



ELSEVIER

Palaeogeography, Palaeoclimatology, Palaeoecology 146 (1999) 99–145

PALAEO

An Early Pleistocene molluscan assemblage from Fiji: gastropod faunal composition, paleoecology and biogeography

Alan J. Kohn*, Ingela Arua

Department of Zoology, University of Washington, Box 351800, Seattle, WA 98195-1800, USA

Received 7 October 1997; revised version received 31 March 1998; accepted 14 July 1998

Abstract

Ecologically important in many modern marine environments as both predators and prey, gastropod molluscs also offer keys to understanding the organization of past biotas. We analyzed Early Pleistocene gastropod shells from the Nasaki Beds in Viti Levu (~1.8 Myr B.P.) to describe and interpret diversity at the species and higher levels, taxonomic and trophic aspects of community composition, and the taxonomic and biogeographic relations of past and present faunas. The assemblage studied probably represents a paleocommunity type that occurred in fine sand sediment in depths of 5–50 m inshore. Gastropods outnumbered bivalves 4:1. At least 320 gastropod species from at least 52 families and 146 genera were present. Neogastropods accounted for 51% of the species and two-thirds of individuals. Numerically the family-groups Nassariinae, Turridae, Olividae and Naticidae dominated. Turridae, Conidae and Naticidae had the most species. Most gastropod species and individuals were probably primary carnivores. About 15% were secondary predators, but these caused significant mortality of other gastropods present. Nearly half of all gastropod species suffered drilling predation, mainly by naticids, and these attacks were nearly always successful. Crabs and other durophagous predators probably killed only about 4% as many gastropods as drillers; a high frequency of shell repairs also suggests that they were less important mortality factors. The Lyellian percentage of the gastropod assemblage exceeds 80%. Two-thirds of the 212 extant species presently occur in Fijian waters; a similar modern fauna occurs in Laucala Bay in 8–25 m. Almost all of the locally extinct but globally extant species whose southern hemisphere distributions are known reach the eastern limits of their ranges west of Fiji, occurring as far east as Indonesia (99%), New Guinea (60%) and Vanuatu (15%). Pleistocene sea level fluctuations likely extensively altered the geographic distributions of gastropods inhabiting tropical subtidal nearshore soft sediments, as previously documented for reef-associated corals and bivalves. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: gastropods; marine paleoecology; predation; paleobiogeography; Pleistocene; Fiji; Nakasi Beds

1. Introduction

Gastropod molluscs are ecologically important in many marine environments as herbivores, as predators, and as prey of other predators. They also of-

fer a key window to reconstructing the organization of past communities, a major goal of paleoecology. Because gastropod shells grow by accretion, adding shell material only along a growing edge, they preserve a record of the animal's life history. This record often provides evidence of trauma from battles with predators, both successful and unsuccessful, throughout the gastropod's life. The fossil record preserves

* Corresponding author. Fax: +1-206-543-3041; E-mail: kohn@u.washington.edu

evidence of such important ecological interactions that occurred as long as 450 million years ago (Carriker and Yochelson, 1968). In some cases, predator as well as prey can be determined from specific types of damage inflicted on a shell, e.g. bivalve shells chipped by *Busycon* (Magalhaes, 1948), spatangoid echinoids drilled by *Cassia* and its relatives (Hughes and Hughes, 1981), and the drilled holes of Muricidae and Naticidae (Berg and Nishenko, 1975; Carriker, 1981; Kitchell et al., 1981).

In shells that become fossilized, such evidence may be preserved for many millions of years. Vermeij (1987, p. 174 ff.) reviews the history of predation on invertebrates from the Early Cambrian. Holes in brachiopod shells indicative of drilling predation first appear in the Late Cambrian. Fishes capable of shell breakage are present from the Devonian. Devonian brachiopods and blastoids were very likely drilled by gastropods (Smith et al., 1985; Baumiller, 1996). Mollusc shells with drilled holes indistinguishable from those of naticids first appeared in the Late Triassic (Fürsich and Jablonski, 1984). Predaceous fishes, crustaceans and molluscs continued to diversify and to evolve increasingly specialized feeding modes that often left distinct marks of feeding activity on the hard remains of their prey (Vermeij, 1987).

The general goal of our study is to seek principles that underlie the organization of marine biotic communities of the past that are the antecedents of those of modern seas. Specifically, we examine Early Pleistocene fossil assemblages at Viti Levu, Fiji, in order to characterize the taxonomic composition, nature of the original habitat, trophic relationships, and biogeography of the gastropods; they were by far the predominant taxon represented. We use the data from these fossils to interpret (1) community composition, including the diversity, abundance, and proportions of taxa; and (2) prey–predator interactions, especially the roles of durophagous and drilling predation, including intensities, success rates, how selectivity of predators relates to prey taxa, size, and anti-predator protective devices.

Following a systematic treatment, we compile the data on the taxonomic characteristics of the gastropod assemblages, test the hypothesis that the assemblage derives from a single ecological community, and estimate attributes of the physical environment, particularly substrate and depth. We synthesize in-

formation on community trophic structure in a qualitative food web, and we demonstrate the pervasive importance of drilling and durophagous predators on the gastropods. We then analyze the biogeographic and paleobiogeographic distributions and paleoecological information of the taxa represented. Finally, we use comparisons with samples from modern communities to infer other paleoecological attributes, and we compare the composition of the fossil assemblage with present-day ecologically analogous assemblages of Fijian waters and elsewhere in the Indo-Pacific region.

2. Materials and methods

2.1. Geological setting

Molluscan fossils were collected at excavations and new exposures of the Nakasi Beds east of Suva and about 1 km west of the Rewa River in southwest Viti Levu, Fiji. These marine deposits are of “grit, sandstone and siltstone” (Wilcoxon and Rodda, 1983) that unconformably overlie the Suva Marl and are overlain by fluvial deposits. Analyses of calcareous nannoplankton indicate that the Nakasi Beds lie within biochronozone N22 (Wilcoxon and Rodda, 1983). Rodda (in litt., 1991) considers it “likely that the strata were deposited during the stage of high sea level in the third-order cycle of Haq et al. (1987) [cycle 3.7, ending 1.6–1.7 Myr B.P.], after the regression at the beginning of that cycle which led to the unconformity between the Suva Marl and the Nakasi Beds.” The maximum age of the Nakasi Beds is thus estimated at about 1.8 Myr B.P., according to the time scale of Hilgen et al. (1993). Their minimum age is about 0.9 Myr B.P. (Johnson, 1991; Rodda, 1994), and we consider them to be of Early Pleistocene age, in conformity with the conclusions in Van Couvering (1997). The Nakasi Beds are more than 60 m thick (Wilcoxon and Rodda, 1983) and presently extend to about 15–20 m above sea level.

2.2. Localities

Saunitambu (18°02'S, 178°29'E). (Loc. 16). Excavations and new exposures at the Saunitambu water treatment plant; April–July 1982.

Waila (18°02'S, 178°31'E). (Loc. 17 = Fiji Mineral Resources Department (MRD) Loc. C3135). Road cut about 800 m west-southwest of Princes Road; April–July 1982.

Waila (18°02'S, 178°31'E). (Loc. 19), Bulldozed surface between MRD locs. C2024 and C2026) (Ladd, 1982, p. 86); April–July 1982.

Tongeravu Island (17°59.8'S, 178°42.2'E) (Loc. 24 = MRD Loc. C4060); June 1985.

2.3. Analytical methods

In order to determine relative abundance of the molluscs and to analyze their condition of preservation, the first 500–900 shells encountered at each locality were collected. Shell fragments were included if they were considered identifiable to genus. These collections are referred to as quantitative random samples (QRS) with respect to taxonomic composition and shell size. Additional specimens of some taxa, referred to as non-random samples (NRS), were also collected.

We applied several independent tests to the data in order to determine whether or not the fossil mollusc assemblages represented a subset of a single biotic community or were admixtures. Information on depth range and habitat from studies of recent members of the same or closely related species was used to estimate these attributes of the fossils and to determine whether the species present likely shared the same environment, particularly the type of sediment in which their shells are now preserved as fossils.

Condition analysis of the shells in the quantitative random samples was used to help determine whether the fossils within an assemblage were uniformly well preserved or comprised a mix of species both preserved in situ and washed in from other, perhaps erosional habitats. The condition of preservation of each gastropod and bivalve in the QRS was assessed by two independent methods, slightly modified from Ogasawara (1977). The first evaluates shell form or degree of intactness graded according to the following standards: 1, form nearly perfect; 2, well preserved but imperfect; 3, fragment but identifiable at least to genus. The second analysis evaluates surface features of the shell: A, as in life; B, slightly etched or worn; C, markedly etched or worn; D, very worn;

no sculpture remaining. This method indicates likely absence of significant transport after death (A and B grades) even if shells are fragmentary (3 grade), as breakage may occur in situ. If wear and dissolution following exposure have occurred, gastropods with predominantly aragonitic shells should be more poorly preserved than mainly calcitic bivalves.

Samples of dried matrix were dissociated by submersion in water, sieved to eliminate particles larger than 2 mm, and analyzed for grain size distribution in an Emery settling tube (Emery, 1938). A sample of Laucala Bay sediment from a depth of 14.5 m was similarly processed.

2.4. Systematic treatment: the taxa of mollusca present

The classification used is based generally on Boss (1982), Hickman (1988), Lindberg (1988), Ponder and Warén (1988), and Mikkelsen (1996). Taxa are ordered as in Vaught (1989); their geologic ranges are taken mainly from Tracey et al. (1993). The systematic account (Section 3) discusses only families represented by 10 or more specimens in our sample. Because “paleoecologists are commonly confronted with the task of gathering for themselves the ecologic information necessary to interpret the fossils” (Dodd and Stanton, 1990, p. 5), each family account provides a summary of its natural history, then briefly summarizes (1) biogeographic, stratigraphic and ecological attributes of the family, (2) numbers of individuals, predominant genera and species found, (3) the present geographic distribution of extant taxa, and paleobiogeographic information, and (4) intensity and success rate of predation, with attribution of predator taxa where possible. Appendix A (**Online Background Dataset**¹) tabulates these data from all families, and it also indicates the authorship of species. In the systematic accounts by family, the numbers of specimens include fragments, but fragments are excluded from analyses of predation. For this reason, some sample sizes differ in the two sections. A full database providing information on each

¹ List of gastropod species in both quantitative random and non-random samples from the Lower Pleistocene Nakasi Beds, Viti Levu, Fiji available at <http://www.elsevier.nl/locate/palaeo>; mirror site: <http://www.elsevier.com/locate/palaeo>, or as a print-out from the first author.

lot is available electronically from the senior author at kohn@u.washington.edu.

For species determinations we have relied on the literature cited in family accounts, examination of the collections of the Australian Museum and the U.S. National Museum of Natural History, and consultation with specialists listed in the Acknowledgments. A few specimens retain portions of their original colour patterns, and the patterns of others fluoresced in the visible range under ultraviolet light (Pitt and Pitt, 1993). The current state of taxonomic knowledge of most groups from the likely depth range of our samples is quite incomplete, so that most determinations are quite tentative. We have come as close as we could, have illustrated shells of common and problematic species, and have deposited voucher specimens in the Australian Museum, Sydney, which holds the most extensive collection of fossils from the Fiji Neogene and Quaternary. Appendix A (**Online Background Dataset**²) indicates those species that we have determined with some confidence.

The numerically dominant species, specimens illustrating successful and unsuccessful predation attempts by both drilling and durophagous predators, and a few modern representatives of the fossil species are illustrated photographically in Plates I–IV. To minimize the disparity in size between the smallest and largest shells but still retain approximate relative shell sizes, small shells are enlarged more than larger ones in the photographs. The shell length in each print was calculated from the formula:

$$N = \frac{K}{1 + e^{a-rt}}$$

where N = shell length in the print in mm, K = 80 mm, a = 0.2, r = 0.027, and t = actual shell length in mm (Kohn, 1992a, p. 4). The figure captions indicate actual shell maximum diameter (MD) or shell length (SL).

2.5. Trophic analysis

Trophic roles of the gastropods represented by fossils were inferred from the literature on modern representatives of extant taxa or close relatives.

All shells were examined for direct evidence of attempted predation and whether or not such attempts were successful. Boreholes made by drilling predatory snails were assigned to the families Naticidae or Muricidae according to the criteria of Arua and Hoque (1989). Naticids drill holes that are beveled or taper inward and the margins are plane or concave, while the sides of holes drilled by muricids are perpendicular or nearly so to the shell surface. Breaks made by durophagous predators were classed as successful or unsuccessful, the latter if the gastropod had repaired its shell and grew after the attack. It was not possible to distinguish breaks made by different types of durophagous predators, but crabs are likely an important cause. Shell damage from some types of crustaceans are specifically characteristic, e.g. from the crab *Calappa* (Shoup, 1968) and the stomatopod *Gonodactylus* (Geary et al., 1991) and were so recorded.

2.6. Paleobiogeography

The same taxonomic works used for species determinations provided data for the estimation of Lyellian percentages, the proportions of species in the fossil record that have survived to the present. They also provided current biogeographic data for these survivor species that allowed comparisons of the Pleistocene and modern composition of the Fijian marine molluscan fauna, and changes in distribution patterns between then and now.

2.7. Analogous recent fauna

To determine similarity in composition of a possible modern analogue of the Nakasi Beds fauna, five stations 8–25 m in depth were sampled on 24 June 1985 by dredging and diving in Laucala Bay, the estuary of the Rewa River, approximately 10 km from the fossil study sites: Sta. 1 — 178°27.7'E, 18°9.5'S, 8.2 m; Sta. 2 — 178°26.8'E, 18°10.1'S, 14.5 m; Sta. 3 — 178°28.1'E, 18°9.9'S, 25 m; Sta. 4 — 178°28.2'E, 18°9.6'S, 24 m; Sta. 5 — 178°29.3'E, 18°9.5'S, 18 m. Sediment grain size distributions were analyzed by the Emery settling tube method (Emery, 1938), and the composition of the benthic gastropod assemblages were compared with those from the Nakasi Beds.

² URL: <http://www.elsevier.nl/locate/palaeo>; mirror site: <http://www.elsevier.com/locate/palaeo>.

3. Systematic account

Most fossils observed in situ were arranged irregularly with respect to bedding plane, but a few were parallel. Most occurred as single shells sporadically throughout the deposit. Lenticular patches of abundant small shells occurred occasionally in sections of coarser sandstone. Mollusc shells were by far the most abundant macrofossils present. Remains of solitary and colonial corals, ectoprocts, echinoids, benthic foraminiferans and calcareous algae were also noted.

Gastropods were by far the numerically dominant group, accounting for about 75% of all molluscan fossils (appendix A, **Online Background Dataset**³). The total gastropod sample consisted of 2893 gastropod shells, of which 2462 were essentially intact. These represented at least 320 species in 146 genera and 52 families.

Class GASTROPODA

‘ARCHAEOGASTROPODS’ (orders PATELLOGASTROPODA, VETIGASTROPODA and NERITOPSINA)

The former Order Archaeogastropoda (e.g. Vaught, 1989) is now generally considered to comprise three order-level taxa. Only three specimens of the Order Patellogastropoda (Lindberg, 1988) or Docoglossa (Salvini-Plawen and Haszprunar, 1987), and only nine of limpet-like Vetigastropoda (Salvini-Plawen and Haszprunar, 1987), all in the Family Fissurellidae, were present. All were small (5–18 mm) and four were broken. All could well have washed into the sediment after death, from their typical hard substrates in shallower water. Most archaeogastropods in the samples were members of the major tropical families Trochidae (53%) and Turbinidae (38%), of the Order Vetigastropoda. A few members of the families Skeneidae (O. Vetigastropoda), and families Phenacolepadidae and Neritidae (O. Neritopsina) were also present.

Family TROCHIDAE

Classification of the large and ancient family Trochidae (Middle Triassic–Recent) has recently ex-

panded to comprise 13 subfamilies, including tropical, high-latitude and deep-sea evolutionary radiations. Most trochids are epifaunal grazers on benthic plants and encrusting invertebrates, but two subfamilies, the Solariellinae (Late Cretaceous–Recent) and Umboniinae (Oligocene–Recent), are particle feeders living on or in soft sediments (Hickman and McLean, 1990). These subfamilies accounted for nearly 80% of the 65 specimens in our samples. *Monilea*, the only umboniine genus present, comprised two-thirds numerically. *M. belcheri* (Plate I, 1, 2) and *M. callifera* were commonest, each comprising about 30% of the sample. Few members of the subfamilies Eucyclinae, Calliostomatinae and Trochinae were present.

Six of the nine identified species of Trochidae are extant, and five of these probably occur in Fiji at the present time. Co-occurrence of the three species of *Monilea* is inconsistent with their modern bathymetric range. According to Cernohorsky (1972, 1978), *M. callifera* occurs intertidally, *M. nucleus*, intertidally and subtidally, and *M. belcheri* in 27–45 m. The latter two species are extant in Fiji, but *M. callifera* presently occurs from New Caledonia westward according to the same author.

Evidence of predation on trochids was uncommon. Only two shells had repair scars, and only nine (16%), all of *Monilea* spp., were drilled (Plate I, 1, 2), seven by naticids.

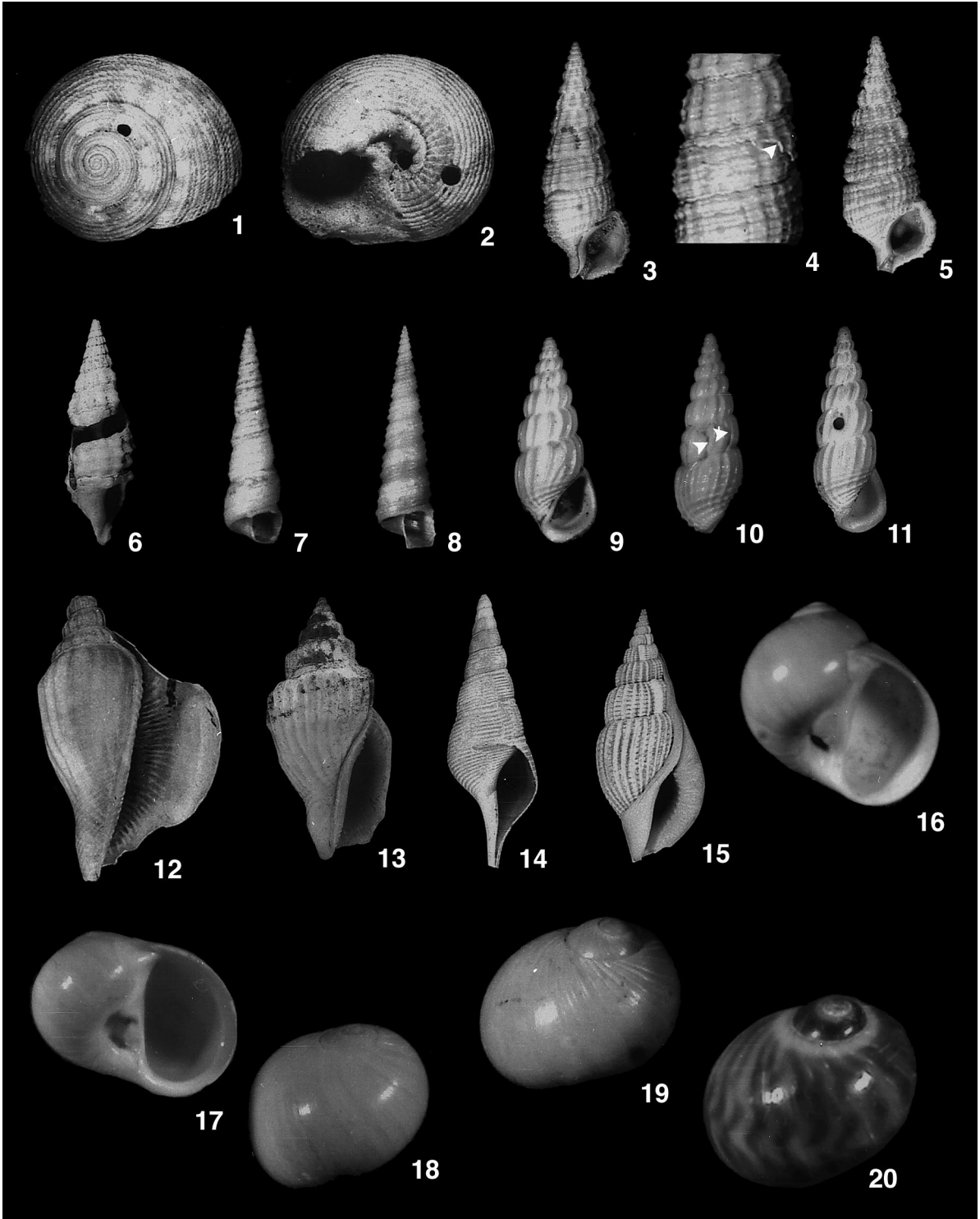
Family TURBINIDAE

While living members of this family are now distinguished from the Trochidae primarily by their conservative radular characters, the turbinids (Permian–Recent) also have relatively thick, usually sculptured, turbinite, conispiral shells, and most species have a nacreous interior shell layer and a calcified operculum (Hickman and McLean, 1990). These authors distinguish nine subfamilies, of which three (Turbininae, Late Cretaceous–Recent; Liotinae, Permian–Recent; and Phasianellinae, Miocene–Recent) are represented here. Turbinids occur worldwide but are most diverse on carbonate substrates in tropical and subtropical regions. They are typically grazers on algae.

Forty-eight shells, fragments and opercula of turbinids were present. The isolated opercula, all of *Turbo* spp., are generally larger than the shells

³ URL: <http://www.elsevier.nl/locate/palaeo>; mirror site: <http://www.elsevier.com/locate/palaeo>.

PLATE I



recovered or represent species of which no shells were present. Thus they are likely to represent additional specimens. The commonest species were *Phasianella graeffei* (11 specimens) and *Turbo squamosus*, the latter represented by 10 characteristically ridged opercula but no shells. *Turbo argyrostoma* (9) and *T. petholatus* (5) were the next commonest species. Five of the six identified species of Turbinidae are extant, and four of these occur in Fiji at present.

Ten of the 30 turbinid shells had repair scars, including one specimen with 3 and one with 4 scars. Four shells, representing three genera, were drilled, all by naticids.

Order NEOTAENIOGLOSSA

The Order Neotaenioglossa (Ponder and Warén, 1988) includes the marine superfamilies of the order more generally known as Mesogastropoda (e.g., Vaught, 1989).

Family CERITHIIDAE

The large family Cerithiidae, with about 25 genera and hundreds of species, is widely distributed geographically; most species occupy sand substrata in shallow water, where they feed on algae, microorganisms and detritus. The shells are usually sculptured, with a high, tapering spire, and ovate

apertures with a crenulated outer lip and relatively long anterior canal (Houbrick, 1988).

The eighth commonest family in our sample, Cerithiidae is divided into three subfamilies (Ponder and Warén, 1988), but all of our specimens belong to the major Subfamily Cerithiinae. The genus *Rhinoclavis* (Oligocene–Recent; Houbrick, 1978) predominated (two-thirds of all individuals). Members of this genus often occur in coral reef-associated habitats on sand or sand and rubble or in sea grass beds. They are “crystalline style-bearing, microphagous detritus-algal feeders” whose guts typically contain algal cells, sand grains, foraminifera and particulate detritus (Houbrick, 1978).

The two extant species of *Rhinoclavis* subgenus *Proclava* commonly co-occur in modern habitats, and they constituted 64% of our sample of the family. Houbrick (1978) treats both species in detail. The widely distributed *R. (P.) sordidula* (Plate I, 3, 4) was commonest (45 individuals). Extant populations of this species occur in the western Indian Ocean and from Indonesia to Japan and Fiji (Plate I, 5); Pliocene and Pleistocene fossils are known from Indonesia, Okinawa, southwest Japan, Guam, and Vanuatu (Houbrick, 1978) as well as Fiji. This species “is confined to fine, sandy or muddy substrates in moderately deep waters” (16–44 m; Houbrick, 1978). From examination of radular characters and fecal pellets Houbrick (1978) suggested that *R. (P.) sor-*

PLATE I

1. *Monilea belcheri*. Dorsal view, showing color pattern and naticid drill hole. Loc. 16. MD = 10.5 mm.
2. *Monilea belcheri*. Ventral view, showing muricid drill hole. Loc. 16. MD = 10.5 mm.
3. *Rhinoclavis sordidula*. Loc. 16. SL = 13 mm.
4. *Rhinoclavis sordidula*, showing shell repair following unsuccessful predation by *Calappa* (arrowhead). Loc. 16.
5. *Rhinoclavis sordidula*. Shell of living specimen, Laucala Bay, Sta. 1, 8 m. SL = 13 mm.
6. *Cerithium columna*, shell probably fatally peeled by *Calappa*. Loc. 16. SL = 15 mm.
7. *Turritella cingulifera*. Loc. 17. SL = 10 mm.
8. *Turritella cingulifera*. Recent, Laucala Bay, Sta. 4, 24 m. SL = 13 mm.
9. *Rissoina bourneae*. Loc. 16. SL = 5.6 mm.
10. *Rissoina bourneae*, showing repair scars (arrowheads). Loc. 16. SL = 6.2 mm.
11. *Rissoina bourneae*, showing naticid drill hole. Loc. 16. SL = 5.7 mm.
12. *Strombus plicatus pulchellus*. Loc. 16. SL = 35 mm.
13. *Strombus labiatus*. Loc. 19. SL = 31 mm.
14. *Tibia powisii*. Loc. 16. SL = 34 mm.
15. *Varicospira cancellata*. Loc. 19. SL = 28 mm.
16. *Natica arachnoidea*. Loc. 16. SL = 6.5 mm.
- 17, 18. *Natica euzona*. Loc. 19. SL = 7 mm.
19. *Natica gualteriana*. Loc. C3136. SL = 6 mm.
20. *Natica gualteriana*. Recent, Laucala Bay, Sta. 1, 8 m. SL = 6 mm.

didula eats the sediment in which it lives. More than half (27) of the shells in our sample were drilled, 16 by naticids and 10 by muricids (1 uncertain); all drilled shells had a single hole. Eighteen had repair scars indicative of unsuccessful attempts by crushing predators, including *Calappa* (Plate I, 4).

The closely related *Rhinochlamys* (*Proclava*) *kochi* (11 specimens) ranked second in abundance. Today it ranges more broadly in the western Indo-Pacific region than *R. (P.) sordidula* Houbriek (1978); it no longer survives in Fiji, although modern populations are known from Vanuatu and New Caledonia. Houbriek (1978) lists Pliocene and Pleistocene fossils from East Africa to Philippines. He also notes that *R. (P.) kochi* occurs on muddy and sandy bottoms from low tide to 60 m; he found gut contents to contain fine to coarse sand and foraminifera, and he also observed that evidence of drilling predation is frequent in museum specimens. Of our ten intact specimens, six were drilled, three of them twice. As in *R. (P.) sordidula*, naticids accounted for 60% of the drilled holes. Six specimens had repair scars.

The second commonest genus in our sample (28% of individuals) was *Argyropeza*, known to live on or in soft sediments in 30 to >900 m (Houbriek, 1980). Stomachs and fecal pellets of *A. divina* examined by Houbriek (1980) contained fine sand, detritus and foraminiferan tests. Both species now occur in the Indian Ocean; *A. divina* ranges eastward to New Guinea, and *C. schepmaniana*, to New Caledonia (Houbriek, 1980) but neither is known from Fijian waters at present. Houbriek (1980) summarized knowledge of the genus, and Kohn (1986) discussed paleoecology of the Fijian specimens and illustrated the shells of both species and a naticid drill hole in one. Nearly one-third of the specimens were drilled, all but one by naticids, and none had repair scars.

Five specimens of the intertidal and shallow subtidal genera *Cerithium* (4 species) and *Clypeomorus* (1 species) made up most of the remaining 12% of the sample. All but one shell was drilled, suggesting the possibility of post-mortem transport to deeper water by hermit crabs or other vectors. One *Cerithium columba* was probably eaten by a *Calappa* (Plate I, 6).

Family TURRITELLIDAE

Geographically the Turritellidae is one of the most widely distributed gastropod families; geologically

the oldest reliable record is Lower Cretaceous (W. Allmon, in litt., 1996). Its members have elongate, tapering shells with a small, round aperture. Spiral shell sculpture is diverse and often complex and varies with geologic age (e.g., Kotaka, 1959, 1978). Turritellids live on or in sand and mud and are both suspension and deposit feeders, collecting fine food particles with the cilia of the ctenidium; the particles are trapped in mucus and passed to the mouth via a large food groove on the floor of the mantle cavity (Graham, 1938; Allmon, 1988).

The family ranked seventh in abundance in our samples. All but two of the 101 specimens were of the genus *Turritella*, and 86% were of one species. Following Shuto (1969), we have identified this as *T. cingulifera* (Plate I, 7). It is the species described and well illustrated by Ladd (1972) from the Fiji Pliocene as *T. fileola* Yokoyama. We accept Shuto's (1969) conclusion that this is conspecific with *T. cingulifera*. The species is widely distributed in Pliocene deposits in Taiwan, Okinawa, southwestern Japan and Philippines, and Pleistocene fossils are also known from southwestern Japan (Shuto, 1969). Although it has not heretofore been reported living in Fiji, we collected numerous specimens in 18–25 m in Laucala Bay, Viti Levu (Plate I, 8).

The only other turritellids were two incomplete shells with all tightly coiled whorls that agree with the description of *Vermicularia* sp. A of Ladd (1972).

A third of the specimens studied had been drilled, more than two-thirds by naticids and the rest by muricids. Nearly a third of the specimens had repair scars, including four with multiple scars.

Family RISSOIDAE

This family, with a fossil record back to the Jurassic, is characterized by high-spired shells usually only a few millimeters long. The animals eat fine algae, deposited detritus, or foraminifera (Ponder, 1985), and are often found among seaweed in shallow water.

The 40 specimens all belonged to the genus *Rissoina* (Subfamily Rissoininae), in which the shell is typically axially and sometimes spirally sculptured and has an ovate aperture. And all are in the subgenus *Rissolina* as revised by Ponder (1985). Four species were present, of which most (35) were probably *R. bourneae* (Plate I, 9–11), described from

the older Suva Formation (Ladd, 1966), and not presently known to be extant. However, the specimens very closely resemble *R. micans* Gould, an extant species occurring in Philippines, according to specimens in the U.S. National Museum of Natural History determined by W. Sleurs. About half of the shells were drilled by naticids (59%) (Plate I, 11) and muricids (41%); almost all (95%) displayed repair scars, frequently two or more scars per shell (Plate I, 10).

Family STROMBIDAE

The Family Strombidae originated in the Late Cretaceous and has been widely distributed in warm waters since (Sohl, 1987). Fewer than 100 species comprise the family at present, and more than half of these are in the genus *Strombus*. Most extant species occur in the Indo-Pacific region, with about 15 presently in Fiji (Abbott, 1960).

The shells of Strombidae vary widely in size and shape. Most have an enlarged last whorl with a long, narrow aperture and expanded, sometimes digitate outer lip. Anteriorly, a characteristic ‘stromboid notch’ accommodates the right eye stalk. The shells often bear varices, axial ribs, and finer spiral sculpture. Strombids feed on filamentous algae and detritus. Most species are “sand-dwelling, shallow-water, tropical and subtropical” (Boss, 1982), and most occur from shallow, subtidal habitats to less than 100 m depth.

Of the five genera represented in our sample (*Lambis* only by a fragment), *Strombus* was the commonest (57%; at least 7 species) followed by *Tibia* (31%; one species) and the now nearly extinct *Varicospira* (7%; one species). All four identified species of *Strombus* remain extant in Fiji. *S. plicatus pulchellus* (Plate I, 12) was the commonest (12 of 26 specimens). According to Abbott (1960), prior fossil records of this species and of *S. labiatus* (Plate I, 13) ($N = 6$) are doubtful, but *S. labiosus* ($N = 6$) and *S. fragilis* ($N = 1$) are known from Pliocene deposits in Indonesia and Vanuatu, respectively. All identifiable specimens of *Tibia* were *T. powisii* (Plate I, 14) ($N = 16$), known from Miocene to Recent in Indonesia, Pliocene to Recent in Philippines, and Pleistocene to Recent in Vanuatu, as well as Pliocene of Fiji (Shuto, 1969; Ladd, 1972, 1982; Robba et al., 1989; Duchamps, 1992). Of the species represented by

fewer individuals, *Terebellum terebellum* and *Lambis crocata* are extant in Fiji, but living *Varicospira cancellata* (Plate I, 15) is now restricted to the Philippines. All nine identified species of Strombidae are extant, and the other seven occur in Fiji today.

Members of all of these genera were drilled. Drilling was most frequent in the thinnest-shelled *Tibia* (4/16, 3 by naticids), and one of the four *Varicospira* individuals was drilled twice (by a naticid and a muricid). *Strombus*, with the thickest shells, was drilled least frequently (3/26; 2 by muricids). Nine specimens of *Tibia* but none of the others had repair scars.

Family CYPRAEIDAE

The shells of Cypraeidae are unmistakable in form; they are globular, hemispherical or ovate-pyriform with a very short, often obscured spire. The surface is glossy as the mantle often extends over the shell in life. The family extends back to the Late Jurassic, and the nearly 200 extant species are well known taxonomically (Burgess, 1985). The main genus of the family is *Cypraea*, although some workers subdivide it. Most species are tropical, primarily in shallow, subtidal habitats where they typically occur epifaunally on hard substrates. The feeding habits are not well known, but most are probably carnivores feeding on encrusting colonial invertebrates such as ascidians and sponges. Some species, especially those most abundant on shallow reef platforms, are known to be herbivorous.

Ten tentatively determined species, all extant in Fiji at present, occurred in our sample of 27 specimens. Most of these (70%) were fragments. Fragments of four specimens were tentatively determined as *C. erosa*, but all other species appeared to be represented by only one or two shells or fragments. The sample probably consists mainly of shells and fragments washed into the sedimenting environment from higher-energy, inshore reef habitats. None of the specimens had repair scars or boreholes.

Family NATICIDAE

The family Naticidae, known from mid-Cretaceous to Recent, comprises about 150 extant species. It was the fourth most abundant family in our samples and the third most diverse in number of species. The shells are small to medium in size and usu-

ally globose with a low spire and large, inflated last whorl. The whorls are either smooth or sculptured with spiral striae. The aperture is usually large and ovate. The operculum may be thin and horny or thick and calcified, and the umbilicus is either open or closed.

Naticids typically occur in broad expanses of sand bottom. They burrow using an expanded foot, often with a large propodium that covers the head and anterior part of the shell. The posterior part of the foot may also expand over the shell. Expansion of the foot is often accomplished by pumping water from the sea into water tubes. The mantle often forms a short inhalant siphon, facilitating respiration while burrowing, but there is no trace of siphon on the shell. Naticids are predators that penetrate the shells of molluscs using the radula and a secretion from an accessory boring organ, located on the ventral surface of the proboscis. They leave a characteristic borehole with beveled or countersunk sides, through which the proboscis penetrates to ingest the body of the prey (Kabat, 1990). They are usually considered to prey on bivalves, but gastropods represented an unusually high proportion of naticid prey in our sample (Section 5.2; Kabat and Kohn, 1986).

The family is usually divided into four subfamilies, Ampullospirinae, Sininae, Polinicinae and Naticinae (Majima, 1989; Kabat, 1991). All are represented in our sample of 207 intact specimens, in 19 species and 7 genera, but only one ampullospirine specimen was present. The genus-level classification of naticids is presently very ambiguous (Kabat, 1991); here we follow that of Schileyko (1977). The Subfamily Naticinae, represented by four subgenera of the genus *Natica*, comprised at least 8 species and 163 specimens, fragments and opercula, or 73% of the sample. *Natica (Tanea) euzona* was the commonest species ($N = 61$), accounting for 27% of all the specimens, followed by *N. (Natica) arachnoidea* (18%) (Plate I, 16–18) and *N. (Notochlis) sp. cf. N. gualteriana* (11%) (Plate I, 19, 20). Polinicinae (2 genera, 6 species) constituted 23% of the individuals, and Sininae (3 genera, 4 species), 4% of the individuals. At least 14 of the species are extant, but only seven of these are known to occur in Fiji at the present time.

The frequency of shell repair by naticids was unusually high, 35% overall and 47% of Naticinae.

Only one of 45 Polinicinae had a repair scar, and only one had a drill hole. In contrast, 25% of naticine shells were drilled, 88% of these by other naticids (see Kabat and Kohn, 1986).

Family CASSIDAE

Shells of this primarily tropical family vary widely in size and thickness. They are ovate to globose with a large, smooth or sculptured last whorl, a short, oblique anterior siphon, and a conical but often short spire. Cassids have a fossil record back to the Upper Cretaceous. Modern species occur from the shallow subtidal to several hundred meters; characteristic habitats are sand and rubble, in which the animals often burrow shallowly. They prey primarily on echinoids and to a lesser extent on asteroids (Hughes and Hughes, 1981).

All but one of the mostly fragmentary specimens belonged to the genus *Phalium*, probably *P. areola* ($N = 6$) and *P. bisulcatum* ($N = 12$). The latter species is known to prey on echinoids (Taylor, 1982). Only one well preserved shell was found, of *P. glabratum* (Plate II, 21). The first two species occur in Fiji at present. Their diets are unknown, but other Indo-Pacific *Phalium* species prey on spatangoid echinoids (Hughes and Hughes, 1981). One specimen of *P. areola* was drilled, probably by a muricid, and the *P. glabratum* had one repair scar (Plate II, 21).

Family TONNIDAE

Shells of the small (<50 species), mainly tropical family Tonnidae are typically large and globose but thin and light, with a very large last whorl and aperture, and short spire. The earliest fossils are Late Cretaceous. Tonnids live from shallow subtidal to abyssal depths, on or buried in sand. Members of the main genus *Tonna* capture holothurians, but other echinoderms, bivalves and crustaceans are also reported as food (Boss, 1982).

Only two of 21 specimens were intact, as might be expected from their fragility. At least five species were present; *T. allium* and *T. sulcosa* (8 and 7 specimens, respectively) were commonest. All identified species are extant, and all but one presently occur in Fiji. There was no evidence of repair scars or drilling predation.

Family FICIDAE

Shells of this small, warm water family (about 10 extant species) are elongate-pyriform with a long aperture with siphonal canal and short spire, and are thin and fragile. Ficids are sand-dwelling, presumably carnivorous gastropods.

One species, *Ficus variegata*, represented by fragments of 15 shells, was present. An extant species, it presently ranges from New Guinea to Philippines and Indonesia, while the closely related *F. ficoides* (Lamarck) now occurs from Fiji westward into the Indian Ocean (Cernohorsky, 1972).

Family RANELLIDAE

This worldwide but mainly warm water family of Late Cretaceous origin (Beu, 1988), previously known as Cymatiidae, includes about 130 Recent species with medium to large, solid, ovate, ventricose or fusiform shells, often with angulate whorls and prominent spiral and axial sculpture. The aperture is often round, with a short to long anterior siphonal canal and usually no anal canal. Although we follow the classification of Ponder and Warén (1988), who included *Distorsio* in the Ranellidae, Subfamily Personinae, Beu (1988) raised the latter to family status on the basis of radular and gut morphology differences.

Ranellids occur on sandy and rocky substrates, from the intertidal zone to several hundred meters. They prey mainly on other gastropods, bivalves, assteroids and echinoids. *Cymatium nicobaricum* feeds on a wide variety of other prosobranch gastropods. Houbriick and Fretter (1969) listed 21 species (in 8 families) of neotaenioglossans and neogastropods, including other *Cymatium* species, as prey of captive *C. nicobaricum* in Hawaii. It has also recently been shown to prey on cultivated tridacnid bivalves (Govan, 1995). *Distorsio reticulata* preys on the polychaete *Phyllochaetopterus* (Taylor, 1982). Many ranellids have larvae that may remain planktonic for months, and some species are very widely distributed.

The six species (in three genera) in the sample of 17 specimens are all extant, and all but one occur in Fiji at present. *Distorsio reticulata* (Plate II, 22–23) was the commonest ($N = 6$). Of the 14 intact shells, three had repair scars, two were drilled by naticids, and one each of *D. reticulata* (Plate II, 23), *Gyrineum gyrinum* (Plate II, 24) and *Cymatium*

nicobaricum had large, irregular holes in the shell likely the result of successful predation by hammering gonodactyloid stomatopods (Geary et al., 1991; Kohn, 1992b). An additional fragment of *G. gyrinum* may also have been the result of stomatopod predation, which affected members of this family more frequently (24%) than any other in the sample.

Other neotaenioglossan families

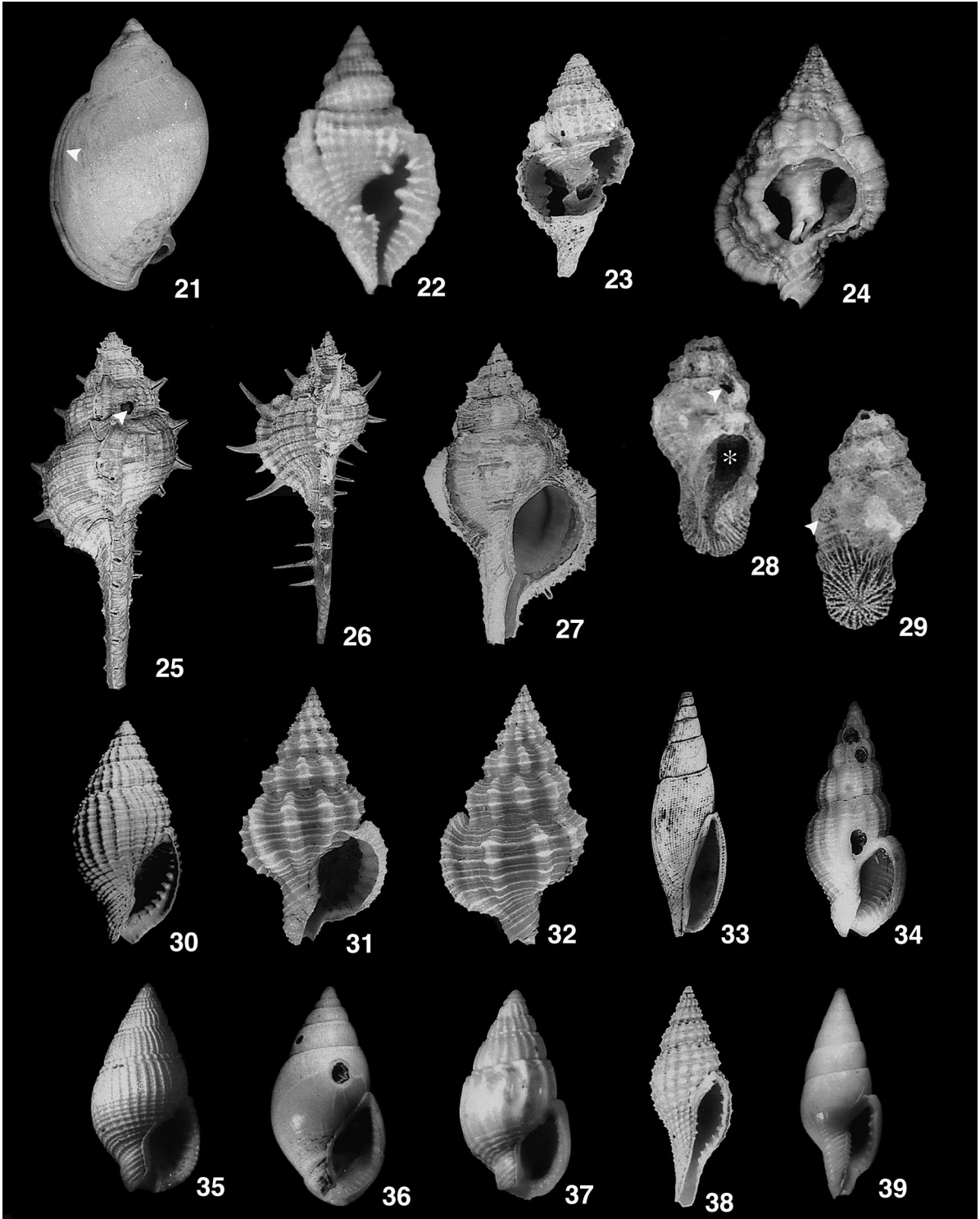
Nine additional families of Neotaenioglossa were represented in the sample by fewer than 10 individuals. Commonest of these was the Bursidae, with 9 specimens of *Bursa rana*, an extant species not known to occur at present in Fiji. Its diet is unknown, but other *Bursa* species prey on polychaetes and sipunculans (Houbriick and Fretter, 1969). The Epitoniidae, a family of parasites primarily on corals, was represented by eight specimens, of which four were *Epitonium sakurarii*, extant in Fiji today. The other families, with 1–6 specimens each, were Plesiotrochidae, Siliquariidae, Vermetidae, Triviidae, Triphoridae and Eulimidae. In addition, one shell of a pelagic heteropod (Family Atlantidae) was recovered.

Order NEOGASTROPODA

Family MURICIDAE

The family Muricidae includes about 700 Recent species of carnivorous gastropods with some of the most complexly sculptured shells, often with long spines. It is a diverse group of predatory snails that feed mainly on other invertebrates such as barnacles, snails, bivalves, tube worms and corals (Fairweather, 1988; Ponder and Vokes, 1988). The earliest known fossils are mid-Cretaceous. The family is currently subdivided into three subfamilies, Muricinae, Thaidinae and Coralliophilinae (Ponder and Warén, 1988), all of which are represented in our samples. In tropical and subtropical shallow waters, muricids inhabit rocky shores, coral reefs and soft bottoms. Fijian Muricidae are typically associated with coral reefs and muddy-sand environments. Cernohorsky (1967, 1969) lists 21 species of Muricinae and 28 species of Thaidinae as extant in Fiji. According to Ponder and Vokes (1988) three of the 23 extant species of *Murex*, *M. aduncospinosus*, *M. tenuirostrum* and *M. pecten*, presently occur in Fiji. Our fossil samples contain the first two of these. None of the 15 extant

PLATE II



Haustellum species now occur in Fiji, but two are present in our samples.

The Subfamily Muricinae arose in the Late Cretaceous in Europe; the oldest *Murex* s.s. date from the Early Miocene, and the stratigraphic range of Indo-Pacific muricids is from Upper Middle Miocene to recent (Ponder and Vokes, 1988).

Nearly three-fourths of the specimens in our sample were Muricinae; the commonest of these (28 of 41 including fragments) was *Murex aduncospinosus* (Plate II, 25), determined from Ponder and Vokes (1988), a member of the Recent Fiji fauna (Plate II, 26). The 13 specimens of Thaidinae represented three genera.

Half of the specimens showed evidence of predation. Eleven Muricinae (46%) were drilled, one twice, nine by naticids (Plate II, 25) and all on the penultimate whorl. One of the drilled specimens also bore an incomplete drill hole. No repair scars from unsuccessful attacks by durophagous predators were observed, but one specimen of *Murex tenuirostrum* showed evidence of successful predation by *Calappa*. Four of the Thaidinae were drilled, two each by naticids and muricids, three had repair scars, one *Morula* sp. appeared to be a victim of *Calappa*, and one was incompletely drilled by a muricid. One specimen of *Morula margariticola* (Plate II, 28, 29) was drilled by a muricid and had

an unrepaired break, probably from a crab, at the outer lip. A peripheral region of cemented sediment in the aperture (below asterisk in Plate II, 29) indicates that a sipunculan probably of the genus *Aspidosiphon* inhabited the shell, and the shell bears one large and one very small solitary coral, *Heterocyathus aequicostatus* (Plate II, 28, 29), a common epibiont of gastropod shells occupied by sipunculans (Hoeksema and Best, 1991).

Family BUCCINIDAE

Formerly considered a group of families comprising the Superfamily Buccinacea (Thiele, 1929), this taxon has been demoted to family status “because there are virtually no characters that constantly and reliably separate them at family level” (Ponder and Warén, 1988). Because these groups, now considered the subfamilies Buccininae, Nassariinae, Melongeninae and Fasciolarinae, have traditionally been considered families, we treat them separately in this section. The Buccinidae (s.l.) was the most abundantly represented family in our sample with 683 specimens of at least 39 species, primarily because of the very large number of Nassariinae.

Subfamily BUCCININAE

The Subfamily Buccininae, considered a family traditionally and in most modern works as well,

PLATE II

21. *Phalium glabratum*, with repair scar (arrowhead). Loc. 24. SL = 32 mm.
22. *Distorsio reticulata*. Loc. 16. SL = 34 mm.
23. *Distorsio reticulata* with large hole suggestive of predation by gonodactyloid stomatopod. Loc. 16. SL = 15 mm.
24. *Gyrineum pusillum* with large hole suggestive of predation by gonodactyloid stomatopod. Loc. 16. SL = 32 mm.
25. *Murex aduncospinosus*, showing naticid borehole (arrowhead). Loc. 16. SL = 75 mm.
26. *Murex aduncospinosus*, recent specimen from Laucala Bay, Sta. 1, 8 m. SL = 50 mm.
27. *Haustellum dolichourus*. Loc. 16. SL = 47 mm.
28. *Morula margariticola*. Ventral view, showing muricid borehole (arrowhead), opening of sipunculan burrow (asterisk), and probably fatal damage by crab to outer lip. Loc. 24. SL = 13 mm.
29. *Morula margariticola*. Dorsal view of specimen in 28, showing large and small (arrowhead) specimens of the solitary coral *Heterocyathus aequicostatus*. Loc. 24.
30. *Phos vitiensis*. Loc. 19. SL = 14 mm.
- 31, 32. *Nassaria acuminata*. Loc. 16. SL = 29 mm.
33. *Metula ibbotsoni*. Loc. 16. SL = 23 mm.
34. *Phos roseatus*, showing one muricid borehole (nearest apex) and two naticid boreholes. Loc. 19. SL = 19 mm.
35. *Nassarius (Zeuxis) concinnus*. Loc. 16. SL = 11 mm.
36. *Nassarius comptus*, showing two boreholes. Loc. C3136. SL = 13 mm.
37. *Nassarius (Niotha) sinusigerus*. Loc. C3136. SL = 9 mm.
38. *Granulifusus* sp. A. Loc. 16. SL = 13 mm.
39. *Mitrella puella*. Loc. 16. SL = 11 mm.

is a diverse, cosmopolitan taxon represented more commonly in temperate and boreal than in tropical regions, in contrast to the Nassariinae and Fasciolarinae. Its earliest fossils are Lower Cretaceous. Tropical members of the Buccininae usually have thick and strong, fusiform to ovate, small to medium-sized shells with a short or moderate-sized siphonal canal. The sculpture is variable but usually includes both axial and spiral elements. Varices are sometimes present but are usually not very prominent. Tropical members of this subfamily occupy sand (*Phos*) or rock and coral habitats (other genera) from shallow subtidal to considerable depths. Most species are carnivorous, feeding primarily on other molluscs and worms or are scavengers. Several *Colubraria* species, including *C. tortuosa* represented here by one specimen, parasitize sleeping parrotfishes (Family Scaridae) by sucking body fluids (Johnson et al., 1995).

The 110 specimens of Buccininae in our sample include representatives of 13 species in eight genera. If considered a family it would rank sixth in abundance and fourth in species richness. Seven of the 11 species identified with confidence are extant, and five of these occur at present in Fiji. *Phos vitiensis* (Plate II, 30), an evidently extinct species originally described from Fiji, comprised nearly half the sample ($N = 48$). As Cernohorsky (1980) indicated, it may well be conspecific with the Miocene–Pliocene *P. dijki* Martin known from Indonesia and Philippines. This species, with low axial and spiral sculpture, had a high frequency of repair scars (0.3/shell) and of predation by borers (27%), with naticids ($N = 7$) and muricids ($N = 6$) each accounting for about half.

The second commonest species was *Nassaria acuminata* (Plate II, 31, 32) (17% of the sample). Cernohorsky (1981) resolved the long-confused taxonomy of this species and discussed its extensive intraspecific variation in shell characters. It is known from the Miocene and Pliocene of Pakistan, Pliocene of India, New Guinea, Indonesia, and Philippines, and Pleistocene of Sabah. Ladd (1977) recorded it from the Pliocene (?) of Vanua Levu and Viti Levu (as *Cymatium rickardi* Ladd). It presently ranges from the Persian Gulf across the northern Indian Ocean, to southern Japan, and south to the Solomon Islands and Queensland, but it is evidently extinct in Fiji. Only

one specimen had a repair scar; the shell bears strong, sometimes varicose axial ribs (Plate II, 31, 32). Six of the 17 specimens were drilled, two of them twice, and most (6/8) by naticids. No specimens of the third commonest species, *Metula ibbotsoni* ($N = 11$) (Plate II, 33) were drilled and only one had a repair scar. All six specimens of *Phos roseatus* were drilled, mostly by naticids; one shell had one muricid and two naticid boreholes (Plate II, 34).

Overall the average numbers of repair scars per shell of Buccininae was 0.26, and 28% were drilled, twice as many by naticids as by muricids.

Subfamily NASSARIINAE

The subfamily Nassariidae is widely distributed in all seas but is most diverse in the Indo-Pacific tropics. Cernohorsky (1984) recognized about 320 Recent and nearly 600 fossil species, most in the main genus *Nassarius*. The earliest record of the family is Upper Cretaceous, but *Nassarius* is known only from Miocene to Recent (Cernohorsky, 1984). The shells are usually small and ovate with convex whorls and a moderately wide, irregularly rounded aperture and a deep siphonal notch but no shell siphon. The outer lip usually bears denticles and is lirate within, and the columella is also usually lirate or wrinkled, and sometimes expanded as a shield. The shell surface is usually sculptured with prominent axial ribs and weaker spiral threads or grooves. Cernohorsky (1984) illustrates multispiral and paucispiral protoconchs of species with planktotrophic and lecithotrophic veligers, respectively.

The subfamily is “a dominant element of shallow waters of the intertidal zone where they sometimes occur in colonies buried in clean or muddy coral sand” (Cernohorsky, 1984). Members of the subfamily also occur subtidally, and to depths exceeding 2000 m.

Species of *Nassarius* are generally considered omnivorous, feeding on other invertebrates, carrion, algae, and detritus (Cadée, 1984; Britton and Morton, 1993, 1994; Taylor, 1993). Of the extant species represented in the Nakasi Beds assemblage, *N. crematus* preys on polychaetes, scavenges, and eats sediment (Taylor and Shin, 1990). The well developed chemosensory ability of *Nassarius* facilitates often violent escape behavior from predators such as naticids (Gonor, 1965).

The genus *Nassarius* is currently divided into 12 subgenera, of which four are present in our sample. However, nearly all of the specimens were in the subgenera *Zeuxis* (7 of the approximately 10 species of *Nassarius* and 70% of the 499 specimens recovered) and *Niotha* (1 species, comprising 21% of the sample). One species (4 specimens) of *Cyllene* was the only member of another genus observed.

Nassarius was the most abundant of all genera in our sample, and the species determined as *N. (Zeuxis) concinnus* (Plate II, 35) was the commonest ($N = 260$; half of all Nassariidae). The spiral sculpture of these specimens was quite variable. About 60 of them agreed very closely with Cernohorsky's (1984) description: "spiral sculpture consists of very fine spiral striae which are either confined to interspaces of axial ribs or override axials rendering these slightly nodulose." However, while the spiral striae of most specimens agreed in their relationship to the axial ribs, they were slightly less fine and thus were separated by flat spiral threads. In this characteristic they agree with *N. pseudomundus* Oostingh (1935) from the Pliocene and Pleistocene of Indonesia, synonymized with *N. (Z.) concinnus* by Cernohorsky (1984). *N. (Z.) concinnus* is presently very widely distributed, from the Red Sea to the Tuamotu Archipelago (Cernohorsky, 1984; Robba et al., 1989). *Nassarius (Z.) comptus* (Plate II, 36) ($N = 116$) and *N. (Niotha) sinusigerus* (Plate II, 37) ($N = 83$) were the next commonest species. Like *N. concinnus*, *N. comptus* occurs throughout most of the Indo-Pacific tropics, but it appears to lack a prior fossil record (Ladd, 1977; Cernohorsky, 1984). Our sample of *N. sinusigerus* possibly includes some specimens of the very similar *N. agapetus* Watson, considered distinct by Cernohorsky (1984). Known from the Pliocene of Indonesia, *N. sinusigerus* is likely the species reported from Fiji as *N. verbeeki* (Martin) by Ladd (1977, p. 52, pl. 17, figs. 17, 18). It is presently distributed throughout the Indian Ocean and western Pacific, reaching the eastern edge of its range at Fiji (Cernohorsky, 1984). All eight of the species determined with some confidence are extant, and seven of these presently occur in Fiji.

About 25% of nassariid shells had repair scars ($N = 126$) and fewer than 20% had drill holes ($N = 85$). Only three shells had multiple drill holes, but one of these was drilled four times and the other

two, three times. Most drillholes (84%) were caused by naticids (Plate II, 36), the rest by muricids. The frequency of drilling highest in *N. sinusigerus* (33%), and only 12–13% in the two other common species.

Subfamily FASCIOLARIINAE

Some members of this subfamily are among the largest gastropods, attaining a shell length of 60 cm. The shell is often spindle-shaped, with an ovate aperture and moderately to very long anterior siphonal canal, especially in sand-dwelling species. The subfamily is of Early Cretaceous origin and is widely distributed in tropical and temperate seas. Some tropical members such as species of *Peristernia* and *Latirus* occur under coral rocks in shallow water. *Pleuroploca*, *Granulifusus* and *Fusinus* are found on sand. Fasciolarini prey on other molluscs and on worms (e.g. Paine, 1963), but knowledge of their feeding biology is very limited.

Our samples contained 5 genera and at least 13 species. The commonest species, *Granulifusus* sp. a (Plate II, 38), comprised nearly half of the sample (20/46 specimens). It was also drilled most frequently (7 naticid holes in 4 shells). The 14 specimens representing 4 species of *Fusinus* were less frequently drilled (4 naticid holes), and had the highest frequency of repair scars, averaging 1.4/shell. Overall, 17 shells had repair scars and 8 of these had more than one. The average was 0.6 repair scar per shell. One third of the shells were drilled, and most of the holes (15/20) were due to naticids.

Family COLUMBELLIDAE

Widely distributed in temperate and tropical waters, the Columbelloididae includes mainly small, shallow water (intertidal to 200 m) gastropods. Its earliest fossil record is Paleocene. Columbelloids often occur on hard substrates or are associated with algae. The family apparently includes herbivores, scavengers and carnivores, and many species may be omnivorous (Hatfield, 1979). The shells are generally fusiform or biconic, with a narrow aperture and denticulate outer lip.

Most columbellids belong to the three genera represented in our samples, *Mitrella*, *Pyrene*, and *Anachis*. Most of the specimens (37/59) belonged to *Mitrella*, and *M. puella* (Plate II, 39) comprised more than half the sample. It presently occurs eastward

only to New Caledonia (Cernohorsky, 1972), and is probably the fossil species described from Fiji as *M. gonzabuensis* by Ladd (1977). This species and *M. ligula* ($N = 13$) had a high frequency of repair scars (0.51) and of drill holes (16 in 13 shells; 11 by naticids and 5 by muricids). Shells of *M. ligula* were drilled significantly more frequently (10 holes in 8 of 14 shells) than *M. puella* (6 holes in 5 of 21 shells) ($G = 4.0$; $P < 0.05$). Three species of *Pyrene* accounted for 25% of the sample; these also had high frequencies of repair (0.53) and boreholes (10 in 8 shells; 7 by muricids and 3 by naticids). The difference in drilling frequency in *Mitrella* and *Pyrene* by the two predator families is nearly significant ($G = 3.80$; $P \approx 0.06$), suggesting that members of the latter genus occur more typically with hard substrates than the former.

Family OLIVIDAE

The family Olividae comprises five genera of predominantly tropical and subtropical, sand-dwelling gastropods. The metapodium of the large foot is expanded into lateral lobes or parapodia that cover all or most of the subcylindrical or spindle-shaped shell and secrete a smooth, glossy outer shell layer. When active, olivids typically leave a broad trail as they burrow just below the sand surface. The smooth shell and expanded metapodium suggest that the animals may move rather rapidly through the sand. When inactive, they may be burrowed down to 5 cm below the surface (Van Osselaer et al., 1993).

Olivids are catholic predators, scavengers and omnivores. The diet of *Oliva sayana* in the Gulf of Mexico includes the bivalve *Donax*, gastropods, and crustaceans (Fotheringham, 1976). The Brazilian *Olivella verreauxii* preys on the *Donax* and on foraminiferans, copepods, amphipods and scaphopods (Marcus and Marcus, 1959). *O. biplicata* in California is reported to prey selectively on foraminiferans (Hickman and Lipps, 1983) and omnivorously on detritus, algae, and living invertebrates (Edwards, 1969a).

The Olividae originated in the Late Cretaceous and, like many neogastropod families, initiated a major radiation in the Miocene. The genus *Olivella* (Cretaceous) is the oldest, *Ancilla* dates from the Paleocene (Davoli, 1989) or Eocene (Kilburn, 1981), *Agaronia* and *Oliva* from the Eocene, and *Olivancil-*

laria from the Oligocene (Davoli, 1989). The family is geographically widely distributed, both living and fossil. It was represented by 12 Mediterranean Basin Miocene species, but became extinct there in the Late Miocene and has not returned (Davoli, 1988, 1989). The genus *Ancilla* is now nearly restricted to the Indian Ocean, extending eastward only to Indonesia (Kilburn, 1981) except for one eastern Pacific species. Davoli (1989) reviews the biogeography, geologic history and paleoecology of the family.

We know of no studies of predation on recent olivids in the Indo-Pacific region. On the U.S. Pacific coast, the well studied *Olivella biplicata* is subject to intensive predation by durophagous crabs, drilling *Octopus* and *Polinices*, as well as by several starfish, shore birds, and man (Edwards, 1969b). Some species of *Oliva*, *Olivella*, and *Ancillista* use the broad foot lobes in a swimming escape response from predators (Wilson, 1969; Farmer, 1970; Phillips, 1977). Davoli (1989) illustrates an Italian Late Miocene specimen of *Oliva dufresni* drilled by a naticid.

The family was the third most numerous in our sample, with 200 well preserved specimens and fragments of 53 others. Most belonged to the genus *Oliva*; three identified and probably at least two other species were present, of which *O. sidelia* (Plate III, 40) (51%) and *O. mustelina* (Plate III, 41) (24%) were by far the commonest species. Both are extant species and both occur in Fiji today, but to our knowledge their natural history is completely unknown. Specimens indistinguishable from *Olivella apicalis*, described and known only from the Recent of Hawaii (Kay, 1979), was the third commonest with 18 specimens (7%) (Plate III, 42), and smaller numbers of two *Turrancilla* species and other unidentified *Olivella* species were also present.

Only 17% of the shells of Olividae were drilled, well below the average of 31% for all gastropod families. Naticids accounted for 82% of the boreholes, as would be expected from the sand habitat of the family. Only one hole was incomplete, and it was in a shell that was also drilled completely. *Oliva sidelia* was drilled much more frequently (27/111) than *O. mustelina* (2/57). Of the 30 specimens of *Olivella* and *Turrancilla*, 4 were drilled, 3 by naticids and one by a muricid. The shell of *Oliva* is quite thick, and because the reflected parapodia secrete additional shell material on the outside, scars indicating

unsuccessful attempted predation by shell breakage may not be detectable. In any case, none of the *Oliva* specimens and only two of other genera had repair scars indicating that they had withstood predation attempts. On the other hand, three specimens of *O. sidelia* appeared to have suffered lethal damage by crabs, probably *Calappa*.

Family HARPIDAE

Harpidae is a small family of mainly large gastropods having rather thin, ventricose shells with a large last whorl, short spire and usually prominent axial ribs but little spiral sculpture. The family contains 18 extant species in two genera, *Harpa* and *Austroharpa*. Except for one Panamic and one West African species, all occur in the tropical Indo-Pacific region (Rehder, 1973; Boss, 1982). The earliest fossil records of the family are Paleocene. Harpids burrow completely in sand, often on coral reefs, during the day, and emerge on the surface at night. They are unusual among neogastropods in preying primarily on crustaceans, both crabs and shrimps (Rehder, 1973).

Our sample contained at least three species of *Harpa*; all are extant and occur in Fiji today. Most of the ten specimens recovered were fragmentary, however, and not identifiable to species.

Family MITRIDAE

The family Mitridae, of Late Cretaceous origin, contains more than 800 species, most in tropical seas and a few in temperate regions. Many species occur intertidally and in shallow subtidal habitats, either buried in clean sand or on the undersides of rocks and coral boulders and in cracks and crevices on reefs. "A small minority live beyond the littoral zone to a depth of 1465 m" (Cernohorsky, 1970). Sand dwelling species may bury deeply, becoming active at the surface at the turn of the tide and at night (Cernohorsky, 1970). Mitrids are specialized predators; as far as is known all species prey exclusively on sipunculans (Kohn, 1975; West, 1990, 1991; Taylor, 1984, 1986, 1993; Kohn et al., 1997), although Cernohorsky (1970) states that sand-dwelling species are attracted to carrion. According to Cernohorsky (1970, 1976), predation on species of Mitridae is fairly frequent, and naticids and muricids are the main predators. In addition, Cernohorsky (1976) stated that members of the Bursidae and Cy-

matiidae will attack mitrids; their predation methods leave no marks on the shells of gastropods.

The stratigraphic range of Mitridae is Upper Cretaceous–Recent. In number of species mitrids typically comprise 3–5% of predatory gastropod assemblages of Senonian (Campanian–Maastrichtian), Eocene and Miocene epochs (Taylor et al., 1980).

Mitridae was the tenth most abundant family in numbers of both individuals and species. All but four of the 73 specimens belonged to the subfamily Imbricariinae. The others were in the nominal subfamily Mitrinae (3) and the Cylindromitrinae (1). By far the commonest in our sample was the species generally known as *Cancilla interlirata* (Plate III, 43, 44), but tentatively placed in *Ziba* by Cernohorsky (1991) pending study of the radula. It accounted for nearly 70% of all mitrids. This species ranges through the entire Indo-Pacific region except for Hawaii, and occurs in depths of 4–340 m. Its fossil record ranges from Middle Miocene to Pleistocene in Indonesia, Late Miocene to Pleistocene in Philippines, and Pliocene fossils are known from India, Okinawa, and Taiwan (Robba et al., 1989; Cernohorsky, 1991).

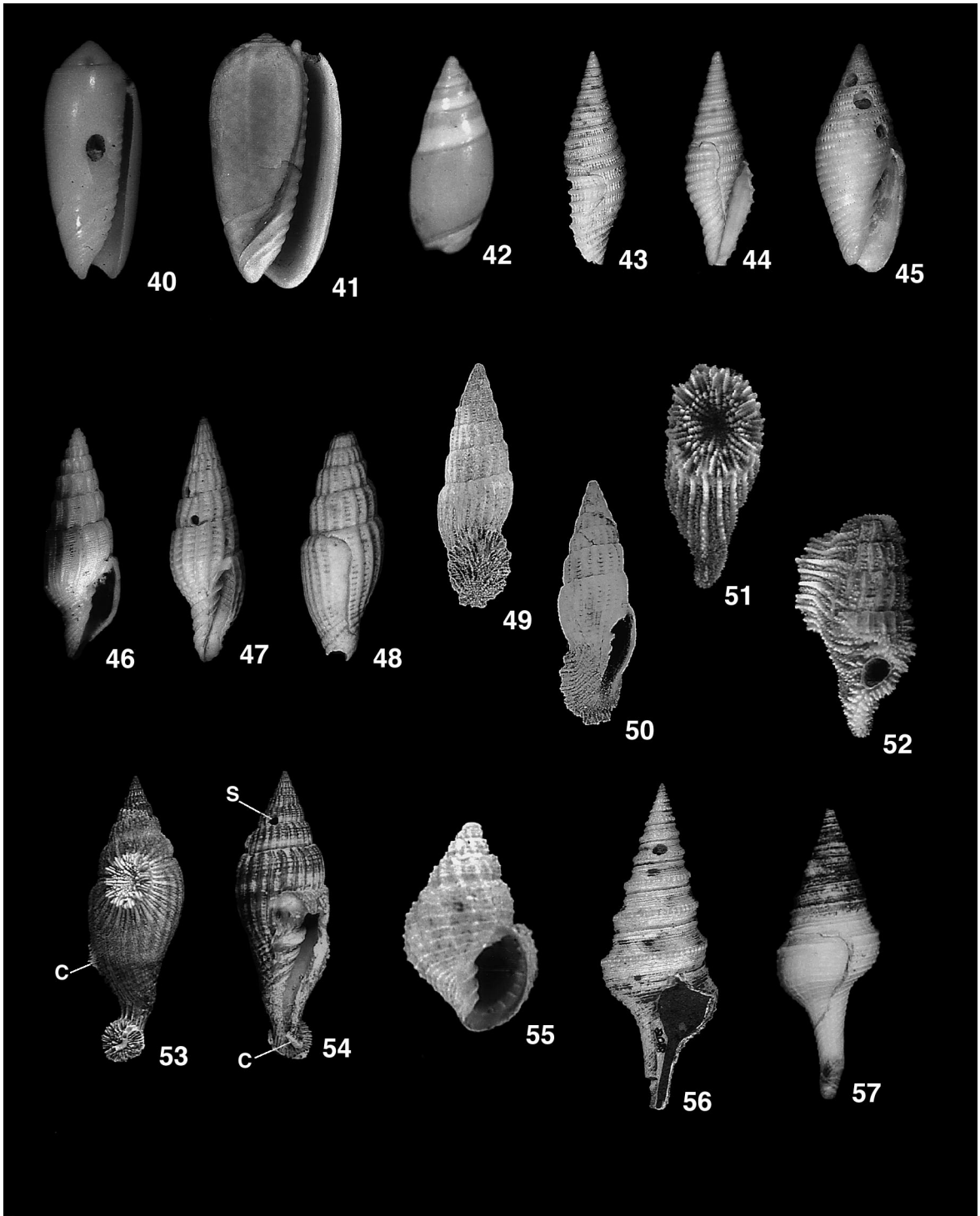
More than 40% of the mitrid shells had been drilled, and several shells had more than one complete hole. Drilling was most frequent in the second commonest species, *Ziba bacillum*, with nine holes in six of the eight shells (Plate III, 45). Of the 50 *Z. interlirata* shells, 23 contained 28 holes, three-fourths of them by naticids. Overall, the frequency was 0.63 boreholes per shell. The number of repair scars indicating unsuccessful predation attempts was also high in the Mitridae, especially in *Z. bacillum*, with an average 1.5 scars per shell. *Z. interlirata* averaged 0.3 scar per shell (Plate III, 44), and among all mitrids the average was 0.7 per shell.

Family COSTELLARIIDAE

The family now known as Costellariidae (Ponder and Warén, 1988) has more often been cited as the Vexillidae or as a subfamily of Mitridae. Like the latter family, its members are "predominantly sand dwellers, but a small percentage of species inhabit the undersides of rocks and coral boulders and crevices of coral reefs" and range to a depth of 924 m (Cernohorsky, 1970). The earliest record of the family is Upper Cretaceous.

The principal genera are *Vexillum*, *Thala*, and

PLATE III



Pusia; they occur in subtropical and tropical regions. The stratigraphic range of the family is Eocene–Recent (Cernohorsky, 1970). Although rather little information is available, costellariids appear to prey mainly on other gastropods. Taylor (1986) recovered remains of the opisthobranch *Alys cylindricus* and no other prey from the guts of two *Vexillum* species from Guam, and four *A. cylindricus* and one polychaete belonging to each of four families were recorded from a third species. *Pusia* and *Thala* are known to prey on prosobranchs (Maes and Ræihle, 1975; Taylor, 1984).

Costellariidae was the ninth commonest family in our samples and the sixth most diverse with at least 11 species, all of *Vexillum*. The commonest, *V. gembacanum* (Plate III, 46) and *V. obeliscus* (Plate III, 47, 48), comprised 45 and 26% of the 80 specimens. The latter species is known from Upper Miocene to Pleistocene in Philippines and Indonesia (Robba et al., 1989) and still lives in Fijian waters, while *V. gembacanum* was described from the Miocene of Java (Martin, 1883–1887).

We know of no prior information on predation on costellariids. More than half (41) of the intact shells were drilled (76% of *V. obeliscus* and 50% of *V. sp. cf. V. gembacanum*), and 11 of these had more than one hole. On average each shell was drilled once.

Remarkably, the maximum number of holes per shell was 5 (Plate III, 47), and multiple drillings accounted for nearly two-thirds of all drill holes (Table 5). As in other families, naticids accounted for the majority of drillholes.

Repair scars from attempted durophagous predation were also common, averaging 0.87 per *Vexillum* shell. *V. obeliscus* repaired damaged shells more frequently than *V. sp. cf. V. radix* (1.2 vs. 0.6/shell). One shell of the former species had six and another had five repair scars. For all *Vexillum* species, half of the scars were on shells that had repaired more than once (Table 8). Two specimens of *V. gembacanum* and one of *V. obeliscus* appeared to have suffered lethal damage by *Calappa* crabs. The outer lips of most other specimens were broken and not repaired, but it is difficult to determine whether this was due to predation or occurred post mortem.

After death, shells of *Vexillum* spp. are sometimes occupied by a ‘hermit’ sipunculan, probably *Aspidosiphon muelleri* Diesing, and solitary corals often colonize the dorsal surface of such shells (Zann, 1980; Hoeksema and Best, 1991; Cutler, 1994). One fossil shell of *V. obeliscus* bore a single coral at the anterior end (Plate III, 49, 50). The aperture was partly filled with sediment, but the hole occupied by the sipunculan was clearly visible (Plate III, 50).

PLATE III

40. *Oliva sidelia*, showing naticid borehole. Loc. 16. SL = 14 mm.
41. *Oliva mustelina*. Loc. 16. SL = 27 mm.
42. *Olivella apicalis*. Loc. 17. SL = 6 mm.
- 43, 44. *Ziba interlirata*. Two views of same specimen showing repair scars. Loc. 16. SL = 11 mm.
45. *Ziba bacillum*, showing multiple boreholes. Loc. 16. SL = 17 mm.
46. *Vexillum gembacanum*. Loc. 16. SL = 13 mm.
47. *Vexillum obeliscus*, showing two of the five boreholes present in the shell. Loc. 16. SL = 24 mm.
48. *Vexillum obeliscus*, showing repair scar. Loc. 16. SL = 18 mm.
- 49, 50. *Vexillum obeliscus* with the solitary coral *Heterocyathus sulcatus* (Verrill). The ventral view (50) shows infilling of aperture and circular opening of burrow (asterisk) likely occupied by a sipunculan. Loc. 24. SL = 15 mm.
- 51, 52. Modern *Vexillum* sp. shell with *Heterocyathus sulcatus* (Verrill). The coral has covered all of the shell aperture except the circular opening of the burrow occupied by a sipunculan, probably *Aspidosiphon muelleri* Diesing. Laucala Bay, Sta. 3, 25 m. SL = 15 mm.
- 53, 54. Recent *Vexillum curviliratum* shell, probably killed by a crab that inflicted lethal damage on the shell (arrowhead). The large specimen of *Heterocyathus sulcatus* (Verrill) on the dorsal surface was alive when collected, the anterior coral was not. Remains of two smaller corals are also present on the shell (c). The hole labeled (s) is one of a pair, the other out of sight to the left, probably the opening of a spionid polychaete that lived in the apical whorls of the shell. It and the presumed sipunculan occupant in the aperture were not recovered. Laucala Bay, Sta. 3, 25 m. SL = 39 mm.
55. *Cancellaria atopodonta*. Loc. 19. SL = 8 mm.
56. *Gemmula speciosa*. Loc. 24. SL = 60 mm.
57. *Gemmula unedo*, showing repair scar. Loc. 16. SL = 42 mm.

The coral is not well preserved but appears to be *Heterocyathus sulcata* (Verrill). This species occurs on Recent *Vexillum* shells in Laucala Bay in 15–25 m (Plate III, 51–54). The one specimen of *V. angustissima* lacked a coral but its aperture contained solidified sediment with an opening that likely indicates the opening of a sipunculan burrow.

Family CANCELLARIIDAE

Although represented by only two species in our sample, this family is noteworthy because the three intact specimens agree in all aspects of shell morphology with a recently described extant species from Philippines, *Cancellaria atopodonta* (Petit and Harasewych, 1986) (Plate III, 55). This species had no prior known fossil record, although Petit and Harasewych (1986) note its close resemblance to a Japanese Pliocene species reported as “*Cancellaria reevei laticostata* (Löbbecke)” by Shuto (1962). Petit and Harasewych (1986) interpreted the unusual (“nematoglossan”) radula of *C. atopodonta* as functioning to penetrate the tissues of prey or the egg capsules of gastropods or cephalopods, enabling suctorial feeding. Subsequently O’Sullivan et al. (1987) demonstrated that at least one species of *Cancellaria* parasitizes sleeping torpedo rays by sucking their blood.

Family TURRIDAE

Richer in species and genera than any other gastropod family in modern seas, the Turridae as traditionally considered is also the oldest of extant neogastropod families. Despite its remarkable evolutionary radiations, phylogenetic patterns in the family have only recently begun to be subjected to analysis (Taylor et al., 1993). The earliest fossil turrids are from the mid-Cretaceous, about 100 million years ago (Powell, 1966). Because of its vast size, the family is usually divided into subfamilies, although most authors recognize that these do not pretend to be phylogenetically informative. Powell (1966) recognized 9 subfamilies. McLean (1971) expanded this to 15, based primarily on radular characters. Kilburn (1983, 1985, 1986, 1988, 1991, 1992, 1993, 1994, 1995) followed Powell’s scheme; other recent treatments have generally been between these extremes, e.g. 12 in Ponder and Warén (1988). The traditional scheme is followed here, although in the most recent revision, Taylor et al. (1993) divide

the Superfamily Conoidea into six families, Drillidae, Pseudomelatominae, Strictispiridae, Turridae, Conidae, and Terebridae. The traditional family Turridae comprises the first four of these as well as six of the seven subfamilies in their family Conidae (Clathurellinae, Conorbinae, Oenopotinae, Mangeliinae, Daphnellinae, and Taraninae. Kilburn (1995) adopted this classification.

The Family Turridae is diverse in all seas. The shells vary widely in size, shape and sculpture but are usually fusiform and share the common feature of an anal slit or sinus on the outer lip, located between the suture and the periphery of the last whorl. Length of the anterior siphonal canal varies widely among different taxa and probably is a reasonably good indicator of substrate preference, species with short siphonal canals (the “clavine facies” of Kilburn, 1988) occupying hard substrates, often under rocks, and those with long siphonal canals (Kilburn’s “turrine facies”) burrowing through sand, usually in deeper water.

Northern hemisphere turrids are predators primarily on polychaetes (Shimek, 1983). Maes (1983) found sipunculan and polychaete remains in the alimentary tracts of several Caribbean turrids, and Taylor (1985) identified 17 species of polychaetes as prey of *Turricula nelliae* in Hong Kong, and Miller (1990) described the feeding mechanism. Most tropical species probably have similar feeding habits, but very little other information exists.

In abundance the Turridae ranked second in our samples only to the Buccinidae (s.l.); both Turridae and Nassariinae were represented by 500 specimens, each accounting for 18% of all gastropods. The formidable taxonomic difficulties surrounding the Turridae render an estimate of the number of taxa difficult, but at least 23 genera and more than 43 species are certainly present. Of the 24 at least tentatively determined species, 15 are extant and 9 of the latter occur in Fijian waters at present.

The Subfamily Turrinae accounted for nearly 60% (292/500) of all turrid specimens, and 91% of these belonged to the genus *Gemmula*. Species in this genus are notoriously difficult to determine, and as Weinkauff stated more than a century ago, “die ganze Gruppe ist indess äusserst verwandt zusammen” (Weinkauff, 1875). Fortunately in most of our specimens sufficient shell pigments persist that can-

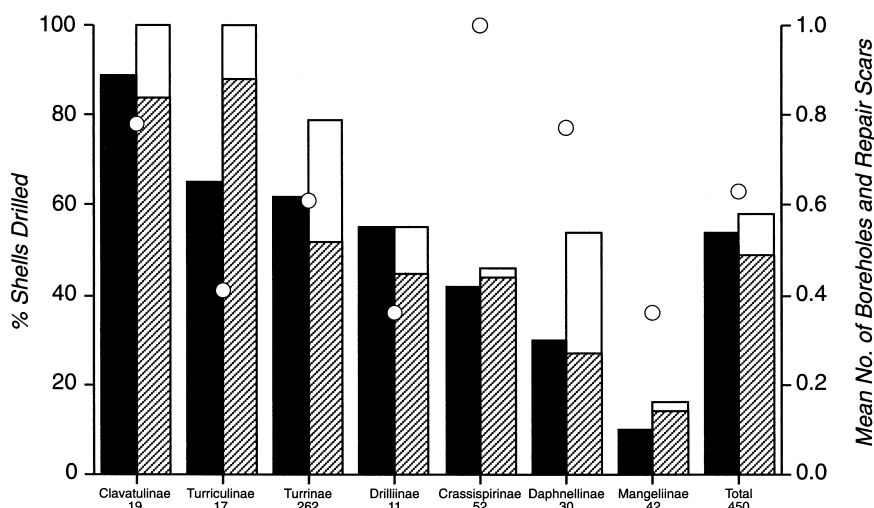


Fig. 1. Intensity of drilling predation on turrid gastropods in the Nakasi Beds. The data are arranged by subfamily in order of frequency of shells drilled by Naticidae and Muricidae, followed by data for all Turridae. Solid histograms indicate per cent of shells with at least one complete borehole (left scale). Hatched histograms indicate mean number of naticid boreholes/shell, and stippled histograms indicate mean number of muricid boreholes/shell (right scale). Circles indicate mean number of repair scars/shell (right scale). Numbers of intact and nearly intact shells examined are shown below subfamily names.

not be seen in visible light but fluoresce yellow under ultraviolet radiation. This character was used in the initial couplet of a preliminary key to *Gemmula* species likely to occur in the Fiji Pleistocene (appendix A, **Online Background Dataset**⁴), based partly on Kilburn's (1983) key to South African *Gemmula* species. The commonest species were *G. speciosa* (Plate III, 56) (41% of Turrinae), and *G. (Unedogemmula) unedo* (Plate III, 57) (15%). Most specimens were less than 50 mm long; the largest found was a *G. (Unedogemmula) unedo* 90 mm long, and the largest *G. speciosa* (Plate III, 56) was 60 mm long, both from Loc. 24. All seven of the identified species of Turrinae recovered are extant, but only three of these occur in Fiji at present. *Gemmula speciosa* is extant but today occurs from the Moluccas westward, and *G. (Unedogemmula) unedo* is now distributed from Japan and Philippines to the Moluccas.

The Crassispirinae, represented mostly by *Inquisitor* sp. cf. *I. angustus* (50% of crassispirines, 6% of all turrids), was the second commonest subfamily (11%), followed by Mangeliinae (9%) and Daphnel-

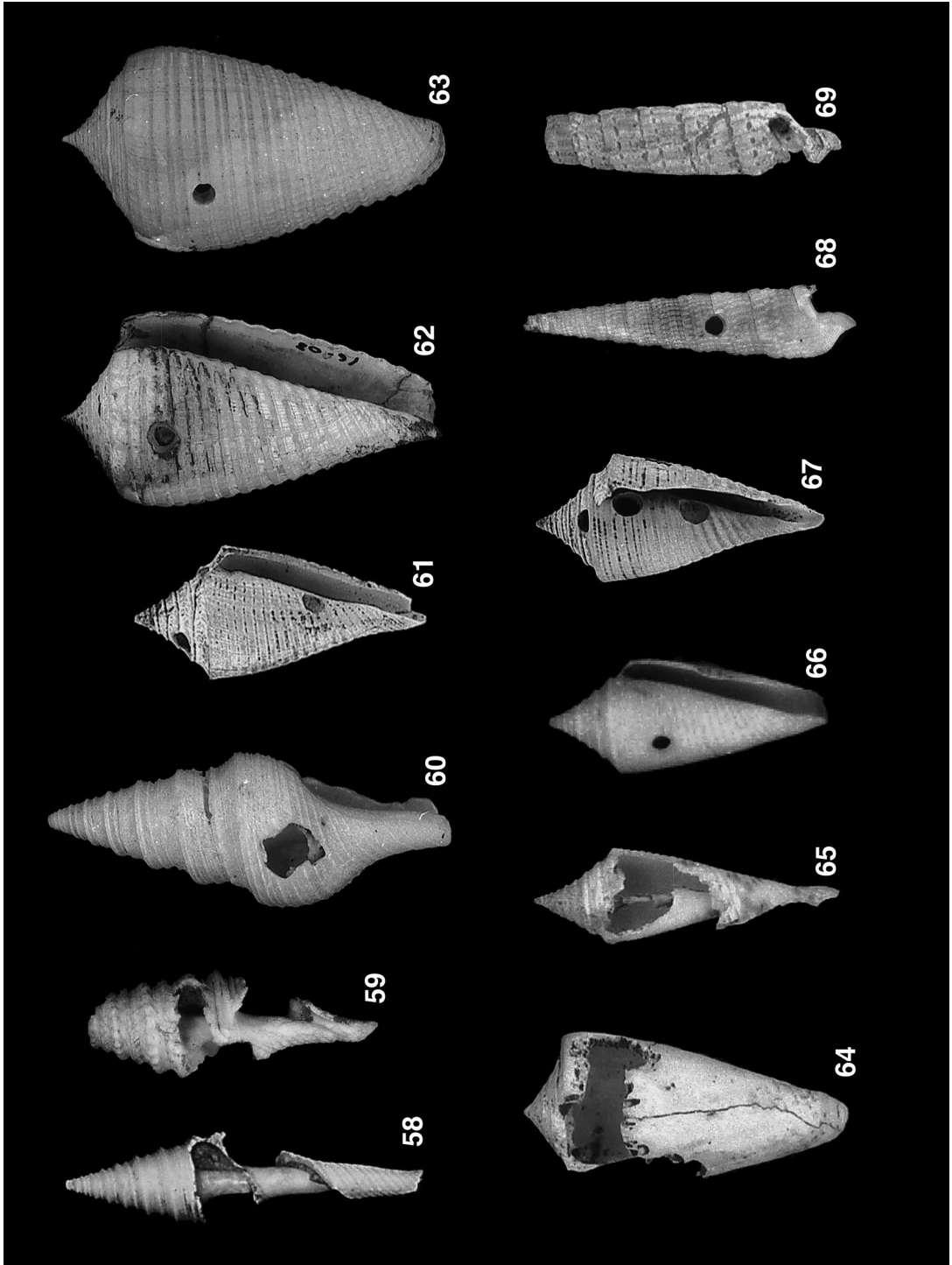
linae (6%). The Turriculinae, Clavatulinae and Drilliinae each comprised less than 5% of the sample.

About 85% of turrid individuals in the sample belong to taxa with plesiomorphic, 'non-toxoglossate' radulas. The only taxa known to have apomorphic, harpoon-like radular teeth were the subfamilies Mangeliinae (44 individuals of at least 12 species in 6 genera) and Daphnellinae (30 individuals of at least 4 species in 3 genera).

Drilling predation on turrids was intense, and 96% of boreholes were complete, indicating successful predation. In all, 54% of turrid shells were drilled, with an average of 0.7 hole per shell (Table 4; Plate III, 56). Except for *Paradrillia* sp. cf. *P. kakegawaensis*, in which all but two of the 19 specimens were drilled, and the Turriculinae in which 11 of 17 shells had 17 boreholes, *Gemmula* suffered the most intense drilling predation (65% of shells drilled; mean of 0.8 boreholes/shell). In the remaining subfamilies, the incidence of drilling predation ranged from 0.2 to 0.6 hole/shell (Fig. 1). Multiple boreholes were most frequent in *Gemmula* (20 specimens drilled twice, 3 specimens with 3 and holes and 2 with 4 holes), Daphnellinae (2 specimens each with 2 and 3 holes), and *Paradrillia* (2 specimens with 3 holes each). One *Eucithara vittata* was drilled

⁴ URL: <http://www.elsevier.nl/locate/palaeo>; mirror site: <http://www.elsevier.com/locate/palaeo>.

PLATE IV



four times. In all 17% of drilled turrid shells had multiple boreholes.

Nearly three-fourths (219/309) of all successful boreholes were caused by naticids, the rest by muricids, except for three of undetermined origin. The proportions differed little among subfamilies, with the exceptions that half of the daphnellids were drilled by predators of each family, and there were few muricid holes in shells of Crassispirinae and Mangeliinae. The substrate preferences of taxa in the clavine and turrine facies mentioned above suggest the hypothesis that the former should be subject to a higher frequency of predation by muricids relative to naticids than the latter. Analysis of the data summarized in Fig. 1, however, shows no statistical difference between the two groups ($G = 2.08$; $P \gg 0.1$; turrine facies including Turrinae, Turriculinae and Clavatulinae; clavine facies including Drilliinae, Crassispirinae, Mangeliinae and Daphnellinae).

Ten specimens (8 belonging to Turrinae and 7 to *Gemmula* spp.) bore evidence of successful predation by crabs, probably mainly *Calappa* (Plate IV, 58, 59), and one specimen may have been preyed on by *Gonodactylus* or a similar stomatopod (Geary et al., 1991) (Plate IV, 60). The average number of unsuccessful predation attempts, indicated by repair scars per shell, was 0.63/shell among all turrids, and as in the case of boreholes little difference between subfamilies representing the turrine (0.58) and clavine (0.70) facies was evident (Fig. 1).

Family CONIDAE

The family Conidae contains more than 500 recent species, almost all in the genus *Conus*, the

largest genus of marine gastropods. Homogeneous in form with usually smooth, conical or biconical shells with a long, narrow aperture, the family is contrastingly diverse ecologically. Primarily tropically distributed, more than half of the species occur in the Indo-Pacific region, but outlying representatives extend to the Mediterranean Sea, on the American coasts to about 35°N, and to 40°S in Tasmania. To our knowledge, all species are predatory. Tropical species tend to have specialized diets, consisting mainly of polychaete annelids. Hemichordate and echiuran worms, prosobranch and opisthobranch gastropods, and fishes are also consumed. In the Indo-Pacific tropics, most *Conus* species inhabit coral reef-associated habitats, attaining highest diversity on subtidal reef platforms (Kohn and Nybakken, 1975; Kohn, 1983a). Other species occupy deeper soft-bottom habitats, some to depths of several hundred meters (Röckel et al., 1995).

Conus originated in the Early Eocene, but the stratigraphic range of the genus in the Indo-Pacific is Upper Eocene to recent. Kohn (1990) traced the historical patterns of diversification in the genus.

Our sample consisted of 120 specimens and more than 50 shell fragments, representing 23 identified species and probably several others among the 14 undetermined specimens. All of the identified species are extant, and 11 of them occur in Fijian waters at present. *Conus eugrammatus* (Plate IV, 61), an extant species that presently occurs only as far east as Queensland in the southern hemisphere, was the commonest species, comprising 17% of the sample. *Conus sulcatus* (Plate IV, 62, 63) extant in Fiji (15%), *C. comatosa* (14%), and *C. orbignyi* (10%),

PLATE IV

58. *Gemmula unedo*, showing probably fatal *Calappa* damage. Loc. 16. SL = 35 mm.
59. *Gemmula speciosa*, showing probably fatal *Calappa* damage. Loc. 16. SL = 15 mm.
60. *Gemmula unedo*, showing probable hole from gonodactyloid stomatopod. Loc. 16. SL = 49 mm.
61. *Conus eugrammatus*, with two muricid boreholes. Loc. 16. SL = 16 mm.
62. *Conus sulcatus*, with naticid borehole. Loc. 16. SL = 35 mm.
63. *Conus sulcatus*, with muricid borehole. Loc. 19. SL = 36 mm.
64. *Conus* sp., showing probable fatal damage from *Calappa*. Loc. 17. SL = 26 mm.
65. Recent *Conus saecularis* from Momi, Viti Levu, Fiji, showing probable fatal damage from *Calappa*. SL = 23 mm.
66. *Conus saecularis*, with naticid borehole. Loc. 16. SL = 12 mm.
67. *Conus eugrammatus*, showing one incomplete and two complete boreholes, at least one of the latter likely drilled after the gastropod's death (see text).
68. *Terebra fenestrata*, with muricid borehole. Loc. 16. SL = 33 mm.
69. *Terebra textilis*, showing repair scar and probably fatal *Calappa* damage. Loc. 19. Estimated SL 15–20 mm.

not known east of New Caledonia, were next in abundance. All other species were uncommon.

Of the common species *C. eugrammatus* had the highest frequency of repair scars (1.0). Over all species the mean frequency was 0.6, considerably higher than the values for reef and shallow sand-dwelling *Conus* species from Guam and Philippines reported by Vermeij (1982: 0–0.35). One shell (Plate IV, 64), unidentified to species, appeared to have been lethally attacked by *Calappa*. Plate IV, 65 illustrates a recent specimen of *C. saecularis* from Fiji apparently eaten by *Calappa*, and Plate IV, 66 shows a fossil *C. saecularis* for comparison. *Conus eugrammatus* and *C. sulcatus* were most frequently subject to drilling predation. Nine of the 18 *C. sulcatus* specimens were drilled, seven by naticids and two by muricids; each had one hole. In addition, four shells had incomplete boreholes. Six of the 20 *C. eugrammatus* shells were drilled, one with two holes and one with three complete as well as an incomplete one. The positions of one complete and the incomplete hole within the broken outer lip (Plate IV, 67) suggest that the shell was drilled after death of the *Conus*, perhaps when it was occupied by a hermit crab. Muricids accounted for most of the holes in *C. eugrammatus*, while naticid holes predominated in the other *Conus* species. In all, one-third of all *Conus* shells (37) were drilled, with a total of 42 complete and 8 incomplete holes. This is a higher ratio (0.2) of incomplete to complete boreholes than in other families. Naticids drilled 74% of the holes.

Family TEREBRIDAE

Members of the family Terebridae have elongate, narrow, multiwhorled shells with a relatively small last whorl and aperture. They mainly burrow in broad expanses of sand in shallow water, where they prey on polychaetes and enteropneusts. The maximum depth record for the family is 260 m (Bratcher and Cernohorsky, 1987). Like the Conidae, terebrids probably evolved from turrid ancestors during the Eocene epoch.

All but a few of the more than 250 Recent terebrid species occur in tropical regions, most in the Indo-Pacific region. They are usually grouped in the three genera *Terebra*, *Duplicaria* and *Hastula*. Only the first two genera were represented in our sample,

and *Terebra* accounted for 39 of the 43 specimens (including fragments) and all but one of the 8 or more species present. All 8 identified species (based on Bratcher and Cernohorsky, 1987) are extant, and 6 of them occur in Fijian waters today. Many of the specimens were rather worn, and it is possible that these had been transported downward from shallower habitats by hermit crabs and sipunculans. *Terebra fenestrata* (Plate IV, 68) and *T. textilis* (Plate IV, 69) were the commonest species, accounting for 33 and 23% of the sample, respectively.

The rather high incidence of repair scars (average of 0.8/shell) is not unexpected, because *Terebra* shells are tightly coiled with many elongate whorls, a shell form that is known to enable successful defense against predators that peel the shell lip (Vermeij et al., 1980). These authors reported frequencies for recent Indo-Pacific terebrids of 20–29 mm and 30–49 mm, similar to the size range in our sample, of 0.6 and 0.9, respectively. Their smaller samples of Pliocene and Pleistocene shells had repair frequencies of 0.4–0.6. Two *Terebra* shells bore the characteristic marks of successful predation by calappid crabs. The results of Vermeij's (1982) experimental data on *Calappa* presented with terebrids of different sizes suggest that the smaller, a *T. textilis* estimated to have been 15–20 mm long (Plate IV, 69), was eaten by a *Calappa* about 40 mm in carapace width. The other specimen, a *Duplicaria duplicaria* probably originally about 35 mm long, was likely eaten by a much larger crab.

Half of the shells (18/35) were drilled; one had three complete boreholes. This contrasts with the much lower rates (10–20%) reported for living and fossil terebrids by Vermeij et al. (1980). Surprisingly, most (14/19) of the holes appeared to have been drilled by muricids (Plate IV, 68), but the worn condition of some shells made attribution difficult. Vermeij et al. (1980) reported that up to 40% of drilling attempts were unsuccessful in Indo-Pacific terebrids, but we found no incomplete boreholes in our specimens.

Subclass HETEROBRANCHIA

Family PYRAMIDELLIDAE

We follow the scheme of Ponder and Warén (1988) in assigning this family to the Order Het-

erostropha of the Subclass Heterobranchia. Pyramidellids are generally small, with elongate, sometimes terebriform, either smooth or sculptured whorls and usually 1–3 columellar folds. The animals live as ectoparasites on a variety of hosts, mainly other molluscs and polychaetes.

The family is represented in our sample by 29 specimens belonging to four genera and at least nine species. The largest were *Otopleura* sp. 19 mm long and *Synola brunnea* 12 mm long, but most shells were 5 mm long or less. It was not possible to determine the rest of the specimens to species, but *Turbonilla*, with 10 specimens of at least three species, was the commonest genus. *Pyramidella* had a high incidence of repair scars (6 on the 5 shells); overall the frequency was 0.4/shell. Ten shells were drilled, and five had multiple holes. One shell had four complete holes; another had two repair scars and one incomplete and one complete hole. Muricids drilled nine and naticids eight of the 17 boreholes.

Family ACTEONIDAE

Usually classified in the Opisthobranchia, this family was reassigned to the Heterobranchia in Mikkelsen's (1996) phylogenetic analysis. Acteonids have solid, ovate or pupiform shells usually with spiral sculpture, and opercula. Their fossil record extends back to the Jurassic (Mikkelsen, 1996). Acteonids occur on soft substrates at depths from the shore down to about 100 m and are predators on cirratulid and sabellid polychaetes (Hurst, 1965; Rudman, 1972). Only 10 specimens, all of *Acteon* aff. *A. teramachii* and *Acteon* sp. occurred in our sample. Two shells were drilled, both by naticids, and only one had a repair scar.

Subclass OPISTHOBRANCHIA

Family RINGICULIDAE

This is a monogeneric family of small opisthobranchs with rounded external shells, usually occurring in muddy sand. Usually considered members of the Order Cephalaspidea, the first phylogenetic analysis of this group suggests that they are basal to it (Mikkelsen, 1996). The fossil record of the family extends back to the Lower Cretaceous (Mikkelsen, 1996). Our sample of 21 specimens includes at least two species, both unidentified. Three shells had re-

pair scars and four were drilled, two each by naticids and muricids.

Family HAMINOEIDAE

The shells of this family are inflated and fragile, external or internal. They range in depth from intertidal to more than 3000 m and geologically from Upper Cretaceous to Recent. Shallow-water species are herbivores or detritivores. The 11 specimens in our sample probably represent four species, most in the largest tropical genus *Atys* but none were determined to species. None were drilled, and only one had a repair scar.

Family SCAPHANDRIDAE

Members of the Scaphandridae also range greatly in depth, from intertidal to more than 2000 m. Their shells are elongate-ovate to cylindrical usually with a sunken spire and involute or projecting apex. Scaphandrids also occur mainly in muddy sand, where they prey on foraminiferans and other molluscs. The sample contained only 10 specimens, representing the genera *Scaphander* and *Cylichna*. One was drilled by a naticid and two had repair scars.

4. Palaeobiodiversity

One cannot assume from the composition of a fossil assemblage that the most abundant species also predominated in the original fauna. Some shells do not fossilize well and may disappear, shells may be washed in to sedimenting environments from other habitats, and taphonomic processes may otherwise alter the assemblage. However, the hypothesis that a fossil assemblage is the in-place residue of the original biotic community is subject to several tests. This hypothesis is supported if replicate samples resemble each other in species composition and abundance, if the species present are known to inhabit substrates like the matrix in which the shells are preserved, if the extant species in the fossil assemblage share a common depth distribution, and if the shells are well-preserved rather than being worn and broken (Ogasawara, 1977; Bennington and Bambach, 1996). This section addresses these tests to the extent permitted by our material.

Table 1
Order-level taxonomic composition of Nakasi Beds gastropods

| Subclass and order | QRS | | Total | | No. of families | No. of genera | No. of species | No. extant/ total No. species. | No. extant in Fiji/ total No. extant |
|-----------------------|-------------------|-----|-------------------|-----|-----------------|---------------|----------------|-----------------------------------|---|
| | Ind. | % | Ind. | % | | | | | |
| <i>Prosobranchia</i> | | | | | | | | | |
| Patellogastropoda | 2 | <1 | 3 | <1 | 1 | 1 | 2 | 1/1 | 0/1 |
| Vetigastropoda | 70 | 4 | 129 | 4 | 6 | 19 | 30 | 16/21 | 11/16 |
| Neotaenioglossa | 402 | 25 | 672 | 23 | 23 | 46 | 103 | 79/84 | 52/79 |
| Neogastropoda | 1086 | 67 | 1961 | 68 | 13 | 66 | 164 | 109/129 | 71/109 |
| <i>Heterobranchia</i> | | | | | | | | | |
| Heterostropha | 21 | 1 | 56 | 2 | 4 | 9 | 15 | 5/6 | 4/5 |
| Opisthobranchia | 38 | 2 | 53 | 2 | 4 | 5 | 7 | 1/1 | 1/1 |
| Pulmonata | 1 | <1 | 1 | <1 | 1 | 1 | 1 | 1/1 | 1/1 |
| Totals | 1635 ^a | 100 | 2893 ^a | 100 | 52 | 146 | 320 | 212/243 | 140/212 |

QRS = numbers of individuals (Ind.) in quantitative random samples from locs. 16 (Saunitabu), 17 and 19 (Waila). Total = QRS + numbers of individuals in non-random samples from these locations and Loc. 24 (Tongeravu).

^a Includes unidentified specimens.

4.1. Taxonomic composition

This study focuses on gastropods because they comprised about 80% of all macrofossils in the assemblage, but bivalves were likely underestimated because many were small and fragile. At least 320 species of gastropods were present, representing 146 genera and 52 families. Neogastropods dominated the samples both by individuals (68% of all gastropods) and species (51%), followed by mesogastropods (= Order Neotaenioglossa; 23 and 32%, respectively). Neogastropods also comprised 67%, and mesogastropods, 25%, of the quantitative random samples from locs. 16, 17 and 19 (Table 1).

The most abundant gastropod family was the Buccinidae (s.l.), representing 24% of the total of 2893 gastropods examined. Most of the buccinids (524/686 or 18% of the total sample) were Nassariinae. Turridae comprised 17% of individuals but was the most diverse family with 43 species (13% of the estimated total of 320 gastropod species). The next commonest family-groups, all with fewer than 10% of the sample, were Olividae, Naticidae, Conidae and Buccininae (Table 2). These six family-groups comprised 62% of all individuals in both the quantitative random and overall samples and 38% of all species (Table 2). The proportions of the eight commonest family-groups were very similar in the overall sample and in the quantitative random samples, indicating that collecting bias in non-random sampling

affected the results minimally (Tables 1 and 2). Appendix A (**Online Background Dataset**⁵) lists the numbers of all species in the sample, and a complete listing of all lots is available via electronic mail from the senior author.

At the family level, the samples from the three most intensively sampled localities (16, 17 and 19) were similar but by no means identical in faunal composition (Fig. 2). Qualitatively, of the 60 species represented by ten or more individuals at these localities, 43 (72%) occurred at all three and only four were found at a single locality. Quantitatively, a different family-group was commonest in the quantitative random sample at each, Turridae at Loc. 16, Nassariinae at 17, and Olividae at 19. Proportional similarity values (PS_i of Kohn and Riggs, 1982) of species in the ten commonest families (those listed in Table 2) ranged from 64% (locs. 16 and 19; 17 and 19) to 68% (locs. 16 and 17).

At the species level, the dominance-diversity pattern of a molluscan fossil assemblage may suggest whether it represents a single original community. In a study comparing Recent and Upper Oligocene assemblages from northern Germany, Janssen (1981) proposed the number of most abundant species comprising 50% of individuals as a criterion of dominance. He suggested that a list containing 3–6

⁵ URL: <http://www.elsevier.nl/locate/palaeo>; mirror site: <http://www.elsevier.com/locate/palaeo>.

Table 2

The ten numerically dominant family-group taxa of Nakasi Beds gastropods in order of abundance in quantitative random samples, their species richnesses, the numbers of extant and extinct identified species, and the general family trophic positions in the community

| Family or Subfamily | QRS | % | Total | % | No. of species | % of species | No. of species extant (F)/ extant (G)/(extant + extinct) | Trophic level and prey |
|---------------------|------|-----|-------|-----|----------------|--------------|--|------------------------|
| Nassariinae | 304 | 19 | 524 | 18 | >13 | 4 | 7/8/8 | O/S |
| Turridae | 252 | 15 | 500 | 17 | >43 | 14 | 9/15/24 | P (polychaetes) |
| Olividae | 160 | 10 | 253 | 9 | 9 | 3 | 3/5/6 | P (molluscs) |
| Naticidae | 140 | 9 | 222 | 8 | >19 | 6 | 8/14/15 | P (molluscs) |
| Conidae | 84 | 5 | 178 | 6 | >23 | 7 | 11/23/23 | P (polychaetes) |
| Buccininae | 70 | 4 | 110 | 4 | 13 | 4 | 5/7/11 | P (varied) |
| Cerithiidae | 66 | 4 | 88 | 3 | 12 | 4 | 6/10/10 | D |
| Costellariidae | 53 | 3 | 80 | 3 | >9 | 3 | 4/7/9 | P (molluscs) |
| Mitridae | 46 | 3 | 79 | 3 | >11 | 3 | 8/11/11 | P (sipunculans) |
| Turritellidae | 45 | 3 | 101 | 3 | 4 | 1 | 1/1/1 | D |
| Sub-totals | 1220 | 76 | 2135 | 74 | >156 | 49 | 62/101/118 | |
| Totals | 1635 | 100 | 2893 | 100 | 319 | 100 | 140/212/243 | |

QRS = numbers of individuals in quantitative random samples from locs. 16 (Saunitabu), 17 and 19 (Waila). Totals = QRS + numbers of individuals in non-random samples from these locations and Loc. 24 (Tongeravu). Extant (F) = extant in Fiji; Extant (G) = globally extant; D = deposit feeder; O/S = omnivore/scavenger; P = predator.

species indicates a single community, while 7–13 species accounting for 50% of individuals indicates a mix of communities. In the Nakasi Beds quantitative random samples, 9–16 species account for 50% of individuals at the three intensively studied localities. However, modern tropical soft bottom communities are known to be more diverse than their temperate counterparts (Sanders, 1968), and this is likely to have been the case in the Early Pleistocene as

well. Thus this result does not provide strong evidence against the hypothesis that the Nakasi Beds assemblage represents a single community.

Recently Bennington and Bambach (1996) more precisely characterized the fossil assemblage collected from a single bed at one outcrop as a local paleocommunity, and they provided tests of relationships to the larger-scale units they termed the paleocommunity and paleocommunity type. They evaluated similarity using two measures, the coefficient of constancy (C_c) and the χ^2 test for heterogeneity. The former weights species by overall abundance in the pooled sample, thus indicating similarity of species composition between samples by both abundance and presence-absence (Table 3; Bennington and Bambach, 1996). In the present study (as in the assemblage of Pennsylvanian molluscs and brachiopods studied by Bennington and Bambach), replicate samples from the same horizon and outcrop, i.e. from the same local paleocommunity, differed markedly in species abundance distributions; all C_c values in pairs were well below 1.0 (Table 3). The χ^2 test for heterogeneity also indicated a highly significant quantitative difference in species composition between subsamples at the one location with subsamples of appropriate size (Table 3).

Lack of sufficiently large replicate samples from our three main Nakasi Beds sites precluded the tests

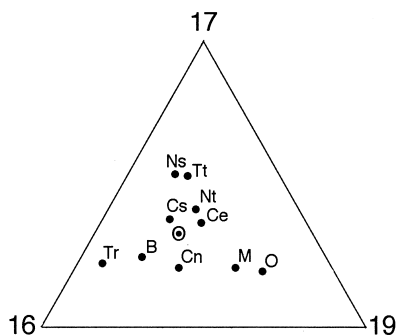


Fig. 2. Distribution of individual fossil shells of the ten commonest families in quantitative random samples at the three most intensively sampled localities (Loc. 16: $N = 508$; Loc. 17: $N = 392$; Loc. 19: $N = 320$). The circled symbol represents the entire sample. The other dots represent families and subfamilies: *B* = Buccininae; *Ce* = Cerithiidae; *Cn* = Conidae; *Cs* = Costellariidae; *M* = Mitridae; *Ns* = Nassariinae; *Nt* = Naticidae; *O* = Olividae; *Tr* = Turridae; *Tt* = Turritellidae.

Table 3

Quantitative random samples of Nakasi Beds gastropods at locations 16, 17 and 19, partitioned into subsamples collected at different times. Constancy (C_c) and heterogeneity χ^2 (Bennington and Bambach, 1996) compare species composition and abundance in replicate samples from the same horizon and outcrop

| Location | Subsample 1 | | | Subsample 2 | | | Total | | C_c | χ^2 |
|----------|-------------|-----|-----|-------------|-----|-----|-------|-----|-------|--------------------|
| | date | S | N | date | S | N | S | N | | |
| 16 | 16IV82 | 22 | 157 | 21IV82 | 14 | 48 | 27 | 205 | 0.62 | – |
| 17 | 20V82 | 48 | 287 | VI82 | 18 | 39 | 59 | 326 | 0.54 | – |
| 19 | 20V82 | 28 | 130 | VI82 | 42 | 127 | 54 | 266 | 0.83 | 59 ($P < 0.001$) |

S = number of species; N = number of specimens. $C_c = (\sum p_j k_j) / n$, where p_j = proportion of species j in the pooled sample, k_j = number of samples containing at least one specimen of species j , and n = number of subsamples. With $n = 2$, C_c varies between 0.5 and 1.0. χ^2 is calculated from the 5 commonest species at Loc. 19; sample sizes at other locations were too disparate to test for heterogeneity.

Bennington and Bambach proposed for the larger between-locality scales. However, for the overall quantitative random samples at these localities, $C_c = 0.75$ ($n = 3$ samples; $S = 79$ species), intermediate in value to those of the replicate subsamples from each locality (Table 3). For the eight commonest species (those with $N > 20$) in the samples from the three localities, the heterogeneity χ^2 was much higher ($\chi^2 = 266$; d.f. = 14; $P < 0.001$), indicating increased variability at the among-locality scale. Thus by the criteria of Bennington and Bambach (1996) the three Nakasi Beds localities would be considered similar local paleocommunities that are components of a paleocommunity type but not of a single paleocommunity.

4.2. Substrate

The single original community hypothesis would be strongly supported if all the species recovered as fossils originally inhabited a substrate like the matrix that presently preserves their shells. This is not completely the case, but extrapolating from the known substrate types of extant species and genera leads to the estimate that three-fourths of the gastropod species present with known or estimated substrate preferences (218/294) and nearly 90% of individuals (2430/2787, excluding parasitic forms), as well as 80% of the bivalves (Arcidae comprised 16%, and *Chama*, 3%, of bivalve individuals), and all of the scaphopods, lived on or in soft sediment. Overall, about 90% of the molluscs present probably occupied in life the sediment type in which they are now preserved.

Particle size analysis of the sand fraction of a sample of matrix from Loc. 16 revealed a sediment predominantly of very fine (73%) and fine (16%) sands (Fig. 3).

4.3. Depth

Precise determination of the depth at which a fossil assemblage lived is difficult, and the recommended independent methods (Brett et al., 1993) were not available in our material. We extracted most depth ranges of extant species from literature records, but most were from other geographic regions or over the entire species range and thus can provide only rough estimates. Nevertheless, they suggest that the most likely depth of the assemblage during life was 5–50 m (Fig. 4). Of the 146 species with depth records, 104 (72%) occur in this depth range; 61% occur in 5–20 m and 65% in 20–50 m, and 71% in 10–50 m. Bathymetric ranges are best known for species of *Conus*, recently reviewed by Röckel et al., (1995). Of the 23 *Conus* species present, 18 or 78% are known to occur in depths of 10–50 m. Some shells of the 23 species restricted to intertidal and shallow subtidal habitats probably washed down into the deeper, sedimenting environments. Transport by hermit crabs is another possibility; however, none of the shells bore clear evidence of having been occupied by hermit crabs, e.g. by the criteria identified by Walker (1992) for temperate zone fossil gastropod shells.

Three anomalously deep species are known only from depths exceeding 200 m. They are *Gemmula cosmoi*, known from off Japan, Taiwan, Mozambique

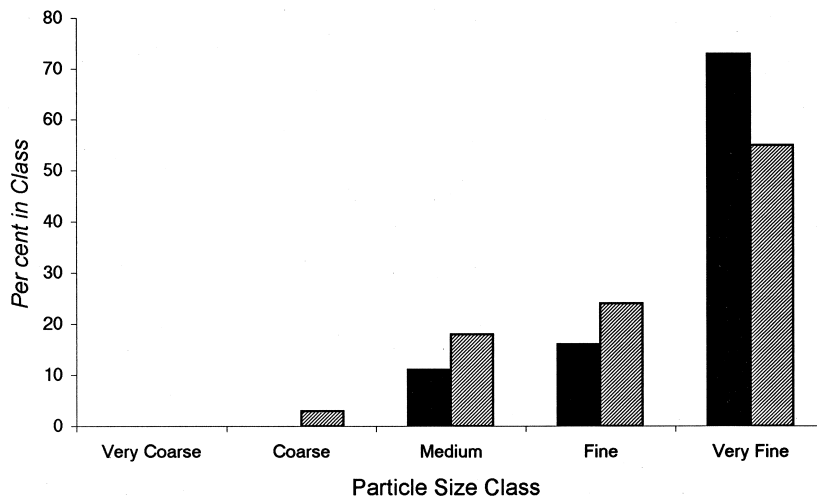


Fig. 3. Particle size distributions of the sand fractions of a dissociated matrix sample from Loc. 16, Nakasi Beds (solid histograms) and a substrate sample from Sta. 2 in Laucala Bay at a depth of 14.5 m (hatched histograms), determined by the Emery settling tube method (Emery, 1938). Each histogram represents the mean of three replicates. The Loc. 16 sample was passed through a 2-mm sieve to remove particles larger than very coarse sand, mainly gastropod shells and foraminifera. The coarse component from Sta. 2 is mainly foraminifera. Very coarse = 1–2 mm; Coarse = 0.5–1 mm; Medium = 0.25–0.5 mm; Fine = 0.125–0.25 mm; Very fine = 0.0625–0.125 mm. The median grain sizes are 0.100 mm at Loc. 16 and 0.119 mm at Sta. 2.

and Natal in 270–490 m (Kilburn, 1983), *Olivella apicalis*, known only from Hawaii in 292–700 m (Kilburn, in litt.), and *Cancellaria atopodonta*, known from Philippines in 300–510 m.

Cumulative plots of the minimum depths (from Fig. 4) of species occurring at the three most intensively collected sites (Fig. 5) show that 65–71% of the species occur in depths <20 m and 78–87% in <50 m. Moreover, the depth distributions of species occurring at the three localities did not differ significantly from one another (in all *K-S* tests, $P > 0.1$). This indicates that all three original assemblages occurred at similar depths.

4.4. Condition analysis

Analyses of preservation of surface features of shells and integrity of form and according to the criteria indicated in Section 2.3 (Ogasawara, 1977) gave generally similar results for gastropods and bivalves and among the different localities (Table 4). About half the specimens of both gastropods and bivalves were in the best preserved category according to both measures. About 90% of both gastropods and bivalves were well or very well preserved with respect to surface and sculpture, and about 80% of both

classes were well or very well preserved with respect to integrity of shell form (Table 4). In addition, a number of specimens retained traces of their original colour patterns (Plate I, 1, 2; Plate III, 41, 42). These results suggest that long-distance transport prior to preservation was not common and support the hypothesis that most were members of a community preserved in situ in a sedimenting environment. Gastropods at Loc. 19 were less well preserved than at the others with respect to both criteria (Table 4; *G* tests for independence; $P < 0.05$).

5. Community trophic structure

5.1. Functional feeding groups and food webs

As indicated in Section 3, the trophic roles of most of the gastropod families and genera, and some of the species in the Nakasi Beds assemblage are reasonably well known. However, estimating food webs of fossil assemblages is fraught with many problems, even with the benefit of direct evidence. Cadée (1984) discusses these and in particular emphasizes evidence for the opportunistic use of different feeding modes by the same species. In our study, charac-

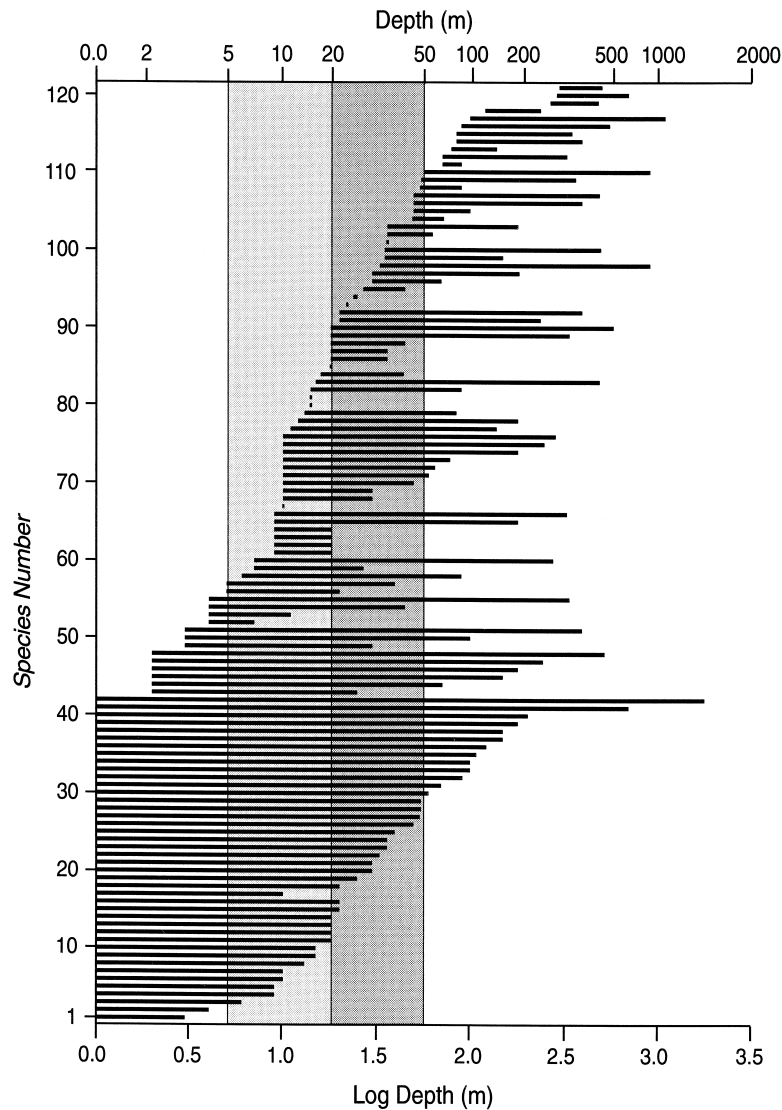


Fig. 4. Bathymetric ranges (plotted as \log_{10} m to compress the range of values) of extant gastropods from the Nakasi Beds. Each bar represents the minimum and maximum reported depths of a species, arranged from shallowest (bottom of figure) to deepest (top). $N = 121$. In addition, 25 species are known only from intertidal or shallow subtidal depths; these cannot be shown on the logarithmically scaled bars. The vertical shaded areas indicate that most species are known from 5–20 m (61%), 20–50 m (65%) and 5–50 m (72%). Literature sources of depth records are available from the first author.

terizing the numerically dominant genus *Nassarius* is especially problematic because of its omnivorous habits: “the feeding preferences of several members of this family are decidedly capricious” (Britton and Morton, 1994, p. 361; see also Cadée, 1984). Excluding *Nassarius*, most gastropods (65% of individuals and 72% of species) in the Nakasi Beds are

carnivores. Considering only families represented by 10 or more specimens in our samples, the carnivore feeding group includes the dominant Turridae and 10 other neogastropod families (and subfamilies of Buccinidae), six neotaenioglossan families (dominated by Naticidae), and three heterobranch families.

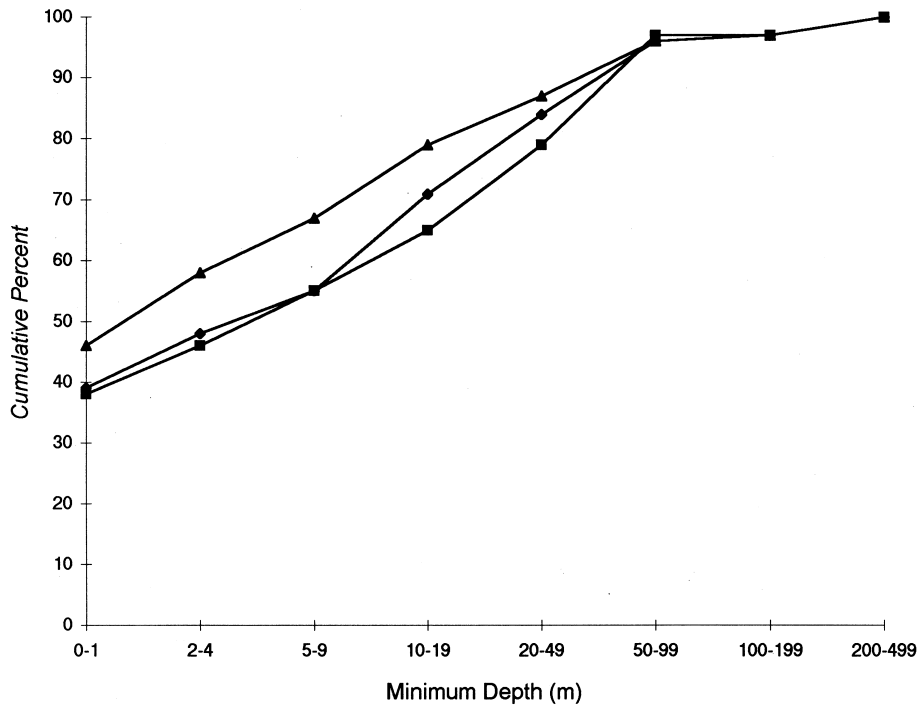


Fig. 5. Cumulative plots of minimum depths of extant gastropod species also collected as fossils in the three most intensively sampled Nakasi Beds localities. The curves do not differ significantly from one another by Kolmogorov–Smirnov tests (all $P > 0.1$). Numbers of species in samples: ◆ = Loc. 16, $N = 100$; ■ = Loc. 17, $N = 65$; ▲ = Loc. 19, $N = 76$.

Following the Nassariinae, members of the five next most abundant family-groups are carnivores. In order of abundance they are the Turridae, Olividae, Naticidae, Conidae and Buccininae. These each comprised 4–17% of both gastropod species and

individuals, and together they accounted for nearly 35% of all species and nearly half (44%) of all individuals (Table 2).

The Cerithiidae, a family of mainly deposit-feeders, ranked next in abundance in the quantitative samples, followed by the carnivorous Costellariidae and Mitridae and the deposit-feeding Turritellidae (Table 2). Fig. 6 shows the qualitative trophic relationships of these, based on diets of modern conspecifics or close relatives and on evidence of predation preserved in the fossil shells themselves. It indicates that some of the predators, particularly in the Naticidae, Muricidae and Conidae and comprising perhaps 10% of the total, are known to be tertiary consumers that prey on other carnivores, including carnivorous gastropods (see also Table 5).

Suspension and deposit feeders comprised 12% of individuals and 16% of species and included four neotaenioglossan families with $N \geq 10$, mainly Cerithiidae, Turritellidae, and the trochid subfamily Moniliinae of the Vetigastropoda, and two hetero-branch families. Families containing primarily herbi-

Table 4
Results of condition analysis of Nakasi Beds gastropod shells, by the method of Ogasawara (1977)

| Criterion | Gastropod shells at locations (%) | | | |
|------------------------------|-----------------------------------|-----|-----|-------|
| | 16 | 17 | 19 | total |
| <i>Surface and sculpture</i> | | | | |
| As in life | 53 | 51 | 35 | 48 |
| Slightly worn | 37 | 41 | 42 | 40 |
| Very worn | 10 | 8 | 23 | 12 |
| <i>Integrity</i> | | | | |
| Nearly perfect | 49 | 49 | 40 | 47 |
| Well preserved | 29 | 30 | 30 | 31 |
| Fragmentary | 22 | 21 | 24 | 22 |
| <i>N</i> | 596 | 494 | 400 | 1490 |

Table 5
Gastropod families most frequently attacked by drilling predators. Families are ordered by per cent of drilled shells

| Family-group | No. of intact shells | No. of boreholes | No. of drilled shells | % of drilled shells | No. of shells > 1 hole | No. of shells with naticid holes | No. of naticid holes | No. of muricid holes | Naticid : muricid ratio | No. of incomplete holes | % of incomplete holes | Frequency in diet (%) of | | Frequency in fossil assemblage (%) (including fragments) |
|----------------|----------------------|------------------|-----------------------|---------------------|------------------------|----------------------------------|----------------------|----------------------|-------------------------|-------------------------|-----------------------|--------------------------|-----------|--|
| | | | | | | | | | | | | Naticidae | Muricidae | |
| Turridae | 450 | 309 | 243 | 54 | 40 | 218 | 87 | 12 | 2.5:1 | 4 | 36 | 30 | 17 | |
| Cerithiidae | 87 | 53 | 46 | 53 | 6 | 34 | 18 | 1 | 1.9:1 | 2 | 5 | 7 | 3 | |
| Costellariidae | 76 | 71 | 38 | 50 | 13 | 48 | 21 | 2 | 2.3:1 | 2 | 3 | 7 | 3 | |
| Mitridae | 73 | 45 | 34 | 44 | 10 | 34 | 11 | 3 | 3.1:1 | 6 | 5 | 4 | 3 | |
| Conidae | 120 | 41 | 37 | 31 | 3 | 31 | 10 | 7 | 3.1:1 | 17 | 5 | 4 | 6 | |
| Buccinidae | 634 | 146 | 127 | 20 | 5 | 114 | 30 | 0 | 3.8:1 | 0 | 16 | 12 | 24 | |
| Naticidae | 207 | 43 | 39 | 19 | 4 | 38 | 5 | 0 | 7.6:1 | 0 | 6 | 2 | 8 | |
| Olividae | 200 | 34 | 34 | 17 | 0 | 28 | 5 | 0 | 5.6:1 | 0 | 4 | 2 | 9 | |
| All Families | 2,462 | 926 | 759 | 31 | 97 | 656 | 257 | 28 | 2.6:1 | 3 | 4 | 2 | 9 | |

vores comprised only 4% of individuals and 7.5% of species and included the Turbinidae (Vetigastropoda) and Strombidae (Neotaenioglossa). The neotaenioglossan family Rissoidae includes herbivores, deposit feeders and consumers of Foraminifera (Ponder, 1985). Because of lack of information on the species represented we divided the family evenly between the herbivore and deposit-feeding categories. Appendix A (**Online Background Dataset**⁶) indicates the general functional feeding group of each family and gives the full data summarized above.

5.2. Predator–prey interactions

Because the accretional shell growth of gastropods provides a record of the animal's entire life history, it often preserves evidence of interactions with predators that attempt to penetrate this armor. Scars on shells indicate successful resistance to a predator's attack and subsequent shell repair by the intended victim. Crushed or peeled shells and holes that completely penetrate shells often indicate successful predation and may serve to identify the perpetrators. The holes made in shells by naticid and muricid gastropods and stomatopod crustaceans provide particularly clear evidence of successful predation, and their special characters often permit identification of the predator, at least to family or genus (e.g. Arua, 1989; Arua and Hoque, 1989; Geary et al., 1991).

5.2.1. Drilling predation

The position of the Naticidae and Muricidae in Fig. 6 indicates that drilling predation was a predominant theme of community trophic relationships. All of the abundant and most of the less common families suffered: 63% of families, 53% of genera, 46% of species, and 31% of individual gastropods were drilled. Almost all boreholes in shells were complete, indicating that drilling predation is generally successful. Most (73%) of the holes indicated predation by naticids, but the presence of muricid holes in 10% of all intact gastropod shells suggests that members of this family are more important predators than the relatively small numbers of muricid shells in the sample (56, or only 2% of all gastropods)

⁶ URL: <http://www.elsevier.nl/locate/palaeo>; mirror site: <http://www.elsevier.com/locate/palaeo>.

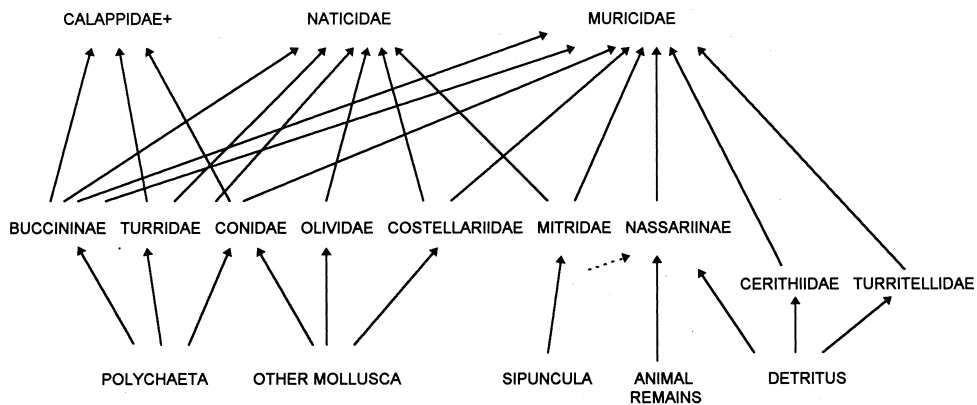


Fig. 6. Qualitative food sub-web showing trophic positions of the dominant gastropod family-groups of the Nakasi Beds assemblage. Arrows point from food to consumer. See systematic section of text for discussion of evidence for predation. + indicates other families of predatory Crustacea in addition to calappids. The dashed line leading to Nassariinae indicates that some members of this subfamily also prey on other invertebrates.

would indicate. In the five most frequently attacked families, naticids accounted for 2–3 times as many boreholes as muricids. The ratio was higher (3.8–7.6 times) in the Naticidae, Buccinidae and Olividae, and overall it was 2.6 : 1 (Table 5).

Table 5 also indicates that Naticidae and Muricidae did not drill gastropods in proportion to their abundance in the sample, suggesting that members of both families were selective predators. This is well documented in Recent representatives (Kitchell et al., 1981; Palmer, 1984). Both naticids and muricids drilled turrids more frequently than would be expected from their abundance: 54% of turrid individuals were drilled, and turrids comprised 36% of naticid and 30% of muricid diets but only 17% of the total gastropod sample (Table 5). Cerithiids and costellariids were nearly as frequently drilled (53 and 50%, respectively) but they represented only 5–9% of muricid and naticid diets. Only 17% of nassariine individuals were drilled, and despite their abundance they comprised only 11 and 7% of the diets of naticids and muricids, respectively. The fact that 17–54% of Olividae, Naticidae, Conidae, Mitridae, Costellariidae and Turridae were drilled (Table 5) documents the importance of secondary carnivores in the assemblage.

In general, shells with surface sculpture (the first four and the sixth families in Table 5) were drilled more frequently (0.47 hole/shell) than smooth shells (0.22 hole/shell), mainly because of the low frequency (17%) of drilled Olividae, the third most

abundant family. Overall only 3% of all boreholes were incomplete, with the highest frequency being 17% in the Conidae (Table 5). This suggests that drilling nearly always results in successful predation once an attack is initiated.

We also observed multiple holes in shells of 14 prosobranch families and the Pyramidellidae, an enigmatic occurrence because a single borehole typically permits successful predation. Multiple boreholes occurred in 13% of all drilled gastropod shells and accounted for 29% of all of the boreholes present (Table 6). They were most frequent in *Vexillum* (Family Costellariidae), which also had the highest observed number of holes per shell, five in five different specimens (Plate III, 47). *Vexillum* also had the highest frequency of evidence of 'hermit' sipunculans, so some multiple holes may indicate predation on subsequent inhabitants of shells after death of their gastropod builders.

5.2.2. Durophagous predation

Gastropod shells often record evidence of encounters with durophagous predators, those that overcome prey by breaking shells, peeling their outer lips, or hammering holes in them (Vermeij, 1983). Such evidence is often more ambiguous than boreholes, because other agents can break shells, especially their thin outer lips, either before or after death of the gastropod. However, certain predaceous crustaceans, particularly xanthid and calappid crabs and gonodactyloid stomatopods, break shells in charac-

Table 6

Gastropod families with most frequent occurrence (>10%) of multiple boreholes (includes only families with >10 drilled shells)

| Family-group | No. of shells with: | | | | | | % of shells with >1 hole |
|----------------|---------------------|------|-----|-----|-----|-----|--------------------------|
| | 1 h | >1 h | 2 h | 3 h | 4 h | 5 h | |
| Costellariidae | 25 | 13 | 4 | 3 | 1 | 5 | 34 |
| Mitridae | 22 | 10 | 7 | 3 | | | 31 |
| Turridae | 199 | 44 | 29 | 8 | 7 | | 18 |
| Rissoidae | 16 | 3 | 3 | | | | 16 |
| Columbellidae | 19 | 3 | 1 | 2 | | | 14 |
| Cerithiidae | 40 | 6 | 5 | 1 | | | 13 |
| Naticidae | 35 | 4 | 4 | | | | 11 |
| All families | 657 | 101 | 65 | 24 | 11 | 5 | 13 |

teristic ways and their attacks are thus recognizable with confidence (Plate I, 4, 6; Plate II, 23, 24; Plate IV, 58–60, 64, 65; Magalhaes, 1948; Shoup, 1968; Geary et al., 1991). In the fossil record, such shells provide strong evidence of the presence in the community of predators that do not fossilize well themselves and thus would not be otherwise detected (see Fig. 6).

In this study, we recognized 21 cases of probably fatal predation by calappid crabs (Table 7). They thus occurred in about 1% of all shells, and all localities were represented. Ten of the attacks were on turrids and seven of these on *Gemmula* spp. Costellariidae and Terebridae were the only other families with more than one successful calappid attack. One *Rhinoclavis sordidula* (Plate I, 4) apparently survived a calappid attack and repaired its shell. Four of the five likely cases of attacks by the stomatopod *Gonodactylus* were on Ranellidae (Plate II, 23, 24). All of these were apparently successful; only one case of shell repair following a *Gonodactylus* attack is known (Kohn, 1992b).

The success rate of other durophagous predators is difficult to determine. However, gastropods often are able to survive attacks by durophagous predators, especially if the crab is able to peel only the thin outer portion of the lip but not the thickened part within. The gastropod later repairs the broken outer lip but preserves a memory of the encounter as an irregular repair scar. Assuming such scars (e.g., Plate I, 4, 10; Plate II, 21; Plate III, 43, 44, 48, 57) result only from predation attempts, their incidence provides a measure of the rate of unsuccessful predation by durophagous predators. In our samples 29% of all

intact gastropod shells bore repair scars, and 20% of these had more than one scar. Most (13%) had two, but some had as many as 5–8 scars. Thus, while all intact shells averaged 0.39 repair scars each, scarred shells averaged 1.3 each (Table 8).

Are gastropod species with frequent repair scars more resistant to durophagous predators than those that rarely bear scars? The latter is not necessarily the case, because their shells may be completely crushed on most occasions. However, shell structure

Table 7

Shells bearing evidence of successful predation by crustaceans

| Family-group | Genera | No. of cases | Plates |
|--|---|--------------|-------------------|
| <i>Predation by Calappa</i> | | | |
| Turridae | <i>Gemmula</i> , <i>Lucerapex</i> , <i>Tomopleura</i> , undet. | 10 | IV, 58, 59 |
| Costellariidae | <i>Vexillum</i> | 3 | |
| Terebridae | <i>Duplicaria</i> , <i>Terebra</i> | 2 | IV, 69 |
| Cerithiidae | <i>Rhinoclavis</i> | 1 | I, 4 ^a |
| Muricidae | <i>Naquetia</i> | 1 | |
| Olividae | <i>Oliva</i> | 1 | |
| Volutidae | <i>Fulgoraria</i> | 1 | |
| Conidae | <i>Conus</i> | 1 | IV, 64 |
| Nassariinae | <i>Nassarius</i> | 1 | |
| <i>Predation by undetermined crabs</i> | | | |
| Strombidae | <i>Strombus</i> | 1 | |
| Muricidae | <i>Morula</i> | 1 | II, 28 |
| <i>Predation by Gonodactylus</i> | | | |
| Ranellidae | <i>Gyrineum</i> , <i>Distorsio</i> , <i>Cymatium</i> | 4 | II, 23, 24 |
| Turridae | <i>Gemmula</i> | 1 | IV, 60 |

^a Plate I, 4 shows a second specimen, with repaired calappid break.

Table 8
Gastropod family-groups with most frequent repair scars. Family-groups (with $N > 30$) are ordered by frequency of repaired shells

| Family-group | No. of intact shells | No. of repaired shells | No. of shells with 1 repair scar | No. of shells with 2 repair scars | No. of shells with 3 repair scars | No. of shells with 4 repair scars | No. of shells with ≥ 5 repair scars | Total No. of repair scars | Mean No. of repair scars/shell (whole sample) | % of shells |
|-----------------|----------------------|------------------------|----------------------------------|-----------------------------------|-----------------------------------|-----------------------------------|--|---------------------------|---|-------------|
| Rissoidae | 40 | 23 | 11 | 4 | 4 | 3 | 1 | 48 | 1.20 | 58 |
| Costellariidae | 76 | 41 | 31 | 4 | 4 | 0 | 2 ^a | 62 | 0.82 | 54 |
| Terebridae | 35 | 18 | 11 | 4 | 3 | 0 | 0 | 28 | 0.80 | 51 |
| Turridae | 450 | 229 | 193 | 26 | 4 | 4 | 2 | 283 | 0.63 | 51 |
| Mitridae | 73 | 35 | 27 | 6 | 0 | 0 | 2 ^b | 52 | 0.71 | 48 |
| Conidae | 120 | 52 | 36 | 13 | 3 | 0 | 0 | 71 | 0.59 | 43 |
| Fascioliariinae | 46 | 18 | 11 | 5 | 2 | 0 | 0 | 27 | 0.59 | 39 |
| Columbellidae | 59 | 21 | 17 | 2 | 1 | 1 | 0 | 28 | 0.48 | 36 |
| Cerithiidae | 87 | 25 | 22 | 2 | 1 | 0 | 0 | 29 | 0.33 | 29 |
| Turritellidae | 96 | 27 | 24 | 3 | 0 | 0 | 0 | 30 | 0.31 | 28 |
| Buccininae | 100 | 24 | 20 | 4 | 0 | 0 | 0 | 28 | 0.28 | 24 |
| Naticidae | 207 | 49 | 34 | 9 | 4 | 2 | 0 | 72 | 0.35 | 24 |
| Nassariinae | 488 | 103 | 88 | 10 | 3 | 1 | 1 | 126 | 0.26 | 21 |
| Strombidae | 47 | 9 | 9 | 0 | 0 | 0 | 0 | 9 | 0.19 | 19 |
| Muricidae | 39 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0.08 | 8 |
| Trochidae | 56 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 0.09 | 4 |
| Olividae | 200 | 2 | 2 | 0 | 0 | 0 | 0 | 2 | 0.01 | 1 |
| All families | 2462 | 722 | 576 | 96 | 30 | 12 | 8 | 950 | 0.39 | 29 |

^a 1 shell with 5 and 1 with 6 repair scars.

^b 1 shell with 5 and 1 with 8 repair scars.

in most families in our samples with low rates of shell repair suggest that they were not subject to intensive predation from shell crushers. Of the numerically dominant families with low repair rates (Table 8), olivids (1% with repair scars) have very thick as well as slippery shells, trochids (9%) have fairly thick shells, most of the muricids in our samples (8%) had long spines on their shells in life (Plate II, 26), and many strombid shells have flaring, thickened outer lips (Plate I, 12, 15).

High incidences of shell repair does not necessarily indicate special resistance to predators, probably mainly crustaceans, that peel outer shell lips. High-spired shells with rather small apertures such as those of *Rissoina* (Family Rissoidae; 58%), *Vexillum* (Costellariidae; 54%), *Terebra* (Terebridae; 51%), many Turridae (51%), and *Ziba* (Mitridae; 48%) (Table 8) may either be more resistant, or may accumulate more scars because of their larger number of whorls, or both. Conversely, low repair frequencies may also indicate high resistance to durophagous predators, for example among thick-shelled Olividae and Trochidae (Table 8).

Cases of successful durophagy often cannot be attributed to a particular predator, but some crabs can be identified at least to family by the pattern of damage they leave on the shell. The best example is *Calappa*, which grasps the outer shell lip in its cheliped. A large, strong tooth on the dactyl is driven through the shell into a space between two strong protuberances on the propodus, crushing a portion of the outer lip. The shell is turned after each bite, and “successive pieces of shell are broken out until the enclosed animal is exposed and removed by the chela or maxillipeds for eating” (Shoup, 1968). This mechanism thus functions like a manual can opener, and leaves a distinctive pattern of shell breakage. *Calappa* attacks are generally fatal (Table 7; Plate IV, 58, 59, 64, 69), but at least one *Rhinoclavis sordidula* survived and repaired its shell following an evident *Calappa* attack (Plate I, 4).

5.3. Size relationships of predators and prey

Estimation of the size of durophagous predators from marks left on the shells of their prey is not possible. However, naticids drill holes whose diameters are proportional to their shell sizes (Ansell,

1960; Edwards and Huebner, 1977; Wiltse, 1980). A detailed analysis of predation by naticids on *Natica arachnoidea*, *N. areolata*, *N. euzona*, and *N. gualteriana* based on material from this study showed that in all cases borehole diameter increased significantly with prey shell size. Extrapolation from the measurements of temperate naticids and their boreholes in the studies cited above (Kabat and Kohn, 1986) suggested that most of the predatory naticids in the Nakasi Beds sample should be in the 10–18 mm shell length range, and this corresponds well to the observed size distribution in our samples.

To assess the broader relationship of naticid predator size and prey size, we measured each borehole diameter and the length of the drilled shell. Fig. 7 summarizes the mean values for each family and indicates a highly significant positive relationship. The slope is an order of magnitude lower than those for individual naticid species in Kabat and Kohn (1986), in part because in the present study we measured inner diameter, but outer diameter in the earlier one, and partly because the absence of larger naticids in the Nakasi Beds constrains the upper limit of borehole size. The latter fact suggests that a curvilinear relationship might more accurately describe the relationship, but a logarithmic function fitted to the data accounts for 48% of the variance, while the linear function explains 53%. In general, as in the more detailed study of naticids as prey of confamilials, larger naticids prey on larger gastropod victims.

Fewer data were available to determine whether prey size increases with muricid predator size across families. Although the trend is again toward a positive relationship, the results are less clear, and the regression explains only 17% of the variance in hole size (Fig. 8).

6. Paleobiogeography

The Lyellian percentage — the proportion of all gastropod species found in the Nakasi Beds fossil assemblage that are extant — is 87%. Because this value is based on both well characterized and tentatively determined species, and the latter groups comprise 238 of the estimated total 320 species present, it must be regarded as a first approximation. More of the mesogastropods (Order Neotaenioglossa) (94%)

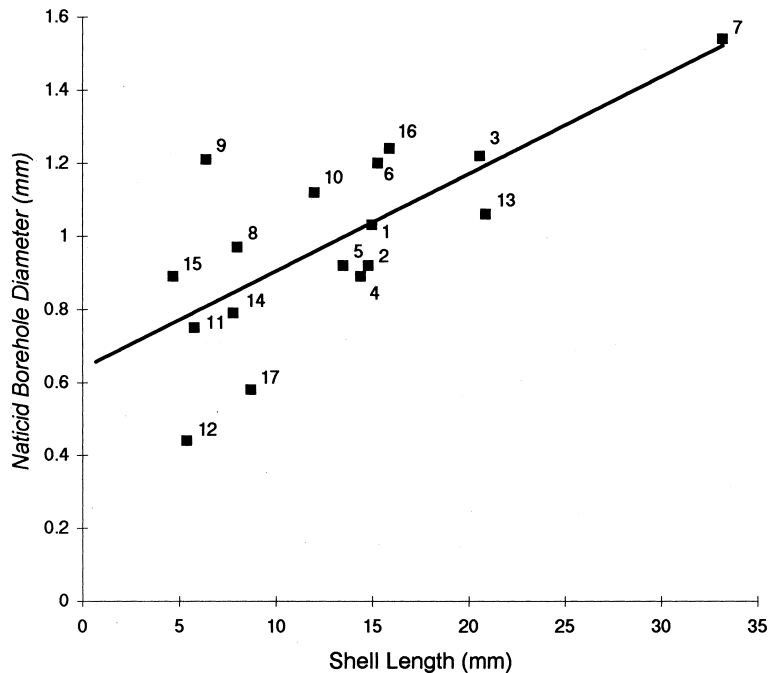


Fig. 7. Relationship between size of naticid predators, estimated by borehole inner diameters, and their prey, indicated by shell length. $Y = 0.027X + 0.638$; $r^2 = 0.53$; $F = 17.2$; $P = 0.001$. ■ indicate mean values of each variable for family-groups numbered as follows, with N (≥ 3 holes measured) indicated in parentheses: 1 = Buccininae (17); 2 = Cerithiidae (25); 3 = Conidae (36); 4 = Costellariidae (60); 5 = Fasciolarinae (16); 6 = Mitridae (32); 7 = Muricidae (13); 8 = Nassariinae (8); 9 = Naticidae (36); 10 = Olividae (30); 11 = Pyramidellidae (8); 12 = Rissoidae (13); 13 = Strombidae (3); 14 = Trochidae (7); 15 = Turbinidae (4); 16 = Turridae (231); 17 = Turritellidae (19).

than neogastropods (84%) are extant (Table 1). Two-thirds of the 212 extant species occur in Fijian waters today; the proportion is constant across all of the major orders and most of the common families (Tables 1 and 2). Of course it is not known whether these species persisted in Fiji through all of the major Pleistocene sea level changes. Among the most species-rich families, frequency of extinction is evidently highest in the Turridae (41%), but the shells of this group are notoriously difficult to determine. All of the Conidae species and all but one of Naticidae are extant, but about half of these no longer occur in Fiji (appendix A, **Online Background Dataset**⁷).

Almost all of the 72 globally extant species that are locally extinct in Fiji but whose southern hemisphere distributions are known reach the eastern limits of their ranges west of Fiji. Six occur as close

as Vanuatu, nearly 60% reach New Guinea, and with one exception all occur in Indonesia (Fig. 9). The exception is *Gemmula speciosa*, of which Recent specimens are known only from off Japan, Taiwan, Mozambique and Natal (Kilburn, 1983). Only two species, *Mitra fulvescens* and *Vexillum caelatum*, appear to miss Fiji but occur farther east in the South Pacific; Samoa is the eastern limit of both ranges (Cernohorsky, 1976; H. Turner, in litt.). As the modern subtidal fauna of Fiji becomes better known in future, these and perhaps other species may also be found to occur there.

7. A modern analogue of the Nakasi Beds fauna

To examine a modern community likely to resemble the fauna preserved in the Nakasi Beds, we sampled the benthos of Laucala Bay, between the Rewa River estuary and the E–W-trending Suva Main Bar-

⁷ URL: <http://www.elsevier.nl/locate/palaeo>; mirror site: <http://www.elsevier.com/locate/palaeo>.

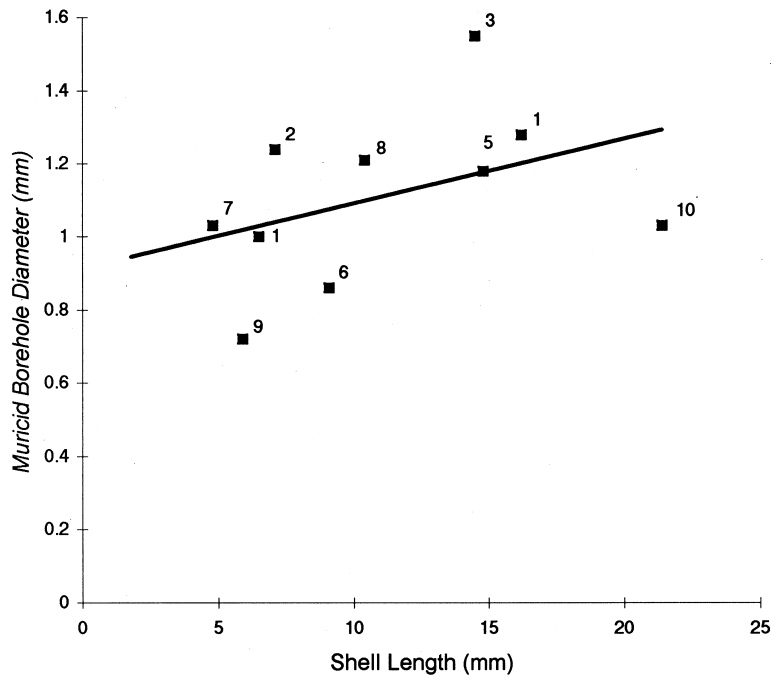


Fig. 8. Relationship between size of muricid predators, measured by borehole inner diameters, and their prey, indicated by shell length. $Y = 0.018X + 0.912$; $r^2 = 0.17$; $F = 1.7$; $P = 0.23$. ■ indicate mean values of each variable for family-groups numbered as follows, with N (≥ 3 holes measured) indicated in parentheses: 1 = Buccininae (8); 2 = Cerithiidae (17); 3 = Conidae (10); 4 = Costellariidae (8); 5 = Mitridae (11); 6 = Nassariinae (11); 7 = Naticidae (4); 8 = Olividae (3); 9 = Pyramidellidae (9); 10 = Turridae (76).

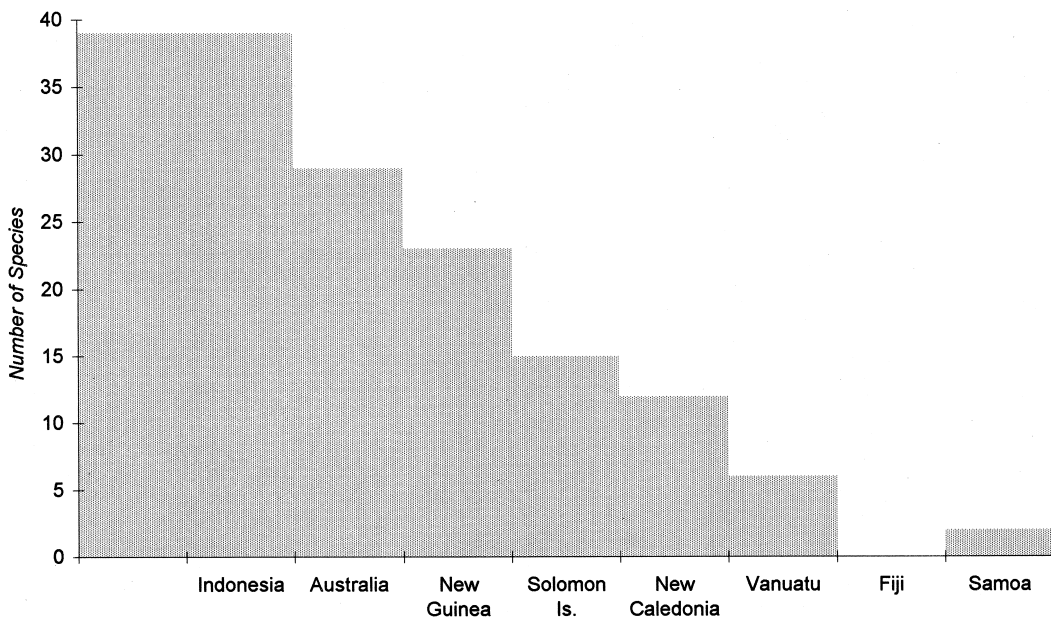


Fig. 9. Modern eastern range limits of extant gastropod species that are locally extinct in Fiji but occur in the Nakasi Beds. The graph plots the cumulative numbers of species from east (right) to west (left).

rier Reef, 10–15 km south-southwest of the Nakasi Beds assemblages studied. We analyzed the modern gastropod fauna sampled at five stations about 2–4 km offshore at depths of 8–25 m by diving and dredging and determined the grain size distribution of a substrate sample from 14.5 m. As in the Nakasi Beds sample, very fine sand predominated, followed by fine sand. Together these fractions constituted 79% of the total, and the median particle size was 0.12 mm, compared with the Nakasi Beds values of 89% and 0.10 mm, respectively (Fig. 3). The higher proportion of finer sand and slightly smaller median particle size at the fossil locality suggests that it derives from a habitat that was farther away from the island and offshore of any contemporaneous coral reefs.

Our sample of the modern benthic gastropod fauna of Laucala Bay contained 361 specimens of 49 shell-bearing species, i.e. an order of magnitude smaller than the fossil sample. The Recent and fossil samples were quite similar in taxonomic composition. Of the 17 families represented in the Laucala Bay sample, the five commonest were all among the 10 commonest in the Nakasi Beds fauna (Table 9), all but two of the 24 genera (*Sthenorytis* and *Neocancilla* of the families Epitoniidae and Mitridae, respectively) also occurred in the Nakasi beds samples, and more than half (54%) of the species were also represented in the fossil samples. The two commonest species, *Rhinoclavis sordidula* and *Turritella cingulifera*, ranked 11th and 5th, respectively, in abundance in the fossil assemblage, and the third commonest, *Nassarius concinnus*, was the most abundant fossil species. *Nassarius* was the commonest genus in the fossil assemblage and second commonest in the Recent sample, and three of the six Recent species present also occurred in the Nakasi Beds. In contrast to the fossil assemblage, bivalves

were almost as common as gastropods. The samples contained 314 specimens, of which the commonest were *Tellina* spp. (40%) and *Malletia* sp. (34%); the bivalves await further study.

Laucala Bay *Rhinoclavis sordidula* suffered the most intensive predation from drillers; 57% of intact shells were drilled. Some had more than one hole, and the mean number of boreholes was 0.78/shell. Several *R. sordidula* shells contained sipunculans, but none had corals attached. *Turritella cingulifera* was drilled half as frequently (28% of shells; mean of 0.3 boreholes/shell). One had two holes and housed a sipunculan. Three of the eight shells of *Vexillum* contained sipunculans (Plate III, 53, 54), the highest frequency of any family. As in a few fossil *Vexillum* (Plate III, 49, 50), these were frequently colonized by the solitary coral *Heterocyathus*. Among the commoner gastropod groups, sipunculans were most frequent in shells of *Nassarius* spp.; they occurred in 12 of 103 intact specimens. None of these bore a coral, and only one was drilled. Overall, nine *Nassarius* specimens had a total of 10 boreholes. The mean number of holes/shell among all gastropods was 0.34, and 26% of gastropod shells were drilled at least once. As in the fossil assemblage, most (about 90%) of the boreholes were due to naticids.

8. Discussion and conclusions

The fossil record provides the only evidence of the antecedents of modern marine benthic communities, of long-term historic trends and changes leading to modern patterns, and of changes over time in the structure of communities in different habitats and in similar habitats in different regions. Although the fossil record preserves neither entire original com-

Table 9

The five commonest gastropod family-groups in samples of a Recent benthic assemblage in Laucala Bay, Viti Levu, Fiji

| Family-group | No. of individuals | No. of genera | No. of species | Commonest species | Species in fossil assemblage? | Family rank in fossil assemblage |
|---------------|--------------------|---------------|----------------|---|-------------------------------|----------------------------------|
| Cerithiidae | 115 | 1 | 1 | <i>Rhinoclavis sordidula</i> Gould | yes | 7 |
| Nassariinae | 108 | 1 | 6 | <i>Nassarius concinnus</i> Powys | yes | 1 |
| Turritellidae | 53 | 1 | 1 | <i>Turritella cingulata</i> Sowerby | yes | 9 |
| Turridae | 18 | 3 | 5 | <i>Lophiotoma indica</i> (Röding), <i>Gemmula</i> sp. | yes | 2 |
| Naticidae | 17 | 1 | 3 | <i>Natica galteriana</i> | yes | 4 |

munities nor original proportions of organisms of different trophic levels, it can reveal evidence of taxonomic composition, relative abundance, and signals of prey–predator interactions adequate to offer insights into the food webs and other aspects of structure of ancient communities. It thus helps to improve understanding of the history and development of modern marine communities.

In the Early Pleistocene Nakasi Beds of southwest Viti Levu Island, Fiji, gastropods dominate the very diverse assemblage of molluscan macrofossils, both with respect to taxonomic richness and abundance. Although many species determinations are tentative, we collected at least 320 gastropod species, representing a minimum of 146 genera in 52 families and comprising about 75% of all molluscan fossils. The high diversity reported here in the nearshore waters of an island conforms to a global pattern elucidated by Jablonski and Flessa (1986). They showed that the Recent faunas of 22 oceanic islands (not including Fiji) included 97% of all marine gastropod families.

The most abundant fossil species may have been the most important members of the original fauna, but of course this is by no means certain. Some species do not fossilize well or at all, and shells may be washed into sedimenting environments from other habitats after death of the gastropod or carried there by subsequent occupants of the shell. In general, however, the state of preservation was very good; at the most intensively studied locations, 80% of shells were well or very well preserved with regard to integrity of shell form, and 90% were well or very well preserved with respect to retention of surface features (Table 4), based on the condition analysis method of Ogasawara (1977). This suggests *in situ* preservation in the animals' original habitat.

For the later Tertiary and Quaternary periods, ecological knowledge of modern taxa can provide data sets that are independent of information derived from fossils and their matrices but that can be combined to enhance understanding of past species and their communities and paleoenvironments (Nehm and Geary, 1994). The present study particularly benefits from this, because an estimated 87% of the gastropod species in the Nakasi Beds assemblage are extant.

Based on independent evidence of the substrates they occupy drawn from studies of Recent con-

specifics and congeners, nearly 75% of gastropod species and about 90% of individuals with known or estimated substrate preferences lived on or in the same type of sediment in which their shells are now preserved as fossils. Combined with the evidence for absence of significant post-mortem transport of the specimens, these results support the hypothesis that the molluscs derive from a single palaeocommunity that occupied the same sediment in which their shells are now preserved as fossils. On the other hand, variability in species-abundance patterns is so high among the three local paleocommunities studied intensively that according to the criteria developed by Bennington and Bambach (1996) they constitute components of a paleocommunity type but not a single paleocommunity.

Attempting to determine the depth at which the original community lived is difficult, because of the tentative identifications of most species and the fact that available data on known depth ranges of extant species are from different geographic regions or from the entire geographic range of the species. Moreover it has not been possible to verify the determinations of most of the species with published depth data. However, 72% of species with available records from the literature occur in 5–50 m, and this is the most likely depth range of the Nakasi Beds assemblage (Fig. 4).

The estimated range, and the fact that the deposits are close to the present coast of the large island of Viti Levu, strongly indicate a nearshore environment. The Nakasi Beds sediment particle size distribution is slightly finer and slightly more well-sorted than the modern sediment of Laucala Bay (Fig. 3), which supports a similar biota 2–4 km from the present coastline but inshore of the modern barrier reef. Possibly in life the Nakasi Beds habitat was somewhat farther from the island and offshore of any contemporaneous barrier reef in somewhat deeper water than modern Laucala Bay.

Not unexpectedly from the high proportions of gastropod species and individuals occupying soft substrates, the predominant family-groups represented in the Nakasi Beds were the Nassariinae, Turridae, Olividae, Naticidae and Conidae. These five proso-branch taxa, listed in order of abundance, comprised nearly 60% of the entire sample. Turridae was the most diverse family at the species level, with 43

species, or 13% of all gastropod species, and the five most abundant families comprised one-third of all species. Few similar quantitative analyses exist for comparison, but the fossil gastropod assemblages of the Eocene Stone City Formation of Texas, studied by Stanton et al. (1981) are remarkably similar in several ways to those of the Nakasi Beds. In the Stone City assemblage, gastropods comprised a smaller majority (56%, vs. 75% in the Nakasi Beds) of the molluscs present, and turrids were the most diverse family, with 20% of all gastropod species and 13% of individuals, compared with 17% and 13%, respectively, in the Nakasi Beds. The five predominant family-groups listed above also account for nearly the same proportions of all gastropod individuals (61%) and species (29%) as in the Nakasi Beds, although their Paleogene age is much older and closer to the origins of these families (Tracey et al., 1993).

If the Nassariinae (18% of individuals, 4% of species) are considered as omnivores or scavengers (Taylor, 1993; Britton and Morton, 1994), then two-thirds of gastropod individuals and three-fourths of the species in the Nakasi Beds assemblage were carnivores. This is a conservative estimate because, as the authors cited above document, Nassariinae are also partly carnivorous. Members of at least three of the next four most abundant families (Turridae, Naticidae and Conidae) all use chemical toxins to aid in overpowering their prey (Kohn, 1983b). In contrast to the dominant carnivores and omnivorous nassariines, only 16% of individuals and 23% of all gastropod species were primary consumers. Here we consider this category to include both suspension- and deposit-feeding detritivores (12 and 16%, respectively) and herbivores (4 and 8%, respectively). In the comparable Eocene Stone City Formation gastropod assemblage, proportions of the major functional feeding groups were even more skewed toward carnivores. Again excluding Nassariinae, carnivores comprised about 90% each of families, genera and species (Stanton et al., 1981).

Predation by drilling gastropods was especially prevalent in the Nakasi Beds assemblage, and the drilling victims in the Nakasi Beds samples were taxonomically highly diverse. More than 60% of all families, and 91% of all those represented by five or more intact specimens, and about half of all species and genera were drilled. Evidence from the

distribution of boreholes among shells indicates that naticids and muricids do not drill gastropod species in proportion to their abundance. Rather, members of both groups prey selectively on turrids, cerithiids and costellariids. However, the latter two families represented only 5–10% of naticid and muricid diets. Although more abundant than turrids, Nassariinae were drilled proportionately less frequently. Most nassariines were much smaller than most turrids, and members of the former group have long been known to have effective escape response from predators (e.g. Weber, 1924).

High drilling frequency of coarsely sculptured shells suggests that ornamentation did not act as an effective deterrence against predation. Similarly, Yochelson et al. (1983) observed that coarsely sculptured scaphopods show a high rate of predation while smooth or finely ribbed forms are almost never bored. Reyment (1966) noted that the strongly sculptured bivalve *Cardium papillosum* is a preferred prey of naticids and muricids in the Western Niger Delta, while many smooth shelled bivalves were free of borings. Although Dudley and Vermeij (1978) and Arua and Hoque (1987) observed that smooth-shelled gastropods and bivalves in their collections were more preferred prey than ornamented ones, this was not the case in the Nakasi Beds, largely because fewer than 20% of the abundant family Olividae were drilled. The reason for this low frequency is unknown, but predators may have found them difficult to manipulate because of their smooth shells with 'slippery slopes' (Vermeij, 1993, p. 117).

Fewer than 3% of the nearly 1000 boreholes we observed failed to penetrate the shells completely, strongly suggesting that attempted drilling predation was almost always successful. By this criterion, drilling by naticids and muricids killed nearly one-third of all gastropods in the sample; the former family was the more important cause by a 3:1 margin. Naticids are known to affect profoundly the abundance, diversity and species composition in communities where they are common. Not only do they reduce these attributes of molluscan assemblages by predation, but their disturbance of surface sediments while feeding decreases the abundance and diversity of other invertebrates (Wiltse, 1980).

Nakasi Beds gastropods appeared to survive attacks by durophagous predators more often than

those by drillers. Nearly 30% of all shells bore one or more scars indicating successful repair following breakage of outer lips, and the mean number of scars/shell was 0.39. Members of families characterized by particularly thick, strong shells, e.g. Olividae and Trochidae, rarely had repair scars. Although evidence is usually lacking to attribute successful attacks to particular durophagous predators some, such as calappid crabs and gonodactyloid stomatopods, leave clearly identifiable damage patterns. These are particularly advantageous for palaeocommunity reconstruction, as they enable recognition of important components of the community that are often not preserved in the fossil record (Table 7; Fig. 6).

The Nakasi Beds palaeocommunity type may possibly be the antecedent of the present-day benthos off the Fijian islands. A modern benthic gastropod fauna we sampled 2–4 km from the present coastline in 5–25 m in Laucala Bay, a sedimenting environment off the estuary of Fiji's largest river, the Rewa, closely resembles the fossil assemblage studied. Gastropods were much commoner than bivalves, and although the modern sample is an order of magnitude smaller, the five most abundant gastropod families were all among the ten commonest in the Nakasi Beds, 92% of the genera and 54% of the species also occurred in the fossil sample, and the three commonest Recent species, *Turritella cingulifera*, *Rhinoclavis sordidula* and *Nassarius concinnus*, were also among the most abundant species in the Nakasi Beds. The modern sediments also resemble the matrix of the Nakasi Beds fossils. Very fine sand was the predominant component of both, but the Laucala Bay sediment was slightly coarser (Fig. 3), perhaps attributable to the more inshore location of Laucala Bay and the influence of stronger currents in the Rewa estuary.

The high Lyellian percentage of the Early Pleistocene Nakasi Beds gastropod assemblage — nearly 90% of the species are extant — allows comparisons with modern faunal composition and geographic distribution patterns. The striking similarities between this assemblage and the modern fauna in Laucala Bay strongly suggest persistence of stable faunal composition and ecological structure of benthic communities over an interval of 1.8 million years.

However, sea levels during the Quaternary fluctuated considerably during about 21 glacial cycles (Harland et al., 1989; Paulay, 1990), and low sea

stands must have resulted in local extinctions in some habitats, as well as the appearance or reappearance of barriers to dispersal. At present we have for comparison samples of only two faunas 1.8 million years apart in age, with no information from intervening glacial cycles. Thus we cannot infer that these species persisted in Fiji throughout the Quaternary. Present Laucala Bay, for example, must have been dry land during the latest Pleistocene glacial stage (Paulay, 1990, fig. 4). Nevertheless, two-thirds (140/212) of the extant species are represented in the Recent Fijian fauna. Of the 72 globally extant species that are locally extinct in Fiji, 69 share a common geographic pattern: they reach the eastern limits of their southern hemisphere distributions west of Fiji. A few of these occur as close to Fiji as Vanuatu, nearly half occur in northern Australia, and all occur in Indonesia (Fig. 9).

Paulay (1990, 1991) demonstrated that Pleistocene sea level fluctuations strongly altered species compositions and shifted geographic distributions of the corals and bivalves inhabiting coral reefs of tropical south Pacific oceanic islands. Our results suggest a similarly dynamic Quaternary biogeographic history of gastropods occupying subtidal soft sediments near these islands. The general pattern of species ranges now constricted to the continental island coasts to the west (Fig. 9) probably reflects local extinctions to the east. Our paleobiogeographic analysis thus supports Paulay's (1990, 1991) hypothesis that sea level changes and the vicissitudes of recolonization by larval dispersal have caused major expansions and contractions of ranges of marine benthic invertebrates during the Quaternary.

We conclude from our paleoecological analyses that the early Pleistocene Nakasi Beds of Viti Levu supported a very diverse palaeocommunity type with more than 300 gastropod species occupying mainly very fine sand sediment, most likely inshore at depths of 50 m or less, and closely resembling the modern fauna of a similar habitat. Carnivorous gastropods and the more omnivorous Nassariinae dominated a complex community trophic organization. Among the former, shell-drilling Naticidae and Muricidae caused particularly widespread mortality among gastropods. Shell-breaking predators were frequent in the community but often attacked gastropods unsuccessfully and were probably much less important

mortality factors. The fossil record has thus yielded insights into the composition, environment, trophic organization, and temporal changes in geographic distributions of paleocommunities as well as enhancing understanding of the history and development of modern marine communities and biodiversity.

Acknowledgements

We gratefully acknowledge the support of NSF Grant INT-9014120. We are especially grateful to the Mineral Resources Department of Fiji for providing research facilities, and we especially thank Peter Rodda for field support and helpful discussions. We thank Johnson Seeto for providing research facilities at the University of the South Pacific and use of the vessel *Nautilus*, and Esther Williams for permitting use of the USP library. We thank Alan Riggs and Gustav Paulay for much expert assistance in the field. For aid in identification of specimens we thank Carole Hickman, Richard Kilburn, Ian Loch, Elsie Marshall, Winston Ponder, Raul Palacios, John Taylor, Hans Turner, Ben Tursch, and Emily Vokes. For logistic support in Fiji we thank the Vidya Rattan family and the late Dr. Ken Gilchrist, and we thank an anonymous referee for constructive criticism of the manuscript.

References

- Abbott, R.T., 1960. The genus *Strombus* in the Indo-Pacific. *Indo-Pac. Mollusca* 1, 33–146.
- Allmon, W.D., 1988. Ecology of Recent turritelline gastropods (Prosobranchia, Turritellidae): Current knowledge and paleontological implications. *Palaios* 3, 259–284.
- Ansell, A., 1960. Observations on predation of *Venus striatula* (da Costa) by *Natica alderi* (Forbes). *Proc. Malacol. Soc. London* 34, 248–249.
- Arua, I., 1989. Gastropod predators and their dietary preference in an Eocene molluscan fauna from Nigeria. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 72, 283–290.
- Arua, I., Hoque, M., 1987. Predation intensity in an Eocene molluscan assemblage from southeastern Nigeria. *Geol. Mijnbouw* 66, 293–296.
- Arua, I., Hoque, M., 1989. Study of the shape of Naticid and Muricid boring in plan view in Eocene prey from Southeastern Nigeria. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 72, 357–362.
- Baumiller, T.K., 1996. Boreholes in the Middle Devonian blastoid *Heteroschisma* and their implications for gastropod drilling. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 123, 343–351.
- Bennington, J.B., Bambach, R.K., 1996. Statistical testing for paleocommunity recurrence: Are similar fossil assemblages ever the same? *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 127, 107–133.
- Berg Jr., C.J., Nishenko, S., 1975. Stereotypy of predatory boring behavior of Pleistocene naticid gastropods. *Paleobiology* 1, 258–260.
- Beu, A.G., 1988. Taxonomy of gastropods of the families Ranelidae (= Cymatiidae) and Bursidae. Part 5. Early history of families, with four new genera and recognition of the Family Personidae. In: Saito Ho-on Kai Spec. Publ. (Prof. T. Kotaka Commem. Vol.), pp. 69–96.
- Boss, K., 1982. *Mollusca*. In: Parker, S.P. (Ed.), *Synopsis and Classification of Living Organisms*, Vol. 1. McGraw-Hill, New York, NY, pp. 945–1166.
- Bratcher, T., Cernohorsky, W.O., 1987. *Living Terebras of the World*. American Malacologists, Melbourne, FL, 240 pp.
- Brett, C.E., Boucot, A.J., Jones, B., 1993. Absolute depths of Silurian benthic assemblages. *Lethaia* 26, 25–40.
- Britton, J.C., Morton, B., 1993. Marine invertebrate scavengers. In: Morton, B. (Ed.), *Marine Biology of the South China Sea*, Vol. 2. Hong Kong Univ. Press, Hong Kong, pp. 357–391.
- Britton, J.C., Morton, B., 1994. Food choice, detection, time spent feeding, and consumption by two species of subtidal Nassariidae from Monterey Bay, California. *Veliger* 37, 81–92.
- Burgess, C.M., 1985. *Cowries of the World*. Gordon Verhoef, Cape Town, 289 pp.
- Cadée, G.C., 1984. ‘Opportunistic feeding’, a serious pitfall in trophic structure analysis of (paleo)faunas. *Lethaia* 17, 289–292.
- Carriker, M.R., 1981. Shell penetration and feeding by naticacean and muricacean predatory gastropods: A synthesis. *Malacologia* 20, 403–422.
- Carriker, M.R., Yochelson, E.L., 1968. Recent gastropod boreholes and Ordovician cylindrical borings. *U.S. Geol. Surv. Prof. Pap.* 593-B, 26 pp.
- Cernohorsky, W.O., 1967. The Muricidae of Fiji (Mollusca: Gastropoda). Part I. Subfamilies Muricinae and Tritonaliinae. *Veliger* 10, 111–132.
- Cernohorsky, W.O., 1969. The Muricidae of Fiji (Mollusca: Gastropoda). Part II. Subfamily Thaidinae. *Veliger* 11, 293–315.
- Cernohorsky, W.O., 1970. Systematics of the families Mitridae and Volutomitridae (Mollusca: Gastropoda). *Bull. Auckland Inst. Mus.* 8, 190 pp.
- Cernohorsky, W.O., 1972. *Marine Shells of the Pacific*, Vol. 2. Pacific Publ., Sydney, 411 pp.
- Cernohorsky, W.O., 1976. The Mitridae of the World. Part I. The Subfamily Mitrinae. *Indo-Pac. Mollusca* 3, 273–528.
- Cernohorsky, W.O., 1978. *Tropical Pacific Marine Shells*. Pacific Publ., Sydney, 352 pp.
- Cernohorsky, W.O., 1980. The taxonomy of some Indo-Pacific Mollusca. Part 7. *Rec. Auckland Inst. Mus.* 16, 171–187.

- Cernohorsky, W.O., 1981. The family Buccinidae. Part I: The genera *Nassaria*, *Trajana*, and *Neoteron*. Monogr. Mar. Mollusca 2, 52 pp.
- Cernohorsky, W.O., 1984. Systematics of the family Nassariidae. Bull. Auckland Inst. Mus. 14, 356 pp.
- Cernohorsky, W.O., 1991. The Mitridae of the world. Part 2. The Subfamily Mitrinae concluded and subfamilies Imbricariinae and Cylindromitrinae. Monogr. Mar. Mollusca 4, 164 pp.
- Cutler, E., 1994. The Sipuncula: Their Systematics, Biology, and Evolution. Cornell Univ. Press, Ithaca, NY, 453 pp.
- Davoli, F., 1988. Olividae Pliocenici nel bacino Mediterraneo? Atti. Soc. Nat. Mat. Modena 119, 19–30.
- Davoli, F., 1989. Olividae (Gastropoda) miocenici: Ultima testimonianza nell'area mediterranea di un clima intertropicale. Boll. Soc. Paleontol. Ital. 28, 101–132.
- Dodd, J.R., Stanton, R.J., Jr., 1990. Paleocology, 2nd ed. Wiley, New York, NY, 502 pp.
- Duchamps, R., 1992. Description d'une nouvelle espèce de *Tibia* (Gastropoda: Strombidae). Apex 7, 47–58.
- Dudley, E.C., Vermeij J.I., G.J., 1978. Predation in time and space: Drilling in the gastropod *Turritella*. Paleobiology 4, 436–441.
- Edwards, D.C., 1969a. Zonation by size as an adaptation for intertidal life in *Olivella biplicata*. Am. Zool. 9, 417–939.
- Edwards, D.C., 1969b. Predators on *Olivella biplicata*, including a species-specific predator avoidance response. Veliger 11, 326–333.
- Edwards, D.C., Huebner, J.D., 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. Ecology 58, 1218–1236.
- Emery, K.O., 1938. Rapid method of mechanical analysis of sand. J. Sediment. Petrol. 8, 105–111.
- Fairweather, P.G., 1988. Movements on intertidal whelks (*Morula marginalba* and *Thais orbita*) in relation to availability of prey and shelter. Mar. Biol. 100, 63–68.
- Farmer, W.M., 1970. Swimming gastropods (Opisthobranchia and Prosobranchia). Veliger 13, 73–89.
- Fotheringham, N., 1976. The winter prey of *Oliva sayana*. Veliger 19, 77–78.
- Fürsich, F.T., Jablonski, D., 1984. Late Triassic naticid drillholes: Carnivorous gastropods gain a major adaptation but fail to radiate. Science 224, 78–80.
- Geary, D.H., Allmon, W.D., Reaka-Kudla, M.L., 1991. Stomatopod predation on fossil gastropods from the Plio-Pleistocene of Florida. J. Paleontol. 65, 355–360.
- Gonor, J.J., 1965. Predator–prey reactions between two marine prosobranch gastropods. Veliger 7, 228–232.
- Govan, H., 1995. *Cymatium muricinum* and other ranellid gastropods: Major predators of cultured tridacnid clams. ICLARM Tech. Rep. 49, 136 pp.
- Graham, A., 1938. On a ciliary process of food-collecting in the gastropod *Turritella communis* Risso. Proc. Zool. Soc. London A 108, 453–463.
- Haq, B.U., Hardenbol, J., Vail, P.R., 1987. Chronology of fluctuating sea levels since the Triassic. Science 235, 1156–1166.
- Harland, W.B., Armstrong, R.L., Cox, A.V., Craig, L.E., Smith, A.G., Smith, D.G., 1989. A Geologic Time Scale 1989. Cambridge Univ. Press, Cambridge, 263 pp.
- Hatfield, E.B., 1979. Food sources for *Anachis avara* (Columbellidae) and a discussion of feeding in the family. Nautilus 93, 90–93.
- Hickman, C.S., 1988. Archaeogastropod evolution, phylogeny and systematics: a re-evaluation. Malacol. Rev. Suppl. 4, 17–34.
- Hickman, C.S., Lipps, J.H., 1983. Foraminiferivory: Selective ingestion of foraminifera and test alterations produced by the neogastropod *Olivella*. J. Foraminiferal Res. 13, 108–114.
- Hickman, C.S., McLean, J.H., 1990. Systematic revision and suprageneric classification of trochacean gastropods. Nat. Hist. Mus. Los Angeles County Sci. Ser. 35, 169 pp.
- Hilgen, F.J., Lourens, L.J., Berger, A., Loutre, M.F., 1993. Evaluation of the astronomically calibrated time scale for the Late Pliocene and earliest Pleistocene. Paleogeography 8, 549–565.
- Hoeksema, B.W., Best, M.B., 1991. New observations on scleractinian corals from Indonesia: 2. Sipunculan-associated species belonging to the genera *Heterocyathus* and *Heterop-sammia*. Zool. Meded. 65, 221–245.
- Houbrick, J.R., Fretter, V., 1969. Some aspects of the functional anatomy and biology of *Cymatium* and *Bursa*. Proc. Malacol. Soc. London 38, 415–429.
- Houbrick, R.S., 1978. The Family Cerithiidae in the Indo-Pacific. Part I: The genera *Rhinoclavis*, *Pseudovertagus* and *Clavocerithium*. Monogr. Mar. Mollusca 1, 130 pp.
- Houbrick, R.S., 1980. Review of the deep-sea genus *Argyropeza* (Gastropoda: Prosobranchia: Cerithiidae). Smithsonian Contr. Zool. 321, 30 pp.
- Houbrick, R.S., 1988. Cerithioidean phylogeny. Malacol. Rev. Suppl. 4, 88–128.
- Hughes, R.N., Hughes, H.P.I., 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). Malacologia 20, 385–402.
- Hurst, A., 1965. Studies on the structure and function of the feeding apparatus of *Philina aperta* with a comparative consideration of some other opisthobranchs. Malacologia 2, 281–347.
- Jablonski, D., Flessa, K.W., 1986. The taxonomic structure of shallow-water marine faunas: Implications for Phanerozoic extinctions. Malacologia 27, 43–66.
- Janssen, R., 1981. Mollusken-Assoziationen und Biotope im norddeutschen Oberoligozän. Natur Mus. 111, 70–78.
- Johnson, H., 1991. Petroleum geology of Fiji. Mar. Geol. 98, 313–352.
- Johnson, S., Johnson, J., Jazwinski, S., 1995. Parasitism of sleeping fish by gastropod mollusks in the Colubrariidae and Marginellidae at Kwajalein, Marshall Islands. Festivus 27, 121–125.
- Kabat, A.R., 1990. Predatory ecology of naticid gastropods with a review of shell boring predation. Malacologia 32, 155–193.
- Kabat, A.R., 1991. The classification of the Naticidae (Mollusca: Gastropoda): Review and analysis of the supraspecific taxa. Bull. Mus. Comp. Zool. 152, 417–449.
- Kabat, A.R., Kohn, A.J., 1986. Predation on Early Pleis-

- tocene naticid gastropods in Fiji. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 53, 255–269.
- Kay, E.A., 1979. *Hawaiian Marine Shells*. Bishop Museum Press, Honolulu, 653 pp.
- Kilburn, R.N., 1981. Revision of the genus *Ancilla* Lamarck, 1979 (Mollusca: Olividae: Ancillinae). *Ann. Natal Mus.* 24, 349–463.
- Kilburn, R.N., 1983. Turridae (Mollusca, Gastropoda) of southern Africa and Mozambique, Part 1. Subfamily Turrinae. *Ann. Natal Mus.* 25, 549–585.
- Kilburn, R.N., 1985. Turridae (Mollusca, Gastropoda) of southern Africa and Mozambique, Part 2. Subfamily Turrinae. *Ann. Natal Mus.* 26, 417–470.
- Kilburn, R.N., 1986. Turridae (Mollusca, Gastropoda) of southern Africa and Mozambique, Part 3. Subfamily Borsoniinae. *Ann. Natal Mus.* 27, 633–720.
- Kilburn, R.N., 1988. Turridae (Mollusca, Gastropoda) of southern Africa and Mozambique, Part 4. Subfamilies Drilliinae, Crassispirinae and Strictispirinae. *Ann. Natal Mus.* 29, 167–320.
- Kilburn, R.N., 1991. Turridae (Mollusca, Gastropoda) of southern Africa and Mozambique, Part 5. Subfamily Taraninae. *Ann. Natal Mus.* 32, 325–339.
- Kilburn, R.N., 1992. Turridae (Mollusca, Gastropoda) of southern Africa and Mozambique, Part 6. Subfamily Mangeliinae, section 1. *Ann. Natal Mus.* 33, 461–575.
- Kilburn, R.N., 1993. Turridae (Mollusca, Gastropoda) of southern Africa and Mozambique, Part 6. Subfamily Mangeliinae, section 2. *Ann. Natal Mus.* 34, 317–367.
- Kilburn, R.N., 1994. Turridae [s.l.] (Mollusca, Gastropoda) of southern Africa and Mozambique, Part 7. Subfamily Crassispirinae, section 2. *Ann. Natal Mus.* 35, 177–228.
- Kilburn, R.N., 1995. Turridae [s.l.] of southern Africa and Mozambique (Mollusca: Gastropoda: Conoidea) Part 8. Conidae: subfamily Mangeliinae, section 3. *Ann. Natal Mus.* 36, 261–269.
- Kitchell, J.A., Boggs, C.H., Kitchell, J.F., Rice, J.A., 1981. Prey selection by naticid gastropods: Experimental tests and application to the fossil record. *Paleobiology* 7, 533–552.
- Kohn, A.J., 1975. Predation on sipunculans. In: Rice, M.E., Todorovic, M. (Eds.), *Proc. Int. Symp. Biol. Sipuncula and Echiura*, Vol. 1, pp. 313–333.
- Kohn, A.J., 1983a. Microhabitat factors affecting abundance and diversity of *Conus* on coral reefs. *Oecologia* 60, 293–301.
- Kohn, A.J., 1983b. Feeding biology of gastropods. In: Saleuddin, A.S.M., Wilbur, J.M. (Eds.), *The Mollusca*, Vol. 5. Academic Press, New York, NY, pp. 1–63.
- Kohn, A.J., 1986. Slip-resistant silver-feet: Shell form and mode of life in Lower Pleistocene *Argyropeza* from Fiji. *J. Paleontol.* 60, 1066–1074.
- Kohn, A.J., 1990. Tempo and mode of evolution in Conidae. *Malacologia* 32, 55–67.
- Kohn, A.J., 1992a. *A Chronological Taxonomy of Conus, 1758–1840*. Smithsonian Institution Press, Washington, DC, 315 pp.
- Kohn, A.J., 1992b. *Conus striatus* survives attack by gonodactylid! *Veliger* 35, 398–401.
- Kohn, A.J., Nybakken, J.W., 1975. Ecology of *Conus* on eastern Indian Ocean fringing reefs: Diversity of species and resource utilization. *Mar. Biol.* 29, 211–234.
- Kohn, A.J., Riggs, A.C., 1982. Sample size dependence in measures of proportional similarity. *Mar. Ecol. Progr. Ser.* 9, 147–151.
- Kohn, A.J., Taylor, J.D., Wai, J.M., 1997. Diets of predatory gastropods of the families Mitridae and Buccinidae in the Houtman Abrolhos Islands, Western Australia. In: Wells, E.F. (Ed.), *The Marine Flora and Fauna of the Houtman Abrolhos Islands, Western Australia*. Western Australian Museum, Perth, pp. 133–139.
- Kotaka, T., 1959. The Cenozoic Turritellidae of Japan. *Sci. Rep. Tohoku Univ. Ser. 2 (Geol.)* 31, 1–135.
- Kotaka, T., 1978. World-wide biostratigraphic correlation based on turritellid phylogeny. *Veliger* 21, 189–196.
- Ladd, H.S., 1966. Chitons and gastropods (Haliotidae through Adeorbidae) from the western Pacific islands. *U.S. Geol. Surv. Prof. Pap.* 531, 98 pp.
- Ladd, H.S., 1972. Cenozoic fossil molluscs from western Pacific islands; Gastropods (Turritellidae through Strombidae). *U.S. Geol. Surv. Prof. Pap.* 532, 79 pp.
- Ladd, H.S., 1977. Cenozoic fossil molluscs from western Pacific islands; Gastropods (Eratoidae through Harpidae). *U.S. Geol. Surv. Prof. Pap.* 533, 84 pp.
- Ladd, H.S., 1982. Cenozoic fossil molluscs from western Pacific islands; Gastropods (Eulimidae and Volutidae through Terebridae). *U.S. Geol. Surv. Prof. Pap.* 1171, 100 pp.
- Lindberg, D.L., 1988. The Patellogastropoda. *Malacol. Rev. Suppl.* 4, 35–63.
- Maes, V.O., 1983. Observations on the systematics and biology of a turrid assemblage in the British Virgin Islands. *Bull. Mar. Sci.* 33, 305–335.
- Maes, V.O., Ræihle, D., 1975. Systematics and biology of *Thala floridana* (Gastropoda: Vexillidae). *Malacologia* 15, 43–67.
- Magalhaes, H., 1948. An ecological study of snails of the genus *Busycon* at Beaufort, N.C. *Ecol. Monogr.* 18, 377–410.
- Majima, R., 1989. Cenozoic fossil Naticidae (Mollusca: Gastropoda) in Japan. *Bull. Am. Paleontol.* 96 (351), 159 pp.
- Marcus, E., Marcus, E., 1959. Studies on ‘Olividae’. *Bol. Fac. Fil., Cien. Lett. Univ. Sao Paulo* 232 (Zool. 22), 99–188.
- Martin, K., 1883–1887. Paläontologische Ergebnisse von Tiefbohrungen auf Java, nebst allgemeineren Studien über das Tertiär von Java, Timor und einiger anderer Inseln. *Samml. Geol. Reichsmus. Leiden Ser. 1 (3)*, 380 pp.
- McLean, J.H., 1971. A classification of the Family Turridae, with the proposal of new subfamilies, genera, and subgenera from the eastern Pacific. *Veliger* 14, 114–130.
- Mikkelsen, P.M., 1996. The evolutionary relationships of Cephalaspidea S.L. (Gastropoda: Opisthobranchia): A phylogenetic analysis. *Malacologia* 37, 375–442.
- Miller, J.A., 1990. The feeding and prey capture mechanism of *Turricula nelliae spurius* (Hedley) (Gastropoda: Turridae). In: Morton, B. (Ed.), *The Marine Flora and Fauna of Hong Kong and Southern China*. *Proc. Second Int. Mar. Biol. Workshop, Hong Kong, 1986*, pp. 979–992.
- Nehm, R.H., Geary, D.H., 1994. A gradual morphologic transi-

- tion during a rapid speciation event in marginellid gastropods (Neogene: Dominican Republic). *J. Paleontol.* 68, 787–795.
- Ogasawara, K., 1977. Paleontological analysis of Omma fauna from Toyama–Ishikawa area, Hokuriku Province. *Japan. Sci. Rep. Tohoku Univ. Ser. 2 (Geol.)* 47, 43–156.
- Oostingh, C.H., 1935. Die Mollusken des Pliocäns von Boemio-joe (Java). *Wet. Meded. Mijnb. Ned. Indie* 26, 1–247.
- O’Sullivan, J.B., McConnaughey, R.R., Huber, M.E., 1987. A blood-sucking snail: The Cooper’s nutmeg, *Cancellaria cooperi* Gabb, parasitizes the California electric ray, *Torpedo californica* Ayres. *Biol. Bull.* 172, 362–366.
- Paine, R.T., 1963. Trophic relationships of 8 sympatric predatory gastropods. *Ecology* 44, 63–73.
- Palmer, A.R., 1984. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. *Oecologia* 62, 162–172.
- Paulay, G., 1990. Effects of late Cenozoic sea-level fluctuations on the bivalve faunas of tropical oceanic islands. *Paleobiology* 16, 415–434.
- Paulay, G., 1991. Late Cenozoic sea level fluctuations and the diversity and species composition of insular shallow water marine faunas. In: Dudley, E.C. (Ed.), *The Unity of Evolutionary Biology*. Dioscorides Press, Portland, OR, pp. 184–193.
- Petit, R.E., Harasewych, M.G., 1986. New Philippine Cancellariidae (Gastropoda: Cancellariacea), with notes on the fine structure and function of the nematoglossan radula. *Veliger* 28, 436–443.
- Phillips, D.W., 1977. Abundance and escape responses of the gastropod mollusc *Olivella biplicata* (Sowerby) to predatory asteroids. *J. Exp. Mar. Biol. Ecol.* 28, 77–86.
- Pitt, W.D., Pitt, L.J., 1993. Ultra-violet light as a useful tool for identifying fossil mollusks, with examples from the Gatun Formation, Panama. *Tulane Stud. Geol. Paleontol.* 26, 1–13.
- Ponder, W.F., 1985. A review of the genera of the Rissoidae (Mollusca, Mesogastropoda, Rissoacea). *Rec. Aust. Mus. Suppl.* 4.
- Ponder, A.W., Vokes, E.H., 1988. A revision of the Indo-West Pacific fossil and Recent species of *Murex* s.s. and *Haustellum* (Mollusca: Gastropoda: Muricidae). *Rec. Aust. Mus. Suppl.* 8, 160 pp.
- Ponder, W.F., Warén, A., 1988. Classification of the Caenogastropoda and Heterostropha—A list of the family-group names and higher taxa. *Malacol. Rev. Suppl.* 4, 288–326.
- Powell, A.W.B., 1966. The molluscan families Speightiidae and Turridae. *Bull. Auckland Inst. Mus.* 5, 184 pp.
- Rehder, H.A., 1973. The Family Harpidae of the world. *Indo-Pac. Mollusca* 3, 207–274.
- Reyment, R.A., 1966. Preliminary observations on gastropod predation in the Western Niger Delta. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 2, 81–102.
- Robba, E., Sartono, S., Violanti, D., Erba, E., 1989. Early Pleistocene gastropods from Timor (Indonesia). *Mem. Sci. Geol. Padova* 41, 61–113.
- Röckel, D., Korn, W., Kohn, A.J., 1995. *Manual of the Living Conidae*. Vol. I, Indo-Pacific. Christa Hemmen, Wiesbaden, 518 pp.
- Rodda, P., 1994. Geology of Fiji. In: Stevenson, A.J., Herzer, R.H., Ballance, P.F. (Eds.), *Geology and Submarine Resources of the Tonga-Lau-Fiji Region*. South Pac. Appl. Geosci. Comm. Tech. Bull. 8, 131–151.
- Rudman, W.B., 1972. Structure and functioning of the gut in Bullomorpha (Opisthobranchia). Part II. Acteonidae. *J. Nat. Hist.* 6, 311–324.
- Salvini-Plawen, L.v., Haszprunar, G., 1987. The Vetigastropoda and the systematics of streptoneurous gastropods (Mollusca). *J. Zool.* A 211, 747–770.
- Sanders, H.L., 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102, 243–282.
- Schileyko, A.A., 1977. Materials on the morphology of the Naticoidae and problems of the taxonomy of the superfamily (Mollusca: Mesogastropoda). *Tr. Okeanol. Inst. Akad. Nauk SSSR* 108, 77–97, in Russian.
- Shimek, R.L., 1983. The biology of the northeastern Pacific Turridae. III. The habitat and diet of *Kurtziella plumbea* (Hinds, 1843). *Veliger* 26, 10–17.
- Shoup, J.B., 1968. Shell opening by crabs of the genus *Calappa*. *Science* 160, 887–888.
- Shuto, T., 1962. Buccinacean and volutacean gastropods from the Miyazaki Group. *Mem. Fac. Sci. Kyushu Univ. Ser. D Geol.* 12, 27–85.
- Shuto, T., 1969. Neogene gastropods from Panay Island, the Philippines. In: Kobayashi, T., Toriyama, R. (Eds.), *Geology and Palaeontology of Southeast Asia*, Vol. 6. Univ. Tokyo Press, Tokyo, pp. 1–250.
- Smith, S.A., Thayer, C.W., Brett, C.E., 1985. Predation in the Paleozoic: Gastropod-like drillholes in Devonian brachiopods. *Science* 230, 1033–1035.
- Sohl, N.F., 1987. Cretaceous gastropods: Contrasts between Tethys and the temperate provinces. *J. Paleontol.* 61, 1085–1111.
- Stanton, R.J., Powell, E.N., Nelson, P.C., 1981. The role of carnivorous gastropods in the trophic analysis of a fossil community. *Malacologia* 20, 451–469.
- Taylor, J.D., 1982. Diets of sublittoral predatory gastropods of Hong Kong. In: Morton, B.S., Tseng, C.K. (Eds.), *The Marine Flora and Fauna of Hong Kong and Southern China*. Proc. First Int. Mar. Biol. Workshop, Hong Kong, 1980, pp. 907–920.
- Taylor, J.D., 1984. A partial food web involving predatory gastropods on a Pacific fringing reef. *J. Exp. Mar. Biol. Ecol.* 74, 272–290.
- Taylor, J.D., 1985. The anterior alimentary system and diet of *Turricula nelliae spurius* (Gastropoda: Turridae). In: Morton, B., Dudgeon, D. (Eds.), *Proc. Second Int. Workshop on the Malacofauna of Hong Kong and Southern China*. Hong Kong Univ. Press, Hong Kong, pp. 175–190.
- Taylor, J.D., 1986. Diets of sand-living predatory gastropods at Piti Bay, Guam. *Asian Mar. Biol.* 3, 47–58.
- Taylor, J.D., 1993. Regional variation in the structure of tropical benthic communities: Relation to regimes of nutrient input. In: Morton, B. (Ed.), *Marine Biology of the South China Sea*, Vol. 2. Hong Kong Univ. Press, Hong Kong, pp. 337–356.
- Taylor, J.D., Shin, P.K.S., 1990. Trawl surveys of sublittoral gastropods in Tolo Channel and Mirs Bay; A record of change

- from 1976–1986. In: Morton, B. (Ed.), *The Marine Flora and Fauna of Hong Kong and Southern China*. Proc. Second Int. Marine Biological Workshop. Hong Kong Univ. Press, Hong Kong, pp. 857–881.
- Taylor, J.D., Morris, N.J., Taylor, C.N., 1980. Food specialization and the evolution of predatory prosobranch gastropods. *Palaeontology* 23, 375–409.
- Taylor, J.D., Kantor, Yu.I., Sysoev, A.V., 1993. Foregut anatomy, feeding mechanisms, relationships and classification of the Conoidea (= Toxoglossa) (Gastropoda). *Bull. Nat. Hist. Mus. London (Zool.)* 59, 125–170.
- Thiele, J., 1929. *Handbuch der systematischen Weichtierkunde*, Teil 1. Fischer, Jena, 376 pp.
- Tracey, S., Todd, J.A., Erwin, D.H., 1993. Mollusca: Gastropoda. In: Benton, M.J. (Ed.), *The Fossil Record 2*. Chapman and Hall, London, pp. 131–167.
- Van Couvering, J.A. (Ed.), 1997. *The Pleistocene Boundary and the Beginning of the Quaternary*. Cambridge Univ. Press, Cambridge, 296 pp.
- Van Osselaer, C., Bouillon, J., Tursch, B., 1993. Studies on Olividae XVII. Data on depth of burrowing, motion and substrate choice of some *Oliva* species. *Apex* 8, 151–158.
- Vaught, K.C., 1989. A classification of the living Mollusca. *American Malacologists*, Melbourne, FL, 189 pp.
- Vermeij, G.J., 1982. Gastropod shell form, repair, and breakage in relation to predation by the crab *Calappa*. *Malacologia* 23, 1–12.
- Vermeij, G.J., 1983. Shell-breaking predation through time. In: Tevesz, M.J.S., McCall, P.L. (Eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*. Plenum, New York, NY, pp. 649–669.
- Vermeij, G.J., 1987. *Evolution and escalation*. Princeton Univ. Press, Princeton, 527 pp.
- Vermeij, G.J., 1993. *A Natural History of Shells*. Princeton Univ. Press, Princeton, 207 pp.
- Vermeij, G.J., Zipser, E., Dudley, E.C., 1980. Predation in time and space: Peeling and drilling in terebrid gastropods. *Paleobiology* 6, 352–364.
- Walker, S.E., 1992. Criteria for recognizing marine hermit crabs in the fossil record using gastropod shells. *J. Paleontol.* 66, 535–538.
- Weber, H., 1924. Ein Umdreh- und ein Fluchtrefflex bei *Nassa mutabilis*. *Zool. Anz.* 60, 261–269.
- Weinkauff, H.C., 1875. *Catalog der Arten des Genus Pleurotoma*, s. str. *Jahrb. Dtsch. Malakozool. Ges.* 2, 273–305.
- West, T.L., 1990. Feeding behavior and functional morphology of the epiproboscis of *Mitra idae* (Mollusca: Gastropoda: Mitridae). *Bull. Mar. Sci.* 46, 761–779.
- West, T.L., 1991. Functional morphology of the proboscis of *Mitra catalinae* Dall 1920 (Mollusca: Gastropoda: Mitridae), and the evolution of the mitrid epiproboscis. *Bull. Mar. Sci.* 48, 702–718.
- Wilcoxon, J.A., Rodda, P., 1983. Calcareous nonnoplankton form the Veisari Sandstone, the Lami Limestone, and the younger strata at Nakasi. *Fiji Miner. Resour. Dep. Rep.* 36, 12 pp.
- Wilson, B.R., 1969. Use of the parapodium as a swimming organ in an ancillid (Gastropoda: Olividae). *Veliger* 11, 340–342.
- Wiltse, W.I., 1980. Effects of *Polinices duplicatus* (Gastropoda: Naticidae) on infaunal community structure at Barnstable Harbor, Massachusetts, USA. *Mar. Biol.* 56, 301–310.
- Yochelson, E.L., Dockery, D., Wolf, H., 1983. Predation on sub-Holocene scaphopod mollusks from southern Louisiana. *U.S. Geol. Surv. Prof. Pap.* 1283, 13 pp.
- Zann, L., 1980. *Living Together in the Sea*. T.F.H. Publ., Hong Kong.