, 1909, 1925, 1929, VERRILL 1880, 1882, 1884). The recent discoveries throw some new light on the problems of the gastropod origin, specially on the role of limpet-shelled forms in the gastropod evolution (HASZPRUNAR 1988ab, 1992ab, HASZPRUNAR & MCLEAN 1996, HICKMAN 1983, MARSHALL 1996). The papers published during the last three years (BECK 1996, HASEGAWA 1997, HASZPRUNAR & MCLEAN 1996, LEAL 1996, MARSHALL 1996, MCLEAN & HARASEWYCH 1995, SIMONE 1996, WAREN 1996ab) contain descriptions of 17 new species (further 8 have been presented but not named yet), redescription and reclassification of another 22 species, establishment of a new genus and a new subfamily. Descriptions of further species are being prepared (MARSHALL, LEAL, MCLEAN – personal communication). This is a proof that this gastropod group still inspires new research. Therefore it seems reasonable to compile in one paper all information on the species included in the superfamilies Cocculinoidea and Lepetelloidea, as well as all data on their habitat, food preferences and distribution areas. The checklist should also give a detailed bibliography of both superfamilies.

CHECKLIST OF COCCULINIFORM LIMPET SPECIES

Superfamily: Cocculinoidea Dall, 1882(a) (Thiele, 1909 emend.)
Family: COCCULINIDAE Dall, 1882(a)
Genus: Cocculina Dall, 1882(a) (type species: Cocculina rathbuni Dall, 1882)
Several species have been referred to the genus Cocculina Dall, 1882(a), however their generic (and family) status has not been recently confirmed by the studies on their anatomies and radulae, these species are listed as “Cocculina”.

Cocculina angulata Watson, 1886 (western Pacific: Philippines)
(CMCLEAN & HARASEWYCH 1995)
“Cocculina” alta Smith, 1894 (southwest Pacific: off New South Wales, 750 m)
“Cocculina” alveolata Schepman, 1908 (Indo-Pacific)
Cocculina baxteri McLean, 1987 (northeastern Pacific: Prince William Sound, Alaska; 424–430 m; on wood) (HASZPRUNAR 1987a)
Fig. 1–8. Shells of cocculiniform limpets. Cocculinidae: 1 – *Cocculina surugaensis* Hasegawa, 1997; 2 – *Cocculina trisulcata* Hasegawa, 1997; 3 – *Coccopigya okutanii* Hasegawa, 1997; 4 – *Coccopigya punctoradiata* (Kuroda et Habe, 1949); Pseudococculinidae: 5, 6 – *Pseudococculina subcingulata* (Kuroda et Habe, 1949); 7 – *Notocrater pustulosa* (Thiele, 1925); 8 – *Copulabysia similis* Hasegawa, 1997. Scale bars: 500 µm (1, 2, 5–8) or 1 mm (3, 4). Published by the courtesy of KAZUNORI HASEGAWA (National Science Museum, Tsukuba, Japan) after HASEGAWA (1997)
Cocculiniformia, Checklist of species 51

(northeastern Pacific: Queen Charlotte Sound, Vancouver Isl., British Colombia; 265 m)  
(DALL 1921, MCLEAN 1987)

*Cocculina cowani* McLean, 1987  
(northeastern Pacific: off Moresby Isl., Queen Charlotte Islands, British Columbia; 1370 m; on wood)  
(HASZPRUNAR 1987a)

*Cocculina craigsmithi* McLean, 1992(a)  
(northeastern Pacific: between Santa Catalina Isl. and San Clemente Isl.; 1240 m; on whale bones)  
(HASZPRUNAR 1987a)

*Cocculina striata* Schepman, 1908  
(northeastern Pacific: off West America)

Genus: *Coccorater* Haszprunar, 1987(a)  
(type species: *Cocculina radiata* Thiele, 1904)

*Coccorater agassizii* (Dall, 1908) (*Cocculina*)  
(eastern Pacific: Gulf of Panama; 1015 m)  
(HASZPRUNAR 1987a, MCLEAN 1987)

*Coccorater pocillum* (Dall, 1890) (*Cocculina/Coccopygia*)  
(western Atlantic: off Tobago; 1600 m)  
(MCLEAN & HARASEWYCH 1995)

*Coccorater portoricensis* (Dall et Simpson, 1901) (*Cocculina*)  
(western Atlantic: off San Juan Harbor, Puerto Rico; 566 m)  
(MCLEAN & HARASEWYCH 1995)

*Coccorater radiata* (Thiele, 1904) (*Cocculina*)  
(eastern Indian Ocean: off Sumatra; 614 m)  
(HASZPRUNAR 1987a)

Genus: *Coccopigya* Marshall, 1986  
(nomen novum pro *Coccopygia* Dall, 1889/a/)  
(type species: *Cocculina spinigera* Jeffreys, 1883)

*Coccopigya barbatula* Marshall, 1986  
(southwestern Pacific: off New South Wales; 384–457 m; on wood)

*Coccopigya compunctum* (Marwick, 1931) (*Tectissium*)  
(early or middle Miocene, NE of Tekaraka, Gisborne District, New Zealand)  
(MARSHALL 1986)

*Coccopigya crebrilamina* Marshall, 1986  
(southwestern Pacific: Whale Island to off Timaru, New Zealand; 833–1514 m; on wood)

*Coccopigya crinita* Marshall, 1986  
(southwestern Pacific: off Timaru, New Zealand; 833–1514 m; on wood)  
(HASZPRUNAR 1987a)
Coccopigya komitica Marshall, 1986
(Otaian, early Miocene, 1.6 km NW of Pakaurangi Point, Kaipara, New Zealand)

Coccopigya latia Warén, 1996(a)
(north Atlantic: off southwestern Iceland; on sunken driftwood)

Coccopigya mikkelenses McLean et Harasewych, 1995
(western Atlantic: off Chateau Belair Bay, St. Vincent, Lesser Antilles; 421 m; on wood)

Coccopigya oculifera Marshall, 1986
(southwestern Pacific: White Island to off Timaru, New Zealand; 248–962 m; on wood)

Coccopigya okutanii Hasegawa, 1997 (Fig. 3)
(northwestern Pacific: Suruga Bay, Honshu, Japan; 205–740 m; on wood)

Coccopigya otaiana Marshall, 1986
(Otaian, early Miocene, 1.6 km NW of Pakaurangi Point, Kaipara, New Zealand)

Coccopigya punctoradiata (Kuroda et Habe, 1949) (Cocculina) (Fig. 4)
(northwestern Pacific: off Tosa, Shikoku; Suruga Bay, Honshu; 120–1708 m; on wood)

Coccopigya spinigera (Jeffreys, 1883/c/) (Cocculina) = Cocculina conspersa Dautzenberg et Fischer, 1897
(northwestern Atlantic: off the northeastern United States to western and southern Iceland, and to north of the Hebrides; also Mediterranean: between Catalonia and Mallorca, and Chafarinas Island, N. Morocco; 200–1534 m; on submersed wood and whale skeletons, also on tubes of xylophagid and teredinid ship-worms)

Coccopigya viminensis (Rocchini, 1990) (Cocculina)
(northwestern Pacific: off Tosa, Shikoku; Suruga Bay, Honshu; 120–1708 m; on wood)

Coccopigya sp. (HASEGAWA 1997)
(northwestern Pacific: Suruga Bay, Honshu, Japan; 180–680 m; on wood)


Fedikovella beanii (Dall, 1882/a/) (Cocculina)
(northwestern Atlantic: Martha’s Vineyard Island, Massachusetts; Martinique; 183–1846 m)
(off Chateau Belair Bay, St. Vincent, Lesser Antilles; 421 m; on wood) (MCLEAN & HARASEWYCH 1995, MOSKALEV 1976)

Fedikovella capulus (Thiele, 1925) (Cocculina)
(western Indian Ocean: Zanzibar Channel; 463 m) doubtfully included in Fedikovella (MCLEAN & HARASEWYCH 1995, MOSKALEV 1976)

Fedikovella caymanensis Moskalev, 1976
(western Atlantic: Cayman Trench; 6740–6800 m; on sunken wood) (MCLEAN & HARASEWYCH 1995)

Genus: Paracocculina Haszprunar, 1987(a)
(type species: Cocculina laevis Thiele, 1904)

Paracocculina cervae (Fleming, 1948) (Cocculina)
(southwestern Pacific: North Cape to Long Sound, New Zealand; 18–891 m; on whale bones, algal holdfast, deep-sunken wood) (HASZPRUNAR 1987a, MARSHALL 1986, 1994)

Paracocculina laevis (Thiele, 1904) (Cocculina)
(eastern Indian Ocean: off Nias Island, Sumatra) (HASZPRUNAR 1987a)

Genus: Teuthirostria Moskalev, 1976
(type species: Teuthirostria cancellata Moskalev, 1976)

Teuthirostria cancellata Moskalev, 1976
(eastern Pacific: off Peru; 5200–5540 m; on cephalopod beaks)

Gen. n., sp. n. (LEAL 1996)
(western Atlantic: Puerto Rico Trench; 8595 m)

Family: BATHYSCIADIIDAE Dautzenberg et Fischer, 1899

Genus: Bathysciadium Dautzenberg and Fischer, 1899
(type species: Bathysciadium conicum Dautzenberg et Fischer, 1899)
=Bonus Moskalev, 1973
(type species: Bonus petrochenkoi Moskalev, 1973) (WAREN 1996b)

Bathysciadium concentricum Dall, 1927
(northwestern Atlantic: off Georgia; 800 m)

Bathysciadium costulatum (Locard, 1897) (Lepeta)
(Atlantic: south of the Azores; 3175 m; on a cephalopod jaw)
=Bathysciadium conicum Dautzenberg et Fischer, 1899
(Atlantic: off Azores, off Spanish Sahara; 1000–2000 m; on cephalopod beaks) (PELSENEER 1899, 1940; WAREN 1996b)

Bathysciadium pacificum Dall, 1908
(eastern Pacific: off Peru; 4115 m; on cephalopod beaks) (WAREN 1996b)

Bathysciadium petrochenkoi Moskalev, 1973 (Bonus)
Bathysciadium rotunda (Dall, 1927) (Cocculina) (northwestern Atlantic: off Fernandina, Florida) (tentatively referred to Bathysciadium by McLean & Harasewych 1995)

Bathysciadium xylophagum Warén et Carrozza, 1996 (in Warén 1996b) (Mediterranean: off Sardinia; 630 m; in holes made by ship-worms in a piece of sunken wood)

Bathysciadium sp. cf. xylophagum Warén et Carrozza, 1996 (in Warén 1996b) (Atlantic: off southwestern Portugal, Josephine Bank; 200 m; on a cephalopod beak)

Bathysciadium n. sp. (1) (Haszprunar 1988a) (southwestern Indian Ocean: off Reunion Island; 2830–2850 m)

Bathysciadium n. sp. (2) (Haszprunar 1988a) (southwestern Indian Ocean: off Reunion Island; 2830–2850 m)

Bathysciadium n. sp. (3) (Warén 1996b) (southwestern Atlantic: northeastern coasts of United States and southwestern coasts of Iceland; 900–1000 m)

Bathysciadium n. sp. (4) (Warén 1996b) (Mediterranean: off Capraia Island; 150 m)

Genus: Pilmus Warén, 1991 (tentatively placed in the Bathysciadiidae by Warén 1993) (type species: Cocculina conica Verrill, 1884)
Pilmus conica (Verrill, 1884) (Cocculina) (northwestern Atlantic: northeastern coasts of United States and southwestern coasts of Iceland; 900–1000 m) (McLean & Harasewych 1995; Warén 1993)

Genus: Xenodonita Warén, 1993 (tentatively placed in the Bathysciadiidae) (type species: Cocculina conica Verrill, 1884)
Xenodonita bogasoni Warén, 1993 (north Atlantic: off western and southwestern Iceland; 260–770 m)
Xenodonita n. sp. (Warén 1993) (eastern Pacific: off Galapagos Islands; on the shell periostracum of Capulus sp.)

species excluded from Cocculinoidea Dall, 1882(a) Acmaea parva var. tasmanica Pilsbry, 1895 = Cocculina meridionalis Hedley, 1903 = Acmaea excentrica Test, 1945 sometimes referred in Cocculina or Notocratère belongs to Propilidium Forbes et Hanley, 1849, Lepetidae Dall, 1869 (Marshall 1986)
Cocculina aethiopica Thiele, 1925 is a basal plate of a barnacle – Crustacea: Cirripedia (Warén 1985)
Cocculina casanica Dall, 1919 is a junior synonym of Lepeta caeca (Müller, 1776) and belongs to Lepetidae Dall, 1869 (McLean 1987)

Cocculina dalli Verrill, 1884 close to Iothia rugosa (Jeffreys, 1883/a/) Lepetidae Dall, 1869 (McLean & Harasewych 1995)
Cocculina lissocoma Dall, 1927 referred to Propilidium Forbes et Hanley, 1849, Lepetidae Dall, 1869 (McLean & Harasewych 1995)
Cocculina maxima Dautzenberg, 1925 belongs to patellogastropod genus Pectinodonta Dall, 1882(a) (Marshall 1985)
Cocculina obtusa Thiele, 1925 probably belongs to patellogastropod genus Pectinodonta Dall, 1882(a) (Marshall 1985)
Cocculina petasus Thiele, 1925 is a basal plate of a barnacle – Crustacea: Cirripedia (Warén 1985)
Cocculina reticulata Verrill, 1885 referred to Propilidium Forbes et Hanley, 1849, Lepetidae Dall, 1869 (McLean & Harasewych 1995)
Cocculina rhyssa Dall, 1925 belongs to patellogastropod genus Pectinodonta Dall, 1882(a) (Hassegawa 1997, Marshall 1985)
Cocculina scabra Kuroda et Habe, 1949 referred to Iothia Forbes, 1849, Lepetidae Dall, 1869 (Hassegawa 1997, Inaba & Oyama 1977)
Cocculina superba Clarke, 1960 referred to Lepetidae Dall, 1869 (McLean & Harasewych 1995)
Cocculina terramachii Kuroda et Habe, 1949 referred to Iothia Forbes, 1849, Lepetidae Dall, 1869 (Hassegawa 1997, Inaba & Oyama 1977)

Genus: Dallia Jeffreys, 1883 (a) (type species: Tectura (Dallia) galeola Jeffreys, 1883/a/) with the species: D. galeola (Jeffreys, 1883/a/), D. pusilla (Jeffreys, 1883/a/) and D. aduna (Jeffreys, 1883/a/) probably belongs to Lepetidae Dall, 1869 (Marshall 1986) but their specific, generic and familiar status is unclear (Dantart & Luque 1994)

Genus: Maoricrater Dell, 1956 (type species: Notoaeanea explorata Dell, 1953) belongs to Lepetidae Dall, 1869 (Hickman 1983, Moskalev 1977)


Superfamily: L e p e t e l l o i d e a Dall, 1882(a) (Thiele, 1908 emend.)

Family: LEPETELLIDAE Dall, 1882(a)
Genus: Lepetella Verrill, 1880 (type species: Lepetella tubicola Verrill et Smith in Verrill, 1880)
Lepetella barrajoni Dantart et Luque, 1994
Genus: *Bogia* Dantart et Luque, 1994
(type species: *Cocculina labronica* Bogi, 1984)
(family uncertain, should be excluded from Lepetellidae according to DANTART & LUQUE 1994)
*Bogia labronica* (Bogi, 1984) (*Cocculina*)
(Mediterranean: Tyrrenhenian Sea; 80–220 m)

Genus: *Sablea* Allen, 1970
(type species: *Sablea minuta* Allen, 1970)
*Sablea minuta* Allen, 1970
(Eocene-Oligocene)
conchologically similar to *Lepetella* Verrill, 1880
(DANTART & LUQUE 1994; STEARNS & DOCKERY 1984)

Genus: *Tectisumen* Finlay, 1927 (type species: *Cocculina clypidellaformis* Suter, 1908) (synonymised with *Lepetella* Verrill, 1880 by WAREN (1972) and HICKMAN (1983) but not by HASZPRUNAR (1988a))
*Tectisumen clypidellaformis* (Suter, 1908) (*Cocculina*)
(southwestern Pacific: deep water off New Zealand, on polychaete *Hyalinoecia tubes*) (DELL 1956, MOSKALEV 1978)
*Tectisumen compropinctum* (Fleming, 1966) (*Lepetella /Tectisumen/*)
(Cenozoic, New Zealand) (MOSKALEV 1978)
*Tectisumen wayi* Finlay, 1927
(southwestern Pacific: off New Zealand)
(MOSKALEV 1978)
*Tectisumen parallela* (Fleming, 1966) (*Lepetella /Tectisumen/*)
(Cenozoic, New Zealand) (MOSKALEV 1978)
*Tectisumen tasmanica* (May, 1920)
(southwestern Pacific: off Australia)

Genus: *Tecticrater* Dell, 1956 (type species: *Cocculina compressa* Suter, 1908) (synonymised with *Lepetella* Verrill, 1880 by WAREN (1972) and HICKMAN (1983) but not by HASZPRUNAR (1988a))
*Tecticrater compressa* (Suter, 1908) (*Cocculina*)
(southwestern Pacific: off New Zealand; 260 m) (DELL 1956, MOSKALEV 1978)
"*Tecticrater* grandis" Crozier, 1966
(southwestern Pacific: off New Zealand)
this species should be probably referred to Lepetellidae Hall, 1869 (MARSHALL, personal information)

Genus: *Bogia* Dantart et Luque, 1994
(type species: *Cocculina labronica* Bogi, 1984)
(family uncertain, should be excluded from Lepetellidae according to DANTART & LUQUE 1994)

Genus: *Sablea* Allen, 1970
(type species: *Sablea minuta* Allen, 1970)

Genus: *Addisonia* Dall, 1882
(type species: *Addisonia paradoxa* Dall, 1882)
*Addisonia brophyi* McLean, 1985
(northeastern Pacific: Santa Barbara Basin to Santa Catalina Basins; 155–174 m; in shark egg cases)

*Addisonia enodis* Simone, 1996
(southwestern Atlantic: off Ubatuba, Sao Paulo St. Brazil, 184 m)

*Addisonia excentrica* (Tiberi, 1855) (*Gadinia*)
  = *Addisonia lateralis* auct., non *Gadinia lateralis* Réquien, 1848
  = *Addisonia excentrica* Jeffreys, 1883(a)
(Mediterranean: Sicily to Corsica; Eastern Atlantic: Bay of Biscay to Guinea Bissau)
  = *Addisonia paradoxa* Dall, 1882(a)
(western Atlantic: Nova Scotia to Jamaica; in empty egg cases of sharks and skates)
(DALL 1882bc, 1889b, MCLEAN 1985, DANTART & LUQUE 1994, WARÉN 1996b)

Subfamily: Helicopeltinae Marshall, 1996

(type species: *Helicopelta rostricola* Marshall, 1996)

*Helicopelta rostricola* Marshall, 1996
(southwestern Pacific: Chesterfield Plateau, Coral Sea; 685–700 m; on a detrital cephalopod beak)

*Helicopelta* n. sp. (MARSHALL 1996)
(southwestern Pacific: southeast of New Caledonia; 750 m; on a detrital cephalopod beak)

species excluded from Addisoniidae Dall, 1882(a)

*Gadinia lateralis* Réquien, 1848
is a junior synonym of *Trimusculus mammilaris* (Linnaeus, 1758) (*Pulmonata*)
(DANTART & LUQUE 1994, WARÉN 1996b)

Family: BATHYPHYTOPHILIDAE Moskalev, 1978


*Bathyphytophilus caribaeus* Moskalev, 1978
(western Atlantic: Cayman Trench; 5800–6500 m; on turtlegrass *Thalassia testudinarum*)

*Bathyphytophilus diagens* Haszprunar et McLean, 1996
(northeastern Pacific: San Diego Trough; 1224 m; on surfgrass *Phyllospadix scouleri*)

*Bathyphytophilus* n. sp. (HASZPRUNAR & McLEAN 1996)
(northeastern Pacific: San Diego Trough; 1207–1234 m; on surfgrass *Phyllospadix torreyi*)


*Aenigmabonus kurilokamtschaticus* Moskalev, 1978
(northwestern Pacific: Kurile-Kamchatka Trench; 6120–6160 m)

Family: CHORISTELLIDAE Bouchet et Warén, 1979
  = CHORISTIDAE auct.

Genus: *Bichoristes* McLean, 1992(b)
(type species: *Bichoristes wareni* McLean, 1992)

*Bichoristes wareni* McLean, 1992(b)
(southwestern Pacific: Norfolk Ridge, south of New Caledonia; 505–515 m)

Genus: *Choristella* Bush, 1897 (type species: *Choristella leptalea* Bush, 1897)

*Choristella hickmanae* McLean, 1992(b)
(northeastern Pacific: Northern Cascadia Abyssal Plain, Strait of Juan de Fuca; 2176 m)
(HASZPRUNAR 1992b)

*Choristella leptalea* Bush, 1897
  = *Choristella brychia* Bush, 1897 (MCLEAN 1992b)
(northeaster Mediterranean: off Martha’s Vineyard Island, Massachusetts; 713–1481 m)

*Choristella marshalli* McLean, 1992(b)
(southwestern Pacific: off New Zealand; 376–1116 m; in empty skate egg case) (HASZPRUNAR 1992b)

*Choristella nofronii* McLean, 1992(b)
  = *Cynthia natiformis* auct., non *Cynthia natiformis* Jeffreys, 1883(b)
(Alboran Sea, westernmost Mediterranean near Spain; 50–100 m; in *Raia* egg cases)
(GUBBIOLI & NOFRONI 1986, HASZPRUNAR 1992b)

*Choristella ponderi* McLean, 1992(b)
(southwestern Pacific: off Australia; 91–552 m; in skate egg case)

*Choristella tenera* (Verrill, 1882) (*Choristes*)
(northeastern Pacific: off Martha’s Vineyard Island, Massachusetts and off Cape Hatteras, North Carolina; 353–580 m; inside an old egg-case of skate *Raia*) (MCLEAN 1992b)

*Choristella vitrea* (Kuroda et Habe in Kuroda et al., 1971) (*Choristes*)
(northeastern Pacific: Sagami Bay, Japan; on egg capsules of shark) (MCLEAN 1992b)

*Choristella* n. sp. (1) (MCLEAN 1992b)
(southwestern Indian Ocean: Mozambique Channel; 3716 m)

*Choristella* n. sp. (2) (MCLEAN 1992b)
(southern Indian Ocean: Mozambique Channel; 3716 m)

*Choristella* n. sp. (3) (MCLEAN 1992b)
(southern Pacific: Norfolk Ridge; 503 m)

*Choristella* n. sp. (3) (MCLEAN 1992b)
(Indo-Pacific: Tanimbar Island, Indonesia; 356–368 m)

*Choristella* n. sp. (4) (MCLEAN 1992b)
(Indo-Pacific: Arafura Sea, off Kai Islands, Indonesia; 390–502 m)

species excluded from Choristellidae Bouchet et Warén, 1979

*Choristes agulhasae* Clarke, 1961
probably in *Trenchia* Knudsen, 1964, Skeneidae
Clark, 1851 (McLean 1992b)

*Choristes agulhasae argentinae* Clarke, 1961
probably in *Trenchia* Knudsen, 1964, Skeneidae
Clark, 1851 (McLean 1992b)

*Choristes carpenteri* Dall, 1896
should be placed in Naticidae Forbes, 1838
(McLean 1992b)

*Choristes coani* Marincovich, 1975
is synonym of naticid *Amauropsis islandica* (Gmelin, 1791) (McLean 1992b)

*Choristes carpenteri* Dall, 1896
probably in *Granigyra* Dall, 1889, Skeneidae
Clark, 1851 (McLean 1992b)

*Choristes nipponica* Okutani, 1964
should be excluded from Choristellidae (McLean 1992b)

*Choristes mollis* Okutani, 1964
probably in *Granigyra* Dall, 1889, Skeneidae
Clark, 1851 (McLean 1992b)

*Choristes carpenteri* Dall, 1896
should be placed in Naticidae Forbes, 1838
(McLean 1992b)

*Choristes coani* Marincovich, 1975
should be placed in Naticidae Forbes, 1838
(McLean 1992b)

*Choristes carpenteri* Dall, 1896
probably in *Trenchia* Knudsen, 1964, Skeneidae
Clark, 1851 (McLean 1992b)

*Choristes carpenteri* Dall, 1896
should be placed in Naticidae Forbes, 1838
(McLean 1992b)

*Choristes elegans* Carpenter in Dawson, 1872
is synonym of naticid *Amauropsis islandica* (Gmelin, 1791) (McLean 1992b)

Cintha naticiformis Jeffrey, 1885(b)
probably in *Trenchia* Knudsen, 1964, Skeneidae
Clark, 1851 (McLean 1992b)
recently to *Xyloskenea* Marshall, 1988, Skeneidae
Clark, 1851 (Warén 1996a)

*Cyclostrema pompholyx* Dall, 1889(a)
should be not referred to Choristellidae (McLean 1992b)

*Cyclostrema valvatoides* Jeffrey, 1883(b)
probably in Skeneidae Clark, 1851 (McLean 1992b)

Family: COCCULINELLIDAE Moskalev, 1971

Genus: *Cocculinella* Thiele, 1909
(type species: *Acmaea minutissima* E. A. Smith, 1904)

*Cocculinella coerecta* (Hedley, 1907) (*Cocculina*)
(southernwestern Pacific: off New South Wales and eastern Victoria; 146–393 m; off Cape Jaffa, S. Australia; 238 m; on fish bones) (Marshall 1986)

*Cocculinella kopua* Marshall, 1983
(southwestern Pacific: off North Cape, New Zealand; 257–327 m) (species of uncertain validity, Marshall 1986)

*Cocculinella minutissima* (E. A. Smith, 1904) (*Acmaea*)
(northwestern Indian Ocean: Arabian Sea; on teleost fish bones) (Haszprunar 1988b)

*Cocculinella osteophila* Marshall, 1983
(southwestern Pacific: Whangaroa Harbour, New Zealand; 13 m; on bone)

*Cocculinella salisburyensis* Ludbrook, 1956
(Pliocene, South Australia)
doubtfully referable to the genus, probably belongs to Lepetellidae Dall, 1882(a) or to Acmaeidae Forbes, 1849 (Marshall 1983)

Family: OSTEOPELTIDAE Marshall, 1987

(type species: *Osteopelta mirabilis* Marshall, 1987)

*Osteopelta ceticola* Warén, 1989
(north Atlantic: off southwestern Iceland between Vestmannaeyjar and Reykjanesridge; on whale bone)

*Osteopelta mirabilis* Marshall, 1987
(southernwestern Pacific: Challenger Plateau, northwest of Chatham Islands and Chatham Rise, New Zealand; 800–955 m; on whale skulls and bones) (Haszprunar 1988c)

(middle Eocene, Waihao Greensand, New Zealand; associated with bones of fossil turtle)

*Osteopelta praeceps* Marshall, 1994
(southernwestern Pacific: Chatham Rise and Challenger Plateau, New Zealand; 372–912 m; on whale bones)

Family: PSEUDOCOCCULINIDAE Hickman, 1983
(the subfamiliar attribution of particular genera may be premature according to McLean 1991)

Subfamily: Pseudococculininae Hickman, 1983

Genus: *Pseudococculina* Schepman, 1908 (type species: *Pseudococculina rugosoplicata* Schepman, 1908)

*Pseudococculina cingulata* Schepman, 1908
(Indo-Pacific: off Indonesia)

*Pseudococculina granulata* Schepman, 1908
(Indian Ocean)

*Pseudococculina gregaria* Marshall, 1986
(southernwestern Pacific: off Southern New Zealand and New South Wales; 384–891 m; on wood) (Haszprunar 1988b)

"*Pseudococculina* rugosoplicata" Habe, 1952
(northwestern Pacific: off Japan)
status not confirmed by recent anatomical studies

*Pseudococculina rugosoplicata* Schepman, 1908
(eastern Indian Ocean: Sunda Sea, Indonesia, 2798 m)

*Pseudococculina subcingulata* (Kuroda et Habe, 1949) (*Cocculina*) (Fig. 5, 6)
(northwestern Pacific: off Tosa, Shikoku; Suruga Bay, Honshu, Japan; 140–490; on wood) (Haszgawa 1997)

*Pseudococculina* n. sp. (1) (Moskalev 1976)
*Pseudococculina* n. sp. (2) (Moskalev 1976)
*Pseudococculina* n. sp. (3) (Moskalev 1976)
*Pseudococculina* n. sp. (4) (Moskalev 1976)
*Pseudococculina* n. sp. (5) (Moskalev 1976)


*Bandabyssia costoconcentrica* Moskalev, 1976

*Kaiparapelta askewi* McLean et Harasewych, 1995 (northwestern Atlantic: 165 km E of Charleston, South Carolina; 194 m) (spongivorous) (WAREN & GOFAS 1996)

*Kaiparapelta singularis* Marshall, 1986 (early Miocene, Pakaurangi Point, Kaipara, New Zealand)


*Kurilabyssia antipodensis* Marshall, 1986 (southwestern Pacific: off New South Wales and southern New Zealand; 823–962 m; on wood) (HASZPRUNAR 1988b)

*Kurilabyssia squamosa* Moskalev, 1976 (northwestern Pacific: Kurile-Kamchatka Trench; 5220 m)


*Mesopelex n.* sp. (to be described by B. A. Marshall according to HASZPRUNAR 1988ab) (southwestern Pacific: off Timaru, New Zealand; 852–876 m)

Genus: *Notocrater* Finlay, 1927

(type species: *Cocculina craticulata* Suter, 1908) = *Punctolepeta* Habe, 1958

(type species: *Punctolepeta minuta* Habe, 1958)

*Notocrater craticulata* (Suter, 1908) (Cocculina) (southwestern Pacific: off Timaru and Dusky Sound, New Zealand; 37–738 m; on wood) (MARSHALL 1986)

*Notocrater gracilis* Marshall, 1986 (southwestern Pacific: off Hicks Bay, New Zealand, 55–73 m; in teredin tubes in wood)

*Notocrater houbricki* McLean et Harasewych, 1995 (western Atlantic: south of Settlement Point, Grand Bahama Island, Bahama Islands; 412 m)

*Notocrater maxwelli* Marshall, 1986 (early Miocene, Pakaurangi Point, Kaipara, New Zealand)

*Notocrater ponderi* Marshall, 1986 (southwestern Pacific: off New South Wales; 165–84 m; on wood) (HASZPRUNAR 1988b)

*Notocrater pustulosa* (Thiele, 1925) (Cocculina) (Fig. 7) = *Punctolepeta minuta* Habe, 1958 (northwestern Pacific: off Japan) (HASEGAWA 1997, MARSHALL 1986)

*Notocrater pustulosa* (Woodring, 1928 non Thiele, 1925) (Cocculina) (Miocene, Jamaica) (MCLEAN & HARASEWYCH 1995) the species should probably receive a replacement name as the name *pustulosa* appears to be preoccupied

*Notocrater youngi* McLean et Harasewych, 1995 (western Atlantic: off Southwest Reef, New Providence Island, Bahamas; 518 m; on palmetto fronds)


*Tentaoculus balantiophaga* Marshall, 1996 (southwestern Pacific: off Castlepoint and western Chatham Rise, New Zealand; 1065–1335 m; on spent skate egg cases)

*Tentaoculus eritmeta* (Verrill, 1884) (Puncturella /Fissurisepta/) (western Atlantic) (MCLEAN & HARASEWYCH 1995)

*Tentaoculus georgiana* (Dall, 1927) (Cocculina) (western Atlantic: off Georgia; 805 m) (MCLEAN & HARASEWYCH 1995)

*Tentaoculus haptricola* Marshall, 1986 (southwestern Pacific: off Jackson Bay, New Zealand; 1027–1041 m; on dorsal surface of carapace of stone crab *Lithodes murrayi* Henderson, 1888)


*Tentaoculus perlucida* Moskalev, 1976 (western Pacific: off New Guinea; 300–450 m)

Subfamily: Caymanabyssiinae Marshall, 1986

Genus: *Caymanabyssia* Moskalev, 1976

(type species: *Caymanabyssia s. str.* Moskalev, 1976)

*Caymanabyssia (Caymanabyssia)* rhina Marshall, 1986 (southwestern Pacific: off White Island, New Zealand; 1075–1100 m; on wood)

*Caymanabyssia spina* Moskalev, 1976 (western Atlantic: off Hicks Bay, New Zealand, 55–73 m; in teredin tubes in wood)

*Caymanabyssia vandoverae* McLean, 1991 (northeastern Pacific: Escanaba Trough, Gorda Ridge; 3362 m; on wood)
*Caymanabyssia (Dictyabyssia) fosteri* McLean, 1991
(East Pacific Rise 11°N; 2700 m; on wood)
*Caymanabyssia (Dictyabyssia) sinespina* Marshall, 1986
(southwestern Pacific: White Island to Jackson Bay, New Zealand; 800–1147 m)
(HASZPRUNAR 1988b)

Genus: *Amphiplica* Haszprunar, 1988(b)
Subgenus: *Amphiplica* s. str. Haszprunar, 1988(b)
(type species: *Amphiplica venezuelensis* McLean, 1988)
*Amphiplica (Amphiplica) concentrica* (Thiele, 1909)
(Pseudococculina)
(Atlantic: north of Azores) (MCLEAN 1988)
*Amphiplica (Amphiplica) knudseni* McLean, 1988
(southwestern Pacific: Tasman Basin, New Zealand; 3610 m) (HASZPRUNAR 1988b)
*Amphiplica (Amphiplica) venezuelensis* McLean, 1988
(western Atlantic: Venezuelan Basin; 3476–5057 m) (HASZPRUNAR 1988b)
*Amphiplica* n. sp. (LEAL 1996)
(western Atlantic: Puerto Rico Trench; 8595 m)
*Amphiplica (Gordabyssia) gordensis* McLean, 1991
(northeastern Pacific: Escanaba Trough, Gorda Ridge; 3305 m; on sulfide crust)

*Colotrachelus hestica* Marshall, 1986
(southwestern Pacific: off Castlepoint and off Kaikoura, New Zealand; 1174–1723 m; on wood)
(HASZPRUNAR 1988b)

Genus: *Copulabyssia* Haszprunar, 1988(b)
(type species: *Cocculina corrugata* Jeffreys, 1883)
*Copulabyssia corrugata* (Jeffreys, 1883/c/) (Cocculina)
(northeastern Atlantic; Tyrrenhian Sea; 100–1778 m; from submersed wood)
*Copulabyssia gradata* (Marshall, 1986) (Pseudococculina)
(southwestern Pacific: White Island and East Cape, New Zealand; 1075–1280 m; on wood)
(HASZPRUNAR 1988b)
*Copulabyssia leptalea* (Verrill, 1884) (Cocculina)
(northern Atlantic: Iceland, north of the Hebrides; from wood bored by shipworms) (MCLEAN & HARASEWYCH 1995)

Genus: *Punctabyssia* McLean, 1991 (subfamiliar status unclear)
(type species: *Punctabyssia tibbettsi* McLean, 1987)
*Punctabyssia tibbettsi* McLean, 1991
(northeastern Pacific; 940–1400 m; on whale skulls) (MCLEAN 1992a)

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