

2.5. Distribution of gastropods within the Cretaceous Tethyan realm

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Summary

Fossil assemblages of different geographical regions and within certain latitudes which are equivalent on the genus or family level indicate temperature-controlled realms in the geologic past. Paleobiogeographically, the Tethys is placed within the Tropical realm of the Mesozoic. In addition to the low-latitude Tropical realm, Warm Temperate, Temperate, and probably also Subpolar marine provinces can be distinguished by the distribution of fossils in Cretaceous rocks. In low latitudes, the horizontal distribution is to a varying degree vertically reproduced.

Like all benthic organisms the gastropods are restricted to specific environments. This distribution pattern is discussed for the nerineaceans (including the itieriids), the actaeonellids (*Actaeonella* and *Trochactaeon*), the cassiopids and the genera *Trajanella* and *Discotectus*. Valid biostratigraphic analyses can be obtained only by comparing stratigraphic ranges within the same environments.

Normally, marine gastropod assemblages of rocky surfaces or patches of hard substrates show high diversities of archaeogastropods. Level bottom communities are characterized by a high diversity of mesogastropods and cephalaspidean opisthobranchs. The evolution of neogastropods allows this group to become increasingly dominant during the Cretaceous; the number of nerineacean genera is in the process of decreasing after the Cenomanian.

The origin of the neogastropods was within the Temperate marine zone. In the Tethyan realm, neogastropods were not recorded prior to the Upper Albian. It is assumed, that the first neogastropods were buccinids which have evolved from deposit-feeding groups.

The Tethyan gastropods were profoundly affected by the terminal Creta-

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ceous events. The extinction of Tethyan gastropods is interpreted as having been primarily caused by a change of surface water temperature distribution in the marine biosphere.

1. Introduction

The composition of aquatic communities is controlled by the chemical and physical environment (BOUCOT, 1981) and by the interactions of their members. Chemical parameters controlling animal life are dependent on such factors as the mineral content of the water, Eh, pH, etc. Physical parameters include such primary factors as water temperature, light intensity and wave length, water pressure, water energy and substrate. In broad, pragmatic terms, only the substrate can be roughly identified by direct evidence through a petrological analysis of the rocks containing the fossil assemblage. The remaining parameters are deduced from observations of sediment structures and the composition and distribution of fossil assemblages by a critical actualistic analysis. However, due to the varying degrees of fossilisation potential within individual taxa large percentages of the ancient living communities are not represented in fossil assemblages.

Water temperature is probably the most critical factor among the physical parameters (BOUCOT, 1981). The distribution of animals is regulated through the physiological effect of water temperature on every single individual of a species or even of taxonomically higher hierarchies to which species may be combined. The temperature dependence is not only due to the fact that the majority of marine invertebrates lives within the range of 0–35° C. Tolerance for maximum and minimum temperatures at which sufficient metabolic rates are maintained is specific for the representatives of a certain species. Temperatures above and below this range are, therefore, lethal for individuals of a taxon. However, it is much more important for the distribution of individual taxa that most organisms require a critical temperature for reproduction (GUNTER, 1957). Water temperature does not only have a primary regulative effect on the distribution of each taxon. The occurrence or non-occurrence of a taxon will influence an entire trophic system.

By far the majority of known megafossil assemblages are of shallow water origin; these assemblages reflect the local surface temperature. Consequently, shallow water assemblages of different geographical regions which contain taxa equivalent on the genus or even family level are indicative of temperature-controlled realms. It is assumed in all conclusions on the distribution of realms in geologic times that the temperature tolerance is a conservative element in the animal-environment relationship (BOUCOT, 1981). The deduction of relative temperature ranges based on the geographic distribution of fossil taxa together with sedimentological data is a rapid, pragmatic, and valid method for recognizing the distribution of temperature-related realms in the past.

2. Cretaceous realms

The various definitions of Tethys and the concept of Mésogée have been discussed by KOLLMANN and by MASSE in this volume. Tethys is utilized here in the sense of KAUFFMAN (1973, 1975) and SOHL (1971, 1987) as a paleobiogeographically defined realm which covers the area of distribution of algal-coral, coral-rudist, or rudist dominated organic framework build-ups. According to the present distribution of bioherms in the marine biosphere, the Tethys has to be considered as being within the Tropical realm during the Cretaceous. This definition does not agree with the original definition of Tethys by SUÈSS (1893), however, it is very convenient to work with. It has been emphasized by KAUFFMAN (1973, 1984) and SOHL (1971, 1987) that the Tethyan realm was not stable during the Cretaceous but has had varyable limits with time.

Gastropods do not provide any evidence for a Supertethys postulated by KAUFFMAN & JOHNSON (1988). It has been shown by BEAUVAIS & BEAUVAIS (1974) that corals are occurring in most parts of the belt considered as Supertethys. Although the distribution is sporadic it provides evidence against a Supertethys with hotter and more saline water than the rest of Tethys. ACCORDI, CARBONE & SIRNA (1982) have demonstrated that Upper Cretaceous coral-algal associations of south Italy are restricted to muddy sands. These sediments show a much lower diversity of rudists than adjoining rudist banks. In descriptions of lower Cretaceous occurrences of the Provence (TURNSEK & MASSE, 1973) and of Spain and Austria (REITNER, 1987) rudists generally occur in different beds than corals. All of these observations strongly support SCOTT, quoted by KAUFFMAN & JOHNSON (1988), that coral-algal dominated and rudist-dominated reef paleocommunities have preferred different habitats.

SOHL (1971, 1987) has developed the concept of a transitional marine belt north and south of the belt with Tropical organic build-ups. In suitable environments, this belt was inhabited by corals and rudists as well as Tethyan gastropods. Like the Tethyan realm this zone was varying in its geographical limits during Cretaceous times; these features can be explained also by comparison with modern marine realms:

According to WELLS (1957), modern coral reefs are best developed at mean annual water temperature between 23–25° C. No significant reefs occur where temperatures during the year fall below 18° C, except for a short period. The distribution of reefs therefore, is restricted to the Tropical belt. Hermatypic corals and calcareous algae, however, are not restricted to this belt but do also occur outside together with other Tropical elements. In fact, they have been reported into latitudes with mean annual temperatures as low as 15° C (WELLS, 1957), where they gradually diminish in number and diversity. These marine zones are called subtropical by VAUGHAN (1940) or Warm Temperate by STEPHENSON (1947). The extent of the zones has been summarized by HEDGPETH (1957).

It may therefore be assumed that the Warm Temperate zone of the Cretaceous marine biosphere is characterized by solitary rudists and corals. In the

Upper Cenomanian these fossil groups were spreading into Europe as far north as Saxony (see the faunas described by GEINITZ, 1872). In the Campanian rudists were found in abundance in southern Sweden (KÜHN, 1949) which is by far the northernmost distribution of this group. In the Maastrichtian corals and rudists were spreading as far north as Maastricht (Holland). It has been shown by SOHL (1971) that equivalent to modern seas, cypraeids are common gastropods of the Cretaceous Warm Temperate zone. This zone forms the southernmost extension of the archaeogastropod family Pleurotomariidae which gains importance further to the north. This gastropod family is therefore of great importance for distinguishing the Tethyan zone from the Temperate zones (SOHL, 1971; KOLLMANN, 1984).

The Warm Temperate marine zone is followed northward by a zone called Temperate in the biological literature. This zone is part of the Boreal zone of paleontologists. Tropical elements are missing; the gastropod faunas are not diverse and characterized by pleurotomariids. This zone seems to agree in its distribution with the Lower Cretaceous Hoplitinid province of OWEN (1971) and the Upper Cretaceous North Temperate realm as defined by the distribution of the cephalopod *Belemnitella* (KEGEL CHRISTENSEN, 1976).

There is not much evidence for a Cretaceous marine province equivalent to the Subpolar province of modern seas. Based on my own observations, a fauna from the island of Nugsuaq, west Greenland, dated as Maastrichtian with ammonites (ROSENKRANTZ, 1970) may represent this marine zone. It contains dominantly shells of infaunally living gastropods, mostly belonging to the opisthobranch group of Cephalaspidea. THORSON (1952) has shown that the percentage of infaunal species is highest in cold water environment of the Subpolar province as life within the sediment provides protection against strong temperature changes. Towards the Tropical zone, the percentage of infaunal species in the total fauna is diminishing while the number of taxa remains approximately the same.

The succession of temperature-controlled biogeographic zones in the northern hemisphere shows that there was, at least temporarily, a higher temperature gradient in the Cretaceous than assumed in the earlier literature (KAUFFMAN, 1973). This agrees with the observations of KEMPER (1987).

3. Vertical successions

Utilizing recent ostracodes, HAZEL (1970) has demonstrated that the temperature-controlled latitudinal marine realms of the Atlantic continental slope are to a certain extent vertically reproduced in lower latitudes. There also are some examples on various fossil groups that can be cited for the Cretaceous; they are:

WIEDMANN (1988) has recorded in the Vascogotic through of northern Spain a Lower Turonian association of mammitid ammonites of northern origin which had lived in water depths below 200 meters while shallow zones were

inhabited by a typically Tethyan fauna with vascoceratid ammonites. Another, yet unpublished example, is the occurrence of a *Belemnitella* in the Upper Maastrichtian "couches de passage" of the Olonos-Pindos zone which was found during field work in association with I. MARIOLAKOS south of Tripolis (Peloponnese, Greece). FLEURY (1980) considers the deposition depth of these sediments to be 2-3000 meters.

Examples involving gastropods include the Upper Aptian fauna of north Tunisia (MONGIN, 1971) which contains forms exclusively described from the Boreal Cretaceous of North Germany (WOLLEMAN, 1900, 1912), England (ABBASS, 1973), the Paris Basin (D'ORBIGNY, 1842-43) and Mangyslak in the Soviet Union (NACKIJ, 1916). A correlation between water depth and faunal composition has been observed in the Upper Cretaceous of the Charente in France by KOLLMANN (1985). Tethyan faunas are restricted here to the regression phases of HANCOCK and KAUFFMAN (1979) while temperate ones with pleurotomariids and large archaeogastropods belonging to the genus *Coelobolma* are associated with transgressive pulses.

4. Systematic inventory of Cretaceous Tethyan and Warm Temperate gastropods

Scholars such as J. WALTHER (1908), DACQUÉ (1926) and DIENER (1925) have already emphasized the fact that an equatorial belt, named by authors southern sea-belt, mediterranean region or Mésogée was characterized not only by rudists, coral reefs and larger Foraminifera but also by *Actaeonella* and *Nerinea* among the gastropods. These genera, in the sense of the older authors, have undergone an extensive taxonomic subdivision. They have been revalorized taxonomically into family (Actaeonellidae) and superfamily (Nerineacea) rank but still can be used together with other forms for characterizing and delimiting the Tethyan realm (SOHL, 1971). In the Warm Temperate zone these gastropods are absent or very rare.

The most common gastropod genera of the Tethyan realm and of the Warm Temperate zone have been compiled by SOHL (1971). Additional observations have been published by SOHL (1987). With the exception of a few modifications, not much is to be added to the general inventory of Cretaceous Tropical and Warm Temperate gastropods (Table 1).

Family or genus	Tropical	Warm Temperate
Trochidae	diverse	few
<i>Discotectus</i>	common	absent
Fissurellidae	common	absent
Pleurotomariidae	absent	common
Neritidae	diverse, abundant	rare
<i>Pileolus</i>	widespread	rare
Cassiopidae	rare	abundant
Turritellidae	few	abundant

Family or genus	Tropical	Warm Temperate
Aporrhaidae	common	common
<i>Harpagodes</i>	common	absent
<i>Perissoptera</i>	rare	common
Naticidae	common	abundant
<i>Tylostoma</i>	abundant	common
<i>Lunatia?</i>	rare	common
Nerineacea	diverse, abundant	absent or very rare
Actaeonellidae	abundant	absent or very rare

Table 1: Tropical and Warm Temperate gastropods. After SOHL (1971, 1987, slightly modified)

5. Occurrence of selected gastropod groups within the Tethyan realm

As stated by BOUCOT (1981), there is a high correlation between substrate type and benthic organisms within the realms. The use of benthic organisms for biostratigraphic correlation, therefore, is efficient only for sediments deposited under corresponding conditions. It should be the general rule never to extend correlation with benthic forms beyond the facies of their biocoenosis. It therefore seems to be of foremost interest to evaluate the life conditions of fossil gastropods. This has been done for some groups abundant in the Tethyan realm (SOHL, 1971). The state of knowledge is rather poor and all generalisations should be treated with caution until such time as more detailed studies become available.

5.1. Nerineacea

The nerineaceans were most diverse from the Upper Jurassic to the end of the Cenomanian. With the end of the Cenomanian the diversity becomes low.

Families and genera of nerineaceans are primarily distinguished by internal plications. The function of these plaits is still not fully understood. Obviously, some of them have served for subdividing the mantle cavity to separate the inhalant water current from the exhalant current. The exhalant current which carried out the waste material from the mantle cavity was expelled through a sutural notch. The position of the sutural notch allowed an expelling of the water well back of the head. It has been emphasized by SOHL & KOLLMANN (1985) that this is a feature characteristic for completely or partly infaunally-living gastropods.

The most striking feature of the nerineaceans is the mass occurrence in "Nerinea beds" which have been reported from virtually all areas of the Tethyan realm. It has been documented by DAUWALDER & REMANE (1979), WIECZOREK (1979) and KUOYOU MONTZAKIS (1987, 1989) that the heavy nerineacean shells are transported only over short distances and that their thanatocoenosis resembles the original biocoenosis to a high extent.

The nerineacean faunas of the earlier Cretaceous described among others by D'ORBIGNY (1842), PICTET & CAMPICHE (1862), PELLAT & COSSMANN (1907), DE BRUN, CHATELET & COSSMANN (1916), DELPEY (1941) and PHELINTSEV (1927, 1931, 1965) show a persistence of Upper Jurassic genera (or families in the not performable narrow taxonomic concept of PHELINTSEV) into the Cretaceous. Most of these genera which have a short siphonal channel (KOLLMANN, 1976) and frequently a hollow columella become extinct during Aptian time. The process of the replacement of this Jurassic-early Cretaceous faunal stock is not yet documented sufficiently.

Observations on the environments of lower Lower Cretaceous nerineaceans are scarce. The analytical studies of WIECZOREK (1979) on Upper Jurassic nerineacean faunas may be applied to lower Lower Cretaceous ones. According to this author, nerineacean assemblages are restricted to environments of the open shelf. WIECZOREK (1979) concluded from sedimentological data that mass occurrences in nerineacean beds occurred in environments with low water energy, stable substrate and slow sedimentation rates. These would have been the optimal conditions for this gastropod group. From the Cretaceous, REY (1979) has reported the occurrence of undertermined nerineaceans from wackestones to packstones of Estremadura (Portugal). These were deposited under relatively low energy conditions, too. WIECZOREK (1979) reported the highest diversity of species from the "bahamite" or grapestone facies of the open shelf. The highest tolerance to environmental conditions has been observed by him in the genera *Nerinea*, *Nerinella* and *Ptygmatis* which extend into mud and pellet mud facies. This agrees with the observations of SHIKAMA & YUI (1973), who have found *Nerinea* but no other nerineacean genera in sediments of various grain sizes.

There are only a few observations on the ecology of upper Lower and Upper Cretaceous nerineaceans. They do not provide a uniform picture of the environmental conditions. ACCORDI, CARBONE and SIRNA (1982) have described an Aptian fauna containing the nerineaceans *Neoptyxis* together with the Ceritacean *Pseudonerinea* (generically determined after the figures in this publication). In Texas, these genera and *Multiplyxis* occur in low energy lagoonal environments (KOLLMANN, DECKER & LEMONE, unpublished). Occurrences in laminated calcarenites of probably high energy foreshore conditions are probably re-deposited.

From strata of probably Cenomanian age of the Rocca di Cave section, CARBONE, PRATURLON, and SIRNA (1971) have recorded representatives of *Plesioplocus* and *Italoptygmatis* (generic determination changed after the figures of the above-mentioned work). According to these authors, the sediments have been deposited in a medium to high energy environment.

Nerineaceans which are herewith assigned to the genera *Nerinea*, *Neoptyxis*, *Haploptyxis* and *Italoptygmatis* have been recorded by ACCORDI, CARBONE & SIRNA (1982) from limestones of Cenomanian to Turonian age. These have been deposited in medium energy environments.

Rich faunas of nerineaceans belonging to the genera *Dalmatea*, *Nerinoides*,

Neoptyxis, *Laevinerinea*, *Plesioptygmatis* and *Haploptyxis* have been found by KOLLMANN (unpublished) in the massif of Akros, close to Epidavros (Greece). These sediments, dated as Cenomanian by DECROUEZ (1977) and MERMIGHIS (1989), consist of wackestones, floatstones, rudstones and grainstones deposited according to MERMIGHIS (1989, 1989a) in a low energy shallow environment of an internal platform.

KOUYOUMONTZAKIS (1985) recorded taxa of the genera *Haploptyxis* (revised, determined as *Plesioptygmatis* by this author) and *Neoptyxis* (the determination could not be verified as no significant specimen has been figured but it seems rather unlikely that it is correct). These occur in Upper Cenomanian to Turonian wackestones to grainstones, indicating a mobile substrate and low energy conditions. *Haploptyxis* is also occurring in the Upper Turonian sands of Uchaux as part of a diverse level bottom community in the sense of THORSON (1957). It has lived on the soft sandy bottom under low energy conditions.

The preferred environment of *Simploptyxis* which is the most common nerineacean of the Eastern hemisphere from Turonian upwards is different (HÖFLING, 1985). In the Gosau Group of the Lattengebirge (Bavaria) this genus has lived in an environment with relatively high water energy at a temporary low sedimentation rate. This agrees with observations of HERM (1977) who has recorded *Simploptyxis* in the Brandenberg area in Tyrol from coarse- to medium-grained sands deposited in unprotected environments of an external lagoon.

These scanty observations suggest the following environmental conditions for the Cretaceous nerineaceans:

1. Lower Lower Cretaceous nerineaceans were living exclusively under low energy conditions of the open shelf and may have had their optimal living conditions on consolidated surfaces.

2. Upper Lower Cretaceous and Upper Cretaceous nerineaceans were inhabiting various environments, but obviously always soft bottom substrates. *Neoptyxis* and *Haploptyxis* were inhabiting a low to medium energy environment. *Plesioplocus* and *Italoptygmatis* have lived under medium to high energy conditions. *Simploptyxis*, which is characteristic for the Upper Cretaceous from the Turonian upwards, was living under high energy conditions.

3. It has to be concluded that beginning with the Aptian nerineaceans were radiating into various environments.

5.1.1. Itieriidae

Itieriidae are well represented in the Cretaceous sediments. Like the Nerineacea mentioned in the previous chapter, the occurrence of lower Lower Cretaceous Itieriidae may be compared with that of the Upper Jurassic. WIECZOREK (1979) has described two genera, *Phaneroptyxis* and *Fibuloptygmatis*, from the Upper Jurassic of the Polish Holy Cross Mountains. These genera are restricted to the grapestone-facies of the carbonate bank which is interpreted to have been deposited in subtidal or intertidal shallow water with restricted water circula-

tion. According to studies by CARBONE, PRATURLON, and SIRNA (1971), *Phaneroptyxis* is ranging stratigraphically upwards into the Upper Cenomanian (there are some doubts concerning this age as all other recordings of this genus are not younger than Barremian). Other occurrences in the platform limestone of the Aquilean Abbruzze Mountains have been described by SCHNARRENBERGER (1901) and PARONA (1909).

Beginning with the Aptian, another group of the Itieriidae developed. Its taxa have a short, beak-like siphonal channel but resemble in its general morphology the Actaeonellidae. Generally, the channel can be observed only in axial sections of shells. This group of itieriids has primarily been distributed in siliciclastic sediments.

One itieriid genus belonging to this group is *Peruviella* which hitherto is known from West Africa (Angola), South America (Brasil, Peru), North America (Texas, British Columbia, unpublished) and the Soviet Union (POJARKOWA & DJALILOW, 1985). The age is Middle to Upper Albian, perhaps also Lower Cenomanian. For details on the distribution see: KOLLMANN & SOHL, 1979; CASSAB, 1982. Observations in West Texas (KOLLMANN, DECKER & LEMONE, unpublished) have shown that this genus occurred under different energy conditions and was exclusively controlled by the substrate (sand-sized sediments). Single specimens, sticking obliquely in the sediment as it has been described for the recent opisthobranch *Acteon* (FRETTER & GRAHAM, 1954) and, consequently, for the Actaeonellidae (SOHL & KOLLMANN, 1985), suggest an infaunal life for this gastropod group.

The genus *Sogdianella* DJALILOW (1972) is belonging to the same itieriid group as *Peruviella*. (*Omphalactaeonella* HACOBIAN (1972) is a younger synonym). This genus is widely distributed around the Mediterranean. *Sogdianella syriaca* (CONRAD) has been recorded from North Africa and Greece (KOLLMANN, 1985, 1987). Other species have been described by PCELINTSEV (1953), HACOBIAN (1976), DJALILOW (1972) and ALIEV & ALIEV (1986) from the southern Soviet Union and by KOLLMANN & SOHL (1979) from the Gosau Group of the Eastern Alps and from North America.

Sogdianella brandenbergensis (KOLLMANN), is the only species known from the Eastern Alps. It has lived in tidal flats (HERM, 1977). Sediments deposited here are coarse sands. In an occurrence in Greece described by KOLLMANN (1987), *Sogdianella* is observed in association with the cerithiids *Diozoptyxis* and *Itruvia*, several nerineaceans, the itieriid *Vernedia* and one *Trochactaeon* species. Similar assemblages have been observed in Armenia (HACOBIAN, 1978, personal observations). The sediments indicate a soft bottom. As in *Peruviella* the distribution was controlled by sediment grain size. Obviously, these genera were subject to infrequent strong water agitation as all gastropod specimens are eroded. Bivalves do not occur in these strata. Additionally, *Sogdianella* is rather common in the Tripolitsa limestone of Greece (KOLLMANN, 1985 and unpublished).

The genus *Eotrochactaeon* HACOBIAN, which is closely related to *Sogdianella*, was until recently only known from coarse-clastic, terrestrially-influenced sediments from the southern Soviet Union (HACOBIAN, 1976), North Africa

(DELPEY, 1940) and Greece (KOLLMANN, 1982). The genus has recently been recorded by KOLLMANN, DECKER & LEMONE (unpublished) from shallow lagoon sediments of the Trinity sequence of West Texas.

The genus *Vernedia* MAZERAN (1912), which has been erroneously placed into the genus *Itruvia* by many authors (see: KOLLMANN & SOHL, 1979; KOLLMANN, 1987), is widely distributed from the upper Lower Cenomanian upwards. In Hölzelsau, Tyrol, *Vernedia* occurs as part of a diverse fauna described by RAHMAN (1967). The environment inhabited by this fauna indicates a sand bottom below wave base. In all other localities known to me, *Vernedia* occurs in large numbers in sands or other coarse clastic sediments and is part of a mollusc fauna of low diversity. As mentioned before under *Sogdianella*, the shells are generally highly eroded and, obviously, have been deposited under high energy conditions.

Summarizing the state of our knowledge on the Itieriidae the following statement can be made: A conservative stock of genera extends from the Jurassic into the Barremian, with single species perhaps also into the Cenomanian. Like the lower Lower Cretaceous nerineaceans, this group is restricted to parts of the carbonate platforms deposited under open shelf conditions. Like the nerineaceans the itieriids began to radiate into other environments in the Aptian.

5.2. Actaeonellidae

The ecology of Actaeonellidae has been treated in detail by KOLLMANN (1965, 1967) and SOHL & KOLLMANN (1985). Therefore, only a short summary of the results together with a discussion of recent literature is given here. Due to the lack of other data only the genera *Actaeonella* and *Trochactaeon* are discussed.

5.2.1. *Actaeonella*

It has been emphasized by KOLLMANN (1965) and by SOHL & KOLLMANN (1985) that *Actaeonella* is restricted to fully marine environments. HÖFLING (1985) has shown that *Actaeonella* occurred in lagoons under quiet water conditions. This agrees with occurrences of *Actaeonella* in the Upper Albian Meule de Bracquagnies of South Belgium (BRIART & CORNET, 1868; MARLIERE, 1939) and the Upper Turonian sand of Uchaux, France (ROMAN & MAZERAN, 1920). In both deposits *Actaeonella* is part of a diverse fauna characteristic for environments below wave base. The same environment has also been described by WAGREICH (1988) for the Santonian upper Streiteck Formation of the Gosau area where *Actaeonella laevis* (SOWERBY) is very abundant.

According to SOHL & KOLLMANN (1985) the sediments in which *Actaeonella* occurs are generally sands or sandy limestones indicative of an unstable bottom. There are only few occurrences known from carbonate platforms. In the area of Kent (Texas) the occurrence of *Actaeonella* is recorded in strongly

bioturbated grainstones of the Buda Formation (KOLLMANN, LEMONE, DECKER, unpublished). *Actaeonella pecosensis* STANTON (1947) has been described from the Devils River Limestone of Texas.

Sedimentological data for these occurrences are not available. The occurrence of *Actaeonella* in the Marble of Almyropotamos (Euboea, Greece) described by KATSIKATSOS & KOLLMANN (1987) involves marbles which are completely recrystallized and do not reveal any prior sedimentological features.

The infaunal life of *Actaeonella* postulated by SOHL & KOLLMANN (1985) has been questioned by HÖFLING (1985) who believes this genus was part of the epifauna living as an active carnivore. It should be emphasized that the position of *Actaeonella* in the sediment, which has been described by SOHL & KOLLMANN (1985) agrees with observations on modern cephalaspidean gastropods which have a documented "bulldozing" mode of action (THAYER, 1983; VERMEJ, 1987). The elongated aperture is after LINSLEY's (1977) "law" nr. 5 characteristic for a water flow from anterior to posterior by passing a single gill. In *Actaeonella*, the water was leaving the mantle cavity by a funnel-shaped exhalant siphon at the posterior end of the shell. This feature is characteristic for the infaunally living cephalaspideans and occurs also in several prosobranch gastropods of the same life mode.

5.2.2. *Trochactaeon*

Similar to *Actaeonella*, a detailed interpretation of the environmental parameters of *Trochactaeon* has been given by KOLLMANN (1967) and by SOHL & KOLLMANN (1985). Otherwise than quoted by HÖFLING (1985), these papers emphasize the high salinity tolerance of *Trochactaeon* compared with *Actaeonella*. The salinity range postulated by the former authors for *Trochactaeon* is extended by HÖFLING (1985). He interprets *Trochactaeon* of the Schneckwand mass occurrence in the Gosau area (Austria) as inhabitants of a hypersaline environment.

Generally, *Trochactaeon* assemblages show a low diversity (HERM, 1977). The substrates inhabited by *Trochactaeon* species range from limestones and shales to coarse sands (HERM, 1977; HÖFLING, 1985; SOHL & KOLLMANN, 1985). As stated by the latter authors, *Trochactaeon* seems to have preferred generally more fine-grained sediments than *Actaeonella*.

According to HERM's (1977) studies on the Upper Cretaceous of Brandenburg (Tyrol), *Trochactaeon* inhabited tidal flats with high energy environments (The *Actaeonella* mentioned by HERM as co-occurring is the iteriid *Sogdianella*. (see SOHL & KOLLMANN, 1986). Sedimentological data of the Schneckwand mass occurrence of *Trochactaeon* in the Gosau basin (HÖFLING, 1985) which was mentioned above suggest a calm, but temporarily agitated water (Plumley-Index II).

Because of high variability within the species of *Trochactaeon* and abundant effects of mechanical wear, and consequent shell repair by deposition of

internal secondary shell layers SOHL & KOLLMANN (1985) concluded that *Trochactaeon* led a dominantly epifaunal life.

5.3. *Trajanella*

The occurrence of *Trajanella* in the "mediterranean" zone of the Cretaceous was first observed by DELPEY (1939). Localities where *Trajanella* occurs include the Turonian faunas of Uchaux (D'ORBIGNY, 1842-43; ROMAN & MAZERAN, 1920), the upper Lower Cenomanian fauna of Hölzelsau (RAHMAN, 1967), the Aptian-Albian Hiraiga Formation of Japan (KASE, 1984), and Cenomanian sandstones east of Horsetown, California (ANDERSON, 1958). The gastropods of these occurrences have been living in environments below the wave base in level bottom communities in the sense of THORSON (1957). In the Upper Cenomanian Pläner of Saxony (GEINITZ, 1871-75; DENINGER, 1905) and the equivalent Korycany Formation of Czechoslovakia (WEINZETTL, 1910), *Trajanella* has been found together with highly diverse faunas in conglomerates. KASE (1984) recorded *Trajanella* from sediments ranging from conglomerates to fine- to medium-grained sandstones together with patellid gastropods and several archaeogastropods. According to KASE (1984), the fauna was living on a rocky bottom. This suggests a wide range of habitats for *Trajanella*.

5.4. *Discotectus*

The Trochid *Discotectus* is recorded as having been distributed in a variety of environments within the Tethyan realm (SOHL, 1971, 1987). HÖFLING (1975) describes *Discotectus* from the Gosau Group of the Lattengebirge in Bavaria. The genus occurs here in a nodular, grey, marly limestone containing irregularly distributed biomorphs and large bioclasts. According to HÖFLING, this originally mobile sediment has been deposited in the calm, temporarily agitated water of a back reef lagoon behind a hippuritid reef barrier. The numerous small specimens of this locality as well as of other alpine occurrences indicate that representatives of this genus may have lived on marine plants. *Discotectus* is also an abundant member of the diverse faunas of flats deposited below the wave base. In West-Texas *Discotectus* has been recorded exclusively on the fringing facies of a rudist reef (KOLLMANN, DECKER, LEMONE, unpublished). It occurs in Uchaux (ROMAN & MAZERAN, 1920), in Hölzelsau, Tirol (RAHMAN, 1967), in the Cenomanian of the Sarthe, France (GUERANGER, 1867; KOLLMANN, 1978), and in the Aptian Tanohata Formation of the Miyako area in Japan (KASE, 1984). There are many other occurrences such as the Plenus zone of Saxony (GEINITZ, 1871-75; DENINGER, 1905), the Korycany Formation of Czechoslovakia (WEINZETTL, 1910), the limestones of the Monti d'Ocre in Italy (PARONA, 1909) and the Edwards Formation (STANTON, 1947) for which no general environment interpretation can be given due to the diversity of facies.

5.5. *Tylostoma*

Tylostoma occurs most commonly in nodular limestones deposited in shelf basins (KOLLMANN, DECKER, LEMONE, unpublished) below storm wave base. In this facies, only internal molds are preserved. *Tylostoma* has been recorded by RAHMAN in Hölzelsau but otherwise representatives of this genus are rare within faunas living on siliciclastic substrates.

Systematically, *Tylostoma* is generally considered to be a naticid (WENZ, 1938–44). The shape of the molds is extremely variable and recordings of larger numbers of species from a single fauna as described by PERKINS (1960) have to be treated with caution.

5.6. *Cassiopidae*

The distribution of *Cassiope* (I do not follow the taxonomy of MENNESIER, 1984, which seems to be too artificial), has been discussed in detail by CLEEVELY & MORRIS (1988). Earlier papers (HERM, 1977; KOLLMANN, 1975) have emphasized the occurrence of this genus in marginally marine to non-marine environments utilizing the studies of MERTIN (1939). CLEEVELY & MORRIS (1988) have pointed out that the family lived in “essentially marine inshore/backshore environments”.

6. Gastropod assemblages

This chapter gives an outline of the composition of those gastropod assemblages that do not consist exclusively of nerineaceans and actaeonellids. For following the evolution of communities it would be most advantageous to compare contemporaneous assemblages of each environment. This poses problems: On one hand the fossil record is not complete; on the other hand there are hardly any faunas known to me from siliciclastic sediments of the lower Lower Cretaceous because of the broad geographic distribution of carbonate platforms (SCHLAGER, 1981).

In the following Cretaceous gastropod assemblages of different stratigraphic levels and substrates are split up into their archaeogastropod, mesogastropod, neogastropods and opisthobranchs taxa. The Mesogastropoda are further split into families (except for the Cerithiacea); the opisthobranchs are divided into Cephalaspidea and Entomotaeniata. The assemblages are discussed at the end of this chapter. To facilitate the reading of this paper the traditional taxonomic classification into orders is used.

6.1. Orgon and Brouzet-les-Alais. The fauna of Orgon has been described by COSSMANN (1916) while the fauna of Brouzet-les-Alais has been described by PELLAT and COSSMANN (1907) and DE BRUN, CHATELET, and COSSMANN (1916). The gastropod fauna is summarized in table 2.

- 26 Archaeogastropoda
- 29 Mesogastropoda belonging to the following families
 - 4 Naticidae
 - 5 Aporrhaidae
 - 1 Purpurinidae
 - 2 Colombellinidae
- 12 Cerithiacea (not subdivided into families)
 - 1 Epitoniidae
 - 3 Rissoidae
 - 1 questionary Omalaxidae (*Pleurotomaria urgonensis* of Cossmann)
 - 5 Pseudomelaniidae
- 24 Opisthobranchia
 - 10 Cephalaspidea
 - 14 Entomotaeniata

Table 2. Composition of the gastropod fauna of Orgon (after PELLAT & COSSMANN, 1916)

The fauna of Brouzet-les-Alais is similar to the fauna of Orgon, as far as the diversity of the nerineaceans and archaeogastropods is concerned. The mesogastropods include aporrhoids and naticids, but the diversity is not as high as in Orgon. The same observation is made with the cephalaspidean opisthobranchs.

6.2. Aquilanian Abruzzos. Diverse faunas of Cenomanian age have been described from the Aquilanian Abruzzos of Italy by SCHNARRENBERGER (1901) and PARONA (1909). The gastropod localities separated by Parona in his faunal list are compared in table 3:

Fossa Agnese	Northern margin of the Fossa Mezza Spada
27 Archaeogastropoda	14 Archaeogastropoda
13 Mesogastropoda	6 Mesogastropoda
4 Naticidae	2 Naticidae
1 Mathildididae	00
6 Cerithiacea	1 Cerithiacea
1 Aporrhaidae	2 Aporrhaidae
00	1 Cypraeidae
1 Colombellinidae	00
2 Neogastropoda	2 Neogastropoda
13 Opisthobranchia	5 Opisthobranchia
00	1 Cephalaspidea
13 Entomotaeniata	4 Entomotaeniata

Table 3. Comparison of Cenomanian gastropod faunas of the Aquilanian Abruzzos (after PARONA, 1909)

6.3. Nodular limestones of the Washita-Edwards group of Texas. The faunas of this widely distributed facies have been investigated by CRAGIN (1893), STANTON (1947), PERKINS (1960) and KOLLMANN, DECKER, LEMONE (in preparation). PERKINS (1960) has shown that the Goodland Formation of the Fort Worth-Weatherford area contains a fauna dominated by bivalves. It has not been explicitly mentioned by this author that the bivalves are preserved as internal molds of articulating specimens. The gastropods listed by PERKINS (1960) are mostly turritellids, aporrhoids and the naticid *Tylostoma*. Additionally, the trochid *Calliostoma*, a cerithiid belonging to the genus *Diozoptyxis* or a closely related genus (*Cerithium bosquensis* of STANTON, 1947) and an hitherto undescribed neogastropod genus (!*Turbo benbrookensis* STANTON) are recorded. Furthermore, this facies has yielded ammonites, many irregular echinoids and solitary corals.

The fauna of the Finlay Limestone Formation of West Texas (KOLLMANN, DECKER, LEMONE, in preparation) has virtually the same composition. Additionally, it contains abundant specimens of the neritid *Otostoma*, and the epitoniid *Confusiscala*. While the other molluscs are represented by internal molds the shell of *Otostoma* is always preserved.

The nodular limestones of the Washita-Edwards Group have been deposited under open shallow marine conditions at low water energy (ROSE, 1972; WILSON & JORDAN, 1983). They represent the facies zone 2 of WILSON (1975).

6.4. Northeastern Japan. The gastropod fauna of the Miyako Group in Japan (KASE, 1984) occurs in siliciclastic rocks of Upper Aptian-Albian age. It is obviously of marginally Tethyan origin. KASE has shown that patelliform species are restricted to conglomerates and to conglomeratic coquinal limestones while other archaeogastropods occur also in fine- to medium-grained sandstones but not in sandy shales. The mesogastropods are mostly restricted to the calcareous sandstones. Only *Trajanella* is abundant in conglomerates. *Cirsocerithium*, 2 genera of aporrhoids, *Gyrodes*, and 2 nerineaceans occur in sandy shales which otherwise show the lowest diversity of gastropods of all sediments of the Miyako Group.

6.5. Losenstein Formation. The Upper Albian fauna of the Losenstein Formation in Austria which was described by KOLLMANN (1976, 1978, 1979, 1982) contains 93 taxa which have undergone transportation. This fauna does not indicate a single level bottom community but represents a series of different environments (KOLLMANN, 1982).

6.6. Hölzelsau, Tyrol. A level bottom community is represented by the upper Lower Cenomanian gastropod fauna of Hölzelsau (Tyrol), described by RAHMAN (1967). See table 4:

- 9 Archaeogastropoda
- 27 Mesogastropoda
- 3 Turritellidae

- 1 Architectonicidae
- 13 Cerithiacea (different families)
- 1 Epitoniidae
- 1 Pseudomelaniidae
- 1 Aporrhaidae
- 1 Cypraeaceae
- 5 Naticidae
- 5 Neogastropoda
- 28 Opisthobranchia
- 15 Entomotaeniata
- 13 Cephalaspidea

Table 4. Middle to Upper Cenomanian gastropods from Hölzelsau, Tyrol (RAHMAN, 1967)

6.7. Uchaux, France. The sand of Uchaux was deposited during the Upper Turonian in the "Golfe rhodanien" (SORNAY, 1950). Its rich and diverse fauna represents a level bottom community. The gastropod fauna described by D'ORBIGNY (1842-43) and ROMAN & MAZERAN (1920) has the following composition (Table 5)

- 9 Archaeogastropoda
- 30 Mesogastropoda
- 4 Pseudomelaniidae
- 1 Epitoniidae
- 4 Naticidae
- 5 Turritellidae
- 1 Xenophoridae
- 5 Cassiopidae
- 5 Cerithiacea (not subdivided into families)
- 1 Strombidae
- 4 Aporrhaidae
- 9 Neogastropoda
- 8 Opisthobranchiata
- 5 Cephalaspidea
- 3 Entomotaeniata

Table 5. Gastropods of the Upper Turonian of Uchaux, France (after ROMAN & MAZERAN, 1920)

6.8. Gosau Group. The Gosauschichten of the older literature do not represent a single facies. They occur in several geographically isolated areas of the Eastern Alps. These are called Gosau Basins after the village of Gosau in Upper Austria. The only comprehensive monograph on the Gosau gastropods (ZEKELI, 1852) is outdated in many respects. Critical revisions of this monograph by REUSS (1853) and STOLICZKA (1865) are outdated, too. More recent papers are those on the gastropods of the surroundings of Brandenburg

		LITHOLOGY	DEPOSITION	GASTROPOD FAUNAS	
L. CAMP.	900	RESSEN FM	Graded conglomerates, sandstone beds of great thickness, shales	no gastropods	
	800	BIBERECK FM	Upper part: Calcareous shales and turbidites Lower part: Shales with sandstone layers	Shelf shale facies	Archaeogastropoda: Low diversity (2 species of Pleuromariidae) Mesogastropoda: Diverse Neogastropoda: Low diversity Opisthobranchia: Low diversity, rare
U. SANTONIAN		SANDKALK MBR	calcareous arenite ("Sandkalkbank")	low energy shallow water environment	
		HOFERGRABEN MBR	Upper part: Hofergraben Mbr. Fossiliferous shales, few sandstones, basal conglomerate	pelite-dominated; deepening to depth of middle shelf	Archaeogastropoda: Low diversity Mesogastropoda: High diversity Neogastropoda: High diversity Opisthobranchia: Low diversity
		HOCHMOOS FM	Lower part: Shales with coquinas and sandstones; rudist limestone	shallow water to extreme shallow water of inner shelf	Mesogastropoda: Mean diversity, abundant Neogastropoda: Low diversity Opisthobranchia: Special Trochactaeon and Nerineacean (Simploptyxis) facies
---	500	GRABENBACH FM	Shale with layers of coarse-grained silt to fine-grained sandstone of variable thickness, megafossils rare	Pelitic shelf sediment with storm layers deposited between mean wave base and storm wave base. Deposition depth 30 - 150 metres	Molluscs rare Archaeogastropoda: 1 species of Calliophylus Mesogastropoda: 1 species of Cerithiacea (Exechocirsus) no Neogastropoda and Opisthobranchia
L. SANTONIAN	300	STREITECK FM	Upper part: Fossiliferous shales with sandstones Lower part: Conglomerate-sandstone-shale cycles	below mean wave base coarsening upwards fan delta	Archaeogastropoda: Low diversity and rare Mesogastropoda and Neogastropoda: High diversity, abundant Opisthobranchia: Low diversity; Actaeonella laevis (SOVERBY) very abundant
	0 m	KREUZGRABEN FM	Reddish conglomerates, subordinate sandstones and shales		
?	100				

Fig. 1: The distribution of gastropods in the lower part of the Gosau sequence (lithostratigraphic column and partly environment interpretation after Wagreich, 1988).

(Tyrol) by SCHENK (1969) and on a gastropod fauna from the Gosau area by KOLLMANN (1980). Monographs on single groups are those on the melanopsids by KOLLMANN (1975, 1984), the nerineaceans by TIEDT (1958) and the actaeonellids by KOLLMANN (1965, 1967).

In the following, the distribution of gastropods in the rock sequence around Gosau is discussed. This sequence has been subdivided into formations by WEIGEL (1937), KOLLMANN (1981) and KOLLMANN & SUMMESBERGER (1982). The formations (figure 1) have been deposited under different conditions (KOLLMANN & SUMMESBERGER, 1982; WAGREICH, 1985, 1988, 1989). The megafossil-bearing sediments of the Gosau area have been considered partly as Turonian by FELIX (1908) and partly as Coniacian by KÜHN (1947). It has been subsequently proved by KOLLMANN & SUMMESBERGER (1982) and SUMMESBERGER (1985) that the gastropod-bearing sequence has been deposited exclusively in the Santonian. The discussion on the gastropod fauna of the different formations is based on FELIX (1908) and published and unpublished personal observations. As a detailed study of the distribution of gastropods is still missing only a general description showing certain trends will be given.

6.8.1. Upper part of the Streiteck Formation. The lower part of the Streiteck Formation is dominated by conglomeratic layers; the upper part is composed primarily of mudstones with siltstone layers. The megafauna is diverse and abundant. It consists mainly of solitary corals, bivalves and gastropods. Archaeogastropods are rare and are represented by a taxon of Trochidae (Angariinae) and one taxon of Turbinidae. Mesogastropod families occurring in this formation are Rissoidae, Turritellidae, Cerithiaceans, Aporrhaidae, and Cypraeidae. Most diverse are the neogastropods with Buccinidae, Galeodidae, Fasciolaridae, Mitridae and Volutidae. Opisthobranchs are especially abundant; they are represented by one species of cephalaspideans, *Actaeonella laevis* (SOWERBY), and by the small nerineacean *Aptyxiella flexuosa* (SOWERBY). According to WAGREICH (1985, 1987) the fossiliferous fine-grained sediments of the upper part of the Streiteck Formation were deposited below the mean wave base (see also the chapter on *Actaeonella*).

6.8.2. Grabenbach Formation. This formation consists of pelitic sediments with layers of fine-grained sand. Megafossils are rare (KOLLMANN & SUMMESBERGER, 1982). The fauna consists of echinoids, inoceramids and nuculids among the bivalves and two species of gastropods, belonging to the trochid *Caliomphalus* and the potamidid *Exechocirsus*. According to WAGREICH (1985, 1987) the Grabenbach Formation was deposited between mean wave base and storm wave base at a depth below 30 meters.

6.8.3. Hochmoos Formation. The facies of this formation are diverse. The lower part consists mainly of mudstones with graded, clastic biogenetic layers and sandstones. Crustacean trace fossils (*Ophiomorpha* and *Thalassinoides*) are abundant.

The gastropod faunas of the Nefgraben and the Wegscheidgraben of the Gosau basin listed by FELIX (1908) are representative for the lower part of this formation. There are two taxa belonging to the archaeogastropod family Trochidae (2 species of *Angaria*). The mesogastropods are represented by the families Cerithiidae, Naticidae, Architectonicidae, Aporrhaidae, Potamididae, Xenophoridae and Rissoidae. The neogastropods are represented by Volutidae, the opisthobranchs by the nerineacean *Aptyxiella flexuosa*. The gastropod fauna is accompanied by diverse bivalve faunas and abundant solitary corals.

According to WAGREICH (1988) the lower Hochmoos Formation has been deposited in shallow to extremely shallow water of the inner shelf under wave influence. A special facies of the Hochmoos Formation is the "Schneckenwand" which shows an accumulation of large *Trochactaeon*. These sediments have been interpreted by HÖFLING (1985) as deposits of an hypersaline lagoon (see also preceding chapter).

The upper part of the Hochmoos Formation is partly formed by the pelite-dominated Hofergraben Member (KOLLMANN, 1981). The gastropod fauna of the Hofergraben as recorded by FELIX (1908) consists of the following: 3 taxa of the archaeogastropod family Trochidae; the mesogastropod families Rissoidae, Turritellidae, Potamididae, Aporrhaidae and Naticidae; the neogastropod families Fasciolaridae, Mitridae, Volutidae and Turridae, a single opisthobranch species which belongs to the Actaeonellidae. The bivalves and corals are very diverse.

The percentage of planktonic forms within the total number of foraminifera is higher in the Hofergraben Member than it is in the underlying part of the Hochmoos Formation (WAGREICH, 1988). This indicates a deepening of the water.

The uppermost part of the Hochmoos Formation is formed by a fine-grained sandstone called Sandkalkbank (WEIGEL, 1937). The gastropods have been described by KOLLMANN (1980). The Archaeogastropoda are represented by 2 taxa of Pleurotomariidae. The Mesogastropoda are most diverse, consisting of: Rissoidae, Architectonicidae, Turritellidae, Potamididae, Aporrhaidae (3 taxa), Xenophoridae and Naticidae. The neogastropod families of the Sandkalkbank are Vexillinidae, Fasciolaridae, Fusinidae, Vasidae and Volutidae. The opisthobranchs comprise Acteonidae and Actaeonellidae. This gastropod fauna is accompanied by corals and a diverse fauna of bivalves (DHONDT, 1987 has recorded 50 taxa) as well as ammonites (SUMMESBERGER, 1979, 1980).

The sediment was deposited in a low energy shallow water environment (KOLLMANN, 1980; WAGREICH, 1988).

7. Environment and composition of gastropod faunas

The preceding characterization shows the fundamental difference between gastropod faunas of carbonate platforms and of fine-grained siliciclastic sediments: The faunas of the carbonates of Orgon, Brouzet-les-Alais, and the Aqu-

lanian Abbruzzos contain a high percentage of archaeogastropods. Modern representatives of this family are generally rasping off algae from rocky surfaces. Among the mesogastropods, cerithiaceans and aporrhoids which are deposit feeders are most diverse. Modern Cerithiaceans are living on hard substrates as well as on muddy bottom sediments (BANDEL & WERNER, 1987); aporrhoids are living buried in the surface layers of soft sediments (PURCHON, 1968). Soft substrates are also inhabited by the naticids and the large number of cephalaspidean opisthobranchs which are ploughing through the sediments searching for food.

This co-occurrence of gastropod groups preferring hard substrates and others living in and on soft substrates is characteristic for carbonate platforms. They provide the conditions for a diverse gastropod life. It also indicates the problem of the magnitude of ecological niches in this environment. This is equally the case in the clastic klippen facies of marginal warm temperate environments as in the Upper Cenomanian of Saxony and Bohemia where diverse faunas of gastropods with different environmental preference have been described by GEINITZ, 1874; DENINGER, 1905; WEINZETTL, 1910; and FRIC, 1911. A similar interpretation is made for the Maastrichtian of Maastricht (Holland) from which diverse gastropod faunas have been described by KAUNHOWEN (1898).

Deeper water environments of carbonate platforms are typically represented by nodular limestones of Texas and other areas of the Cretaceous Tethyan realm. The gastropod fauna consists mostly of large deposit feeders (turritellids, aporrhoids) and *Tylostoma* which systematically is placed within the carnivorous naticids. Nerineacea and actaeonellids, typical for the shallow water Tethyan sediments, are lacking in this facies. The number of archaeogastropoda is low. In West Texas the neritacean *Otostoma* is common in horizons with abundant oysters (KOLLMANN, LEMONE, and DECKER, unpublished) which may have formed the substratum for this archaeogastropod.

While the shallow water environments of the carbonate platforms provided sufficient hard surfaces for the growth of algae this was not the case on the level bottoms (Hözlensau, Uchaux, Gosau). The communities are therefore characterized by low diversities of archaeogastropods. The number of taxa is decreasing with the grain size of the substrate. This has been shown by KASE (1984) for the Miyako Group. The Cenomanian fauna of Hözlensau and the Turonian fauna of Uchaux are both found to occur in sandy-silty sediments and yield 9 archaeogastropod taxa each. With the exception of heavy-shelled neritopsids and a large fragmentary form determined as *Astele* by RAHMAN (1967), the archaeogastropods of Hözlensau are small and may have lived as well on the sediment surface as on aquatic plants. This especially may be the case for small forms of *Discotectus* which are very abundant in fine-grained sediments of the Gosau Group (HÖFLING, 1985). In addition to Hözlensau, the fauna of Uchaux shows large representatives of the trochid *Angaria* which also occurs in fine-grained sediments of the Gosau Group and was, because of its size, undoubtedly living on the bottom surface.

The main constituents of the faunas of Hölzelsau and Uchaux are the deposit-feeding cerithiaceans, among them the aporrhoids and the turritellids (for their ecology see ALLMON, 1980). This agrees with observations of JABLONSKI & BOTTJER (1983) that epifaunal deposit feeding molluscs prevail where the substrate becomes soft and muddy. In this respect, the gastropod faunas of the level bottoms resemble those of the nodular limestones but are much more diverse.

The same is the case with the carnivorous and ectoparasitic gastropod groups. The nodular limestones contain the naticid *Tylostoma* which occurs in large numbers and epitoniids. The level bottom assemblages of both, Hölzelsau and Uchaux, have yielded the carnivorous mesogastropod families Epitoniidae, Cypraeidae and Naticidae, further neogastropods and cephalaspidean opisthobranchs. The Entomotaeniata are diverse in Hölzelsau but are represented by only 2 species in Uchaux. This is consistent with the extinction of most nerineacean genera at the end of the Cenomanian.

As in the assemblages reviewed before the mesogastropods of the Streiteck Formation, the Hofergraben Member of the Hochmoos Formation and of the "Sandkalk-Bank" forming the uppermost part of the Hochmoos Formation are dominated by various cerithiacean families; among those abundantly represented are turritellids and aporrhoids. According to WAGREICH (1989), the sediments of these sequences have been deposited below the wave base (Streiteck Formation) of a "middle shelf" and in an environment with rare storm events. The fauna of the lower Hochmoos Formation which has been deposited in shallow to extremely shallow water is not as diverse, although the mesogastropod families represented are the same as in the other formations.

Neogastropods are dominating the Gosau gastropod faunas. This is due to the general development of this group in the Tethyan realm during the Cretaceous (see below). The diversity is low in the lower Hochmoos Formation which was deposited in shallow to extremely shallow water. In this part of the sequence the neogastropods are exclusively represented by Volutidae.

Opisthobranchs are occurring mainly in special facies, such as the lagoonal sediments of the Schneckwand with its mass-occurrence of the actaeonellid *Trochactaeon*. Others contain abundant forms of the nerineacean *Simpleptyxis* which is characteristic for the late Cretaceous after the Upper Turonian.

An unique feature is the occurrence of archaeogastropods belonging to the pleurotomariids in the "Sandkalk-Bank" which indicates a cold-water influence (KOLLMANN, 1980). This also is indicated by several bivalve taxa occurring mainly in the temperate marine zone (DHONDT, 1987).

A special facies is represented by the Grabenbach Formation of the Gosau area. Only 2 gastropod genera are represented here: the trochid *Calliomphalus* and the cerithiacean *Exechocirsus*. The low diversity of this fauna and especially the co-occurrence of the protobranch bivalve genus *Nuculana* indicates after KAUFFMAN (1976) a relatively poor benthonic environment. *Calliomphalus* is one of the few archaeogastropod genera which occur in the Upper Cretaceous

Ripley Formation of the Atlantic Coastal Plain (SOHL, 1960) and was probably feeding on organic material deposited on the sediment surface.

8. Evolution of Cretaceous gastropods

In the Permian and Triassic, the diverse stock of Palaeozoic archaeogastropods which formed a high percentage of the soft substrate communities was largely replaced by the deposit feeding and carnivorous mesogastropods. This gastropod group gained dominance at the end of the Triassic. It is especially diverse in fine-grained sediments where the potential for preservation is greatest. The turritellids, which are among the most common gastropods of soft substrates deposited from the Lower Cretaceous upwards, do not occur in shallow water sediments of the Tethyan realm before the Upper Albian (KOLLMANN, 1979; n. b., the Lower Albian fauna from the Corbières, France, described by MONGIN, 1985 is not Tethyan in its composition).

Synchronously with the rise of the mesogastropods, the archaeogastropod families dominant in the Mesozoic and Cenozoic evolved. Modern representatives of these families are primarily grazers that are no longer restricted to soft substrates. Their diversity is highest on surfaces with sufficient algal growth, especially on rocks or patches of rock in shallow environments.

An important step in the evolution of gastropods is the first occurrence of the neogastropods which took place in the Cretaceous. The oldest fossil records of neogastropods are from the Hauterivien Hradiste Formation (Grodischer Schichten) of the Silesian nappe of the Western Carpathians (ASCHER, 1906) and of Barremian sediments of North Germany (WOLLEMAN, 1900; KOLLMANN, 1982). According to JOBLONSKI & POTTER (1990) these forms are problematic and may belong to mesogastropod groups as colombellinids. Actually, they have nothing in common with the colombellinids which have narrow dentate apertures. The forms discussed here have a short channel and are Buccinidae. This family is therefore occurring earlier in the geologic history than any of the Muricea of which earliest representatives have been found at the Aptian-Albian boundary in North Germany (WOLLEMAN, 1903). This fact is in opposition to PONDER's (1973) opinion who believes that the Muricea are closest to the most primitive neogastropod type because of their unspecialized pallial cavity.

PONDER (1973) has indicated that the first evolutionary steps of neogastropods are within the Tropical marine zone. The fossil record disagrees with this view as all neogastropods earlier than Upper Albian have been found in the Temperate zone. The spreading into the Warm Temperate zone and into the Tethyan realm did not take place prior to this time (STANTON, 1947; KOLLMANN, 1976). The composition of assemblages presented in the preceding chapter clearly develops the gradual increase of neogastropod families in the Tethyan realm during the Upper Cretaceous. This agrees with TAYLOR and others (1980) who have stated that most predatory prosobranch families have evolved

in higher latitudes and not in the tropics, although these groups show a strong latitudinal gradient increasing towards the equator in modern seas. This has been explained by MARGALEF (1968) who has called the tropical belt a refuge of types which settled there because of the stable climate but have originated in higher latitudes where the climatic fluctuation was more severe.

Opisthobranchs are diversifying considerably in the Mesozoic, too. The opisthobranch order Cephalaspidea of which earliest fossil representatives are known from the Lower Carboniferous (KOLLMANN & YOCHELSON, 1976) gives rise to a large number of genera and species (KITTL, 1894; HAAS, 1953) in the Triassic. The cephalaspideans have sturdy shells and consequently have developed an adequate fossil record. Modern cephalaspideans are primarily living infaunally and are generally carnivorous (e. g. ANDREWS, 1971; NORDSIECK, 1972). The evolution of the cephalaspideans is part of the evolution of bulldozing forms since the Permian (THAYER, 1983).

Actaeonellids and nerineaceans are the only gastropod groups of family and higher level in the taxonomic hierarchy which are restricted almost totally to the Tethyan realm. It may be puzzling that they are considered as opisthobranchs. Although they are extraordinarily large, compared with modern cephalaspideans the Actaeonellids are put into this opisthobranch group because of a sutural notch and a heterostrophic larval shell (KOLLMANN, 1967; SOHL & KOLLMANN, 1985). The earliest representatives of this group are species of *Cylindrites* of Middle Jurassic age. The major development took place in the higher Lower Cretaceous and in the Upper Cretaceous. The diversification of the actaeonellids as shown by SOHL & KOLLMANN (1985) is connected with spreading of the Atlantic and by the consequent interruption of the gene flow. This happened in the Coniacian for Trochactaeon. This is according to SOHL (1967) the time of a general change of American gastropod faunas.

Compared with modern opisthobranchs, many of the nerineaceans are equally extraordinary in size as are the actaeonellids. They are merged into the order Entomotaeniata COSSMANN together with the much smaller Pyramidellacea. The nerineaceans occur first in the Liassic (PCHELINTSEV, 1965). The major evolutionary pulses of the nerineaceans occurred between the Upper Jurassic and the Cenomanian on the open shelf. At our present stage of knowledge no provincialism of nerineaceans can be documented prior to the higher Upper Cretaceous. This indicates a high dispersal potential due to a long larval stage.

9. Instead of a foot-note: Remarks on the origin of neogastropods

A characteristic morphological feature of the neogastropod shell is the siphonal channel. This channel supports the siphon which serves to maintain an inhalant current of water into the pallial cavity. The water current on its way to the ctenidium which is a respiration organ passes the osphradium. This is particularly complex in carnivorous gastropods and may aid in the detection of the prey. As the inhalant siphon is directing the water current toward the

osphradium, this development is clearly an advantageous morphogenetic feature.

The origin of the neogastropods certainly will remain always as a lively subject for discussion of their early history. Necessarily, this history is deduced from shell morphology of fossil forms which hardly can ever be reconciled with the anatomy based on soft part morphology of modern forms. A review of the different opinions has been assembled by TAYLOR and others (1980). These authors believe that the neogastropods originate from the Triassic to Upper Cretaceous family Purpurinidae ZITTEL. COSSMANN (1906) included in this family shells of diverse groups varying considerably in morphology. Many taxa belonging to this family do actually resemble neogastropods by their possession of an anterior notch, the shape of the aperture, and the sculpture.

Nevertheless, considerable doubt remains as all representatives of the Purpurinidae seem to have lived in warm water zones. As explained above the origin of neogastropods must be sought in the Temperate marine zone. The neogastropods must have evolved from a group that is represented in the Temperate zone, too.

One group from which the neogastropods may have evolved are the Amberleyacea which occur in the Temperate and the Warm Temperate zone. Representatives of this group which are closely related to each other occur in level bottom communities of the North German Lower Cretaceous. This seems to be unlikely for herbivorous forms. The nutrients and the physical conditions have been too uniform to generate a genetic pressures which may have led to the differentiation of different taxa. It therefore has been concluded by KOLLMANN (1982) that the amberleyaceans were carnivores and that the species may have evolved through different food preference. The amberleyaceans would seem to be a serious candidate for the origin of neogastropods, although, admittedly, the shell morphology is not nearly as convincing as that of the Purpurinidae.

The PONDER (1973) scenario has the neogastropods evolving from an archaeogastropod or a mesogastropod still possessing anatomical features of archaeogastropods (a "primitive" mesogastropod after PONDER). PONDER believes that the origin of neogastropods is related to a change from grazing to the feeding on a colonial animal. This is in accordance with his opinion that muricids are closest to the origin of neogastropods as this family is generally living on hard surfaces and therefore could have performed the step as described by changing its diet.

Actually, the fossil record is opposite to this opinion. Earliest known neogastropods have lived on soft bottoms which did not allow an algal growth. The Buccinids which are the first neogastropod group in the fossil record probably have evolved from deposit feeders by digesting small animals or carrion. The very general food of Buccinidae (TAYLOR and others, 1980) confirms this opinion. In this evolutionary concept, the neogastropods developed methods and devices which led from browsing towards active predatory hunting (Fig. 2). There is no absolute necessity for neogastropods to evolve from forms which already had a developed siphonal channel. It was only with the adoption of

TURONIAN	use of toxic secretion	Turridae
<hr/>		
CENOMANIAN		Volutidae
<hr/>		
ALBIAN		Cancellariidae Fasciolaridae Mitridae
<hr/>		
APTIAN	benthic hunting	Muricidae
<hr/>		
BARREMIAN	scavenging and feeding on sessile organisms	Buccinidae

Fig. 2: Evolution of neogastropod feeding in the Cretaceous.

carnivorism and the subsequent increasing metabolism that a device was developed for obtaining sufficient food. This device was the siphonal channel which together with the osphradium allowed the efficient location of prey.

10. Tethyan gastropods at the beginning and at the end of the Cretaceous

The Tethyan gastropod faunas do not show any dramatic changes at the Jurassic-Cretaceous boundary. This may be due to the fact that Tethyan gastropods are known only from carbonate platforms which obviously were not affected by environmental changes at this time.

With the exception of *Tylostoma* which occurs in abundance in the Danian sediments of Denmark and Greenland (KOLLMANN & PEEL, 1983) typically Tethyan groups did not survive the Cretaceous-Tertiary boundary. They shared this fate with other major Tethyan groups such as the rudists, most hermatypic coral genera (BEAUVAIS & BEAUVAIS, 1974) and significant numbers of the planktonic foraminifera. As these fossils have lived in shallow environments they are generally not associated with groups which allow an exact dating of the sediments. For this reason it is impossible to document the fact of whether

the extinction occurred synchronously at a single event for all above-mentioned Tethyan groups or over a longer time-span.

If one examines the record of the extinction and decimation of selected fossil taxa at the end of the Cretaceous the following occurs: The majority of the affected taxa are within the Tethyan realm. The warm temperate and the cold temperate zone seem to be much less affected by the terminal Cretaceous event(s). It has been pointed out by KOLLMANN (1979a) that Lower Danian gastropod faunas do not show any differentiation related to water temperatures. A warm temperate fauna was extended from Central Asia and North Africa into Greenland. The faunas on both sides of the Atlantic are different which probably is related to the breakdown of the equatorial current of the Atlantic. This clear separation of faunal provinces ends with the Thanetian where the temperature-controlled marine zones are re-established. It seems therefore that the extinction of Tethyan gastropods was primarily caused by a change of surface water temperatures. A bolide impact which should have effected the entire gastropod fauna, is definitely not proved by the paleontological record.

11. Gastropods and the "Mesozoic Revolution"

VERMEJ (1977, 1978) has drawn attention to the fact that predation was spreading in the Mesozoic among different animal classes. He has called this evolutionary important process "Mesozoic Revolution". The gastropods are affected in two ways by this process: On the one hand they developed a sturdiness of shells to resist predation (VERMEJ, 1977, 1978); on the other hand carnivorous gastropod groups gained steadily in importance. This does not only concern the opisthobranchs and the neogastropods among the prosobranchs, but also the mesogastropods. TAYLOR and others (1980) have pointed out that the carnivorous mesogastropod groups Naticacea, Cymatiidae, Bursidae, Cassidiidae, Tonnidae and Ficidae had their first occurrence in the Mesozoic or at the Cretaceous-Tertiary boundary. The Naticidae which after KITTL (1892) and HAAS (1953) were already diverse in the Triassic obviously have changed their feeding methods during Mesozoic. Naticid drillholes do not occur before the Upper Albian where they have been documented with some frequency in the Blackdown Greensand (TAYLOR and others, 1980). SOHL (1969) correlated the occurrence of the drillholes with the first occurrence of the naticid subfamily Polynicinae.

The reason for the spreading of predation has been explained by VERMEJ (1977) as a response to the breakup of continents which according to VALENTINE (1969) and VALENTINE and MOORES (1970) created numerous biogeographic provinces as a consequence of geographic isolation. This certainly may explain the burst of biotic diversification of benthic groups following the interruption of the gene flow between members of population. Genetic isolation will lead to the development of different non interbreedable species which consequently may be broken up taxonomically into higher systematic hierarchies.

This taxonomic procedure is totally artificial showing the grade of similarity between species which form the base of the hierarchy. It does not represent the rise of predation itself because in mature ecosystems the amount of energy transferred through the various trophic levels is about the same at equal physical conditions (TAPPAN, 1968, 1971 a, b), independent of the number of taxa.

TAYLOR and others (1980) have pointed out that "the diversification and adaptive radiation of predatory families during the late Cretaceous may have arisen as a consequence of competitive interaction between taxa, giving rise to broad habitat separations and specializations upon particular food type". The increase in predation requires an increase in prey availability in the same environment which, consequently, can be only the result of a higher primary (phytoplankton) production. TAPPAN (1968, 1971 a, b) has shown that the fossil record indicates as well an increase of the number of phytoplankton taxa as an increase of phytoplankton production in the Jurassic. This is probably controlled by changes in ocean physiography. This increase in phytoplankton productivity which is deduced from an increase of the oxygen level is probably the actual reason for the "Mesozoic Revolution" which has affected virtually all marine environments.

Acknowledgments

Funding by the Austrian Science Foundation and by the Austrian IGCP Committee is gratefully acknowledged. I am grateful to Prof. David V. LEMONE of the University of Texas at El Paso for his help in improving the style of the manuscript.

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