

SPECIES CHECKLIST OF MURICIDAE (MOLLUSCA: GASTROPODA) IN THE SOUTH CHINA SEA

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ABSTRACT. - The checklist was compiled from published material. A total of 130 species of extant muricid gastropods present in the South China Sea is listed, with brief introductions to subfamilies and genera. Of the subfamilies recognized in the family Muricidae, the Muricinae contains 54 species, Muricopsinae with 5 species, Typhinae and Ocenebrinae each has two species, and Rapaninae comprises 67 species. There were no species belonging to the subfamilies Tripterotyphinae and Trophoninae. Where possible, recent illustrated references for each species are given. The coralliophilids are considered a separate family and therefore not listed.

INTRODUCTION

The family Muricidae is the second largest family in the Neogastropoda with 500–600 Recent species (Boss, 1971; Taylor, Morris & Taylor, 1980). Its members have a fairly recent origin in the Cretaceous (Sohl, 1969; Taylor, Morris & Taylor, 1980) and they are exclusively marine with a global distribution. A concise conchological definition of the members of this family still eludes us, although they can generally be distinguished from other neogastropod families by the presence of varices, tubercles or spines (Thiele, 1931; Wenz, 1941). The operculum has either a marginal or lateral ('purpuroid') nucleus, while the stenoglossan radula consists of a central row of rachidian teeth flanked on each side by lateral teeth. Each rachidian tooth usually has three cusps, and smaller denticles may be present. The lateral teeth are often sickle-shaped, whose edges may bear denticles. Anatomically they are characterized by having a terminal buccal mass inside the proboscis, and an accessory boring organ in the sole of the foot. In many genera a pair of accessory (tubular) salivary glands is present in addition to a pair of acinous salivary glands. The proboscis, accessory boring organ and accessory salivary glands are features associated with their predatory habits (Carriker, 1981). The radular retractor muscles by-pass the nerve ring, there is often a large gland of Leiblein, and the stomach has a broad caecum. These distinct features make muricid gastropods amongst one of the more highly derived members in the superfamily Muricoidea (Kantor, 1996).

Within this anatomically well-defined group, however, attempts to sub-divide its members have been less successful, and there is considerable uncertainty as regards the groupings of

genera within the family (Ponder, 1972). Initial attempts at subfamilial taxonomy include Tryon (1880) who divided the Muricidae into two groups, the Muricinae and the Purpurinae. Cossmann (1903), who proposed a subfamilial classification based on the shell and operculum, divided the Muricidae into four subfamilies, the Muricinae, Ocenebrinae, Typhinae and Rapaninae. He considered Purpuridae a distinct family separate from the Muricidae. In contrast Thiele (1931) did not recognize subfamilies, perhaps in view of the similarities in the morphology of their radula based on the work of Troschel (Troschel, 1866–93). Based on anatomical data (but pending a comprehensive phylogenetic analysis), it seems reasonable to assign Rapaninae (=Thaidinae of authors) subfamilial status (see also Ponder, 1973; Emerson & Cernohorsky, 1973; Fretter & Graham, 1985), despite opinions favouring the recognition of a separate family (Clench, 1947; Keen, 1971; Golikov & Starabogatov, 1975; Radwin & D'Attilio, 1976; Harasewych, 1984). As regards the remaining subfamilies, there is presently little consensus as to what natural groupings are recognizable within the Muricidae. Between three and eight subfamilies have been assigned to the Muricidae (see e.g., Wenz, 1941; Emerson & Cernohorsky, 1973; Ponder & Warén, 1988; Houart, 1995; Vokes, 1996a,b) including Muricinae, Muricopsinae, Typhinae, Tripterotyphinae, Ergalataxinae, Ocenebrinae, Rapaninae (formerly Thaidinae/Drupinae of authors, following Kool, 1993a,b) and Trophoninae (formerly Tritonaliinae).

A partial revision of the genera and their relationships was accomplished recently (Kool, 1993a, b) which clarified the positions of Ocenebrinae and Rapaninae. The two subfamilies were re-defined based on the anatomy of type species (Kool, 1993b).

The muricids have recently been a subject of some concern from a somewhat unrelated standpoint: the phenomenon of imposex. Imposex, or the imposition of male sexual characteristics on females, was shown to be caused by tributyltin (TBT), the active toxic ingredient of anti-fouling paints used on ships' hulls (see review by Gibbs & Bryan, 1996). In addition, the degree of imposex is dependent on the extent of exposure to TBT. In view of the specificity of the snails' response, it has been suggested that these snails could be effective semi-quantitative bioindicators of the pollutant in coastal waters. Quantitative determination of TBT via chemical methods is tedious and time-consuming, and muricids (especially rapanines) appear to be ideal indicator animals since they are often abundant in the intertidal zone. Although the use of TBT is prohibited for smaller vessels, the high costs of using alternative means of controlling biofouling on large vessels still favour the use of organotins in anti-fouling paints. If reliable dose-response relationships can be established for the common species of muricids, then these snails can be useful bioindicators of marine pollution. However, before this can be done, the species concerned must be identified. Efforts to understand and establish a taxonomy of muricids have been hampered by the lack of taxonomists. There are also inherent difficulties in coming to terms with intra- and inter-specific variation that occur amongst members of this family. In this context, a checklist that gives an idea of what is present in the South China Sea is necessary. This paper serves to provide a preliminary checklist of the Muricidae of the South China Sea, as well as gives a brief introduction to the various subfamilies and genera presently recognized.

MATERIALS AND METHODS

The following list was mainly compiled from published material, including several recent monographs. Detailed synonymy, descriptions and comparisons of closely related species are therefore not given. However, recent references that provide informative figures of the

species listed below are included. The following regional checklists of molluscs were utilized during the compilation: Fischer (1891, 1970) and Kurozumi, Kosuge & Tsuchiya (1989) for Gulf of Thailand; Kuroda (1941) for Taiwan; Kuroda, Habe & Oyama (1971) for Taiwan and southern Japan; Chuang (1973), Way & Purchon (1981), Angot (1984) and Middlefert (1997) for peninsular Malaysia; Yen (1935), Zhang (1976, 1980), Qi et al. (1983) and Huang (1994) for the Chinese coast, and Taylor (1994) for Hong Kong. Distributional data were obtained from the abovementioned lists as well as from Radwin & D'Attilio (1976), Cernohorsky (1972, 1978a), Kilburn & Rippey (1982), Wilson (1994), Tan (1995) and other relevant sources. The subfamilial classification adapted from Radwin & Attilio (1976) is mainly for convenience and does not necessarily reflect phylogenetic relationships.

Abbreviations used: EAF—East Africa, incl. Madagascar; IND—Indian Ocean and Indian subcontinent; SEA—Southeast Asia; NEA—Northeast Asia, including Hong Kong, Taiwan and Japan; PAC—Pacific Ocean; AUS—tropical Australia; PHI—Philippine Islands.

RESULTS

Rapaninae Gray, 1853

The close similarities in the anatomy of the type species of *Rapana* and *Thais* were recently pointed out by Kool (1993a). As a consequence the Thaidinae of authors is now replaced by the nomenclaturally older subfamily Rapaninae.

Rapana Schumacher, 1817 (type species: *Rapana rapiformis* (Born, 1778) by S.D.)

This is a well-known genus with three species distributed in the South China Sea (Zhang, 1980). They are found subtidally and are consumed as food by man. Their shell is distinctive in having a large body whorl with a correspondingly large aperture while having a low spire. A thin calcitic layer is present on the surface of the shell. The rachidian teeth have three large cusps but the marginal cusps are conspicuously absent. A comb-like region is present instead on the outer sides of the lateral cusps on the rachidian.

Rapana bezoar (L., 1758)

Fischer (1970) list; Zhang (1980); Morton (1994) ecology, egg capsules
IND, SEA, NEA

Rapana rapiformis (Born, 1778)

Huang (1994) list; D'Asaro (1991); Knudsen (1994) as *bulbosa*; (= *bulbosa* Dillwyn, accord. to Kuroda, 1941 and Zhang, 1980)
EAF, IND, SEA, NEA, PAC, AUS

Rapana venosa Valenciennes, 1880

Huang (1994) list; (= *R. thomasiana* and *R. pechiliensis*, accord. to Huang, 1994)
EAF, IND, SEA, NEA

Drupa Röding, 1798 (type species: *Drupa morum* Röding, 1798 by S.D.)

(consisting of the subgenera *Drupa*, *Ricinella* and *Drupina* according to Emerson & Cernohorsky (1973))

This genus is loosely distinguished from other rapanines by its shell, whose aperture is narrow and occluded by columellar and outer lip teeth. *Drupa* species are confined to the Indo-Pacific (Emerson & Cernohorsky, 1973). They are generally predators of polychaetes although they also feed on vermetids, crustaceans, sipunculids and even fishes (Taylor, 1982, 1983; Thomas & Kohn, 1990).

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<i>Drupa (D.) morum morum</i> Röding, 1798	Huang (1994); Emerson & Cernohorsky (1973) EAF, IND, SEA, NEA, PAC, AUS
<i>Drupa (D.) ricinus ricinus</i> (L., 1758)	Huang (1994); Emerson & Cernohorsky (1973) EAF, IND, SEA, NEA, PAC, AUS
<i>Drupa (R.) ricinus albolabris</i> (Blainville, 1832)	Huang (1994) EAF, IND, SEA, NEA, PAC, AUS
<i>Drupa (R.) rubusidaeus</i> Röding, 1798	Huang (1994); Emerson & Cernohorsky (1973) EAF, IND, SEA, NEA, PAC, AUS
<i>Drupa (Drupina) grossularia</i> Röding, 1798	Huang (1994); Emerson & Cernohorsky (1973) SEA, NEA, PAC, AUS
<i>Drupa spathulifera</i> (Blainville, 1832) [= <i>Drupa rubusidaeus</i> Röding, 1798 accord. to Emerson & Cernohorsky, 1973]	Huang (1994)

Drupella Thiele, 1925 (type species: *Purpura elata* Blainville, 1832 [= *Drupella cornus* (Röding, 1798) according to Fujioka (1982), Wilson (1992) and Turner (1994)] by S.D.) Species of *Drupella* are specialist predators of coral polyps and the genus is distinguished from other rapanines in having extremely long, thin lateral teeth (Thiele, 1925). They are confined to the coral reefs of the Indo-Pacific. The shells and radulae show considerable intraspecific variation and this has resulted in taxonomic problems (Fujioka, 1982; Johnson & Cumming, 1995). In some species apertural colour varies from white to purple, while the radulae of several species show sexual dimorphism, with males having larger and more massive rachidian teeth compared to the females (Fujioka, 1982). It is not known if all members of this genus are sexually dimorphic. The biology and ecology of *Drupella cornus* have been reviewed by Turner (1992, 1994). Most species are found in the subtidal zone, although *D. concatenata* can occur on *Acropora* in the low intertidal zone (pers. obs.).

<i>Drupella concatenata</i> (Lamarck, 1822) [= <i>Drupella rugosa</i> (Born, 1778)] [= <i>Drupella fragum</i> (Blainville), accord. to Zhang, 1976]	Fischer (1970); Zhang (1976); Johnson & Cumming (1995) EAF, IND, SEA, NEA, PAC, AUS
<i>Drupella cornus</i> (Röding, 1798)	Turner (1992, 1994) EAF, IND, SEA, NEA, PAC, AUS
<i>Drupella elata</i> (Blainville, 1832) [= <i>Drupella cornus</i> Röding, 1798 accord. to Fujioka, 1982]	Zhang (1976)
<i>Drupella fragum</i> (Blainville, 1832)	Fujioka (1986); Johnson & Cumming (1995) NEA, AUS
<i>Drupella minuta</i> Fujioka, 1984	Fujioka (1984, 1986) NEA

Purpura Bruguiere, 1789 (type species: *Purpura persica* (L., 1758) by S.D.) The genus *Purpura* is often loosely distinguished from *Thais* species in having largish shells, large apertures and bearing a concave columella. It differs from *Rapana* in not having an external calcitic layer on the shell, and its rachidian teeth bear prominent marginal denticles, unlike those of *Rapana* where the marginal denticles are replaced by fine surface undulations (see Kool, 1993a).

<i>Purpura persica</i> (L., 1758)	Yen (1935); Kuroda (1941); Kool (1993a) SEA, NEA, PAC, AUS
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- Purpura rudolphi* (Lamarck, 1822) Kuroda (1941)
 [=*Purpura panama* Röding, 1798 accord.
 to Kilburn & Rippey, 1982]
- Purpura panama* Röding, 1798 Fujioka (1986)
 EAF, IND, SEA, NEA
- Nassa* Röding, 1798 (type species: *Nassa picta* Röding, 1798 [=*Nassa sarta* (Bruguière, 1789) according to Kool, 1993a] by S.D.)
 According to Houart (1996), of the four *Nassa* species in the Indo-Pacific, only *N. sarta* is found in the South China Sea. He distinguished *N. francolina* as having 98–102 spiral cords on the last whorl as opposed to *N. sarta* which has only 59–62 spiral cords.
- Nassa sarta* (Bruguière, 1789) Kuroda (1941); Maes (1966); Houart (1996)
 SEA, NEA, PAC, AUS
- Thais* Röding, 1798 (Type species: *Thais nodosa* (L., 1758) by S.D.)
 This cosmopolitan genus contains a plethora of species that eludes definitive groupings (Cooke, 1919; Tan, 1995), although many genera based on shell morphology have been proposed, e.g., *Cuma*, *Cymia*, *Menathais*, *Reishia*, *Stramonita*, *Thaisella*, *Thalessa*, etc. Although the type species of the genus, *Thais nodosa*, has a shell that is very different from most Indo-Pacific *Thais* species, intraspecific variation that is observed in some species cautions us against using shell shape as a generic character.
- Thais aculeata* (Deshayes, 1844) Tan (1995); Demond (1957) as *T. hippocastanum* (L.)
 EAF, IND, SEA, NEA, PAC, AUS
- Thais armigera* (Link, 1802) Kuroda (1941); Tröndle & Houart (1992)
 EAF, IND, SEA, NEA, PAC, AUS
- Thais bitubercularis* (Lamarck, 1822) Tan (1995)
 EAF, SEA, AUS
- Thais bufo* (Lamarck, 1822) Kuroda (1941); Tan (1995)
 EAF, IND, SEA, AUS
- Thais clavigera* (Küster, 1858) Kuroda (1941); Tan (1995)
 SEA, NEA
- Thais distinguenda* (Dunker & Zeebor, 1866) Kuroda (1941); Tan (1995)
 EAF, IND, SEA, NEA, PAC, AUS
- Thais gradata* (Jonas, 1846) Fischer (1971); Tan (1995)
 SEA, NEA
- Thais intermedia* (Kiener, 1836) Kuroda (1941); Cernohorsky (1969)
 EAF, IND, SEA, NEA, PAC, AUS
- Thais javanica* (Philippi, 1848) Kuroda (1941); Tan (1996b)
 IND(?), SEA, NEA
- Thais jubilaea* Tan & Sigurdsson, 1990 Tan & Sigurdsson (1990)
 SEA
- Thais lacera* (Born, 1778) Kuroda (1941); Fischer (1970); Tan (1995)
 [=*Thais carinifera* (Lamarck, 1822) accord.
 to Mienis, 1985; Tan, 1995]
 EAF, IND, SEA, NEA
- Thais luteostoma* (Holten, 1802) Kuroda (1941); Tan (1995)
 NEA
- Thais malayensis* Tan & Sigurdsson, 1996b Tan & Sigurdsson (1996b)
 IND(?), SEA

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<i>Thais marginatra</i> (Blainville, 1832)	Kuroda (1941); Tan (1995) EAF, IND, SEA, PAC
<i>Thais muricoides</i> (Blainville, 1832)	Tan (1995) IND, SEA, PAC, AUS
<i>Thais rufotincta</i> Tan & Sigurdsson, 1996a	Tan & Sigurdsson (1996a) IND(?), SEA
<i>Thais rugosa</i> (Born, 1798)	Kuroda (1941); Tan (1995) IND, SEA
<i>Thais squamosa</i> (Pease, 1868)	Tan (1995) EAF, IND, SEA, NEA, PAC, AUS
<i>Thais tuberosa</i> (Röding, 1798)	Kuroda (1941); Demond (1957) EAF, IND, SEA, NEA, PAC, AUS
<i>Thais turbinoides</i> (Blainville, 1832)	Tan (1995) SEA, PAC, AUS

Mancinella Link, 1807 (type species: *Mancinella alouina* (Röding, 1798) by S.D.)

Members of this genus are generally distinguished from the closely related *Thais* species in having a radula whose rachidian teeth have three massive cusps that are devoid of marginal or inner denticles. However, sexual dimorphism has been observed in two of three species (Fujioka, 1985; Tan, 1995) listed below, and there appears to be intraspecific variation as to the absence or presence of denticles on the rachidian (Tan, 1995).

<i>Mancinella alouina</i> (Röding, 1798)	Kuroda (1941); Tan (1995) EAF, IND, SEA, NEA, PAC, AUS
<i>Mancinella echinata</i> (Blainville, 1832)	Kuroda (1941); Tan (1995) SEA, NEA, AUS
<i>Mancinella echinulata</i> (Lamarck, 1822)	Kuroda (1941) IND, SEA, NEA

Morula Schumacher, 1817 (type species: *Morula uva* (Röding, 1798) by S.D.)

The genera *Morula*, *Cronia*, *Ergalatax*, *Muricodrupa*, *Spinidrupa*, *Trachypollia*, *Orania* and *Cytharomorula* have recently been used (e.g., Houart, 1995; Vokes, 1996a) but they have not been defined rigorously. Members of the genus *Morula* are generally distinguished from *Thais* species in having radulae whose rachidians bear lateral cusps that do not give rise to inner denticles. Rather, the inner denticles arise from the base of the rachidian. Also, unlike members of the genus *Thais*, the animal is often pigmented green (Tan, 1995) (also in the case of *Drupa*, *Drupella*, *Cronia* and *Ergalatax*; pers. obs.), and the attached surface of the operculum bears multiple adventitious layers (Tan, 1995).

<i>Morula anaxares</i> (Kiener, 1836)	Kuroda (1941); Tan (1995) EAF, IND, SEA, NEA, PAC, AUS
<i>Morula aspera</i> (Lamarck, 1816) [= <i>Morula uva</i> Röding, 1798 accord. to Cernohorsky, 1972]	Kuroda (1941); Zhang (1976) EAF, IND, SEA, NEA, PAC, AUS
<i>Morula borealis</i> (Pilsbry, 1906)	Zhang (1976) NEA
<i>Morula cariosa</i> (Wood, 1828) [= <i>Drupella fenestrata</i> (Blainville, 1832) in Zhang (1976) as <i>Drupa cancellata</i> (Quoy & Gaimard)] [= <i>Drupella cancellata</i> (Quoy & Gaimard, 1833, accord. to Cernohorsky, 1978b)]	Fujioka (1986) EAF, IND, NEA

<i>Morula ceylonica</i> (Dall, 1923)	Tan (1995) IND, SEA, PAC
<i>Morula funicula</i> (Wood, 1828)	Tan (1995) EAF, SEA, PAC, AUS
<i>Morula fusca</i> (Küster, 1862)	Tan (1995) EAF, IND, SEA, NEA, PAC, AUS
<i>Morula granulata</i> (Duclos, 1832)	Zhang (1976); Tan (1995) EAF, IND, SEA, NEA, PAC, AUS
<i>Morula mutica</i> (Lamarck, 1816)	Kuroda (1941); Emerson & Cernohorsky (1973) IND, PAC(?)
<i>Morula musiva</i> (Kiener, 1836)	Yen (1935); Tan (1995) EAF, SEA, NEA, PAC
<i>Morula ochrostoma</i> (Blainville, 1832) [= <i>Morula cavernosa</i> (Reeve, 1846) accord. to Cernohorsky, 1976]	Zhang (1976) EAF, IND, SEA, NEA, PAC, AUS
<i>Morula porphyrostoma</i> (Reeve, 1846)	Tan (1995) SEA, PAC, AUS
<i>Morula spinosa</i> (H. & A. Adams, 1853)	Tan (1995) EAF, IND, SEA, NEA, PAC, AUS
<i>Morula uva</i> (Röding, 1798)	Zhang (1976); Kool (1993a) EAF, IND, SEA, NEA, PAC, AUS

Cronia H. & A. Adams, 1853 (type species: *Purpura amygdala* Kiener, 1836 by monotypy)
Some genera, e.g., *Ergalatax* (see Cernohorsky, 1976) and *Muricodrupa* (see Fujioka, 1986)
have been considered to be subgenera of *Cronia* in view of the resemblance of their radula
to that of *Cronia amygdala*, the type species.

<i>Cronia margariticola</i> (Broderip, 1833)	Tan (1995); Cernohorsky (1982) EAF, IND, SEA, NEA, PAC, AUS
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Ergalatax Iredale, 1931 (type species: *Ergalatax recurrens* Iredale, 1931 by O.D.)
This genus was first proposed by Iredale (1931) where he assigned *Ergalatax recurrens* as
the type species. This species was subsequently acknowledged to be a junior synonym of
contracta Reeve, 1846 (see Tan, 1995). The family Ergalataxinae was erected by Kuroda,
Habe & Oyama (see Kuroda, Habe & Oyama, 1971) and Houart (1996) has assigned several
genera to this subfamily (e.g., *Cronia*, *Maculotriton*, *Muricodrupa*, *Orania*, *Pascula*). In
addition, Vokes (1996a) included *Spinidrupa*, *Cytharomorula*, *Lataxiena*, *Lindapterys* and
Daphnellopsis in her treatment of this subfamily. However there is little support to isolate
these genera from the others that are considered to be members of Rapaninae and hence this
subfamily is considered here synonymous with Rapaninae.

<i>Ergalatax contractus</i> (Reeve, 1846)	Taylor (1994); Tan (1995) SEA, NEA
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Bedeve Iredale, 1924 (type species: *Trophon hanleyi* Angas, 1867 by S.D.)

<i>Bedeve birileffi</i> (Lischke, 1871)	Radwin & D'Attilio (1976) NEA
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Maculotriron Dall, 1904 (type species: *Triton bracteatus* Hinds, 1844 by O.D.)

Maculotriron digitalis (Reeve, 1844)

Demond (1957)
NEA, PAC

Maculotriron serrialis (Deshayes, 1834)

Kuroda (1941) as var. *longia* (Pilsbry & Vanatta)
"Indo-Pacific"

Vexilla Swainson, 1840 (type species: *Vexilla picta* Swainson, 1840 [= *Vexilla vexillum* (Gmelin, 1791) accord. to Kool, 1993a] by S.D.)

This genus is distinguished by its form of shell and peculiar form of its radula. Kay (1979) and Kool (1987) have observed *Vexilla vexillum* feeding on sea urchins.

Vexilla vexillum (Gmelin, 1791)

Kay (1979); Kool (1993a)
NEA, PAC

Vexilla lineata A. Adams, 1853

Kay (1979)
PAC

Pinaxia H. & A. Adams, 1853 (type species: *Pinaxia coronata* H. & A. Adams, 1853 by monotypy)

In spite of its superficial resemblance to *Vexilla* in shell morphology, the radula of *Pinaxia* is typically thaidine in appearance (see e.g., Kool, 1993a). *Pinaxia versicolor* has been observed to drill the mussel *Brachidontes* (Kay, 1979).

Pinaxia versicolor (Gray, 1839)

Kay (1979); Kool (1993a)
IND, NEA, PAC

[=*Conothais citrina* Kuroda according to Kool, 1993a]

Vitularia Swainson, 1840 (type species: *Vitularia tuberculata* Swainson, 1840 [= *Murex miliaris* Gmelin, 1791 accord. to Radwin & D'Attilio, 1976] by O.D.)

Vitularia miliaris (Gmelin, 1791)

Radwin & D'Attilio (1976); Cernohorsky (1980)
IND, PAC, AUS

Vitularia crenifera (Montrouzier in Souverbie, 1861)

Cernohorsky (1980)
SEA(?)

Muricinae Rafinesque, 1815

The subfamily Muricinae comprises many genera that have an aragonitic shell and bearing opercula with a terminal, subterminal or (rarely) subcentral nucleus (Ponder & Vokes, 1988). Their radulae consist of rachidian teeth bearing three large and two small intermediate cusps (Ponder & Vokes, 1988). Most are found subtidally although several species can be found in the intertidal zone. The subfamily includes well-known genera such as *Murex*, *Chicoreus*, *Aspella* and *Dermomurex*. The Indo-Pacific species of *Murex* (s.s.) and *Haustellum* have been subject of a recent review by Ponder & Vokes (1988); *Chicoreus* species have been reviewed by Houart (1992).

Murex L., 1758 (type species: *Murex tribulus* L., 1758, by S.D.)

Murex tribulus L., 1758

Ponder & Vokes (1988); Huang (1994)
EAF, SEA, NEA, PAC, AUS

<i>Murex tenuirostrum</i> Lamarck, 1822	Ponder & Vokes (1988) IND, SEA, PAC, AUS
<i>Murex carbonnieri</i> (Jousseaume, 1881)	Ponder & Vokes (1988) EAF, IND, SEA
<i>Murex troscheli troscheli</i> Lischke, 1868	Ponder & Vokes (1988); Huang (1994) SEA, NEA, PAC
<i>Murex aduncospinosus</i> Sowerby, 1841	Ponder & Vokes (1988); Huang (1994) SEA, NEA, PAC
<i>Murex trapa</i> Röding, 1798	Ponder & Vokes (1988); Huang (1994) IND, SEA, NEA
<i>Murex falsitribulus</i> Ponder & Vokes, 1988	Ponder & Vokes (1988) SEA, NEA
<i>Murex occa</i> Sowerby, 1834	Ponder & Vokes (1988) SEA
<i>Murex altispira</i> Ponder & Vokes, 1988	Ponder & Vokes (1988) SEA
<i>Murex brevispina ornamentalis</i> Ponder & Vokes, 1988	Ponder & Vokes (1988) SEA
<i>Murex pecten pecten</i> Lightfoot, 1786	Ponder & Vokes (1988); Huang (1994) EAF, IND, SEA, NEA, PAC
<i>Murex spectabilis</i> Ponder & Vokes, 1988	Ponder & Vokes (1988) PHI only
<i>Murex ternispina</i> Lamarck, 1822 [= <i>Murex nigrispinosus</i> Reeve, 1845]	Ponder & Vokes (1988); Huang (1994) Kuroda (1941); Ponder & Vokes (1988); Huang (1994) IND, SEA, NEA

Haustellum Schumacher, 1817 (type species: *Murex haustellum* L., by tautonomy)

The genus *Haustellum* differs from *Murex* species in having apertural denticles on the inner lip, and in the absence of labral teeth on the outer lip. Anatomically they differ little except that in *Murex* the pallial vas deferens forms a muscular ejaculatory duct at the base of the penis, while in *Haustellum* the pallial vas deferens is non-muscular and is either an open groove or the line of fusion is visible externally (Ponder & Vokes, 1988).

<i>Haustellum haustellum haustellum</i> (L., 1758)	Ponder & Vokes (1988); Huang (1994) EAF, IND, SEA, NEA, PAC, AUS
<i>Haustellum rectirostris</i> (Sowerby, 1841)	Ponder & Vokes (1988); Huang (1994) NEA
<i>Haustellum gallinago</i> (Sowerby, 1903)	Ponder & Vokes (1988) NEA
<i>Haustellum multiplicatus bantamensis</i> (Martin, 1895)	Ponder & Vokes (1988) PHI only
<i>Haustellum dentifer</i> (Watson, 1883)	Ponder & Vokes (1988) SEA
<i>Haustellum dolichourus</i> Ponder & Vokes, 1988	Ponder & Vokes (1988) EAF, IND, SEA
<i>Haustellum kiiensis</i> (Kira, 1959)	Ponder & Vokes (1988); Huang (1994) as <i>Murex</i> <i>kiiensis</i> Kira NEA
<i>Haustellum mindanaoensis</i> (Sowerby, 1841)	Ponder & Vokes (1988) SEA

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Chicoreus Montfort, 1810 (type species: *Murex ramosus* L., 1758 by O.D.)
(comprising the subgenera *Rhizophorimurex*, *Triplex*, *Siratus* and *Chicopinnatus*, according to Houart, 1992)

Members of the genus *Chicoreus* are generally characterized by the presence of frondose varices and distinct split siphonal canals. Many species are found in the South China Sea. The Indo-Pacific species of *Chicoreus* and *Chicomurex* have recently been reviewed by Houart (1992). He divided the genus *Chicoreus* into four groups based mainly on the morphology of the shell (including the protoconch) and the radula. Many species of *Chicoreus* have direct or lecithotrophic development (Houart, 1992).

<i>Chicoreus</i> (<i>R.</i>) <i>capucinus</i> (Lamarck, 1822)	Houart (1992); Huang (1994) SEA, PAC, AUS
<i>Chicoreus</i> (<i>C.</i>) <i>asianus</i> Kuroda, 1942	Houart (1992); Huang (1994) NEA
<i>Chicoreus</i> (<i>C.</i>) <i>bundharmai</i> Houart, 1992	Houart (1992) SEA
<i>Chicoreus</i> (<i>C.</i>) <i>ramosus</i> (L., 1758)	Houart (1992); Huang (1994) EAF, IND, SEA, NEA, PAC, AUS
<i>Chicoreus</i> (<i>T.</i>) <i>palmarosae</i> (Lamarck, 1822)	Houart (1992); Huang (1994) EAF, SEA, NEA, PAC
<i>Chicoreus</i> (<i>T.</i>) <i>saulii</i> (Sowerby, 1834)	Houart (1992); Huang (1994) EAF, SEA, NEA, PAC
<i>Chicoreus</i> (<i>T.</i>) <i>torrefactus</i> (Sowerby, 1841)	Houart (1992); Huang (1994) EAF, IND, SEA, NEA, PAC, AUS
<i>Chicoreus</i> (<i>T.</i>) <i>microphyllus</i> (Lamarck, 1822)	Houart (1992); Huang (1994) EAF, IND, SEA, NEA, PAC, AUS
<i>Chicoreus</i> (<i>T.</i>) <i>strigatus</i> (Reeve, 1849)	Houart (1992) PHI, NEA, PAC
<i>Chicoreus</i> (<i>T.</i>) <i>axicornis</i> (Lamarck, 1822)	Houart (1992); Huang (1994) EAF, IND, SEA, NEA, PAC, AUS
<i>Chicoreus</i> (<i>T.</i>) <i>banksii</i> (Sowerby, 1841)	Houart (1992); Huang (1994) SEA, NEA, PAC, AUS
<i>Chicoreus</i> (<i>T.</i>) <i>brunneus</i> (Link, 1807)	Houart (1992); Huang (1994) EAF, IND, SEA, NEA, PAC, AUS
<i>Chicoreus</i> (<i>T.</i>) <i>cnissodus</i> (Euthyme, 1889)	Houart (1992); Huang (1994) IND, SEA, NEA
<i>Chicoreus</i> (<i>T.</i>) <i>territus</i> (Reeve, 1845)	Houart (1992) SEA, AUS
<i>Chicoreus</i> (<i>T.</i>) <i>aculeatus</i> (Lamarck, 1822)	Houart (1992); Huang (1994) EAF, SEA, NEA
<i>Chicoreus</i> (<i>T.</i>) <i>nobilis</i> Shikama, 1977	Houart (1992) IND, PHI, NEA, PAC
<i>Chicoreus</i> (<i>S.</i>) <i>alabaster</i> (Reeve, 1845)	Houart (1992); Huang (1994) PHI, NEA
<i>Chicoreus</i> (<i>S.</i>) <i>pliciferoides</i> Kuroda, 1942	Houart (1992); Huang (1994) PHI, NEA, PAC, AUS
<i>Chicoreus</i> (<i>Ch.</i>) <i>orchidiflorus</i> (Shikama, 1973)	Houart (1992) IND, PHI, NEA, PAC
<i>Chicoreus</i> (<i>T.</i>) <i>brevifrons</i> (Lamarck, 1822)	Huang (1994)(a Caribbean species accord. to Houart, 1992) NEA

Chicoreus orientalis Zhang, 1965 Huang (1994) (= *C. asianus* Kuroda accord. to Houart, 1992)
NEA

Chicomurex Arakawa, 1964 (type species: *Murex superbus* Sowerby, 1889 by O.D.)
Houart (1992) considered *Chicomurex* to be distinct from *Chicoreus* mainly due to radular differences, with *Chicomurex* species having more teeth on the radula ribbon. Also, the central cusp on the rachidian teeth is large and massive relative to the lateral cusps, unlike in *Chicoreus* where it is short and often smaller than the lateral cusps (Houart, 1992).

Chicomurex laciniatus (Sowerby, 1841) Houart (1992); Huang (1994)
EAF, IND, SEA, NEA, PAC, AUS

Chicomurex problematicus (Lan, 1981) Houart (1992)
PHI, NEA, AUS

Chicomurex superbus (Sowerby, 1889) Houart (1992); Huang (1994)
PHI, NEA, AUS

Chicomurex venustus (Rehder & Wilson, 1975) Houart (1992)
IND, PHI, NEA, PAC, AUS

Naquetia Jousseaume, 1880 (type species: *Murex triqueter* Born, 1778 by S.D.)
Houart (1992) distinguished *Naquetia* from *Chicoreus* on the basis of the absence of foliaceous varicial spines on the shell.

Naquetia barclayi (Reeve, 1858) Houart (1992)
IND, PHI, NEA, PAC, AUS

Pterynotus Swainson, 1833 (type species: *Murex pinnatus* Swainson, 1822 [= *Purpura alata* Röding, 1798 according to Radwin & D'Attilio, 1976] by S.D.)
Members of this genus have wing-like varices. The genus *Marchia* is here considered a synonym (or at most a subgenus) of *Pterynotus*.

Pterynotus tripterus (Born, 1778) Huang (1994); as *Marchia triptera* in Radwin & D'Attilio (1976)
"Indo-Pacific"

Pterynotus elongatus (Lightfoot, 1786) Huang (1994); as *Marchia elongata* in Radwin & D'Attilio (1976)
"Indo-west Pacific"

Pterynotus alatus (Röding, 1798) Huang (1994); Radwin & D'Attilio (1976)
IND, NEA

Pterynotus bipinnatus (Reeve, 1845) Huang (1994); as *Marchia bipinnata* in Radwin & D'Attilio (1976)
"Indo-west Pacific"

Pterynotus pinnatus (Swainson, 1822) Taylor (1994) (= *P. alatus* accord. to Radwin & D'Attilio, 1976)
IND, NEA

Aspella Mörch, 1877 (type species: *Ranella anceps* Lamarck, 1822 by monotypy)

Aspella producta (Pease, 1861) Radwin & D'Attilio (1976)
EAF, IND, SEA, NEA, PAC, AUS

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Lataxiena Jousseaume, 1883 (type species: *Lataxiena lataxiena* Jousseaume, 1883 [= *Trophon fimbriata* Hinds, 1844 accord. to Radwin & D'Attilio, 1976] by tautonomy)

<i>Lataxiena fimbriata</i> (Hinds, 1844)	Radwin & D'Attilio, (1976); Cernohorsky (1978a); Taylor (1994) list IND, SEA, NEA, AUS
<i>Lataxicna bimucronata</i> (Reeve, 1846)	Tan (1995) as <i>Bedevea</i> SEA, PAC
<i>Lataxicna blosvillei</i> (Deshayes, 1832)	Tan (1995) as <i>Bedevea</i> SEA, PAC

Muricopsinae Radwin & D'Attilio, 1971

This subfamily has been delineated on the basis of their radula and operculum. The radula has rachidian teeth that have a raised central cusp, while the operculum has a terminal nucleus (Radwin & D'Attilio, 1971; Vokes, 1978). No information is available regarding their anatomy. Two species have been recently described from the Bohol Straits and Okinawa (D'Attilio & Myers, 1985).

<i>Favartia balteata</i> (Sowerby, 1841)	Cernohorsky (1978a) IND, SEA(?), AUS
<i>Favartia (Murexiella) leonae</i> D'Attilio & Myers, 1985	D'Attilio & Myers (1985) PHI, NEA
<i>Favartia peasei</i> (Tryon, 1880)	Cernohorsky (1978a) "Indo-Pacific"
<i>Favartia (Murexiella) rosamiae</i> D'Attilio & Myers, 1985	D'Attilio & Myers (1985) PHI, NEA
<i>Favartia salmonea</i> (Melvill & Standen, 1899)	Cernohorsky (1978a) IND, SEA(?), AUS

Ocenebrinae

The Ocenebrinae comprises temperate and polar genera (e.g., *Ocenebra*, *Urosalpinx*, *Nucella*, *Acanthina*), and its members are distinguished by two synapomorphies: a thick external calcitic layer, and the accessory boring organ is separate from and anterior to the ventral pedal gland (Kool, 1993b). Only one genus (*Pteropurpura*) appears to be present in the South China Sea, and their anatomy is unknown.

Pteropurpura Jousseaume, 1880 (type species: *Murex macropterus* Deshayes, 1839 by O.D.) This genus comprises species with moderately high spires and wing-like varices. It is placed in the Ocenebrinae by virtue of its operculum, radula and fused siphonal canal (Radwin & D'Attilio, 1976). However the anatomy of *Pteropurpura* appears not to have been examined in any detail, and until this is done its placement in this subfamily is provisional.

<i>Pteropurpura adunca</i> (Sowerby, 1834)	Radwin & D'Attilio (1976); Huang (1994) NEA
<i>Pteropurpura plorator</i> (Adams & Reeve, 1849)	Radwin & D'Attilio (1976); Huang (1994) NEA

Typhinae

Members of this subfamily are distinguished by having tubular anal and siphonal canals whose walls completely enclose the canals. A review of conchological characters used in their classification was reviewed by Vella (1961).

Monstrotyphis Habe, 1961 (type species: *Typhis tosaensis* Azuma, 1960 by O.D.)

Monstrotyphis tosaensis (Azuma, 1960) Radwin & D'Attilio (1976)
NEA

Typhina Jousseaume, 1880 (type species: *Typhis belcheri* Broderip, 1833 by O.D.)

Typhina ramosa (Habe & Kosuge, 1971) Radwin & D'Attilio (1976)
SEA, NEA

Tripterotyphinae

Species in this family have three varices per whorl (as opposed to Typhinae with 4–5 varices per whorl), but otherwise similar in shell morphology to the Typhinae (Houart, 1991). No records are available for the South China Sea.

Trophoninae

Kool (1993b) suggested that *Trophon geversianus* (Pallas, 1774) the type species of *Trophon* is closely related to *Nucella* and *Ocenebra*, the latter two genera being recently grouped in the Ocenebrinae (Kool, 1993b). The subfamily Trophoninae presently contains species confined to the temperate and boreal regions in the northern and southern hemispheres.

DISCUSSION

A total of 130 muricid species is recorded from this study. The South China Sea covers an area of about 2,318,000 km² and is defined by more than 18,000 km of coastline, straddling about 20 latitude degrees north of the equator. The northern half (sometimes called the South China Sea basin) is deep with depths of more than 1000m, while the southern half forms part of the Sunda shelf with depths less than 1000m. The number of muricids in the South China Sea compares favourably with those found on the west coast of tropical America (109 species; Keen, 1971), Japan (120 species; Fujioka, 1986), Australia (180 species; Wilson, 1994) and the Philippines (between 111 and 127 species; Springsteen & Leobrera, 1986; Vermeij, 1996) (see Table 1). This is not surprising in view of the fact that the South China Sea is part of the Indo-West Pacific province, which is biologically diverse by any standard. However, the subfamilies represented differ considerably depending on the region in question. Most muricids reported from the South China Sea either belong to the subfamily Muricinae or Rapaninae, with five species in the Muricopsinae and only two species each in the subfamilies Typhinae and Ocenebrinae. No trophonine or tripterotyphine species are reported in the literature. Slightly more than half the total number of muricid species in the South China Sea are shallow water rapanines. This is somewhat different from the cases of Australia and tropical Central America, where there occur substantial number of species belonging

to the Muricopsinae and Typhinae (Table 1) from a wide range of depths. The South China Sea also lacks trophonine and ocenebrine species that are common in the northern or southern temperate seas (e.g., Strebel, 1904; Bouchet & Warén, 1985; Wilson, 1994), although 14 species of trophonines have been recorded (mostly from deep water) from Central America (Keen 1971). The lack of records concerning such deep water muricids in the South China Sea as well as the absence of muricopsine and typhine species is interesting, and the phylogenetic implications have yet to be addressed. On the other hand, the dearth of species other than those belonging to the Rapaninae or Muricinae could be simply because the region is still relatively unexplored, and it is likely that more species will be discovered in the future.

At the generic level, the 130 species are represented by 25 genera of muricids from the South China Sea, which is in contrast to those of tropical America where 109 species are assigned to 35 muricid genera (Kay, 1971). Similarly, 180 species of muricids are assigned to 54 genera in Australia (Wilson, 1994), and 109 species to 35 genera in Central America (Keen, 1971) (see Table 1). Hence the ratio of the number of species to the number of genera is between 2 and 4 in Australia, Japan, South Africa and Central America, but this ratio climbs to 5 in the South China Sea and the Philippines. Does this mean that the South China Sea is rich in species but poor in generic diversity? Present delineation of genera based on shell morphology is at best questionable and somewhat arbitrary (Kool, 1993a; Tan, 1995). This is not only true for tropical genera, but applies to temperate genera as well (e.g., *Trophon*; Bouchet & Warén, 1985). Radular differences are often complicated by sexual dimorphism and intraspecific variation in rachidian morphology (Fujioka, 1982, 1985; Tan, 1995). At present there is no single morphological character that can distinguish between the different genera, and anatomical characters are still unknown for many muricid genera. It is likely therefore that, for example, South China Sea species presently assigned to the genus *Thais*

Table 1. Distribution of species in six subfamilies of the Muricidae from Australia, Japan, the Philippines, South Africa, Central America and the South China Sea. Species in the subfamily Tripterotyphinae have been incorporated into the subfamily Typhinae.

Geographical region (reference)	Number of species in each subfamily						Total number of genera	Total number of species
	Rapaninae	Muricinae	Muricopsinae	Ocenebrinae	Typhinae	Trophoninae		
Australia (Wilson, 1994)	69	59	18	0	16	18	54	180
Japan (Fujioka, 1986)	64	35	7	1	1	12	32	120
Philippines (Springsteen & Leobrera, 1986)	43	54	13	0	0	1	26	111 (127; Vermeij, 1996)
South China Sea (this study)	67	54	5	2	2	0	25	130
South Africa (Kilburn & Rippey, 1982)	23	7	1	7	0	2	19	40
Central America (Keen, 1971)	21	33	25	5	11	14	35	109

may form other natural groupings at the generic level. Phylogenetic analyses involving a wide range of characters would help to resolve some of the present uncertainties concerning generic placement of species.

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