FOOD SPECIALIZATION AND THE EVOLUTION OF PREDATORY PROSOBRANCH GASTROPODS

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ABSTRACT. Predatory prosobranch gastropods from the Neogastropoda, Tonnacea, and Naticacea feed upon a wide variety of invertebrate prey. They are an extremely diverse trophic group comprising some twenty-six families, most of which are found at tropical or subtropical latitudes. Empirical evidence suggests that competition has been an important process in shaping the diets and habitats of related species and, over a longer time period, of the different families. Nearly all the predatory families first appeared in a massive adaptive radiation in the late Cretaceous and it is probable that the major habitat and feeding adaptations were acquired at this time. The present-day steep latitudinal gradient in diversity and the importance of Buccinidae at high latitudes were developed during and since the Miocene. In the Campanian–Maastrichtian, and perhaps for most of the Upper Cretaceous, times, predators were more diverse at higher than at lower latitudes, which is the reverse of the present-day situation. The late Cretaceous diversification of gastropods coincided with similar radiations in other predatory and non-predatory groups of marine animals. The continental fragmentation/ diversity model probably best accounts for these massive changes in the composition of marine faunas.

MARINE prosobranch gastropods are one of the most diverse groups of animals. They encompass a broad array of feeding types, including algal grazing, suspension and deposit feeding, grazing upon sedentary animals, parasitism, and predation, and thus may be found at several trophic levels in marine communities. The diversity and functional range of gastropods is too great for them to be treated as a unified whole, and there is clearly little interaction in competitive or evolutionary terms between gastropods belonging to different trophic groups. The object of this paper is to examine the evolution of one trophic group, the predators. This group is extremely diverse, comprising some 5000–6000 species (Boss 1971), classified into twenty-six families (after Ponder 1973). In most areas of the world at least half of the gastropods present may be classified as predators. Predators are here defined as carnivores which seek out and consume generally whole prey organisms (Curio 1976). Predatory gastropods are also numerically important in many shallow-water, particularly tropical, communities.

We know that most groups of gastropods classified today as predators did not appear until the late Cretaceous (Sohl 1964*a*) and their appearance formed part of the 'Mesozoic marine revolution' recently documented by Vermeij (1977*a*) and contributed greatly to the apparent steep increase in diversity of marine benthos towards the end of the Mesozoic described by Valentine (1969, 1973). This relatively rapid evolution of predatory gastropods, which feed today mostly upon invertebrate prey, would have had important effects upon the structure of marine benthic communities. In this paper we document the diversification of the predatory gastropod families, and attempt to relate their evolution and present high diversity to dietary and habitat specializations.

Predatory prosobranch gastropods are found today in a few families of the order Mesogastropoda, but most species are from families of the order Neogastropoda. The mesogastropod groups concerned are the superfamily Naticacea and the five families of the Tonnacea (Cymatiidae, Tonnidae, Bursidae, Cassididae, and Ficidae). Some families from both the Archeogastropoda and Mesogastropoda are carnivores, feeding by grazing upon sedentary animals such as sponges, ascidians, and coelenterates. As this behaviour is little different from grazing upon plants, these families are not considered here, although we acknowledge that there is a gradation of feeding habits from omnivorous browsers to hunting predators. Some species from the Neogastropoda and Tonnacea are not strictly predators, but in most cases they belong to families in which the

majority of other members show predatory behaviour. The gastropod subclass Opisthobranchia also contains many predatory species, but many are either shell-less or possess very fragile shells and their geological history is difficult to evaluate.

When compared with algal grazing, for example, the act of predation involves a complex sequence of behaviour on the part of the predator. This behaviour may consist of processes of search, evaluation, pursuit, capture, immobilization, penetration, and consumption (Menge 1974; Black 1978). Predators differ in anatomical and behavioural adaptations from gastropods of other feeding categories. Ponder (1973) has documented many of the features by which predatory Neogastropods differ from other prosobranchs. These differences mainly involve modification and elaboration of the foregut and radula, including the formation of an extensible proboscis, a well-developed siphon, and the elaboration of the chemo-sensory osphradium by an increase in the surface area by folding. The nervous system is modified, with the concentration of the ganglia into the nerve ring around the oesophagus. Also with the Neogastropoda many of the major anatomical differences between the families are centred upon the feeding structures. Similar modifications are seen in the mesogastropod superfamilies Naticacea and Tonnacea. It was thought that the neogastropods were derived from the higher mesogastropods, but it is now recognized that the anatomical similarities are the results of convergence (Ponder 1973).

COMPETITIVE INTERACTIONS BETWEEN PREDATORS

In studies of groups of closely related species (guilds, taxocenes) of predatory gastropods in such families as the Conidae (Kohn 1959, 1968; Kohn and Nybakken 1975; Leviten 1976, 1978), Muricidae (Taylor 1976, 1977, 1978a; Bernstein 1974), Terebridae (Miller 1970), Melongenidae and Fasciolariidae (Paine 1962, 1963, 1966a), and Buccinidae (Nagai and Suda 1976), species have been shown to divide available ecological resources, frequently by fine differences in habitat or food. Nevertheless, in tropical environments there is often a good deal of habitat overlap between species, and Kohn (1971, p. 343) concludes that 'the strategy of specializing upon different prey species in the same microhabitat is more advantageous to the co-occurring species than specializing upon different microhabitat patch types'. Frequently, clear dietary differences exist between similar species occupying similar microhabitats. The habitats and diets amongst coexisting species are thought to have arisen over ecological and evolutionary time by competitive interactions between species, resulting in specializations which effectively partition the available resources between the coexisting species. There has been considerable controversy concerning the relative roles of competition, predation, disturbance, and other factors in organizing communities (Connell 1975, 1978). However, Menge and Sutherland (1976) point out that the relative importance of competition in organizing guild structures will change from lower to higher trophic levels; with competition expected to be much more important at higher trophic levels.

The evidence for historical competition is necessarily largely circumstantial, but recently Kohn (1978) has shown that *Conus miliaris* at Easter Island has a much broader diet than when it coexists with other *Conus* species in other parts of its geographic range. Similarly, a muricid *Cronia margariticola* has a broader diet and habitat at Hong Kong than in the more central parts of its range, where more potential predators are present (Taylor 1980). The ideas of food and habitat division can be extended more broadly to the family level. If one of the main mechanisms resulting in habitat and dietary specializations between species is the competitive interaction between taxa, then the specializations of gastropod families are the sum of the specializations of the constituent species, which have arisen over evolutionary time.

Diets of predatory gastropods

In view of the fact that many of the main anatomical differences between neogastropod families concern the structures associated with feeding and digestion, it is clear that a knowledge of the diets of these families is essential to an understanding of their adaptive radiation and evolution. However, except for the Naticacea and Muricidae, we have little direct evidence of the diet of fossil predatory gastropods and our interpretation of the habits of fossil gastropods depends upon information from

related Recent species. Although the diets of some families are quite well known, for instance the Conidae (Kohn 1959, 1968; Kohn and Nybakken 1975; Leviten 1976, 1978), Fasciolariidae (Paine 1963, 1966a), and Muricidae (Bernstein 1974; Taylor 1976, 1978a), much of the information on other families is widely disseminated throughout the literature and is often highly anecdotal in nature. The detailed quantitative information assembled for Conidae by Kohn and his associates is unequalled in any other family. The available information on the diets of predatory prosobranchs is summarized in Table 1. For many families the data are woefully sparse, and for some, namely the

TABLE 1. Major prey items in the diets of predatory prosobranch families. The most important prey for each family in heavy type.

predator families	Gastropods	Bivalves	Sedentary polychaetes	Errant polychaetes	Sipunculids	Enteropneusts	Decapod crustacea	Small crustacea	Cirripedes	Echinoids	Asteroids	Holothurians	Ophiuroids	Ascidians	Priapulids	Brachiopods	Hydroids	Corals	Fish	Foraminifera	Ostracods	Algae	Carrion
NATICACEA	✱	✱																		*	*		
CYMATIIDAE	*	✱	*	*		*				*	*	*		*		*						*	*
BURSIDAE			*	✱	*					*	*		*										
CASSIDIDAE										✱													
TONNIDAE												✱											
FICIDAE										*													
MURICIDAE	✱	✱	*	*	*		*	*	✱	*		*				*		*					*
CORALLIOPHILIDAE																		✱					
COLUMBELLIDAE			*	*				*						*			*					*	*
BUCCINIDAE	*	✱	✱	✱	*		*	*	*	*				*	*								✱
MELONGENIDAE	✱	✱																					
NASSARIIDAE			*	*				*															✱
FASCIOLARIIDAE	✱	✱	✱					*															*
VASIDAE			✱	*	✱																		
VOLUTIDAE	✱	✱																					
OLIVIDAE	*	✱	*																	*	*		*
HARPIDAE							✱																
MARGINELLIDAE	✱																			*			
MITRIDAE	*				✱																		
VEXILLIDAE	*																						
CANCELLARIIDAE	*																						
TURRIDAE			✱	*																			
CONIDAE	✱	*	✱	✱		*													✱				
TEREBRIDAE			✱	✱		*																	

Ficidae, Cancellariidae, and Columbariidae, are virtually non-existent. However, for the other families some broad dietary patterns emerge which are instructive in considering the evolution of predators.

The mesogastropod families Cassididae, Tonnidae, Bursidae, and Cymatiidae are the only families which regularly eat echinoderms; the Cassididae eating echinoids (Moore 1956; Hughes and Hughes 1961), the genus *Charonia* of the Cymatiidae eating asteroids, and holothurians (Percharde 1972; Thomassin 1976), the Tonnidae eating holothurians (Grange 1974), and the Bursidae eating, amongst other things, ophiuroids, echinoids, and crinoids (Taylor 1978a). Crustacea are eaten by only a few families; the Harpidae feed upon decapods (Rehder 1973), whilst a few species of Buccinidae, Nassariidae and Muricidae regularly take smaller free-living crustacea. Only the Buccinidae and Muricidae eat barnacles. Sipunculids are the main prey of the species of Mitridae so far studied (Kohn 1970; Taylor 1976, 1978a), but are eaten by only a relatively small number of species from other families.

Polychaetes are amongst the most diverse groups of macroinvertebrates and they figure extensively in the diets of predatory gastropods. The worms differ considerably in size, habits and mobility and this variety is reflected in different predatory gastropod families tending to take different types of polychaete prey. Some families eat only sedentary polychaetes, such as the Sabellidae and Terebellidae, others take the predatory errant groups such as the Nereidae and Eunicidae. Some families are polychaete specialists, and many species of the families Conidae, Terebridae and Turridae eat polychaetes exclusively, whilst species in other families may eat polychaetes regularly but not exclusively.

Molluscs are also eaten by many gastropod families and here again there is a broad variation in the type of mollusc taken depending upon the size, mobility, and habits of the prey and predator. Thus, although the Muricidae generally eat sedentary molluscs such as epifaunal bivalves and sedentary or slow-moving gastropods, other families, such as the Naticidae, Cymatiidae, Volutidae, and Conidae can feed upon more mobile gastropods. There is some overlap in diet of these dominantly predatory families with the browsing carnivores of the Archaeo- and Mesogastropoda. For instance, species of the Neogastropod family Coralliophilidae feed exclusively upon coelenterates (Robertson 1970; Hadfield 1976) as do a few species of Muricidae (Taylor 1976, 1978a) and Columbellidae (Bandel 1974). Some Cymatiidae and Vexillidae feed upon ascidians (Laxton 1971; Morton and Miller 1968), whilst some Columbellidae and *Apollon natator*, a species of Cymatiidae, feed upon algae (Bandel 1974; Marcus and Marcus 1962; Taylor 1980). Additionally Scheltema (1964) reports *Nassarius obsoletus*, a species with a crystalline style, as a deposit feeder.

Many gastropods will feed upon carrion when available; the best-known families having this habit are the Nassariidae and Buccinidae (Brown 1971; Lloyd 1971; Taylor 1978b). However, many observations have been made in unnatural conditions such as aquaria and baited traps (Arnaud 1970) and the natural diet of some of the species, such as *Buccinum undatum*, also includes a wide variety of live prey, particularly polychaetes (Taylor 1978b). Similar observations have been made upon the genus *Bullia* (Nassariidae) in which carrion is taken when available (Brown 1971), but gut samples of *Bullia mauritiana* reveal a diet consisting largely of live-taken polychaetes and small, sand-dwelling crustacea. Some *Conus* species are well known for their ability to catch small fish, especially gobies (Kohn 1959; Kohn and Nybakken 1975). Unexpected prey items have been reported for some predators, for example *Priapulus* is eaten by *Neptunea antiqua* (Taylor 1978b) and dogfish egg cases bored by *Natica* (Ansell 1961). The prey most commonly taken by predatory gastropods are polychaetes and bivalve molluscs which are eaten by species from twelve and nine families respectively. The Cymatiidae, Bursidae, Muricidae and Buccinidae might be considered the more generalist families in taking a wide variety of major prey categories, whilst other families such as the Mitridae, Cassididae and Turridae appear to be relatively specialized.

Methods of attack

An extensive array of behavioural and mechanical devices is used by predatory gastropods for immobilizing and gaining access to their prey.

Some predators merely thrust their proboscis into their prey, and down the tubes of animals such as sedentary polychaetes or vermetid gastropods, or wait for bivalve prey to open before inserting their proboscis. Species of Melongenidae, Fasciolariidae, Buccinidae, and some Muricidae wedge the lip of their shell aperture between the valves of bivalve prey allowing the insertion of the proboscis; Nielsen (1975) illustrates this for *Buccinum undatum*. This behaviour has been elaborated in some Melongenidae and Muricidae where species of *Busycon* and *Muricanthus fulvescens* chip the edges of thicker-shelled bivalve prey until there is sufficient space to insert the shell lip and proboscis between the valves (Carriker 1951; Paine 1963, 1966*a*; Wells 1958). In the Volutidae (Ponder 1970) and some Olividae (Marcus and Marcus 1959; Olsson and Crovo 1968) the bivalve or gastropod prey is enveloped in the large foot until apparently asphyxiated and partially open. In the Harpidae the crustacean prey is held in the propodium and foot, and a sticky fluid released which envelops and immobilizes the prey. The drilling of shelled prey is known from three predatory prosobranch taxa, the Naticacea, Muricidae, and the Cassididae. Day (1969) suggests that *Argobuccinum* of the Cymatiidae could drill holes, but there is no evidence of this from actual feeding observations. Similarly, another cymatiid, *Monoplex australasiae*, has been reported as drilling bivalves, but this was not confirmed in a detailed study by Laxton (1971). Some species of the mesogastropod family Capulidae can also drill bivalves (Orr 1962; Matsukuma 1978) but these species do not kill the bivalve and can be classed as parasites. The drilling process in the Muricidae has been reviewed by Carriker and van Zandt 1972, and Carriker and Williams 1978, and in the Naticidae by Ziegelmeier (1954). Drilling of echinoid tests by the Cassididae has been shown by Hughes and Hughes (1971). The shell-drilling process in the Muricidae and Naticacea involves mechanical radular scraping combined with chemical secretions from the accessory boring organ, in the foot of Muricidae and in the proboscis of Naticacea. A recent review by Carriker and Williams (1978) suggests that a combination of enzymes, inorganic acid, and chelating agents is involved in the chemical phase of shell penetration by both naticid and muricid gastropods.

The use of toxic secretions to immobilize prey is known in several families; some species of Cymatiidae squirt a venom at their mollusc prey (Houbrick and Fretter 1969), and the vexillid *Thala floridana* uses a toxic secretion to immobilize prey after the proboscis has touched the prey (Maes and Raeihle 1976). The toxoglossan families Turridae, Terebridae, and Conidae utilize a toxic secretion produced by the venom gland. The venom is injected into the prey following puncture of the victim by the dart-like radula teeth (Kohn 1959; Pearce 1966). In some Terebridae there is no venom apparatus, and in *Terebra gouldii* the proboscis is applied closely to the enteropneust prey and rapidly everted (Miller 1975). In some groups, particularly those feeding upon errant polychaetes, such as the Buccinidae, Muricidae, Bursidae, and Vasidae the methods of attack and prey immobilization are unknown, although venoms have been reported (Pearce and Thorson 1967; Fänge 1958).

Habitats of predators

Studies of coexisting similar species of predatory gastropods such as the Conidae (Kohn 1959, 1968; Kohn and Nybakken 1975), Melongenidae and Fasciolariidae (Paine 1962, 1963), and Muricidae (Taylor 1976, 1978*a*; Bernstein 1974) have shown differences in habitat occupation patterns between potentially competing species. These differences involve such factors as substrate preferences, zonation along some intertidal gradient, such as wave exposure or length of emersion, differences in microtopography, or by size of the predator, allowing exploitation of different sizes of microhabitat. Although most studies have been in the tropics, Nagai and Suda (1976) show clear habitat separation amongst similar species of *Neptunea* in the Bering Sea, and Okutani (1968) shows depth partitioning amongst species of Volutidae and Buccinidae in Sagami Bay, Japan. Some circumstantial evidence for broader-scale partitioning comes from the two toxoglossan families Terebridae and Conidae. Both families are probably descended from a common ancestor; they have similar food-gathering apparatus and commonly occur at the same localities. However, the two families show quite different habitat preferences; the Terebridae are entirely confined to sandy substrates, whilst the Conidae occur in a number of habitats including rubble, hard reef-platform, and coral areas, with only a few species of *Conus* occurring in the same habitats as the Terebridae.

Most of the twenty-six families of predatory gastropods live partly upon soft substrates; only thirteen families contain species which regularly occur upon hard substrates, and of these only the Coralliophilidae, which live upon skeletonized coelenterates, are exclusive to hard substrates. The Muricidae is the most diverse family which regularly inhabits hard substrates; its large subfamily Thaiinae has diversified extensively upon rocky intertidal shores where the species are important members of food webs throughout the world (Connell 1961, 1970; Paine 1966b; Taylor 1976; Luckens 1970; Phillips 1969). Other families containing species which regularly occur upon hard substrates are the Cymatiidae, Bursidae, Buccinidae, Columbellidae, Fasciolariidae, Mitridae, Vexillidae, Turridae, and Cassididae. By contrast, the families Olividae, Terebridae, Harpidae, Ficidae, Tonnidae, and Naticidae are confined exclusively to soft substrates. Species of the Marginellidae and Buccinidae are found in freshwater habitats in south-east Asia (Jutting 1956; Brandt 1974).

Size variations in predators

Predatory gastropods exhibit a large variation in size from the large volutid *Melo* (500 mm) and the melongenid *Syrinx* (700 mm) down to tiny Turridae at 1–4 mm. Morphological differentiation between guilds of coexisting species presumably reflecting resource partitioning has often been inferred to be the direct evolutionary consequence of competition. Size differences between predators may allow division of resources by size, smaller predators in general taking smaller prey items which are generally more abundant and often occur in monospecific aggregations. Large predators, which tend to feed upon larger prey, are usually less specialized in diet (Schoener 1974) as demonstrated for *Pleuroploca* in the Fasciolariidae by Paine (1963). Size differences between coexisting species of intertidal muricid gastropods, probably reflecting the dietary differences, are illustrated in text fig. 1;
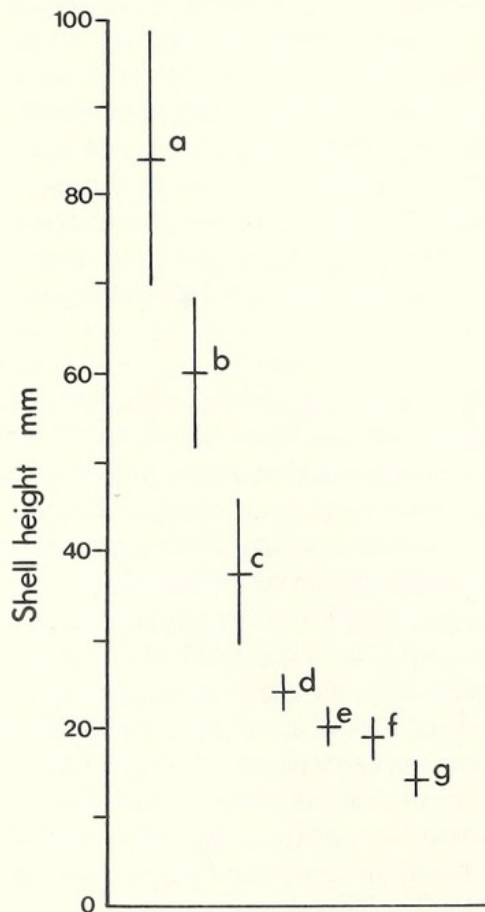
TEXT-FIG. 1. Shell height (mean and standard deviation) of seven coexisting species of muricid gastropod on a shallow sublittoral rocky shore in Tolo Channel, Hong Kong (from Taylor 1980). Species a. *Chicoreus microphyllus*; b. *Chicoreus brunneus*; c. *Mancinella echinata*; d. *Drupella rugosa*; e. *Drupella contracta*; f. *Morula spinosa*; g. *Cronia margariticola*.

although other guilds of species in other predatory gastropods, for example the Conidae, need not show such differences (Leviten 1978). Size differences between taxa may allow greater division of habitat space and small species can occupy microtopographic features of the substrate unavailable to larger species. Large species frequently forage over a number of habitat types, each representing the sole habitat for smaller species.

Other selection pressures may be influencing these size adaptations, for small species are vulnerable to a greater range of predators and environmental stresses than larger species, and the latter may effectively 'grow out' of predation pressure. In *Conus* species, small body size is a liability in sublittoral habitats where predation is intense and large body size is a disadvantage on intertidal benches where predation is less but wave action is strong and shelter becomes important (Leviten 1978). Some families such as the Volutidae, Melongenidae, Muricidae, Vasidae, and Tonnidae contain many large species, whilst others such as the Marginellidae and Turridae are dominated by rather small species. In other families there is more size variation, but the over-all size characteristics of the various families tend to reflect the major niche dimensions of the particular family.

DISTRIBUTION OF PREDATORY GASTROPODS

We know that in common with many other animal groups (Stehli 1968) there are strong latitudinal gradients in the species and family diversities of predatory gastropods, and also that there are large changes in the composition of predatory faunas with latitude (Taylor and Taylor 1977). Hence, in order to interpret the changes in diversity and taxonomic composition of predatory gastropod faunas during and since the Cretaceous we must examine the present-day patterns of gastropod distribution in some detail. It has recently been argued by Osman and Whitlach (1978) that the latitudinal species diversity gradient is a function of the spherical shape of the Earth. They pointed out that the area of the Earth's surface occupied by the tropics and subtropics is much greater per degree of latitude than the extratropical zones, and will thus support more species. However, for continental shelf habitats this argument does not hold, because most continental margins trend north–south and the shallow shelf areas are actually greater at higher than at lower latitudes. Osman and Whitlach (1978) have further argued that because of the shape of the Earth there is greater spatial separation and hence greater isolation of tropical faunas, which encourages higher diversity. Higher-latitude faunas are supposed to be less spatially separated, with consequently greater faunal mixing and lower diversity. In fact, tropical faunas exhibit great similarity over large areas, witness the enormous, but uniform Indo-Pacific marine province extending from East Africa to the central Pacific. Moreover, Arctic faunas are not as uniform as might be expected; for instance, Clarke (1974) has documented the considerable east–west changes in the molluscan faunas of the northern North Atlantic and Baffin Bay.

Gastropod faunas were examined from localities throughout the world, but in the interests of simplicity only the distributions for north–south trending continental margins are presented here. The data used were extracted from monographs and faunal lists which vary in quality and completeness, but the over-all trends are clear. Predictably, the number of families and species of predatory gastropods show a strong latitudinal gradient increasing towards the Equator. This trend is illustrated in text-fig. *2a–d* for a number of continental margins for which adequate faunal information is available. A rather rapid change in family richness at around latitude 40° N. is particularly marked in the western and eastern Atlantic and this has been discussed by Taylor and Taylor (1977). The two other continental margins examined show a more even diversity gradient. The diversity of species within families was estimated in two ways, by the Shannon diversity index H' (Pielou 1977) and by the rarefaction method (see Raup 1975). Both H' and rarefaction curves show similar trends, with a steep decline in diversity towards higher latitudes (text-fig. *3a–d*). In the eastern Atlantic the rarefaction curves show two groupings, with a high-diversity group from sites south of latitude 35–40° N. and a low-diversity group from stations north of this latitude (Taylor and Taylor 1977, fig. 4). Similar groupings are seen in the western Atlantic, but more gradual changes in diversity are seen on the Pacific coast of north America and upon the Atlantic coast of South America.
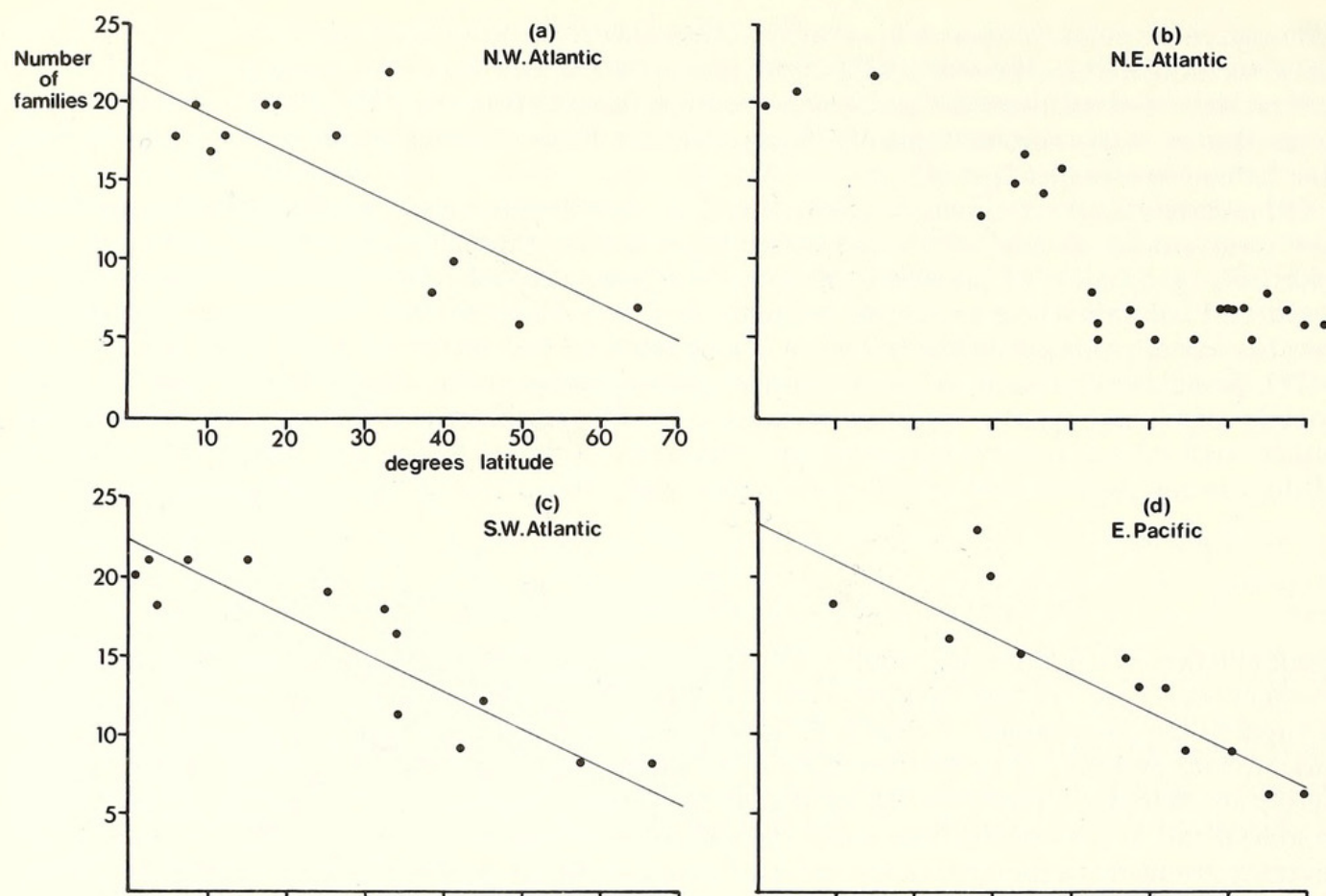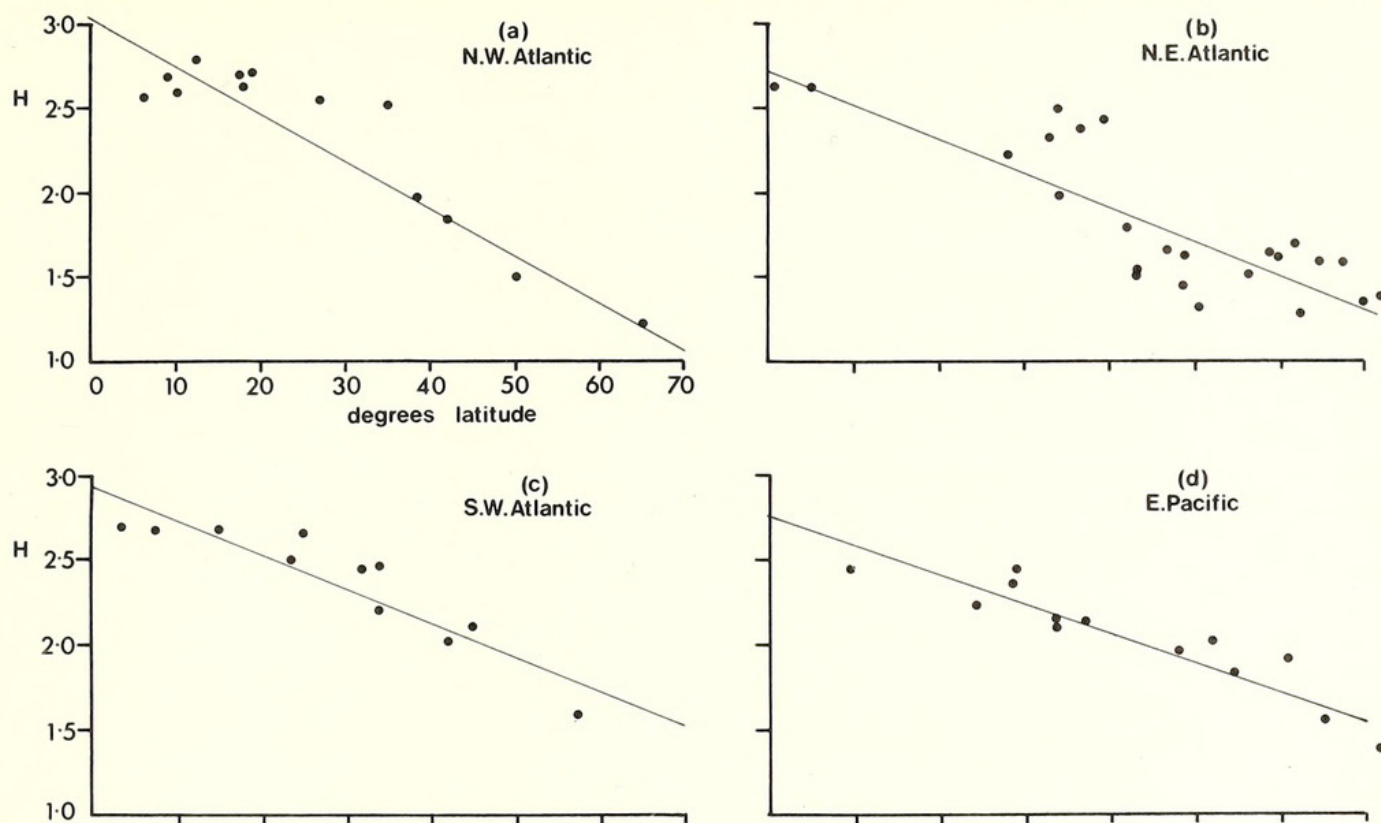
TEXT-FIG. 2a–d. Variation in the numbers of Recent predatory gastropod families with latitude along four continental margins. Lines are linear regressions. Source of data:

a. NW. Atlantic: Abbott (1958), Altena (1975), Coomans (1962), Dall and Simpson (1901), Houbrick (1968), Johnson (1915), Jong and Kristenson (1965), Macpherson (1971), Nowell-Usticke (1959), Olsson and McGinty (1958), Perry and Schwengel (1955), Porter (1974), Provancher (1891).

b. NE. Atlantic: Bellon-Humbert (1971), Cadée (1968), Cornet and Marche-Marchad (1951), Dautzenberg (1898), Dautzenberg and Durouchoux (1913), Fischer (1899), Geerts (1969), Hägg (1905), Knight (1901), Leche (1878), MacAndrew (1850), MacAndrew and Woodward (1864), Marche-Marchad (1958), Marine Biological Association (1957), Nobre (1932, 1937), Norman (1879, 1902), Ohdner (1915), Pasteur-Humbert (1962), Rendall (1956), Sneli (1974), Sparck and Thorson (1933), Thorson (1941, 1944), Tomlin (1923), Tomlin and Shackleford (1914, 1915).

c. SW. Atlantic: Barattini (1951), Carcelles (1950), Castellanos (1967), Matthews and Kempf (1970), Powell (1951), Rios (1975), Scarabino (1977).

d. E. Pacific: Adams (1852), Bernard (1970), Bishop and Bishop (1973), Dall (1874), DuShane and Poorman (1967), Eyerdam (1924), Keen (1964), MacGinitie (1959), McLean (1961, 1969), Oldroyd (1924–1927), Smith and Gordon (1948), Willett (1919).

Faunal composition

On all the north–south gradients there is a distinct change in faunal composition at the family level. At high latitudes two families, the Buccinidae (as Buccinulidae in many Antarctic references) and the Turridae, contain proportionally the highest number of species, whilst at lower latitudes species are much more equitably distributed amongst more families. The rise in importance of the Buccinidae along a number of north–south continental margins is shown in text-fig. 4a–d. At high latitudes approximately 45% of predatory species belong to the Buccinidae, but at low latitudes they form only about 5% of species. There is a rapid change in the slope of the curves at around latitudes 35–40° N. and S. The comparative success of the Buccinidae at high latitudes has been attributed to their

TEXT-FIG. 3*a-d*. Variation in the diversity of species (H′, Pielou 1977) within Recent predatory gastropod families along four continental margins. Lines are linear regressions. Data as for text-fig. 2*a-d*.

generalist feeding habits (Taylor 1978*b*). The family Turridae is relatively diverse at all latitudes but together with the Buccinidae it is the most important predatory family at high latitudes (text-fig. 5). The few data that are available suggest that the Turridae feed mainly upon deposit-feeding polychaetes (Pearce 1966; Taylor 1979; Shimek 1977). Thus, although specialized, they are exploiting a stable resource in a strongly seasonal environment while the food-supply to algal grazers or suspension feeders is strongly limited during the winter months.

Depth distribution

As well as the latitudinal differences in distribution between predatory families there are pronounced differences along the depth gradient. The total number of prosobranch gastropods decreases into deeper water and this is also true of the predatory species. Clarke (1962) catalogued the species recorded from abyssal depths (greater than 1828 m, originally 1000 fms.) and although seventeen families of predatory gastropods have been recorded, six of these are represented by a single species. Most of the other species belong to just a few families with 58% of them belonging to the Turridae, 13% to the Buccinidae, 7% to the Naticacea, 5% to the Muricidae, and 4% to the Tonnidae. This general pattern is reflected in individual samples, for instance on the Deutschen Tiefsee Expedition (Thiele 1925), in virtually all the samples taken below 500 m at least 50% of the species are Turridae. A similar pattern was described by Okutani (1968) in a survey of archibenthal and abyssal gastropods from Sagamai Bay, Japan, where 34% of the predatory species belong to the Turridae and 24% to the Buccinidae. As yet, little taxonomic information is available from recent deep-sea work using more efficient sampling techniques, but Rex (1976) reports that between 478 and 4862 m in the western Atlantic 74·5% of predatory prosobranch species belong to the Turridae. Predator diversity increases to a depth of about 2500 m and then declines towards the abyssal plain where most gastropods are deposit feeders. Knudsen (1964) reviews the gastropods found from hadal depths (below 6000 m) where only fourteen species are known and of these six are predators belonging to the Naticidae, Cancellariidae, and Buccinidae. The Turridae, so diverse at abyssal depths, are notably absent.
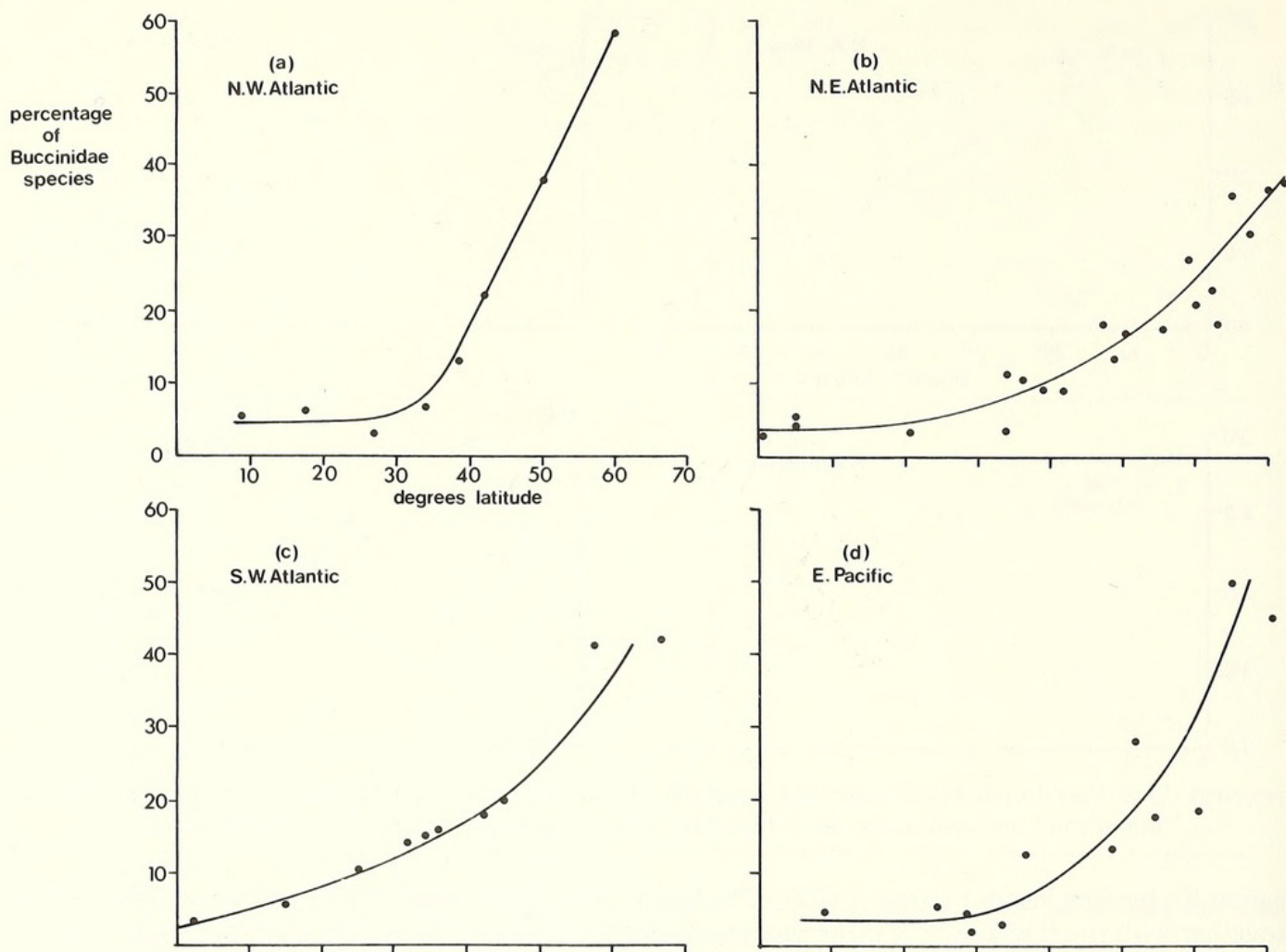
TEXT-FIG. 4a–d. Latitudinal variation in the percentage of Buccinidae species out of the total predatory gastropod fauna for Recent samples along four continental margins. Curves fitted by eye. Data extracted from references cited in text-fig. 2a–d.

ORIGIN OF PREDATORY GASTROPODS

The predatory prosobranch gastropods as discussed in this paper comprise three major groups, the two superfamilies Naticacea and Tonnacea of the Mesogastropoda and the families of the order Neogastropoda. The phylogenetic relationships between and within these three groups are imperfectly understood, but our ideas concerning the origins and relationships of the three groups are briefly reviewed following.

Naticacea. The Naticacea have the longest history of any of the predatory groups and are known back to at least the lower Jurassic. The superfamily is characterized by unornamented, globular, rather featureless shells; this makes their ancestry difficult to ascertain. Moreover, the anatomical features of living species have so far given no real clues to relationship (Fretter and Graham 1962). The Triassic to Jurassic family, the Coelostylinidae, is a probable stem group for many later mesogastropod families, and includes many species with globular, unsculptured shells, very similar in morphology to those of the naticids. We believe that the naticids, along with several other groups of mesogastropods, may have had their origins with this family.

Tonnacea. The Upper Jurassic–Cretaceous family Columbellinidae have shells with distinct anterior and posterior apertural canals, frequently with denticulate outer and inner apertural lips. Upper Jurassic members of the family vary from forms with constricted and then flared apertures, resembling Cymatiidae, through others where the internal shell layer covers one side of the outside of the shell, to an extreme where in the adult state the outer shell layers are completely covered by inner shell layers, indicating extensive reflexing of the mantle over

the dorsal surface of the shell. Columbellinids from the Aptian and Albian include forms with shell characters resembling those of the Cymatiidae, Bursidae, and Cassididae and the derivation of these families from the Columbellinidae is probable. The Cypraeacea (excluding the Triviidae and Eratoidae) were probably derived from those columbellinids in which the extensive reflection of the mantle occurred. The Columbellinidae were in turn probably derived from *Diarthema*, a Middle Jurassic genus placed in the Strombacea, which as well as having many aporrhaid features, has incipient anterior and posterior canals, an apertural constriction, and an extension of the inner shell layer to form an expanded inner lip. The Columbellinidae probably thus shared a common ancestor with the Strombacea, and in turn gave rise to the Cypraeacea and Tonnacea.

Neogastropoda. In his broad survey of the Neogastropoda Ponder (1973) was unable to find anatomical justification for the present superfamilial divisions of the Neogastropoda. His revised classification, which has yet to gain acceptance, proposes three broad divisions which he calls superfamilies; the Conacea, comprising the toxoglossate families Terebridae, Turridae, and Conidae; the Cancellariacea with one family and the Muricacea consisting of all the other seventeen families. The three superfamilies differ considerably in the organization of the foregut, and in Ponder's view each evolved separately from an early neogastropod ancestor before the elongation of the snout to form a proboscis. Although the Neogastropods have traditionally been regarded as originating by progressive elaboration from the higher Mesogastropods such as the Tonnacea, Ponder (1973) presented clear evidence that indicates that the two groups have independent origins and to some extent show parallel development of anatomical features. On the basis of a number of anatomical characters shared between the Neo- and Archaeogastropoda, but not the Mesogastropoda, Ponder proposed that the Neogastropoda were derived from an Archaeogastropod or primitive Mesogastropod ancestor. Following Knight *et al.* (1954), Ponder thought that the extinct family Subulitidae had some of the characters required in an ancestral Neogastropod. These included an anterior notch, sometimes a columellar fold and a non-nacreous shell. Knight *et al.* (1954) derived the Nerinacea, Muricacea, and Buccinacea from the Subulitacea and suggested that in turn the Nerinacea gave rise to the Volutacea and Conacea. The link suggested between the Neogastropods, Subulitacea, and Nerinacea seems to depend mainly on the presence of an anterior canal and columellar folds. The anterior canal has certainly evolved more than once amongst unrelated groups of prosobranchs such as the Cerithiacea, Purpurinidae, and Tonnacea, and although an important feature it is not in itself sufficient reason for linking the groups. In fact there is no certainty of the relationship between the Nerinacea and the Subulitacea. The Nerinacea typically have strong columellar folds and an opisthobranch-like opisthocline aperture. The internal folds could be interpreted as having supported a channelled ciliated mantle resembling the mantle caecum and similar structures in the opisthobranchs (Fretter and Graham 1962). The heterostrophic protoconch reported for some Nerinacea (Bigot 1896) which might further support their placement in the Opisthobranchia, has not been confirmed; nevertheless, this character has been independently evolved in other gastropods.

A more likely derivation of the Neogastropods would seem to us to lie in the middle Triassic to Upper Cretaceous family the Purpurinidae, many of which have an anterior notch and a range of apertural shapes and
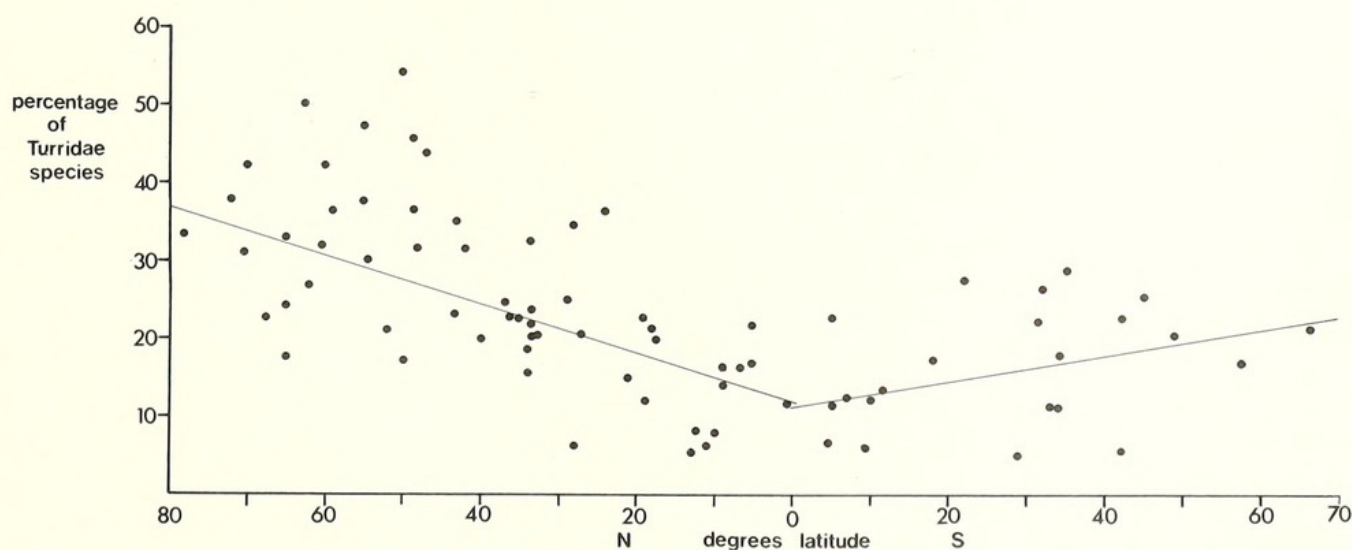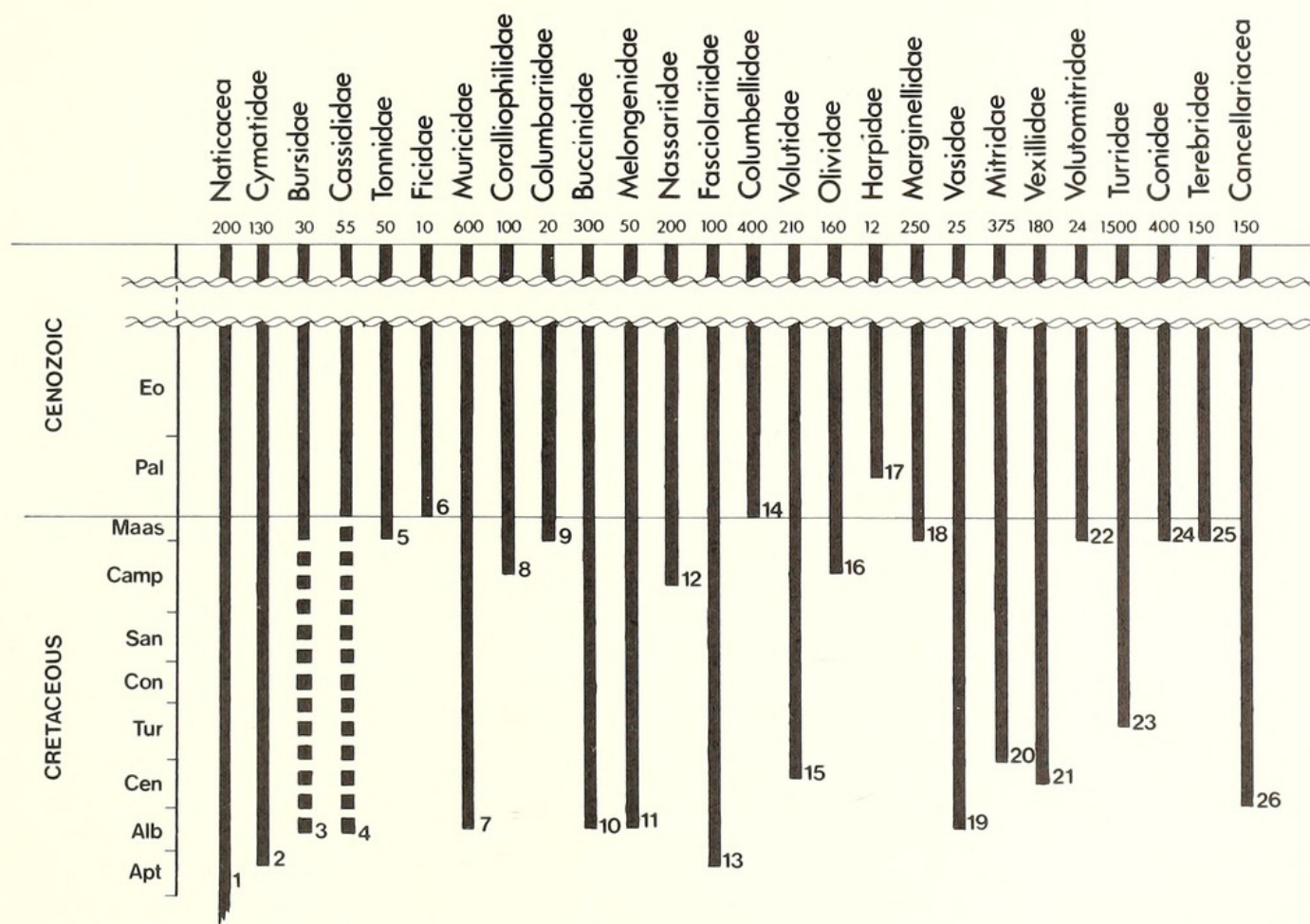

TEXT-FIG. 5. Variation in the percentage of Turridae species in the total predatory gastropod fauna with latitude for Recent faunas. Lines are linear regressions. Data mainly from sources listed in text-fig. *2a–d.*

shell sculpture comparable to that of the Neogastropoda. As with the Naticacea, it seems most likely that the Purpurinidae are an offshoot of the Coelostylinidae. We suggest that the Cancellariacea, Conacea, and Muricacea (*sensu* Ponder 1973) share a common ancestor in the Purpurinidae. An initial branching separated the Cancellariacea, with their distinctive anatomical features and radula from the common ancestor of the Muricacea and the Conacea (text-fig. 6). Some Purpurinidae are very similar in shell morphology to cancellariids. The Muricacea and Conacea have a number of features in common and some Turridae show close resemblances in shell morphology and anatomical characters, other than the anterior alimentary system, with the Fasciolariidae. However, the second major split in the evolution of the Neogastropods involved the separation of the Conacea from the Muricacea, the two groups differing mainly in the organization of the anterior alimentary system. The common ancestor of the two families should have possessed five teeth in each radular row, a feature found in some living Turridae but not in the Muricacea which have three teeth or less.

TEXT-FIG. 6. Summary of possible relationships amongst the Neogastropoda and Naticacea with the wholly extinct families Coelostytinidae and Purpurinidae. 1. Number of branches for the Coelostylinidae and Purpurinidae merely indicates a number of forms. 2. Muricacea *sensu* Ponder (1973), i.e. includes all Neogastropod families except the Conacea and Cancellariacea.

ANALYSIS OF FOSSIL GASTROPOD FAUNAS

The first records of species recognizable as belonging to the various predatory families are shown in text-fig. 7 together with the relevant references. The assignment of some of the early species to families is rather subjective, for members of related families tend to resemble each other more closely, than later in their evolutionary history. Correct assignment to a family often depends upon tracing the details of species lineages, and in many cases this information is just not available for Cretaceous gastropods. Modifications to the ranges shown in text-fig. 7 are to be expected but the broad pattern of diversification is unlikely to be greatly altered. More interesting perhaps than recording the first appearance of the different families, is the pattern of the incorporation of these families into faunas and communities and how these patterns have changed with time. For instance, some families appeared relatively early in the Upper Cretaceous but were neither diverse nor numerically very important until much later, whilst other families apparently diversified rapidly. A basic assumption made here is that fossil gastropods which have similar shell morphology to their living relatives had similar habits. Although studies of the functional morphology of the gastropod shell are still in their infancy, Vermeij (1973) and Linsley (1977) have shown a strong relation of shell shape to habit. Moreover some characters of shell shape are related to modifications of the food-gathering apparatus; for example, the fish-eating species of *Conus* generally have broad, flared apertures when compared with polychaete-eating species. More direct evidence comes from the appearance of muricid-like drill holes in bivalves of the Albian, at the same time as the first unambiguous muricid gastropods (see below) which confirms the assumption.

Data for the study were obtained from many monographs and faunal lists, and the sources are listed with each diagram. The data vary considerably in quality and completeness, a problem particularly acute in fossil faunas from both very high and very low latitudes. However, some broad patterns emerge which transcend this rather variable data. Lists of faunas were examined from the Miocene, Eocene, and the Cretaceous, time units selected as giving adequate sampling to establish the broad patterns of predatory gastropod evolution. Some reassignment of species to families was necessary, particularly with older literature. Families were used as the basic taxonomic unit, for Sepkoski (1978), using models and empirical evidence, has shown that the higher taxa parallel the patterns and kinetics of species diversification even when the information loss due to incomplete sampling of the fossil record masks these patterns in the species themselves. Palaeolatitudes were estimated using the palaeocontinental maps of Smith and Briden (1977).

TEXT-FIG. 7. First appearance and stratigraphic ranges of predatory prosobranch families from the Aptian onwards. Numbers at the foot of the bars refer to references and notes below; numbers at the head of the bars give an approximate estimate of the number of Recent species in each family (partly from Boss 1971). 1, Sohl (1969); 2, Morris and Cleevely (unpub.); 3, Morris and Cleevely (unpub.); 4, Morris and Cleevely (unpub.); 5, Wenz (1938); 6, Wenz (1938); 7, Sohl (1969) and others; 8, Sohl (1964*a*); 9, Darragh (1969); 10, Morris and Cleevely (unpub.) Buccinidae are probably a polyphyletic group; 11, Morris and Cleevely (unpub.); 12, *Buccinopsis* in Sohl (1964*a*), Nuttall *pers. comm.*; 13, Morris and Cleevely (unpub.); 14, Glibert (1973); 15, Stephenson (1952); 16, Sohl (1964*a*); 17, Rehder (1973); 18, Ponder (1973); 19, Morris and Cleevely (unpub.) Vasidae may be a polyphyletic group; 20, Cernohorsky (1970), the designation of Cretaceous species to this or the following family is rather subjective; 21, Cernohorsky (1970); 22, Cernohorsky (1970); 23, Stoliczka (1867–1868); 24, Powell (1966); 25, Powell (1966); 26, Stephenson (1952), if *Palaeadmete* can be accepted as a Cancellariacean.

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Diversity changes with time

The diversity of predatory gastropod families and of species within families from various faunas from the Upper Cretaceous to the present day is shown in text-figs. 8 and 9. There is a steady increase in diversity from the Aptian to the Turonian, with a further larger increase in the Campanian-Maastrichtian. This steep increase continues to the Eocene (few faunas were sampled for the Paleocene) and then flattens off to the Miocene and Recent. As will be shown below, the diversities of low-latitude predatory faunas in the Campanian-Maastrichtian are low, and are thus shown
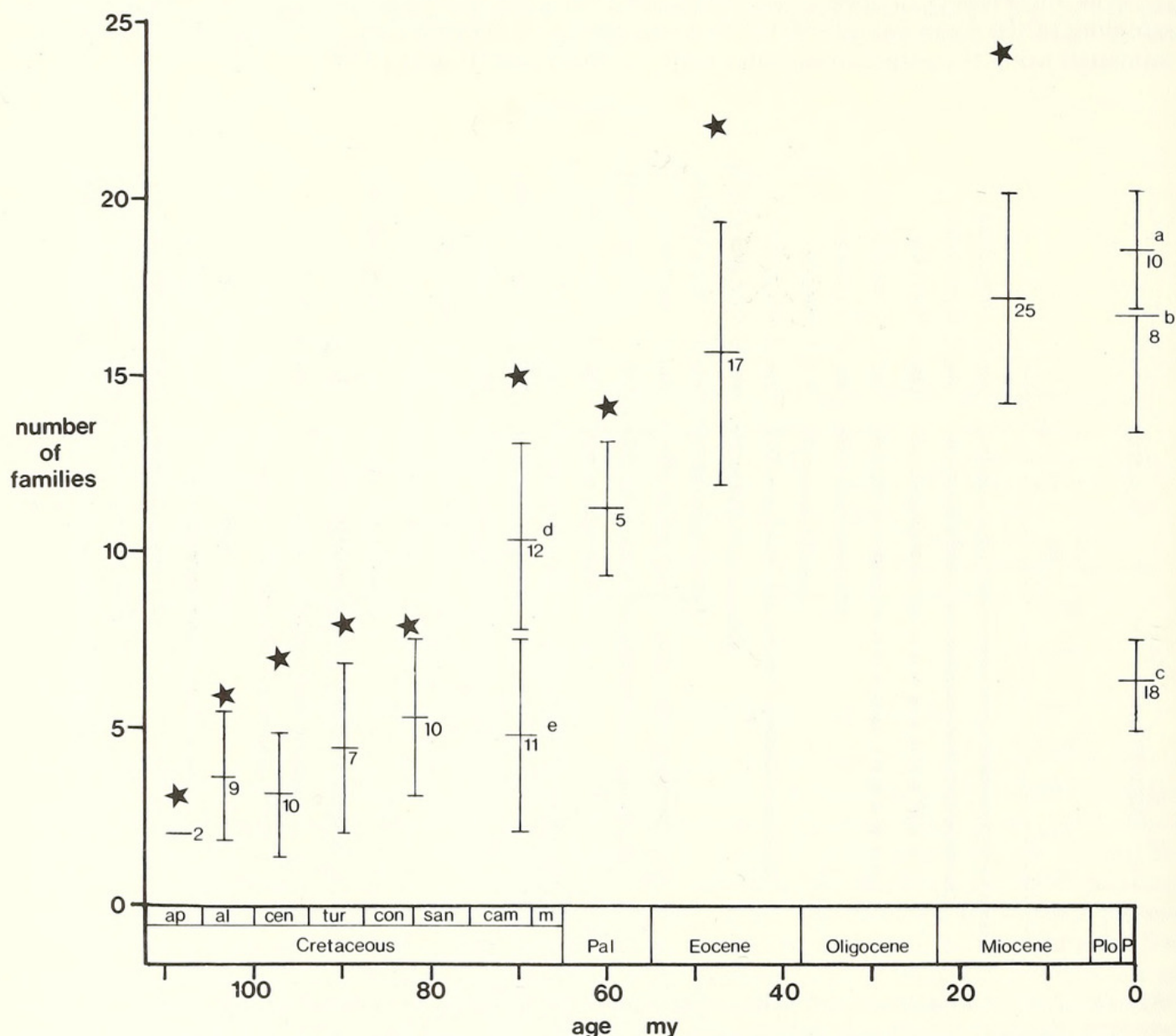
TEXT-FIG. 8. Number of predatory gastropod families in faunas from the Upper Cretaceous to the Recent. Data have been grouped for the Cenomanian–Turonian, Coniacean–Santonian, and Campanian–Maastrichtian stages. In view of the large diversity differences between high and low latitudes in the Campanian–Maastrichtian, the faunas have been split into two groups: (d) faunas from north and south of palaeolatitude 23·5° N. and S.; and (e) faunas from within palaeolatitudes 23·5° N. and S. Three Recent points are shown for comparison: (a) NW. Atlantic S. of 40° N.; (b) NE. Atlantic S. of 40° N.; (c) NE. Atlantic N. of 40° N. Bars show means, standard deviations, and the number of faunas sampled, except for the Aptian, which shows the mean and range. Stars indicate the maximum number of families recorded in any fauna of that age. Data sources as for text-figs. 2a–d, 11a–d, and 12a–b with the additions of Nagao (1934) and Cleevely (unpub.) for the Aptian.

separately from the extra-tropical faunas. Several Recent values are included because of the strong latitudinal variations which occur today. The diversification appears to take place in two phases, the first from the Albian to the Santonian, and the second from the Campanian to the Eocene. However, the curve is broadly similar to the exponential rises seen in other evolutionary expansions in which major taxonomic groups radiate into new adaptive zones of 'unoccupied ecospace' (Van Valen 1971; Stanley 1977; Sepkoski 1978). The rate of diversification flattens off, possibly when an equilibrium condition is reached at which the rate of origination of new taxa is balanced by extinction. The initial exponential rise need not necessarily mean that speciation rates are higher, alternatively, extinction rates may be lower (Rosenweig 1975).

Rarefaction curves for species within families for individual Cretaceous faunas are shown in text fig. 10, these confirm the more or less progressive increase in diversity to the Maastrichtian stage. Rarefaction curves for most Cenozoic faunas and low-latitude Recent faunas are slightly higher than the Maastrichtian curves.
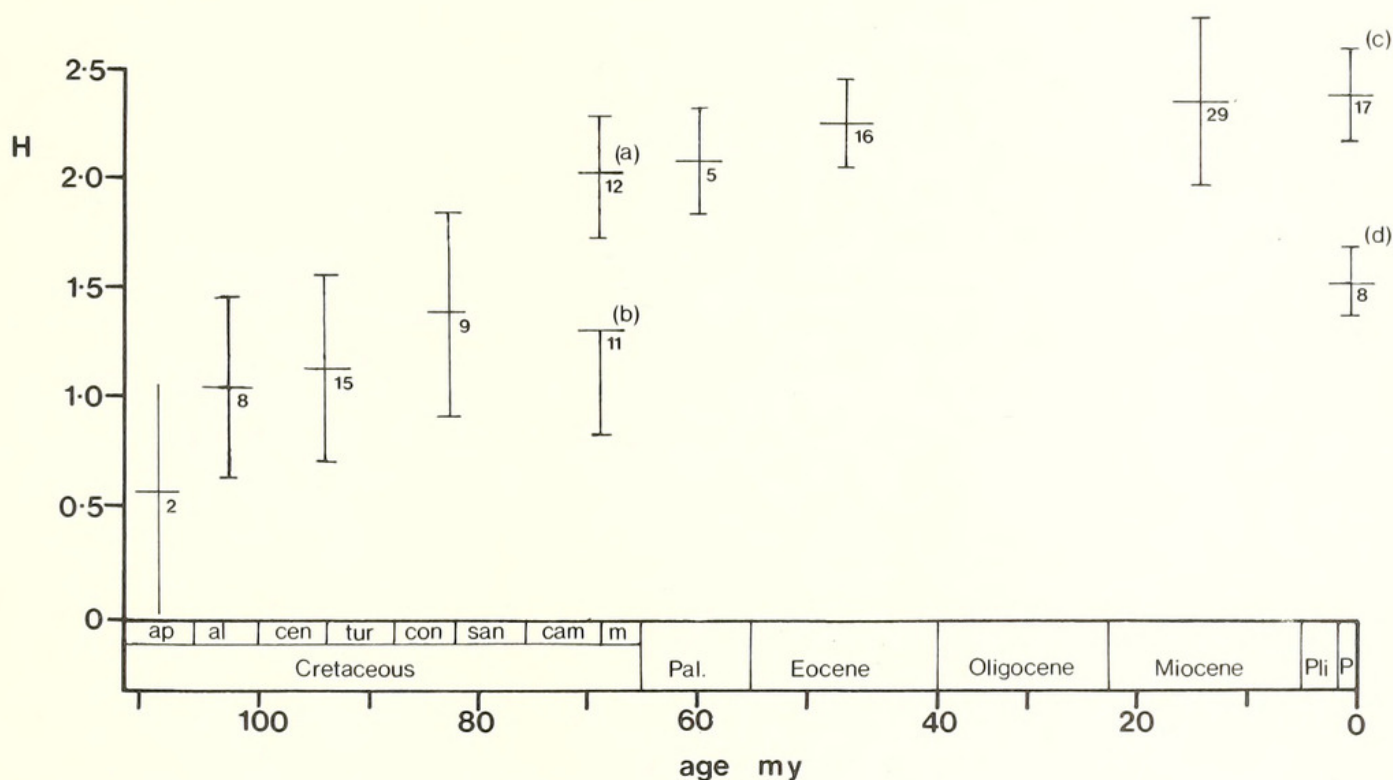
TEXT-FIG. 9. Diversity of species within families (H′) for Cretaceous faunas from the Aptian to the Recent. Bars show means, standard deviations and sample sizes. Data sources and other comments as for text-fig. 8.

Latitudinal distribution of fossil gastropods

If the strong latitudinal gradient in species diversity seen in Recent predatory gastropod faunas, particularly as exhibited in the eastern Atlantic, existed in the past, then the patterns of increasing diversity through time may represent a response to environmental gradients. A low diversity recorded from a particular geological period may not represent a low global diversity but merely that all the faunas sampled came from a particular latitudinal range or similar environmental regimes. Thus in order to interpret correctly the changes of diversity with time it is necessary to examine the latitudinal distributions of gastropods at the particular time concerned.
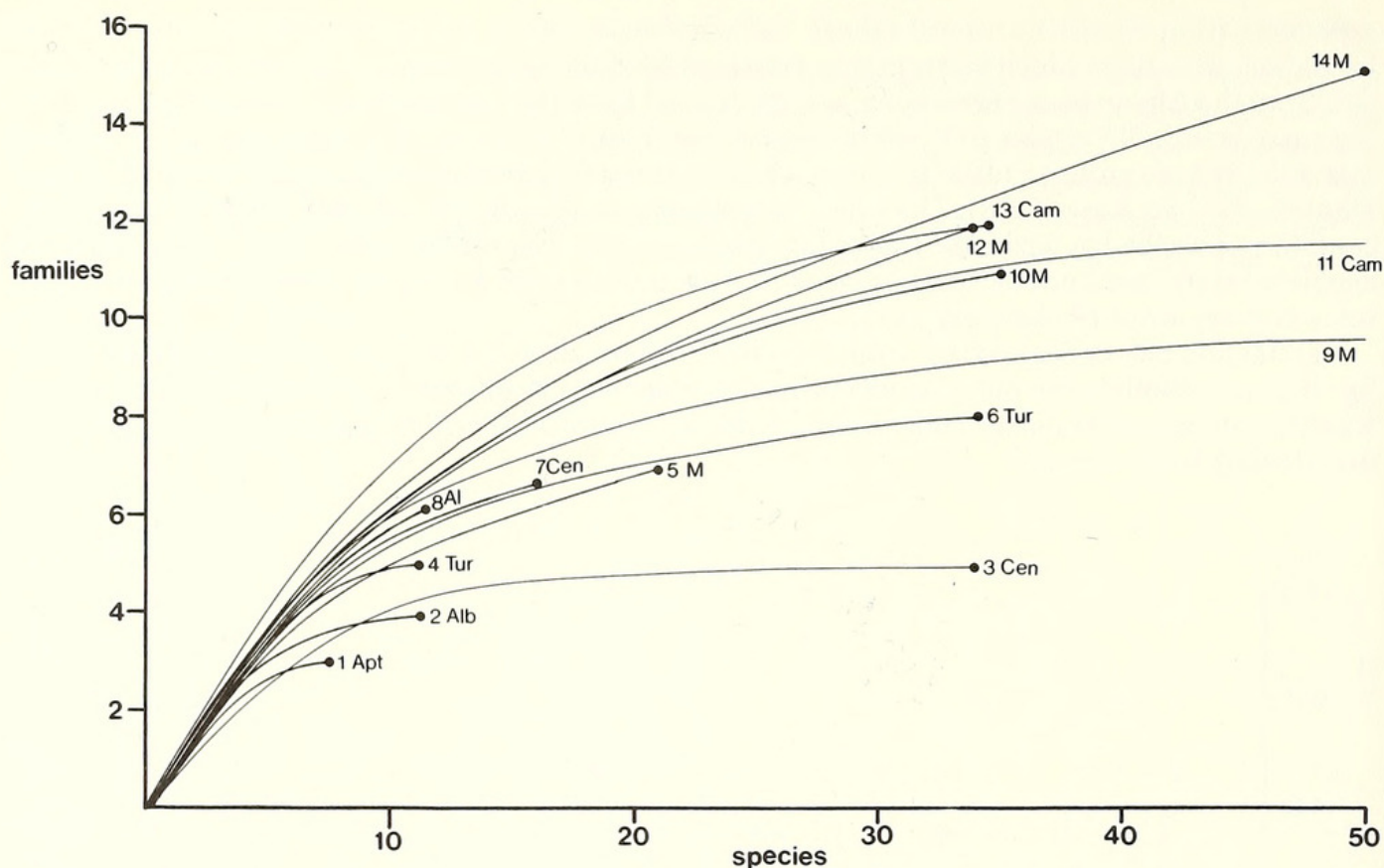
TEXT-FIG. 10. Rarefaction curves (Raup 1975) of species in families for some of the most diverse Cretaceous faunas. Abbreviations represent Cretaceous stages. 1, Aptian, England (Morris and Cleevely, unpub.); 2, Loriol (1862); 3, Stephenson (1952); 4, Roman and Mazeran (1920); 5, Erikson (1974); 6, Stoliczka (1867–1868); 7, Geinitz (1874); 8, Blackdown Greensand (Morris and Cleevely, unpub.); 9, Stephenson (1941); 10, White (1888); 11, Sohl (1964a); 12, Stoliczka (1867–1868); 13, Sohl (1964b); 14, Kaunhowen (1898).

The latitudinal distribution of predatory families during various stages of the Upper Cretaceous is shown in text fig. 11. For the Albian, Cenomanian-Turonian, Coniacean-Santonian there are slightly more families at latitudes 30–40° N. and S. than at lower latitudes, although the number of families at all latitudes if fairly low. However, in Campanian-Maastrichtian times there is a pronounced diversity gradient with tropical faunas having less than half the number of species than faunas from higher latitudes. This gradient is of some interest, for it is, of course, in the opposite direction to that of the present day where most predatory families are found in tropical latitudes.

By the Eocene (text-figs. 12b and 13b), low-latitude predatory families were much more diverse, but although there is a slight gradient towards the poles this is not statistically significant. It is possible that if more well-collected and described low- and high-latitude faunas had been available this gradient may have been a little steeper. In the Miocene (text-figs. 12a and 13a) the predator diversity curve decreases polewards and is similar in form to the present-day gradient on the west coast of North America. Unfortunately, insufficient data points were available to separate Lower, Middle, and Upper Miocene faunas which may have illustrated the progressive effects of polar cooling in the late Miocene as evidenced from other sources (e.g. Addicott 1970b). Tropical diversities in the Miocene were about the same as at the present day, but European Miocene faunas were much richer in predatory gastropods than the equivalent eastern Atlantic latitudes today.
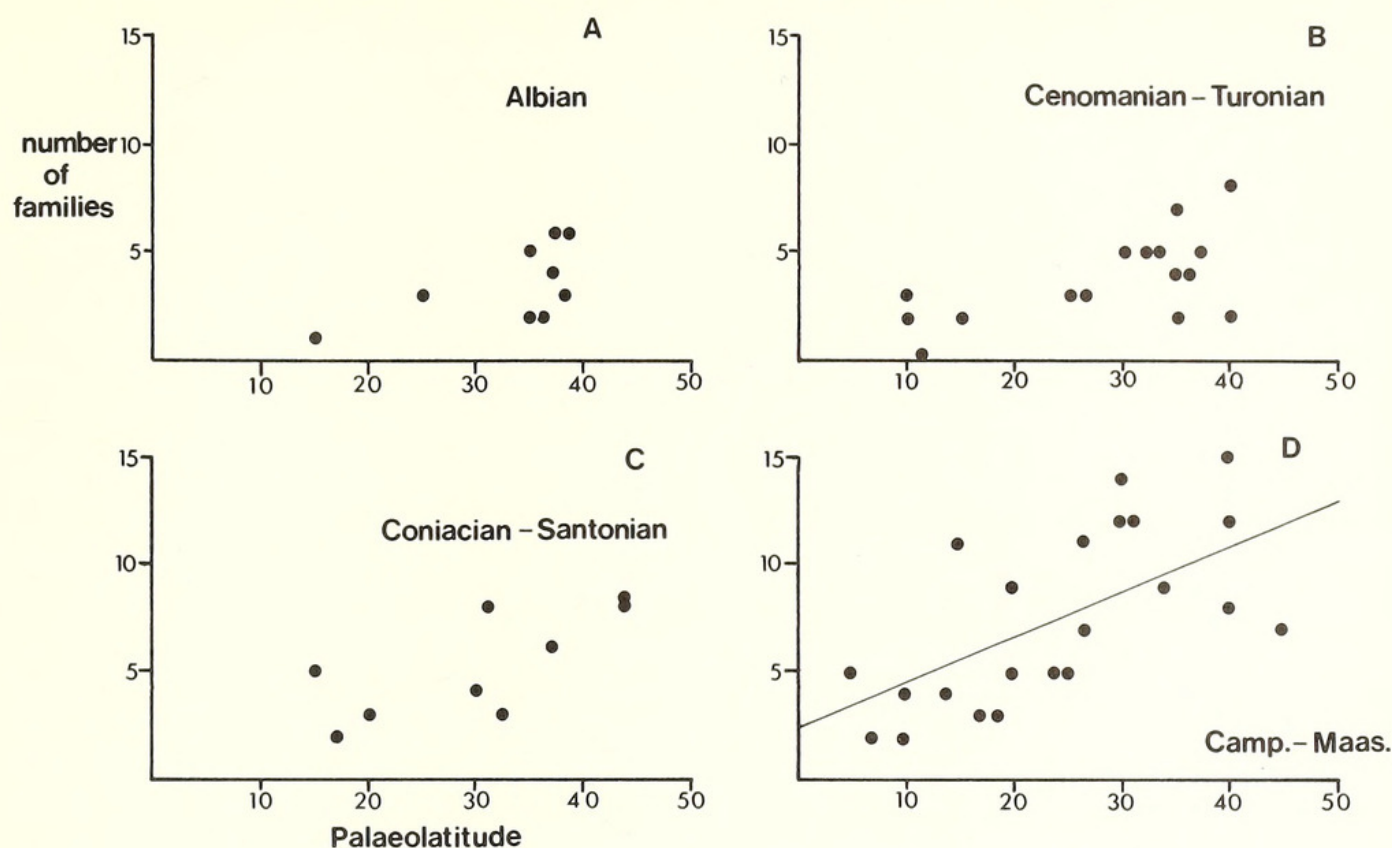
TEXT-FIG. 11*a–d*. Variation in the number of predatory gastropod families with palaeolatitude for various Upper Cretaceous stages. Lines are linear regressions. Data extracted from the following sources:

a. Albian: Allison (1955), Kollmann (1977, 1978), Loriol (1882), Mongin (1977), Morris and Cleevely (unpublished lists B.M. (N.H.)), Pervinquière (1912), Stanton (1947), Wollemann (1906).

b. Cenomanian-Turonian: Abbas (1963), Andert (1934), Archaic (1837), Blanckenhorn (1927), Chiplonkar and Badve (1972), Collignon (1934), Delpey (1940), Geinitz (1874), Hayami and Kase (1977), Parona (1909), Pchelintsef (1954), Pervinquière (1912), Roman and Mazeran (1920), Stephenson (1952), Stoliczka (1867–1868).

c. Coniacean-Santonian: Andert (1934), Blanckenhorn (1927), Böse (1923), Delpey (1938), Morris and Cleevely (unpublished), Nagao (1939), Pchelintsef (1954), Pervinquière (1912), Rennie (1945).

d. Campanian-Maastrichtian: Abbass (1963), Albanesi and Busson (1974), Collignon (1949, 1971), Douvillé (1904), Erikson (1974), Holzapfel (1888), Imlay (1937), Kaunhowen (1898), Krymgol'tz (1974), Morris and Cleevely (unpublished Rept. Ecuador), Myers (1968), Olsson (1934), Pervinquière (1912), Riedel (1932), Sohl (1964*a*, 1964*b*, 1967), Sohl and Mello (1970), Stephenson (1941), Stoliczka (1867–1868), White (1888).

Northern and southern hemisphere faunas plotted on the same 0–50° axis. Palaeolatitudes estimated from Smith and Briden (1977).

Compositional changes in fossil faunas

The Recent model shows that compositional changes occur with latitude, and such changes are also to be expected in fossil faunas as well as changes through geological time as a result of evolutionary replacement by more successful forms. In Cretaceous faunas from the Albian to the Campanian, the families Naticacea, Fasciolariidae, Volutidae, and Cancellariidae were generally the most diverse of the predatory taxa. Table 2 shows the percentage of various predatory families in various faunas of the Cenomanian-Turonian. Other families such as the Muricidae, Vasidae, and Melongenidae were diverse in some faunas. In the extra-tropical faunas of Campanian-Maastrichtian times, many more families such as the Turridae, Mitridae, Olividae, and Cymatiidae make an appearance (Table 3) but the most diverse families were clearly the Fasciolariidae and the Volutidae which form an average of
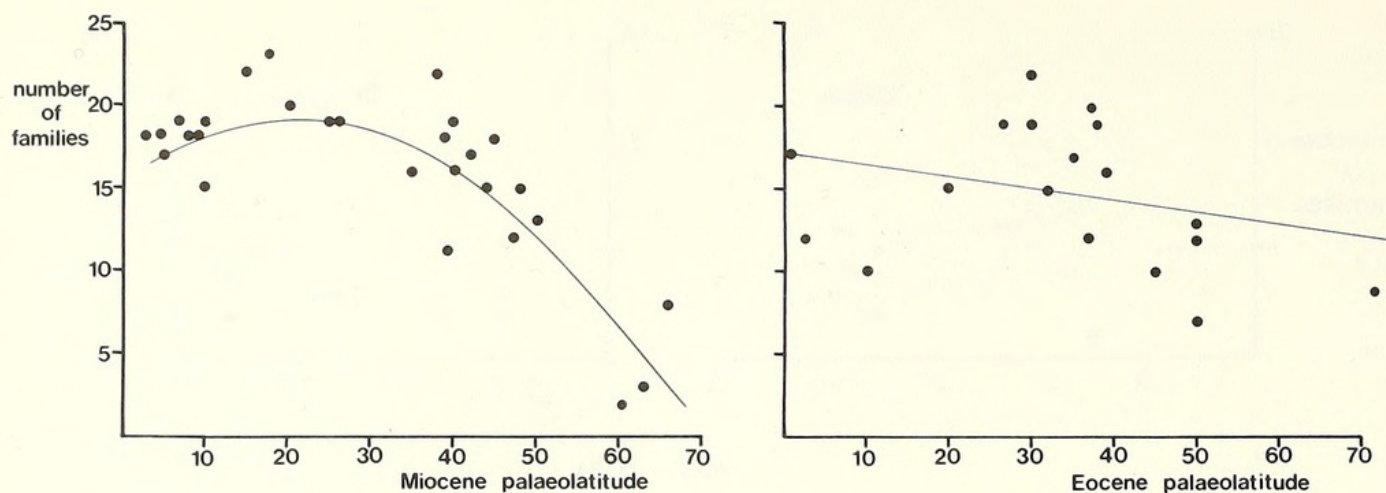
TEXT-FIG. 12a–b. Variation in the number of predatory gastropods with palaeolatitude for (a) Miocene faunas and (b) Eocene faunas. Curve in 12a is a five-point running mean, and line in 12b is a linear regression. Data extracted from:

a. Miocene faunas: Addicott (1970a), Beets (1941), Gardner (1936–1947), Glibert (1952a, b, Turridae from Peyrot, 1938), Hinsch (1977), Hornes (1851–1856), Ilona (1954), Ilyina (1963), Itojgawa et al. (1974), Iwasaki (1962), Jung (1965, 1969, 1971), Kanno (1971), Ludbrook (1973), Mansfield (1937), MacNeil (1973), Maury (1917), Nordsieck (1972), Olsson (1964), Pannekoek (1936), Perrilliat (1972–1973), Rasmussen (1968), Rutsch (1934), Sorgenfrei (1958), Strausz (1966), Uozumi (1962), Vredenburg (1925), Weaver (1942), Woodring (1957–1973).

b. Eocene faunas: Cossmann (1895–1898), Cossmann and Pissaro (1898–1901, 1911), Curry et al. (1968), Eames (1952, 1957), Glibert (1938), Iqbal (1972), Ludbrook (1973), Martin (1914, 1931), O'Gorman (1923), Olsson (1928), Ortmann (1902), Oyama et al. (1960), Palmer (1937, Turridae from Harris 1937), Vokes (1939), Weaver (1942), Zinsmeister and Camacho (in press).

Northern and southern hemisphere faunas plotted on the same 0–80° axis. Palaeolatitudes estimated from Smith and Briden (1977).
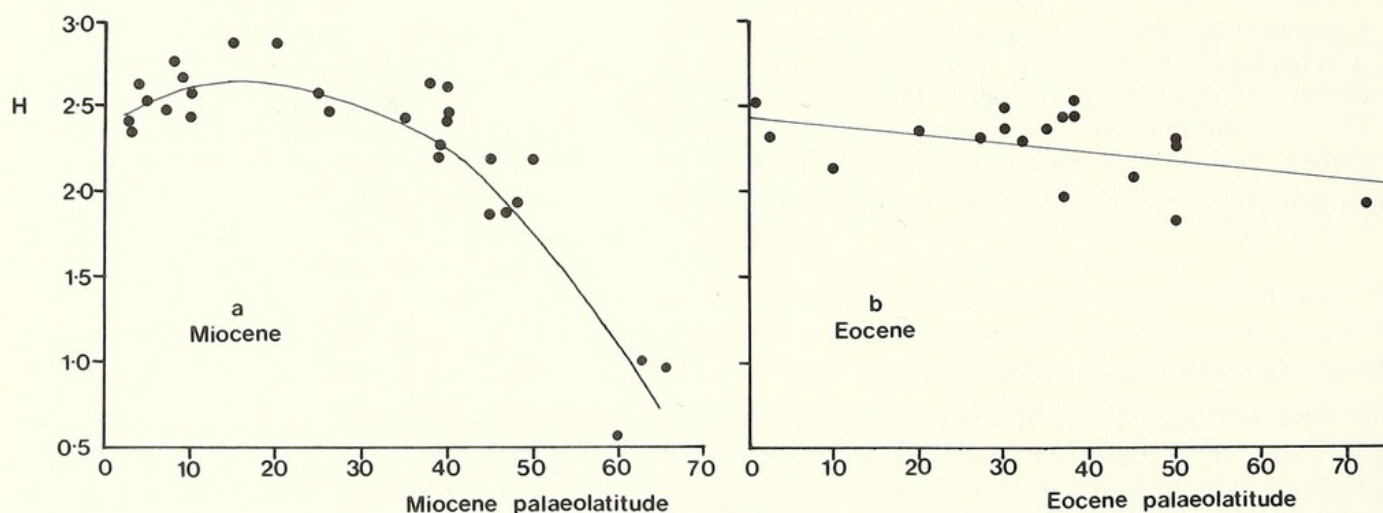
TEXT-FIG. 13a–b. Variation in the diversity of species within families (H′) with palaeolatitude for (a) Miocene and (b) Eocene faunas. Data as for text-fig. 12a–b. Curve in 13a is a five-point running mean, and line in 13b is a linear regression.

TABLE 2. Percentage of species in different predatory families in some Cenomanian–Turonian faunas.

	Woodbine Fm. Stephenson (1952)	Saxony Geinitz (1874)	S. India Stoliczka (1867–1868)	C. Asia Pchelinsef (1953)	Germany Andert (1934)
Naticacea	23·5	22·2	21·2	38·5	38·5
Cymatiidae		5·6	3·0		
Muricidae	5·9	16·7			
Buccinidae		22·2			
Melongenidae			12·1		
Fasciolariidae	11·8	5·6	12·1		23·0
Vasidae			12·1	3·8	15·4
Volutidae	38·2	5·6	30·3	50·0	15·4
Cancellariidae	20·6	22·2	3·0	3·8	7·7
Turridae			6·1		
Families	5	7	8	5	5
Species	34	18	33	26	13

20 and 13% of the predatory faunas respectively. The Fasciolariidae are particularly diverse in faunas from the south-eastern United States where they formed up to 25% of species. In tropical faunas of the Campanian-Maastrichtian, predators were neither diverse nor common, and Tethyan faunas typically contain a few species of Naticacea, Fasciolariidae, and Volutidae. The common naticid in these faunas is *Tylostoma*, a genus generally restricted to Tethyan faunas.

Sohl (1971) has documented the sharp compositional boundary between the tropical Cretaceous and sub-tropical temperate gastropod faunas that existed from Neocomian to Maastrichtian times in the Caribbean–North American area. A similar sharp faunal change existed between other Tethyan and higher-latitude faunas. The Tethyan faunas were characterized by abundant rudistid bivalves (Kauffman 1973) and acteonellid and nerineid gastropods. As discussed above, only relatively few predatory prosobranch gastropods occur in these faunas and these are relatively uncommon. Although changes did occur, these Tethyan faunas were extremely conservative and stable throughout the Upper Cretaceous, and it appears that most of the predatory prosobranch families first evolved at higher latitudes and not in the tropics as their present-day distributions would suggest.
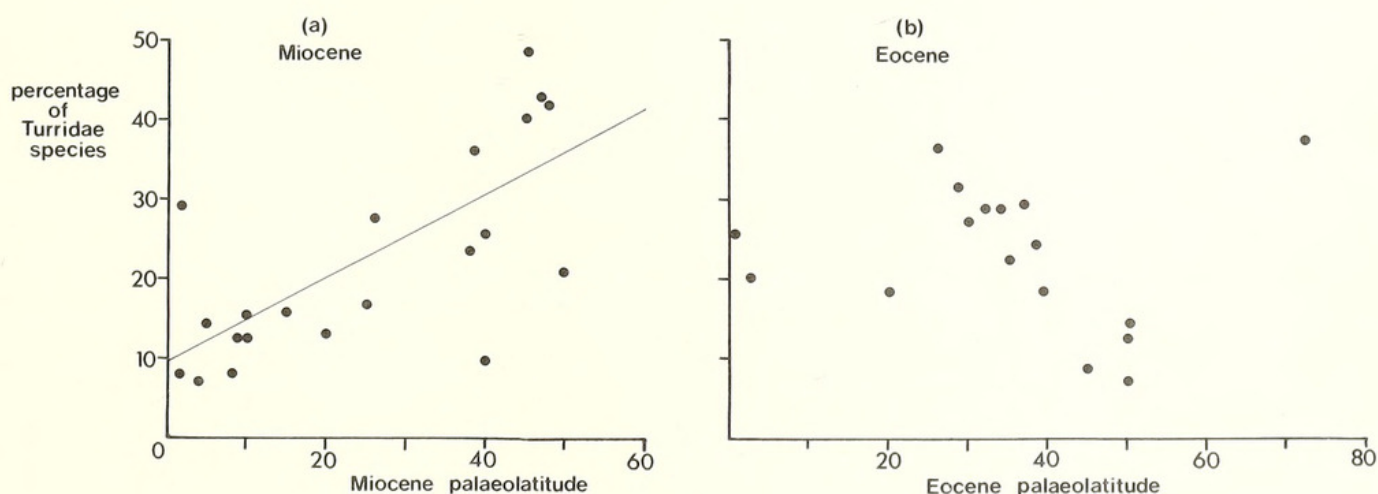
TEXT-FIG. 14*a–b*. Variation in the percentage of Turridae species in the total predatory gastropod fauna with paleolatitude for (*a*) Miocene and (*b*) Eocene faunas. Data sources as for text-fig. 12*a–b*.

TABLE 3. Percentage of species in different predatory families in some Campanian–Maastrichtian faunas. Some minor families omitted.

	Ripley Fm. Sohl (1964a)	Coffee Sand Sohl (1964b)	Merchantville Fm. Sohl and Mello (1970)	Maastricht Kaunhowen (1898)	S. India Stoliczka (1867–1868)	Navarro Gp. Stephenson (1941)	Owl Creek Fm. Sohl (1964a)	NE. Brazil White (1888)	Aachen Holzapfel (1888)
Naticacea	7·3	11·8	19·0	22·0	32·3	11·3	6·3	37·1	
Cymatiidae	2·2			4·0	8·8				
Muricidae	8·0	6·9	9·5	2·0		5·2	4·8	8·6	3·2
Coraliophilidae	1·5	2·9					3·2		
Buccinidae	5·8	14·7	4·8	2·0	5·9	9·3	7·9	8·6	6·5
Melongenidae	8·8	5·9	4·8	2·0	5·9	2·1	6·3		6·5
Fasciolariidae	25·5	14·7	23·8	14·0	2·9	2·7	20·6	11·4	6·5
Vasidae	6·6	11·8	9·5	4·0	2·9	10·3	9·5		13·0
Olividae	3·6	2·9		2·0	2·9	1·0	7·9	2·9	
Volutidae	12·4	8·8	9·5	12·0	14·7	11·3	19·0	8·6	29·0
Mitridae		2·9		4·0	2·9				9·7
Cancellariidae	6·6	5·9	14·3	16·0	14·7	11·3	4·8	5·7	16·1
Turridae	10·2	11·8	4·8	10·0	2·9	15·5	7·9	5·7	
Families	14	12	9	15	12	10	12	10	8
Species	137	34	21	50	34	97	63	35	31

TABLE 3. Percentage of species in different predatory families in some Campanian–Maastrichtian faunas. Some minor families omitted.

	Ripley Fm. Sohl (1964a)	Coffee Sand Sohl (1964b)	Merchantville Fm. Sohl and Mello (1970)	Maastricht Kaunhowen (1898)	S. India Stoliczka (1867–1868)	Navarro Gp. Stephenson (1941)	Owl Creek Fm. Sohl (1964a)	NE. Brazil White (1888)	Aachen Holzapfel (1888)
Naticacea	7·3	11·8	19·0	22·0	32·3	11·3	6·3	37·1	
Cymatiidae	2·2			4·0	8·8				
Muricidae	8·0	6·9	9·5	2·0		5·2	4·8	8·6	3·2
Coraliophilidae	1·5	2·9					3·2		
Buccinidae	5·8	14·7	4·8	2·0	5·9	9·3	7·9	8·6	6·5
Melongenidae	8·8	5·9	4·8	2·0	5·9	2·1	6·3		6·5
Fasciolariidae	25·5	14·7	23·8	14·0	2·9	2·7	20·6	11·4	6·5
Vasidae	6·6	11·8	9·5	4·0	2·9	10·3	9·5		13·0
Olividae	3·6	2·9		2·0	2·9	1·0	7·9	2·9	
Volutidae	12·4	8·8	9·5	12·0	14·7	11·3	19·0	8·6	29·0
Mitridae		2·9		4·0	2·9				9·7
Cancellariidae	6·6	5·9	14·3	16·0	14·7	11·3	4·8	5·7	16·1
Turridae	10·2	11·8	4·8	10·0	2·9	15·5	7·9	5·7	
Families	14	12	9	15	12	10	12	10	8
Species	137	34	21	50	34	97	63	35	31

Both of the gastropod families, the Acteonellidae and the Nerineidae which dominate Tethyan tropical faunas are now considered to belong to the subclass Opisthobranchia. Most Nerineidae were probably infaunal gastropods inhabiting carbonate sands and muds. Although they have no obvious living relatives they may have been deposit feeders. On the other hand, although the relationships of the Acteonellidae with living shelled opisthobranchs are obscure, their morphology is generally similar. However, although most shelled opisthobranchs are predators, particularly upon other molluscs and polychaetes, some of the larger animals such as *Bulla*, *Hydatina*, and *Haminoea* are herbivorous (Thompson 1976). Thus there are no clear indications from comparisons with living forms whether acteonellids were herbivores or carnivores. Their great abundance in some deposits might suggest a herbivorous habit, but the light, buoyant shells of opisthobranchs often accumulate in post-mortem aggregations. If the Acteonellidae were predators, then it might be suggested that their abundance in tropical faunas during the late Cretaceous excluded the predatory prosobranch families which had apparently originated at higher latitudes. However, although the acteonellids are frequently abundant in Tethyan faunas they are not particularly diverse, and if morphological diversity gives some idea of a diversity of habits, then one would not expect a great variety of feeding types amongst them. By contrast, predatory prosobranchs exhibit such a diversity of food specializations, that exclusion by acteonellids was probably unlikely.

By the Eocene, the distribution patterns had changed considerably (Table 4), with the Turridae being the most diverse family in most samples and generally comprising some 25% of the species (text-fig. 15). The importance of the Turridae continued into the Miocene and in faunas from the European area up to 45% of species may be turrids. Families such as the Fasciolariidae and Volutidae which were diverse during the Cretaceous and formed a high proportion of the total predatory fauna were by the Eocene much less important and along with many other families formed only a relatively small proportion of the total predatory fauna. Although latitudinal gradients in faunal composition are not steep in the late Cretaceous and Eocene faunas, there are marked compositional changes in the Miocene. The Turridae are very important at higher latitudes, but at lower latitudes they comprise

TABLE 4. Mean percentage of species in different predatory families in faunas from the Cenomanian to the Miocene. Minor families omitted.

	Cenomanian–Turonian	Campanian–Maastrichtian	Eocene	Miocene
Naticacea	28·8	13·9	12·0	6·7
Cymatiidae	1·7	1·5	4·0	2·1
Ficidae			1·8	1·3
Cassididae			3·0	2·7
Muricidae	4·5	4·2	5·2	7·2
Columbellidae			1·2	3·9
Buccinidae	4·4	6·6	8·5	5·3
Nassariidae			1·9	6·9
Melongenidae	2·4	5·3	1·4	0·5
Fasciolariidae	10·5	20·5	8·1	4·4
Vasidae	6·3	9·6	0·3	0·5
Olividae		2·3	4·4	3·6
Volutidae	27·9	13·4	5·8	1·5
Marginellidae			3·4	1·8
Mitridae		2·9	3·9	5·0
Cancellariidae	11·5	7·8	3·8	5·6
Turridae	1·2	9·2	25·2	25·4
Conidae			3·6	6·3
Terebridae			1·0	5·2
No. of faunas sampled	5	10	10	17

only about 14% of the species; however, the two other toxoglossate families Conidae and Terebridae are more diverse at these lower latitudes. The Nassariidae, Fasciolariidae, and Cancellariidae also form a slightly greater proportion of the total predatory species at higher latitudes.

The importance of the Turridae has continued to the present day (text-fig. 5), especially in offshore and deep-sea sediments. The importance of the Buccinidae at high latitudes which is so pronounced in the present day, in all oceans, is a relatively recent occurrence from the late Miocene onwards and its development was not detected in this analysis; although some faunas from the late Miocene of northern Japan show an abundance of Buccinidae (Uozumi 1962; Chinzei 1978). The evolution of the important buccinid genus *Neptunea* in the northern Pacific has recently been documented by Nelson (1978) who shows how the group arose in the Miocene, spread around the northern Pacific, and then entered the Atlantic in the Plio-Pleistocene.
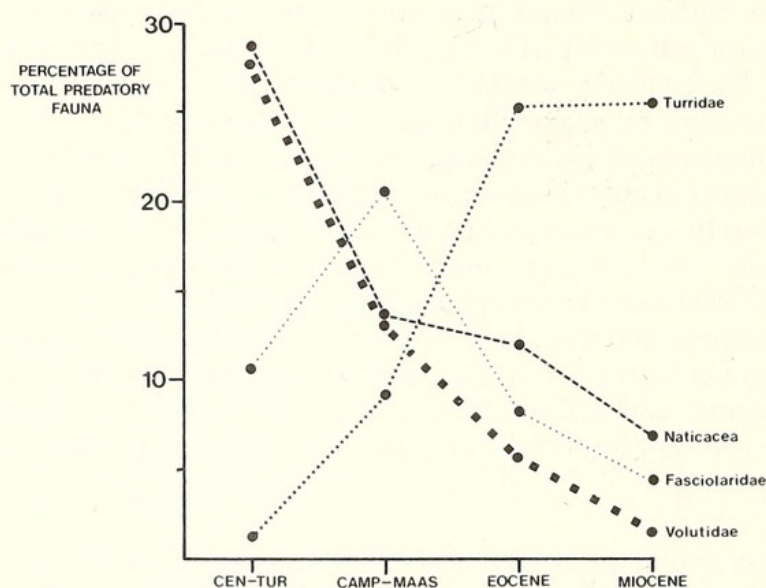
TEXT-FIG. 15. Changes in the relative proportions of various major families in the total predatory fauna from the Cenomanian–Turonian to the Miocene. Time axis not to scale.

Direct evidence of predation by fossil gastropods

Direct evidence of the activities of predatory gastropods in fossil faunas is afforded mainly by these predators which drill holes into shelled prey, that is, the Mesogastropod groups Naticacea and Cassididae and the Neogastropod family Muricidae. Another Mesogastropod family the Capulidae contains species which bore holes but these may be regarded as parasites (Matsukuma 1978). Predatory hole drilling is known in other molluscs particularly in the octopus (Wells 1978), the opisthobranch *Okadaia* (Young 1968), and in the predatory species of the terrestrial pulmonate gastropod family the Zonitidae (Mordan 1977). The last are true predators, other reports of shell boring in pulmonates seem to be instances of radulation for calcium carbonate.

The drilling activities of the Naticacea and Muricidae have been well documented, and Carriker and Yochelson (1968) suggest the criteria by which boreholes produced by gastropods should be recognized. There is an extensive literature concerning boreholes throughout the Cenozoic (e.g. Taylor 1970; Hoffman *et al.* 1974; Fischer 1966; Thomas 1976; Reyment 1966, 1967), and although boreholes have been attributed to gastropods throughout the Mesozoic and Palaeozoic, we agree with Carriker and Yochelson (1968) and Sohl (1969) that most pre-upper Cretaceous holes are equivocal in nature and generally uncommon.

The earliest unequivocal drillholes that we know of, and which occur in some abundance, are from the Albian Blackdown Greensand of south-west England, a little earlier than the Cenomanian records of Sohl (1969) and Fischer (1962, 1964); although borings attributed to gastropods have been recorded in some Aptian brachiopods of England (Laurie 1977). In the Blackdown Greensand both naticid and muricid drill holes occur in epifaunal and infaunal bivalves. The potential predators in the Blackdown Greensand include several naticid species and two or three species of muricid. Sohl (1969) observes that by the Campanian-Maastrichtian a wide variety of bivalves and gastropods were bored by predatory gastropods. Evidence of boring by Cassididae into the tests of echinoids is much less common, but examples are known from the Eocene (figured by Sohl 1969) and from the Oligocene (figured by Beu *et al.* 1972). Although the Naticacea have been in existence since at least the lower Jurassic, unambiguous naticid drill holes did not appear until the mid Cretaceous. Sohl (1969) correlates the beginning of the shell-drilling habit with the appearance of species of the subfamily Polynicinae; most naticaceans prior to the Albian belonged largely to the subfamily Ampullospirinae which were apparently not shell borers. In some Recent species such as *Polynices duplicatus* (Edwards 1975; Edwards and Huebner 1977) about 25% of the prey are not bored and it is possible that pre-Albian naticids may have eaten molluscan prey without hole drilling, but they would have been limited in the types of bivalve prey they could attack in this way.

The first appearance of convincing muricid drill holes corresponds quite well with the first appearance of muricid gastropods, and forms such as *Hillites*, *Sargana*, and *Rapana*-like forms are quite common in the lower part of the Upper Cretaceous. Some Recent species of Melongenidae, Fasciolariidae, and Buccinidae which wedge and chip at the valve margins of bivalve prey frequently suffer damage to the outer lip of the shell aperture. Nielsen (1975) illustrates the characteristic breakage and repair produced by these activities in *Buccinum undatum*, and these patterns should be recognizable in fossil gastropods.

DISCUSSION AND CONCLUSIONS

Competition has been an important evolutionary force that has led to niche separation, specialization, and diversification (Pianka 1974). Empirical studies from living predatory gastropods strongly suggest that in the tropics at least, competitive interactions have been important in determining the habitat, occupation patterns, size and diets of gastropods at the specific level, and over a longer timespan at the familial level.

The rapid diversification and adaptive radiation of predatory families during the late Cretaceous may have arisen as a consequence of competitive interactions between taxa, giving rise to broad habitat separations and specializations upon particular food types. Selection will favour those phenotypes which maximize the energy extracted from particular food types, which results in anatomical and behavioural modifications to cope more efficiently with particular food types or habitats. The predators may have become canalized into particular prey or habitat types, and later diversification mainly occurred within these particular adaptive zones. For example, the specialized behaviour and anatomical modifications which enable the Cassididae to catch and eat echinoids are not very suitable for catching other prey types such as infaunal polychaetes. By contrast, some families have retained or acquired generalist feeding habits or habitat preferences which, as in the case of the Buccinidae, have resulted in diversification at high latitudes.

Amongst the earliest predatory gastropods are species from the families Fasciolariidae, Volutidae, Vasidae, Muricidae, Cymatiidae, and the superfamily Naticacea. These are families which today feed largely upon rather slow-moving or sedentary prey such as bivalves, gastropods, and sedentary polychaetes. The diet of the Cancellariidae, another family important in early faunas, is unknown. Of the three most diverse families in Albian to Campanian faunas the large Fasciolariidae use both the proboscis and the edge of the shell to gain entry into bivalve prey, whilst smaller species use only the proboscis to feed upon tube-living polychaetes (Paine 1966*a*). From what is known of the Volutidae, they feed upon gastropods and bivalves, and the Naticacea are well known for their shell drilling of molluscan prey.

Predatory taxa adept at catching more mobile prey were neither diverse nor abundant until the Campanian-Maastrichtian, when the Turridae became more important, but by the Eocene, this family of polychaete specialists is the most diverse in many faunas. Other specialist families such as the Cassididae, Tonnidae, Harpidae, Conidae, and Terebridae did not appear until the late Cretaceous or early Palaeocene. By comparison with living forms the feeding methods of gastropods became
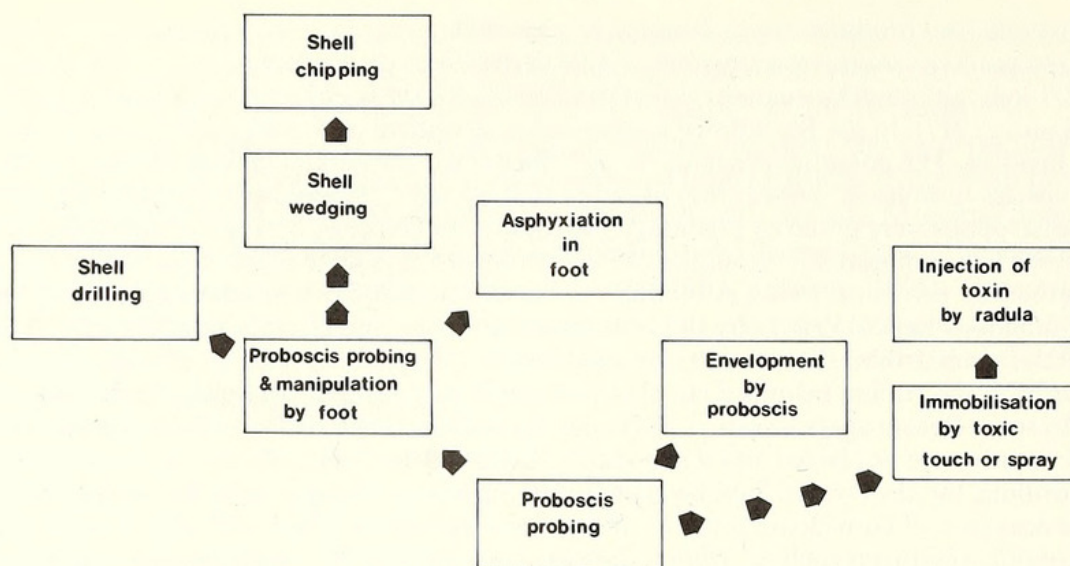
TEXT-FIG. 16. Possible radiation of feeding behaviour in predatory prosobranch gastropods. See text for discussion.

more elaborate during the Upper Cretaceous. A possible radiation of gastropod feeding methods based upon observations of living animals is shown in Text-fig. 16. The co-evolution of predators and prey is important: as predators became more adept at catching and extracting prey, the prey species in turn evolved anti-predation devices and behaviour, such as the development of escape reactions, the selection of more cryptic habitats, shell thickening, and the elaboration of shell sculpture. Predatory gastropods probably developed from carnivorous forms feeding upon sedentary animals such as sponges and ascidians, as the Fissurellidae, Cypraeidae, Triphoridae, and Eratoidae do today. From this carnivorous habit the ability to feed upon slightly more mobile prey (sedentary polychaetes, other molluscs) developed. Initially predators may have developed better prey-seeking devices, with the elaboration of the osphradium and the anterior nervous system. The proboscis was developed for gaining access to the prey. Sedentary soft-bodied prey such as ptychoderid worms may be swallowed whole by the eversion of the proboscis. Free-living prey would have been held and manipulated by the foot and from this probably developed the feeding method employed by the Volutidae, Harpidae, and Olividae of holding and asphyxiating the prey in the foot, sometimes with the secretion of large quantities of mucus. An elaboration of the foot-grasping behaviour is the use of the outer shell lip of the gastropod to wedge between the valves of bivalve prey whilst the proboscis is inserted. In some groups this behaviour probably developed into the use of the shell lip for chipping the edges of bivalve prey.

Today zonitid pulmonate snails penetrate the shells of their snail prey by mechanical means only (Mordan 1977). Selection may have favoured those predators producing calciphagic enzymes, acids, and chelating agents from either the proboscis or the foot which allowed more efficient penetration of the shells. At first drill holes may have been concentrated at valve margins, a habit practised by some naticids today; but later, perhaps because of increased protection of the valve margins, and by the increased perfection of the drilling technique of the predators, the normal drill position moved towards the dorsal part of the shell, although this varies with prey and predator species. Similar drilling techniques also arose independently in the Cassididae. Predatory gastropods which eat more active prey evolved the use of a toxic secretion, usually produced by modified oesophageal glands, to immobilize their prey after location. Some predators deliver the toxin by touch, as in *Thala*, a vexillid (Maes and Raeihle 1976) or squirt it as in some Cymatiidae (Houbrick and Fretter 1969), and in the toxoglossan families (Turridae, Terebridae, and Conidae) the radula teeth have become modified into hollow darts, down which the toxin flows after the prey has been impaled. The venom apparatus is not homologous in the families mentioned but they represent different ways of performing the task of delivering the venom and immobilizing the prey.

The main adaptive zones of predatory gastropods were probably established between Campanian and Eocene times. The constraints upon the width of the adaptive zone occupied by predatory prosobranch gastropods, other than anatomical or functional limitations, were and are probably the competitive effects of other predators of benthic invertebrates, notably opisthobranch gastropods, decapod crustacea, and teleost fish. Predation by other animals on predatory gastropods may have been limiting in certain environments. Although obviously new taxa have evolved during the Cenozoic, they have probably made little difference to the main adaptive zones of each family. For instance, the species of the genus *Drupa* of the Muricidae, which evolved fairly recently (Emerson and Cernohorsky 1973) feed upon similar prey to the Conidae and Mitridae, and occupy broadly similar habitats. Similarly, a small number of muricid species, notably in the genus *Drupella*, feed upon coral polyps, which are the dominant food of the family Coralliophilidae (Taylor 1976, 1978*a*), yet they represent small numbers of species when compared with those within the main adaptive zone of the Muricidae. More usually there have been massive diversifications within one broad feeding type or habitat as, for example, the several hundred extant species of polychaete feeding Conidae, the 550 genera of Turridae (Powell 1966), and the multitude of species of intertidal Muricidae.

A remarkable feature of the predatory prosobranch radiation is the approximately coeval appearance of the Tonnacea and the unrelated Neogastropod families, as well as a smaller, less spectacular radiation amongst the Naticacea. Many of the morphological adaptations of the Tonnacea parallel those within the Neogastropoda, and the shell-drilling habit arose independently and at approximately the same time within the Tonnacea, Naticacea, and Muricacea. The radiation of predators was not confined to gastropods, for as Vermeij (1977*a*) has pointed out, the late Mesozoic saw massive diversifications in predatory teleost fish (Greenwood *et al.* 1966) and crabs with crushing chelae (Vermeij 1977*b*). These, together with the major diversifications which occurred in non-predatory groups such as siphonate heterodont bivalves (Stanley 1977), echinoids (Kier 1974), and cheilostome Bryozoa (Schopf 1977) formed part of the major reorganization of marine communities which Vermeij (1977*a*) dubbed the 'Mesozoic marine revolution'. This contributed greatly to the steep increase in total diversity at the end of the Mesozoic documented by Valentine (1969, 1973) and the subject of much recent debate (Bambach 1977; Raup 1976; Sepkoski 1976; Signor 1978). The appearance of major groups of new predators armed with new techniques of hunting and catching prey had profound effects upon the structure and adaptations of benthic marine animals. The specializations of the predators are so diverse that probably no group of invertebrates would have escaped their effects. For instance, the rise in importance of siphonate bivalves documented by Stanley (1977) suggests that bivalves were effectively being 'driven underground' by the severe predation intensity on epifaunal and surface burrowers. Changes in gastropod shell morphology were probably also associated with increased predation pressure. In some communities today, such as the intertidal rocky shore, gastropods may be the dominant predators (Paine 1966; Menge 1978).

The most satisfactory explanation of the late Mesozoic diversification is the continental fragmentation-diversity model developed by Valentine and Mores (1970). As well as providing the isolation of faunas necessary for diversification, the development of north–south aligned continental margins resulted in an increase in the number of marine provinces from the relatively few of the Mesozoic to the chains of provinces along N.–S. continental margins as in the Cenozoic and Recent (Valentine, Foin, and Peart 1978). Additionally, Kauffman (1975) has stressed that the last extensive inundations of cratonic areas all over the world occurred during the Cretaceous. This flooding, which occurred as a series of major pulses, combined with the almost global development of warm-water marine climatic environments, provided vast new areas for the proliferation and dispersal of marine animals. The development of new shallow-water habitats coupled with the isolating effects of continental fragmentation probably encouraged rapid diversification of unrelated groups of marine animals.

The numerous latitudinal faunal boundaries of the Cenozoic and Recent, formed by temperature discontinuities, may be unique in the Phanerozoic record, and the latitudinal thermal gradient in the Mesozoic was apparently lower and more gentle compared with the Neogene and Recent. Addicott

(1970b), for instance, documents the increase in provinciality of west American molluscan faunas throughout the Cenozoic with the late Miocene cooling producing the greatest provinciality of faunas. This increasing provinciality produced the diversifications of predatory gastropods seen during the Cenozoic, but generally within adaptive zones established during the Late Cretaceous and early Paleogene. Nevertheless, the adaptive radiation of predatory prosobranch gastropods is one of the more remarkable diversifications in the evolutionary history of the Mollusca and the invertebrates.

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