

# Coral barnacles: Cenozoic decline and extinction in the Atlantic/East Pacific versus diversification in the Indo-West Pacific

A. Ross<sup>1</sup> and W.A. Newman<sup>1</sup>

## ABSTRACT

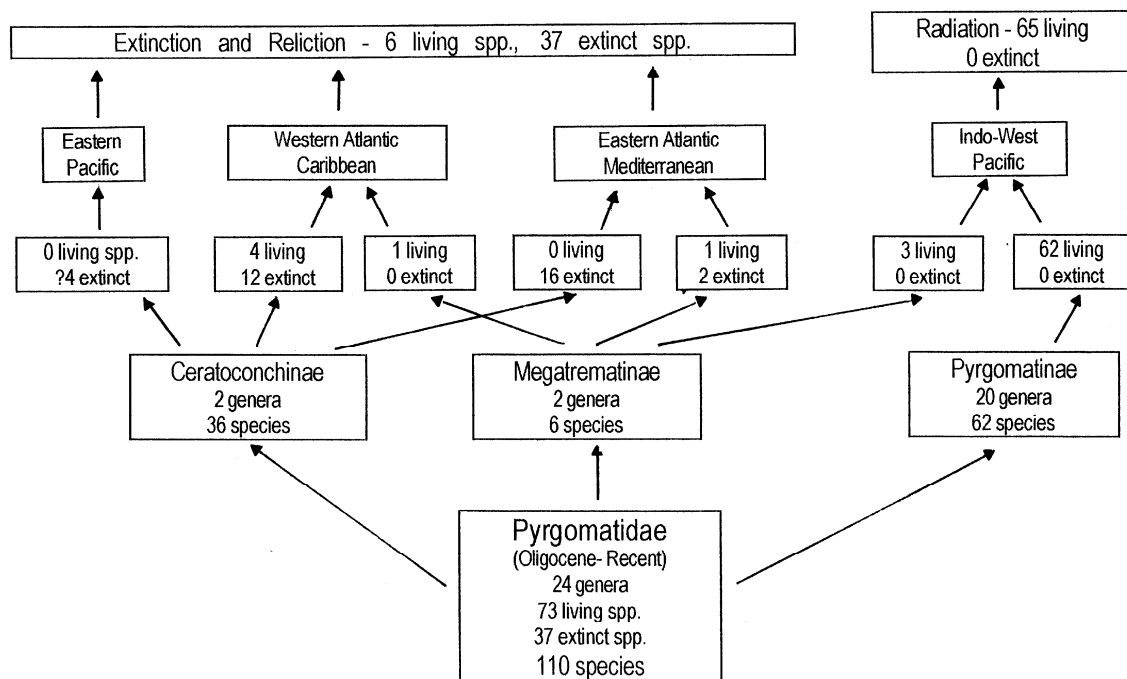
The pyrgomatid coral barnacles, first appearing in the late Oligocene of the western Atlantic, underwent a Miocene diversification unparalleled by any other group of sessile barnacles. Diversification in the Indo-Pacific (eastern Tethys) coincided with retreat of the tropics from higher latitudes, especially in the Atlantic. Fragmentation of the tropics, due to the breakup of the Tethys seaway, and wholesale extinctions of their host corals beginning in the Oligocene of Europe, Mediterranean and eastern Pacific resulted in relictual distributions and regional endemism. This was followed by Neogene extinctions of many host coral genera in the western Atlantic which were not replaced by originations. The exceptional diversity of pyrgomatids now evident in the Indo-Pacific was tied to the survival and radiation of the corals found there. Curiously, our knowledge of pyrgomatid numbers and diversity has shifted from the Indonesian to peripheral centers of distribution.

**Keywords** Cirripedia, Pyrgomatidae, Biogeography.

## Introduction

The pyrgomatids are obligatory symbionts or parasites that have undergone numerous adaptations for living on some 200 different coral, hydrozoan and sponge hosts (Ross and Newman 1973, Ogawa and Matsuzaki 1992). Aside from an extensive fossil record they are well represented today by 67 living taxa (Figs. 1-2).










The pyrgomatids, beginning with a six-plated wall and separable opercular plates (Newman and Ladd 1974a), and progressing to a single-plated wall with two inseparable opercular plates (Table 1) had an archaeobalanid ancestry. This is based on shell morphology, growth patterns (Ross and Newman 1973, 2000), cirral and other behaviors (Anderson 1992), and sperm ultrastructure (Healy and Anderson 1990).



**Fig. 1** Extinction and reliction versus radiation in the Pyrgomatidae. Within the Mediterranean, Atlantic and eastern Pacific, six species are extant and more than 30 extinct whereas none is extinct in the Indo-Pacific. Comparing these faunas there are 10 times the number of Indo-Pacific species; our studies suggest well over 100 species. Numbers of species given here reflects work in progress; Table 1 lists only nominal taxa.

<sup>1</sup> Scripps Institution of Oceanography, La Jolla, California 92093-0202, USA

**Table 1** List of nominal pyrgomatids; genera and higher taxa in approximate phylogenetic order, species alphabetically; asterisk (\*) denotes type species, dagger (†) extinct taxa. Geologic time range follows name of each genus. Wall and opercular plate patterns (6 x 4; 4 x 4; 1 x 4 etc.) are indicated diagrammatically and each applies to the taxa immediately following. *Ceratoconcha voksae* (early Miocene, Chipola Fm.), *C. aderca* (early Pliocene, Tamiami Fm.) and *Moroniella cystosa* (early Pliocene, Tamiami Fm.) from Florida, mentioned by Zullo and Portell (1992b), not listed below, are *nomina nuda*.

Family Pyrgomatidae Gray, 1825	Tribe Pyrgomatini Gray, 1825	
Subfamily Ceratoconchinae Newman & Ross, 1976	<i>Cantellius</i> Ross & Newman, 1973 [Rec.] 	<i>P. projectum</i> Nilsson-Cantell, 1938
<i>Eoceratoconcha</i> Newman & Ladd, 1974 [Oligo.-Plio.] 	<i>C. acutum</i> (Hiro, 1938)	<i>P. sinica</i> (Ren, 1986)
† <i>E. kugleri</i> Newman & Ladd, 1974*	<i>C. albus</i> Ren, 1986	<i>Neopyrgoma</i> Ross & Newman, 2001 [Rec.]
† <i>E. renzi</i> Newman & Ladd, 1974	<i>C. alphonsei</i> Achituv, 2001	<i>P. lobata</i> (Gray, 1825)
† <i>E. weisbordi</i> Zullo & Portell, 1991	<i>C. arcuatum</i> (Hiro, 1938)	<i>Trevathana</i> Anderson, 1992 [Pleist.-Rec.]
<i>Ceratoconcha</i> Kramberger 1889 [M. Mio.-Rec.] 	<i>C. brevitertium</i> (Hiro, 1938)	<i>T. dentata</i> (Darwin, 1854)* [Rec.]
† <i>C. barbadensis</i> (Withers, 1926)	<i>C. euspinulosa</i> (Broch, 1931)	<i>T. orientale</i> (Ren, 1986) [Rec.]
† <i>C. cladangiae</i> (Kolosváry, 1949)	<i>C. gregarius</i> (Sowerby, 1823)	<i>T. paulayi</i> Asami & Yamaguchi, 2001 [Rec.]
† <i>C. coniocystata</i> Newman & Ladd, 1974	<i>C. hiroi</i> Galkin, 1982	<i>Savignium</i> Leach, 1825 [L. Mio.-Rec.]
† <i>C. costata</i> (Seguenza, 1876)*	<i>C. iwayama</i> (Hiro, 1938)	<i>S. crenatum</i> (Sowerby, 1825)*
† <i>C. creusoides</i> Newman & Ladd, 1974	<i>C. madreporae</i> (Borradale, 1903)	<i>Darwiniella</i> Anderson, 1992 [Rec.] 
† <i>C. darwiniana</i> (Prochazka, 1893)	<i>C. octavus</i> Ross & Newman, 1973	<i>D. conjugatum</i> (Darwin, 1854)*
† <i>C. diplocona</i> (Seguenza, 1876)	<i>C. pallidus</i> (Broch, 1931)	<i>Nobia</i> Sowerby, 1839 [L. Mio.-Rec.]
† <i>C. domingensis</i> (DesMoulin, 1866)	<i>C. preobrazhenskij</i> Galkin, 1982	<i>N. grandis</i> Sowerby, 1839*
<i>C. floridana</i> (Pilsbry, 1931)	<i>C. pseudopallidum</i> (Kolosváry, 1947)	<i>N. halomitrae</i> (Kolosváry, 1948)
† <i>C. fuchsii</i> (Prochazka, 1893)	<i>C. quintus</i> Ross & Newman, 1973	<i>N. orbicellae</i> (Hiro, 1934)
† <i>C. jungi</i> Newman & Ladd, 1974	<i>C. secundus</i> (Broch, 1931)	<i>Neotrevathana</i> Ross, 1999 [Rec.]
† <i>C. kojumdjievae</i> (Kolosváry, 1962)	<i>C. septimus</i> (Hiro, 1938)	<i>N. elongatum</i> (Hiro, 1935)*
† <i>C. lata</i> (Seguenza, 1876)	<i>C. sextus</i> (Hiro, 1938)	<i>Cionophora</i> Ross & Newman, 2000 [Rec.] (2)
† <i>C. minuta</i> Newman & Ladd, 1974	<i>C. sinensis</i> Ren, 1986	<i>C. soongi</i> Ross & Newman, 2000
† <i>C. miocaenica</i> (Prochazka, 1893)	<i>C. sumbawae</i> (Hoek, 1913)	<i>C. guilluamae</i> Achituv, 2000
† <i>C. multicostrata</i> (Seguenza, 1876)	<i>C. transversalis</i> (Nilsson-Cantell, 1938)*	Tribe Pyrgopsellini Ross & Newman, 1995
† <i>C. noszkyi</i> (Kolosváry, 1949)	<i>C. tredecimus</i> (Kolosváry, 1947)	<i>Pyrgopsella</i> Zullo, 1967 [Rec.]
† <i>C. oranienensis</i> (Moissette & Saint Martin, 1982)	<i>Hiroa</i> Ross & Newman, 1973 [Rec.]	<i>P. annandalei</i> (Gruevel, 1903)* 
† <i>C. paucicostata</i> Young, 1989	<i>H. stubbingi</i> Ross & Newman, 1973*	<i>P. stellula</i> Rosell, 1973
† <i>C. phryxa</i> (Pajaud, 1976)	<i>Arossella</i> Anderson, 1993 [Rec.]	Tribe Hoekiini Ross & Newman, 1995 
† <i>C. prefloridana</i> (Brooks & Ross, 1960)	<i>A. lynnae</i> Ross, 2000*	<i>Echoekia</i> Ross & Newman, 1995 [Rec.]
† <i>C. quadratoradiata</i> Newman & Ladd, 1974	<i>Creusia</i> Leach, 1817 [Rec.] 	<i>E. chaos</i> Ross & Newman, 1995*
<i>C. quarta</i> (Kolosváry, 1947)	<i>C. spinulosa</i> Leach, 1818*	<i>E. nyx</i> Ross & Newman, 1995
† <i>C. rangi</i> (DesMoulin 1866)	<i>Galkinia</i> Ross & Newman, 1995 [Rec.]	<i>Parahoekia</i> Ross & Newman, 1995 [Rec.]
† <i>C. sanctacrucensis</i> (Baluk & Radwanski, 1967)	<i>G. angustiradiata</i> (Broch, 1931)	<i>P. aster</i> Ross & Newman, 1995*
† <i>C. sturi</i> (Prochazka, 1893)	<i>G. decima</i> (Ross & Newman, 1973)	<i>Hoekia</i> Ross & Newman, 1973 [Rec.]
† <i>C. trolia</i> (Abel, 1927)	<i>G. indica</i> (Annandale, 1924)*	<i>H. fornix</i> Ross & Newman, 1995
Subfamily Megatrematinae Holthuis, 1982	<i>G. supraspinulosa</i> Ogawa, 2000 [Rec.]	<i>H. monticulariae</i> (Gray, 1831)*
<i>Megatrema</i> Sowerby, 1823 [Plio.-Rec.] 	<i>Wanella</i> Anderson in Ross 1999 [Rec.]	<i>H. mortenseni</i> Ross & Newman, 1995
<i>M. madreporum</i> (Bosc, 1801)*	<i>W. andersonorum</i> Ross, 1999 	<i>H. philippensis</i> Ross, 2000
† <i>M. costatum</i> (Seguenza, 1876)	<i>W. milleporae</i> (Darwin, 1854)*	<i>Ahoekia</i> Ross & Newman, 1995 [Rec.]
<i>M. anglicum</i> (Sowerby, 1823)	<i>W. snelli</i> (Kolosváry, 1950)	<i>A. chuangi</i> Ross & Newman, 1995
<i>M. oulastreae</i> (Utinomi, 1962)	<i>Pyrgoma</i> Leach, 1817 [Rec.]	<i>A. microtrema</i> Ross, 2000
<i>Pyrgomina</i> Baluk & Radwanski, 1967	<i>P. cancellatum</i> Leach, 1818*	<i>A. tanabensis</i> Ross & Newman, 1995*
† <i>P. seguenzai</i> Baluk & Radwanski, 1967 [Plio.]	<i>P. japonica</i> (Weltner, 1897)	<i>Australhoekia</i> Ross & Newman, 2000 [Rec.]
Subfamily Pyrgomatinae Gray, 1825	<i>P. kuri</i> Hoek, 1913	<i>A. cardenae</i> Ross & Newman, 2000*

Pyrgomatid paleobiogeography reflects adaptations to the diversity and distribution of their hosts. The history of the corals and their exceptional diversity in some areas, and decline or extinction in others, is tied to tectonic and climatic changes bordering the Tethys seaway (Rosen 1984, Wilson and Rosen 1998), and the narrow regime within which they thrive. The global maximum species diversity of corals today is in the Indo-Pacific (Veron 1995). Although Indo-Pacific pyrgomatids underwent a concomitant rapid diversification during the Neogene the wide spectrum of fossils suggests a pre-Miocene radiation no later than the early late Oligocene in the Caribbean (Zullo in litt., cf. Wilson and Rosen 1998).

Tropical provincialism began with the collision of Africa and Eurasia (20-17 Ma), severing the Indian Ocean from the Atlantic (Rosen 1984). This was followed by the Messinian "salinity crisis" (6 Ma) resulting in the extinction and later replacement of the tropical Mediterranean fauna by a warm temperate one. The partial closure of the Indonesian (ca. 7 Ma; Wilson and Rosen 1998) and complete closure of the Panamic seaways (3.5 Ma) completed development of tropical provincialism for

the pyrgomatids and their hosts. The western Atlantic coral fauna suffered a further decline, the "Plio-Pleistocene faunal turnover," in which about 90% of the Mio-Pliocene species and 37% of the genera went extinct with no new generic originations since (Budd et al. 1993).

## Biogeography

### The Ceratoconchinae

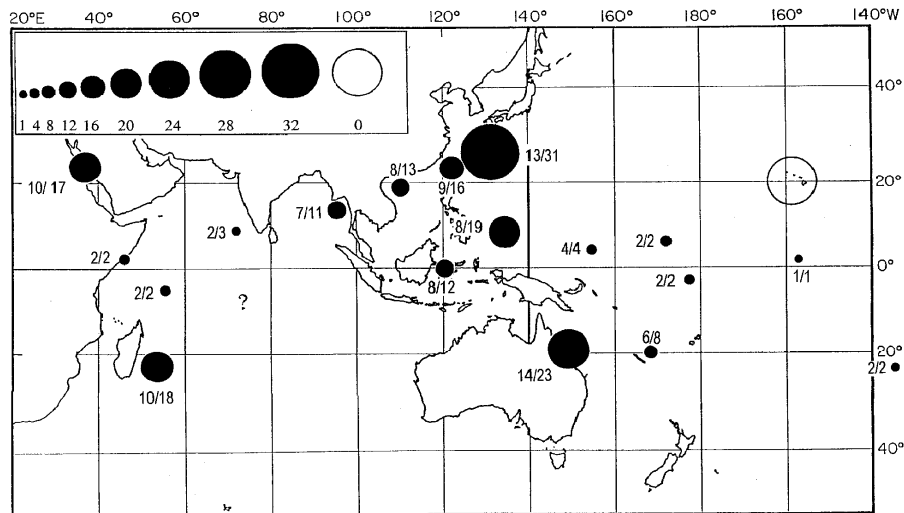
*Eoceratoconcha* first occurs in the early Miocene of Jamaica, and then middle Miocene of Trinidad (Newman and Ladd 1974a), and Pliocene of Florida (Zullo and Portell 1990, 1991). None is known from the Paratethyan region, and not one is living today. Thus, the center of origin for the Ceratoconchinae could well be the Caribbean.

The derived *Ceratoconcha* appear in the Oligocene of Puerto Rico (Zullo in litt.), early Miocene of Jamaica (Newman and Ladd 1974a), Florida (Zullo and Portell 1991, 1992), middle Miocene of Trinidad (Newman and Ladd 1974a), Mio-Pliocene of Cuba (Withers 1953), late Pliocene of Florida (Brooks and Ross 1960, Weisbord

1972, Zullo and Portell 1991), and Pleistocene of Barbados (Withers 1926). In the Mio-Pliocene there were several species of *Ceratoconcha* in southeastern California at the northern end of the Imperial Seaway (33°57'N, unpubl.). There are at least four living species, known from the western Atlantic: Brazil (Young 1988), Belize (Highsmith et al. 1983), Trinidad (Bacon 1976), Dominican Republic-Haiti (DesMoulins 1867), Jamaica (Scott 1987), Barbados (Scott 1987), Texas (Pequenot and

Ray 1974), Florida (Pilsbry 1931, Wells 1966) and Bermuda (Zullo et al. 1972, Bromley 1978, Southward 1986).

Based on fossil evidence, *Ceratoconcha* reached its greatest diversity (15 spp.) in the middle to early late Miocene in Paratethys (Baluk and Radwanski 1967a, 1967b), other records are for Spain and Algeria (Moissette and Saint Martin 1990). Extinction in Europe and northern Africa, stemming from the interaction of tectonics, glacio-eustatic sea level changes, and local climate followed during the Messinian "salinity crisis".



**Fig. 2** Known Indo-Pacific localities having two or more taxa. Japan and the Ryukyu Is. Have more species, but less generic diversity compared to Australia. No taxa occur in Hawaii. Eleven fossil taxa in five extant genera (late Miocene to Holocene) occur in Japan, Ryukyu Is, Fiji and Marshall Is., but likely represent living forms. Fractions indicate actual number of genera/species known at a given locality. Dot on the right, beyond 140°W and below the 20°S tick mark represents records from the Tuamotu Is. The limited number of genera in the Indo-Malayan region likely reflects a collecting bias in our data.

Central American plate tectonics late in the Miocene led to closure of the trans-isthmian seaway between the Caribbean and eastern Pacific (Pindell and Barrett 1990). The recent, poorly developed, scattered and relatively young reefs in the eastern Pacific contain almost wholly Indo-Pacific taxa (Veron 1995). A combination of paleotectonic activity, followed by rapid sedimentation, increased upwelling and shoaling of the thermocline (Kennett et al. 1985, Newman 1992) likely accounts for their demise there. This niche was soon occupied by a few eurytopic Indo-Pacific coral taxa and by the late Pliocene to Recent archaeobalanid, *Hexacreusia* (Ross 1962, Zullo 1967, Zullo et al. 1972, Johnson and Ledesma-Vázquez 1999).

Existing evidence supports a ceratoconchine dispersal from the Caribbean to the Mediterranean. Based on negative evidence, further support comes from the absence of *Ceratoconcha* in the Red Sea or bordering areas.

#### The Megatrematinae

Megatrematines, lacking any Miocene records, occur in the early Pliocene of Sicily (Moroni 1967), late Plio-

cene of Crete (Baluk and Radwanski 1967c), and the Plio-Pleistocene of Italy (Withers 1953). They also occur in the Coralline Crag of England (Tilbrook 1997) and Pleistocene to Holocene deposits in Japan (Sakakura 1934, Asami and Yamaguchi 1997).

Closure of the Iberian portal likely signaled the demise of *Megatrema* in the Mediterranean (6 Ma). With refilling of the Mediterranean, *M. anglicum*, now ranging from the British Isles (Rees 1962, 1966) to Nigeria (Stubbings 1967) northern Angola (Zibrowius in litt.), and eastward to Meteor Bank (Young 1998), Madeira and Canary Is. (Zibrowius in litt.), re-invaded and is the only nominal megatrematine known to occur there (Relini 1980, Moissette and Saint Martin 1990, Roca 1992), although there appears to be another species at Oran, Algeria (cf. Relini 1980). In northern Africa, *M. anglicum* extends from Oran, (Moissette and Saint Martin 1990) east to Cap Bon, northeastern Tunisia (Zibrowius in litt.). Parenthetically, the notion that *M. anglicum* in Japan is the same as that now found in the eastern Atlantic has not been convincingly demonstrated (cf. Ogawa and Matsuzaki 1994, 1995, Asami and Yamaguchi 1997).

There is one record for a Pleistocene megatrematine in the Falmouth Formation on the north coast of Jamaica (Portell in litt.) but no records for the eastern Pacific. Why they seemingly never ranged this far to the west, despite favorable westward currents (Iturralde-Vinent and MacPhee 1999), is unknown. The sole species in the Caribbean today, *M. madreporarum*, occurs in Brazil (Young 1988), Tobago (Bacon et al. 1984) Bonaire (Southward 1975) Jamaica (Scott 1987), Barbados (Scott 1987) and Florida (Ross and Newman 1973).

In the Indo-Pacific, living taxa are known from the Great Barrier Reef (unpubl.), Rottneest I., Western Australia (Jones 1993), Japan and Ryukyu Is. (Utinomi 1967, Ogawa and Matsuzaki 1995, Asami and Yamaguchi 1997) South China Sea (Ren 1986) and Gambier Is (unpubl.). There are records (Broch 1931, Hiro 1935, Nilsson-Cantell 1938) for what purports to be *M. anglicum*, but the descriptions or discussions of these are inadequate and likely apply to taxa now found in Japan (Utinomi 1967, Ogawa and Matsuzaki 1995). Despite a presence in the Indo-Pacific, megatrematines never attained a diversity comparable to the pyrgomatines.

#### The Pyrgomatinae

By no later than the middle Miocene the seaway between the Mediterranean and Indian Ocean was severed (Rögl 1998), thereafter the pyrgomatid faunas in the two provinces became sharply differentiated. Although recognizably different, migration from one to the other region was possible up until this time, but *Ceratoconcha*, from which the pyrgomatines are likely derived, failed to survive in the Indian Ocean. The wholly Indo-Pacific Pyrgomatinae includes three morphologically and ecologically distinct tribes (Table 1; Ross and Newman 1995).

Pyrgopsellini. - Sponge-inhabiting pyrgomatines are not likely to fossilize because they have a chitinous basis and a partly chitinous wall. Among the known species, one is from the Andaman Is., another from Hong Kong and the Philippines (Rosell 1975).

Hoekiini. - This tribe includes wholly parasitic species which occur only on a few species of *Hydnophora* (Ross and Newman 1995, 1999, Ross 2000). If there is a fossil record, if not by their characteristic and fragile amoeboid wall, it will likely be for the calcareous portion of the basis, which has an amoeboid outline.

Pyrgomatini. - This tribe encompasses some 60 or so species, and has a diversity of shell characters far greater than any other pyrgomatids. Fossil records include *Nobia* and *Savignium*, from the late Miocene and Pleistocene of Fiji and the Marshall Is. (Pilsbry 1945, Newman and Ladd 1974b, Newman et al. 1976), and *Trevathana* in the Pleistocene of Japan (Mimoto 1991). All others are from Holocene terraces in Japan, including *Cantellius*, *Darwiniella* and *Galkinia* (Asami and Yamaguchi 1997). The paucity of records provides no clue as to the time of origin and subsequent diversification of the Indo-Pacific fauna, but noteworthy, genera representing modern forms appear in the late Miocene.

#### Conclusions

Pyrgomatids probably originated in the Paleogene of western Tethys and hence extant populations in the Atlantic and Indo-Pacific represent Tethyan relicts. Despite broad scale extinctions in the west, the greatest diversity of forms occur in the Indo-Pacific where pyrgomatids underwent an extensive radiation. Western Atlantic pyrgomatids, like their coral hosts, are far less diverse than they were during the Neogene (Budd et al. 1993). By comparison, there are some 100 coral genera in the tropical Atlantic, and about 1000 in the Indo-Pacific, and instructively the proportion of pyrgomatids in the two regions, 7 to 69, is comparable.

Contrary to previous studies (Ross and Newman 1973, Newman et al. 1976) the distribution patterns of either Indo-Pacific genera or species does little to amplify their history. The center of distribution was once thought to be the Malaysian Triangle. However, this "center of distribution" has disappeared for pyrgomatids, partly because our knowledge has shifted largely from expedition-based collections to research centers that are generally peripheral to the deep tropics.

**Acknowledgments** This paper is dedicated to H S Ladd (1899-1982), V.A. Zullo (1936-1993) and H. Utinomi (1910-1979) all of whom contributed in many ways. We thank colleagues, friends and institutions for providing specimens over the past 40 years. Financial support was provided, in part (to AR), by the American Museum of Natural History. A Contribution of the Scripps Institution of Oceanography, new series.

#### References

- Anderson DT (1992) Structure, function and phylogeny of coral-inhabiting barnacles (Cirripedia, Balanoidea). *Zool J Linn Soc* 106: 277-339.
- Asami K, Yamaguchi T (1997) Distribution of living and fossil coral barnacles (Cirripedia; Pyrgomatidae) in Japan. *Sess Org* 14: 9-16.
- Bacon PR (1976) The Cirripedia of Trinidad. *Stud Fauna Curaçao Carib Is* 50: 1-55.
- Bacon PR, Hubbard R, Southward AJ (1984) New records of cirripedes from Trinidad and Tobago. *Stud Fauna Curaçao Carib Is* 57: 77-91.
- Baluk W, Radwanski A (1967a) Genus *Creusia* Leach, 1817, (Cirripedia) in the Croatian Miocene. *Geol Vjesnik, Zagreb* 20: 137-152.
- Baluk W, Radwanski A (1967b) Miocene cirripeds domiciled in corals. *Acta Palaeo Polonica* 12: 457-521.
- Baluk W, Radwanski A (1967c) *Pyrgomina* gen. n., an aberrant cirriped and its Pliocene and Recent representatives. *Bull l'Acad Polonaise Sci, Sci Biol* 15: 691-695.
- Broch H (1931) Papers from Dr. Th. Mortensen's Pacific expedition 1914-1916. LVI. Indomalayan Cirripedia. *Vidensk Meddel Dansk Naturh Foren* 91: 1-146.
- Bromley RG (1978) Bioerosion of Bermuda reefs. *Palaeogeogr Palaeoclimatol Palaeoecol* 23: 169-197.

- Brooks HK, Ross A (1960) *Pyrgoma prefloridanum*, a new species of cirriped from the Caloosahatchee Marl (Pleistocene) of Florida. *Crustaceana* 1: 353-365.
- Budd AF, Stemann TA, Johnson KG (1993) Late Cenozoic turnover in the Caribbean reef coral fauna. *Abstr Prog, Paleont Soc Spec Publ* 6: 43 pp
- DesMoulins C (1867) Liste des principaux fossiles recueillis par les membres de la société a Cazeneuve dans le Calcaire de Bazas pendant l'excursion de la 50e Fête Linnéene. *Act Soc Linn Bordeaux* 26 (ser. 3, v. 6): 293-344.
- Healy JM, Anderson DT (1990) Sperm ultrastructure in the Cirripedia and its phylogenetic significance. *Rec Austr Mus* 42: 1-16.
- Highsmith RC, Lueptow RL, Schonberg SC (1983) Growth and bioerosion of three massive corals on the Belize barrier reef. *Mar Ecol Prog Ser* 13: 261-271.
- Hiro F (1935) A study of cirripeds associated with corals occurring in Tanabe Bay. *Rec Oceanogr Wks Japan* 7(1): 1-28.
- Iturralde-Vinent MA, MacPhee RDE (1999) Paleogeography of the Caribbean region: implications for Cenozoic biogeography. *Bull Amer Mus Nat Hist* 238: 1-95.
- Johnson ME, Ledesma-Vázquez J (1999) Biological zonation on a rocky-shore boulder deposit: upper Pleistocene Bahía San Antonio (Baja California Sur, Mexico). *Palaios* 14: 569-584.
- Jones DS (1993) The barnacles of Rottneest Island, Western Australia, with descriptions of two new species. In: Wells FED, Walker I, Kirkman H, Lethbridge R (eds) *Proc 5th Int Mar Biol Workshop: The marine flora and fauna of Rottneest Island, Western Australia*. Western Australian Museum, Perth: 113-133.
- Kennett JP, Keller G, Srinivasan MS (1985) Miocene planktonic foraminiferal biogeography and paleo-oceanographic development of the Indo-Pacific region. *Geol Soc Amer Mem* 63: 197-236.
- Mimoto K (1991) Cirripedian fossils from the Pleistocene deposits of the southwestern part of Kochi Prefecture, Shikoku. *Fossils* 51: 15-23.
- Moissette P, Saint Martin JP (1990) Cirripedes Pyrgomatidae actuels et fossils d'Oranie (Algeria). *Rev Paleobiol* 9: 37-47.
- Moroni MA (1967) Ricerche su *Balanus milensis* e *Pyrgoma costatum* del Pliocene Siciliana. *Lavori Ist Geol Univ Palermo* 5: 1-28.
- Newman WA (1992) Biotic cognates of eastern boundary conditions in the Pacific and Atlantic: relicts of Tethys and climatic change. *Proc San Diego Soc Nat Hist* 16: 1-7.
- Newman WA, Ladd HS (1974a) Origin of coral-inhabiting balanids (Cirripedia, Thoracica). *Verhandl Natur Gesell Basel* 84: 381-396.
- Newman WA, Ladd HS (1974b) Occurrence of modern coral-inhabiting barnacles in the Miocene of Fiji and the Marshall Islands (Cirripedia, Balanomorphia). *Int Symp Indo-Pacific Reef Biology, University of Guam* (Abstract page 29).
- Newman WA, Jumars PA, Ross A (1976) Diversity trends in coral-inhabiting barnacles (Cirripedia, Pyrgomatinae). *Micronesica* 12: 69-82.
- Nilsson-Cantell CA (1938) Cirripedes from the Indian Ocean in the collection of the Indian Museum, Calcutta. *Mem Indian Mus* 13: 1-81.
- Ogawa K, Matsuzaki K (1992) An essay on host specificity, systematic taxonomy, and evolution of the coral-barnacles. *Bull Biogeograph Soc Japan* 47: 87-101.
- Ogawa K, Matsuzaki K (1994) First records of *Megatrema anglicum* (Balanomorpha, Pyrgomatidae) from Japan, with some ecological notes. *Bull Biogeograph Soc Japan* 49: 71-86.
- Ogawa K, Matsuzaki K (1995) Host influence on the morphology of coral-inhabiting barnacles revealed by morphometric analyses of *Megatrema* with the revision of the genus. *Bull Biogeograph Soc Japan* 50: 21-37.
- Pequenot LH, Ray JP (1974) Crustacea and other arthropods. In: Bright, T.J., Pequenot, L.H. (eds) *Biota of the West Flower Bank*. Gulf Publ Co, Houston: 232-288.
- Pilsbry HA (1931) The cirriped genus *Pyrgoma* in American waters. *Proc Acad Nat Sci Phila* 83: 81-83.
- Pilsbry HA (1945) Barnacles. In: Ladd HS, Hoffmeister JE (eds) *Geology of Lau*. Bernice P. Bishop Mus Bull 181: 371-372.
- Pindell J, Barrett SF (1990) Geological evolution of the Caribbean region; a plate tectonic perspective. In: Dengo G, Case JE (eds) *The geology of North America*. Vol. H, The Caribbean region. Geological Society of America, Boulder: 405-432.
- Rees WJ (1962) The distribution of the coral, *Caryophyllia smithii* and the barnacle *Pyrgoma anglicum* in British waters. *Bull Brit Mus (Nat Hist), Zool* 8: 403-418.
- Rees WJ (1966) Further notes on the distribution of *Caryophyllia smithii* Stokes and Broderip and *Pyrgoma anglicum*. *Ann Mag Nat Hist ser* 13, 9: 289-292.
- Relini G (1980) Guide per riconoscimento delle species animali delle acque lagunari e costiere italiane. 2. Cirripedi toracici. *Consiglio Nazionale de Ricerche*: 1-122.
- Ren X (1986) Studies on Chinese Cirripedia (Crustacea), VII. Family Pyrgomatidae. *Stud Mar Sinica* 7: 129-158.
- Roca I (1992) Primera cita de *Megatrema anglicum* (Sowerby, 1823) (Cirripedia, Crustacea) recogido sobre *Leptopsammia pruvoti* (Lacaze-Duthiers, 1897) (Scleractinia, Anthozoa) en las costas de Baleares (Mediterraneo occidental). *Bol R Soc Espana Hist Nat (Sec Biol)* 88: 31-37.
- Rögl F (1998) Paleogeographic considerations for Mediterranean and Paratethys seaways (Oligocene to Miocene). *Ann Naturhist Mus Wien* 99A: 279-310.
- Rosell NC (1975) On two noteworthy balanids (Cirripedia Thoracica) from the Sulu Archipelago, Philippines. *Crustaceana* 29: 206-214.

- Rosen BR (1984) Reef coral biogeography and climate through the late Cainozoic: just islands in the sun or a critical pattern of islands. In: Benchley P (ed) Fossils and climate. John Wiley and Sons Ltd. London: 201-262.
- Ross A (1962) Results of the Puritan-American Museum of Natural History expedition to western Mexico. 15. The littoral balanomorph Cirripedia. Amer Mus Novitates 2084: 1-44.
- Ross A (2000) Coral-eating barnacles: wall morphology and the descriptions of two new species. Sess Org 17: 45-56.
- Ross A, Newman WA (1973) Revision of the coral-inhabiting barnacles (Cirripedia: Balanidae). Trans San Diego Soc Nat Hist 17: 137-174.
- Ross A, Newman WA (1995) A coral-eating barnacle, revisited (Cirripedia, Pyrgomatidae). Contrib Zool 65: 129-175.
- Ross A, Newman WA (1999) A new coral-inhabiting barnacle from Taiwan (Cirripedia: Pyrgomatidae). Zool Stud 38: 387-390.
- Ross A, Newman WA (2000a) *Pyrgoma kuri* Hoek, 1913: a case study in morphology and systematics of a symbiotic coral barnacle (Cirripedia: Balanomorph). Contrib Zool 68: 245-260.
- Ross A, Newman WA (2000b) A new coral-eating barnacle: the first record from the Great Barrier Reef, Australia. Mem Queensland Mus 45:585-591.
- Sakakura K (1934) Pleistocene *Pyrgoma* from Tiba Prefecture. J Geol Soc Japan 41: 575-581.
- Scott PJB (1987) Associations between corals and macroinfaunal invertebrates in Jamaica, with a list of Caribbean and Atlantic coral associates. Bull Mar Sci 40: 271-286.
- Southward AJ (1975) Intertidal and shallow water Cirripedia of the Caribbean. Stud fauna Curaçao Caribbean Is 46: 1-53.
- Southward AJ (1986) Class Cirripedia (barnacles). In: Sterrer W (ed) Marine fauna and flora of Bermuda. A systematic guide to the identification of marine organisms. John Wiley and Sons, New York: 299-305.
- Stubbings HG (1967) The cirriped fauna of tropical west Africa. Bull Brit Mus (Nat Hist), Zool 15: 227-319.
- Tilbrook KJ (1997) Barnacle and bivalve associates of bryozoan-coral symbiosis from the Coralline Crag (Pliocene) of England. Tertiary Res 18: 7-22.
- Utinomi H (1967) Comments on some new and already known cirripeds with emended taxa, with special reference to the parietal structure. Publ Seto Mar Biol Lab 15: 199-237.
- Veron JEN (1995) Corals in space and time: the biogeography and evolution of the Scleractinia. Comstock / Cornell University Press, Ithaca.
- Weisbord NE (1972) *Creusia neogenica*, a new species of coral-inhabiting barnacle from Florida. Tulane Stud Geol Paleont 10: 59-64.
- Wells HW (1966) Barnacles of the northwestern Gulf of Mexico. Quart J Florida Acad Sci 29: 81-95.
- Wilson MEJ, Rosen BR (1998) Implications of paucity of corals in the Paleogene of SE Asia: plate tectonics or centre of origin? In: Hall R, Holloway JD (eds) Biogeography and Geological evolution of SE Asia. Backhuys Publ, Leiden: 165-195.
- Withers TH (1926) Barnacles of the *Creusia-Pyrgoma* type from the Pleistocene of Barbados. Ann Mag Nat Hist 9 (97) 17: 1-6.
- Withers TH (1953) Catalogue of fossil Cirripedia in the Department of Geology. Vol. III. Tertiary. British Museum (Natural History, London.
- Young PS (1988) Recent cnidarian-associated barnacles (Cirripedia, Balanomorph) from the Brazilian coast. Rev Brasileira Zool 5: 353-369.
- Young PS (1998) The Cirripedia (Crustacea) collected by the "Fisheries Steamer Meteor" in the eastern Atlantic. Arquivos Mus Nac 58: 1-54.
- Zullo VA (1967) On the identity of some specimens assigned by Darwin, 1854, to *Balanus allium* Darwin (Cirripedia, Thoracica). Crustaceana 13: 126-127.
- Zullo VA, Portell RW (1990) The coral barnacle *Eoeratoconcha* Newman and Ladd, 1974 in the Pliocene of southern Florida. Abstracts with Programs. Geol Soc Amer 22: 71 pp
- Zullo VA, Portell RW (1991) A new species of *Eoeratoconcha* Newman and Ladd, 1974 (Cirripedia, Archaeobalanidae) from the Pliocene of Florida. J Paleo 65: 271-276.
- Zullo VA, Portell RW (1992) Paleobiogeography of Florida Neogene barnacles. Abs Vol. The 3rd Bald Head Island conference on coastal plains geology. Hilton Head Island, South Carolina. Nov. 1992: 61-65.
- Zullo VA, Beach DB, Carlton JT (1972) New barnacle records (Cirripedia, Thoracica). Proc Calif Acad Sci ser 4, 39(6): 65-74.