Paleoecological aspects of the Lower Oligocene Paisslberg Formation of Bad Häring (Lower Inn Valley, Tyrol) based on molluscs and carbonates

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Löffler, S.-B. & Nebelsick, J. H., 2001: Paleoecological aspects of the Lower Oligocene Paisslberg Formation of Bad Häring (Lower Inn Valley, Tyrol) based on molluscs and carbonates. – In: Piller, W. E. & Rasser, M. W. (Eds.): Paleogene of the Eastern Alps. – Österr. Akad. Wiss., Schriftenr. Erdwiss. Komm. 14: 641–669, 5 Figs., 2 Tabs., 4 Pls., Wien.

Abstract: A detailed study of molluscs and carbonates from the Lower Oligocene Paisslberg Formation (Lower Inn Valley, Austria) allows palaeoecological investigations of the depositional environment. This formation is dominated by calcareous marls containing a rich, historically well known mollusc fauna. Carbonates present as autochthonous limestones and allochthonous debris flow deposits show a variety of different facies.

The rich mollusc fauna consisting of 142 taxa (58 gastropods, 81 bivalves, 3 scaphopods) allows trophic and substrate relationships to be analysed. Gastropods are dominated by carnivores, with subordinate detritivores and herbivores; suspensivores are very rare. Bivalves are dominated by suspensivores; detritivores and carnivores are subordinate. The taxonomic structure method based on Recent distributions of subclasses respectively orders implies that the marls were deposited in a deeper sublittoral to upper bathyal depositional environment. The mollusc fauna is dominated by thermophilous elements.

The carbonates occur as autochthonous limestones and allochthonous proximal debris flow deposits (Werlberg Member) as well as distal debris flow deposits within the marls of the Paisslberg Formation. Biotic components within the carbonates were distinguished as photoautotrophs, symbiotrophs, suspensivores and polytrophs. A deepening-up depth gradient recognized with the transition from the coralline algal to coralline algal – bryozoan to bryozoan facies is reflected in the trophic analysis with a change from photoautotrophs and symbiotrophs to suspensivores. Differences in substrate relationships and turbulence as seen in a change from the coral – coralline algal to the coralline algal to the foraminiferal facies are, however, not reflected in the trophic analysis.

Zusammenfassung: Mollusken und Karbonate aus der unteroligozänen Paisslberg-Formation von Bad Häring (Unterinntal, Österreich) sind Gegenstand detaillierter paläoökologischer Untersuchungen. Diese Formation – bisher in der Literatur bekannt als "Zementmergel" – wird aufgebaut aus grünlichdunkelgrauen Mergelkalken mit eingeschalteten autochthonen Kalken sowie allochthonen "Debris Flow"-Ablagerungen.

Auf der Grundlage der umfangreichen Molluskenfauna (58 Gastropoda-, 81 Bivalvia- und 3 Scaphopoda-Taxa) werden Aussagen bezüglich Lebens- und Ernährungsweisen durch die Analyse ihrer trophischen Struktur und Substratansprüche ermöglicht. Bei den Gastropoden liegt die Dominanz bei den Carnivoren, gefolgt von den Detritivoren und Herbivoren; sehr stark unterreprä-

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sentiert sind die Suspensionsfiltrierer. Innerhalb der Bivalven überwiegt der Anteil an Suspensivoren, untergeordnet sind die detritivoren und carnivoren Ernährungsmodi. Durch die Anwendung der "Taxonomic Structure Method", die sich auf die quantitative Verteilung systematischer Einheiten höherer Kategorien innerhalb rezenter Molluskengemeinschaften gründet, kann die Lage des Sedimentationsraumes der Mergelkalke auf einen Tiefenbereich zwischen unterem Sublitoral und oberem Bathyal präzisiert werden. Die Molluskenfauna zeichnet sich durch ein großes Spektrum an thermophilen Elementen aus.

Die Mergelkalke der Paisslberg – Formation bestehen aus autochthonen und allochthonen Kalken (Werlberg Member) sowie aus distalen "Debris Flow"-Ablagerungen. Unter den beteiligten Organismen innerhalb der Karbonatablagerungen lassen sich photoautotrophe, symbiotrophe, suspensivore und polytrophe Vertreter erkennen. Mit dem Übergang von der Corallinaceen- über die Corallinaceen-Bryozoen- bis zur Bryozoen-Fazies wird ein bathymetrischer Gradient von flach nach tief offenbar, der in der trophischen Analyse im Wechsel von photoautotrophen und symbiotrophen zu suspensivoren Organismen aufgezeigt wird. Unterschiede in Substratbeziehungen und Wasserturbulenz, ersichtlich im Wechsel von der Korallen-Corallinaceen- über die Corallinaceen- bis hin zur Foraminiferen-Fazies, werden jedoch in der trophischen Analyse nicht reflektiert.

Keywords: Molluscs, Carbonates, Oligocene, Palaeoecology, Microfacies, Trophic Analysis, Substrate Relationships

Contents

1. INTRODUCTION

The rich molluscan assemblage and varied carbonate microfacies of the formation presented in this paper potentially allow for a detailed reconstruction of a number of important ecological parameters. These include variation in light intensity, nature of the substrate, degree of turbulence and nutrient supply as well as the presence of ecological gradients related to depth. These can be deduced through actualistic comparisons to Recent representatives of the mollusc families and genera concerning feeding strategies and substrate preferences. Ecological information from the carbonates is obtained by comparing limestone fabrics, dominant components and component relationships determined through the standard method of microfacies analysis. Problems of reconstructing ecological parameters from the molluscs include incomplete data due to taphonomic and collection phenomena ranging from aragonite dissolution, tectonic deformation to missing small fauna. A more fundamental problem is the question to what degree actualistic

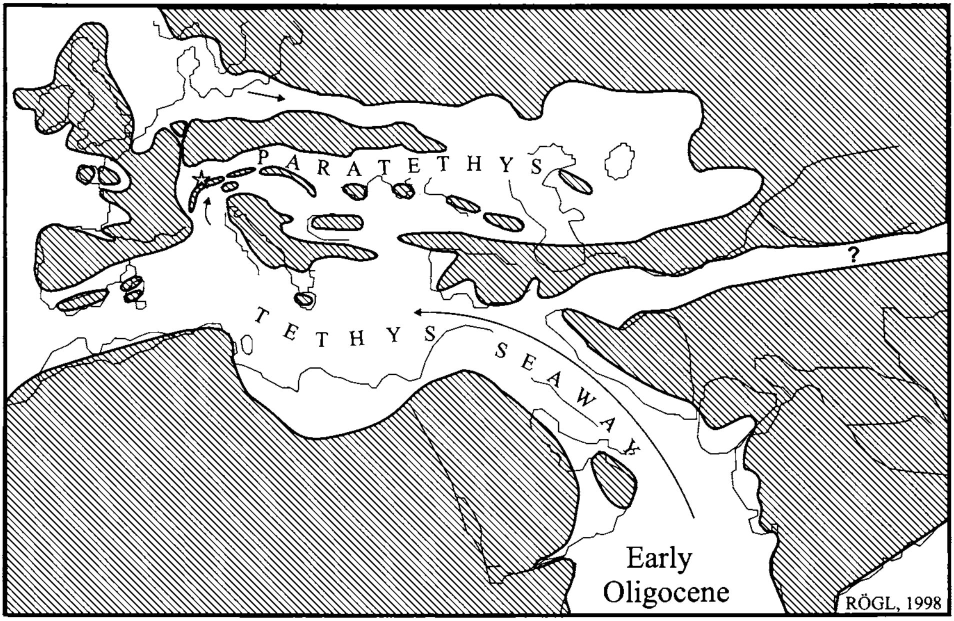


Fig. 1: Palaeogeography of the Mediterranean area during the Early Oligocene (Rupelian, Kiscellian). Redrawn from Rögl (1998). Star denotes study area.

comparisons can be applied to Early Oligocene faunal and floral associations.

The molluscs and carbonates of the Lower Inn Valley are of general interest as they represent the beginning of the Paratethys (Fig. 1) which developed as a separate biogeographic entity through plate tectonic movements and the raising of the Alpine chain (see Rögl, 1998). The characteristic molluscan fauna lead to the first recognition of the distinct faunal province of the Paratethys which forms the basis for the definition of the Kiscellian stage of the regional stratigraphic framework of the Central Paratethys (e.g., Báldi 1979, 1984, 1986). The carbonates in the Lower Inn Valley represent one of the few Oligocene carbonates of the Paratethys (compare Kaiser et al., this volume).

Bad Häring (formerly "Häring") is known as a classic fossil locality for the European Paleogene. Rich plant fossils from the laminated bituminous marls ("Bitumenmergel") of the Bergpeterl Member within the Häring Formation were already described in 1853 by C. v. Ettingshausen. The highly diverse macrofauna from the calcareous marls (formerly "Zementmergel") of the Paisslberg Formation (with anthozoans, brachiopods, gastropods, bivalves, scaphopods, cephalopods, crustaceans, echinoderms and vertebrates – especially fish) have been described by Gümbel (1861), Mayer (1861), Dreger (1892, 1902, 1904), Schlosser (1923), Schachl (1939) and Löffler (1999). Studies on the microfossils including foraminifers, nannoplankton, pollen and spores have been made, e.g., by Lühr (1962), Lindenberg (1962, 1965), Cicha et al. (1971), Schnabel & Draxler (1976), Hochuli (1978), Hagn (1981), Dohmann (1991), Scherbacher (2000) and Scherbacher et al. (this volume). Microfacies analyses of the limestones within the Paisslberg

Formation have been conducted by NEBELSICK et al. (1996) and NEBELSICK et al. (2001) with special emphasis on the main constituents which consist of coralline algae, foraminifera, corals and bryozoans. A comprehensive synopsis of the palaeontological, sedimentological, tectonic and palaeogeographic aspects of the Paleogene sediments is given in LÖFFLER (1999), NEBELSICK et al. (2001) and ORTNER & STINGL (this volume). The lithostratigraphic units formally defined by ORTNER & STINGL for the Lower Inn Valley Cenozoic (this volume) are used in this paper.

A detailed study of the rich and historically well known molluscs of the Lower Oligocene calcareous marls of the Paisslberg Formation of the Bad Häring area, including a systematic revision and aspects of the ecology is given in LÖFFLER (1999). Investigations concerning the microfacies of the carbonates within the Paisslberg Formation are presented in NEBELSICK et al. (2001). This paper contains a synthesis of these two different approaches thus obtaining a more complete picture of the palaeoecology of the Paisslberg Formation.

1.1. Study area and lithostratigraphy

Late Eocene to Late Oligocene sediments lying transgressively above units of the Northern Calcareous Alps are exposed in the Lower Inn Valley between Rattenberg/Kramsach (Tyrol/Austria) in the SW and Reit im Winkel (Bavaria/Germany) in the NE. Detailed investigations to the sedimentology and lithostratigraphy of the single units within the Lower Inn Valley Tertiary can be found in STINGL (1990), KROIS & STINGL (1991), KROIS et al. (1991), STINGL & KROIS (1991), KROIS (1992), ORTNER (1996), NEBELSICK et al. (2001) and especially ORTNER & STINGL (this volume) and are briefly summarised here.

In the Bad Häring area (Fig. 2), sedimentation begins with the continental to shallow marine Häring Formation consisting of clastic sediments (conglomerates, sandstones, calcareous marls) of the Lengerergraben Member, and coal measures together with bituminous marls of the Bergpeterl Member. The Paisslberg Formation follows above the Häring Formation as well as transgressing directly above basement rocks. The Paisslberg Formation consists of both shallow water sediments (including carbonates of the Werlberg Member) as well as shallow to deeper water calcareous marls. Debris flow deposits containing allochthonous carbonates are interbedded within the marls. The Paisslberg Formation is well exposed at the type locality in the large Bergpeterl Quarry SSE of Bad Häring at the northern side of the Paisslberg mountain (see ORTNER & STINGL, this volume). The deepening of the depositional environment within the Paisslberg Formation is attributed to both local tectonic subsidence and a general rise in eustatic sea level. The occurrence of turbidites in the following Unterangerberg Formation is attributed to an increase of clastic input. Finally, in the Late Oligocene, an intense fall in sea level as well as continuing high sedimentation rates of clastics lead to the development of fluvial sands and conglomerates of the Oberangerberg Formation.

1.2. Biostratigraphy

In the older literature, the stratigraphic correlation of the calcareous marls of the Paisslberg Formation alternates between NP 21 (HOCHULI, 1978) and NP 22 (CICHA et al., 1971; SCHNABEL & DRAXLER, 1976; STEININGER et al., 1976; DOHMANN, 1991). Samples taken

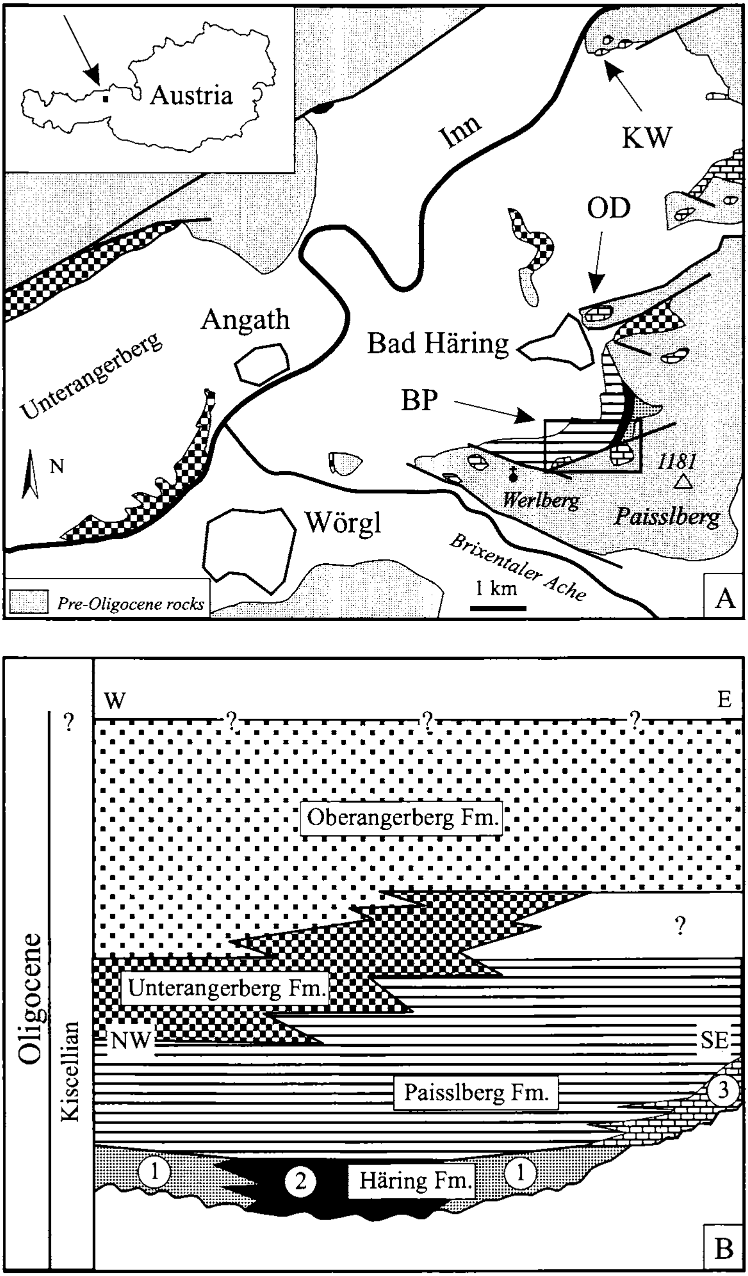


Fig. 2: A) General location of the study area and distribution of lithologic units; BP = Bergpeterl Quarry, KW = Kufsteiner Wald, OD = Osterndorf; B) Facies development of the Lower Inn Valley Tertiary; 1 = Lengerergraben Member; 2 = Bergpeterl Member; 3 = Werlberg Member; for details see Ortner & Stingl, this volume.

over the whole profile of the Bergpeterl Quarry profile (Fig. 3) investigated by E. MARTINI (University of Frankfurt/M.) demonstrate nannoplankton zone NP 22 (*Helicosphaera reticulata*-Zone). This zone is defined as the "Interval from the last occurrence of *Cyclococcolithus formosus* KAMPTNER to the last occurrence of *Reticulofenestra umbilica* (LEVIN)" (MARTINI, 1971: 761). Common species of this zone which were also found in the profile are *Isthmolithus recurvus* DEFLANDRE and *Reticulofenestra umbilica* (LEVIN), whereas *Cyclococcolithus formosus* KAMPTNER is already missing. Some redeposited Cretaceous species were also discovered; for detailed information see LÖFFLER (1999: 12).

2. MATERIAL AND METHODS

All the material used for this investigation was collected from the Paisslberg Formation in the Bad Häring area and environs (Fig. 2). The profile of the Paisslberg Formation in the active Bergpeterl Quarry shown in Fig. 3 was taken in May 1997.

The basis for the systematic revision of the gastropods, bivalves and scaphopods by LÖFFLER (1999) (Tab. 1) is the extensive collection at the University of Innsbruck (Institut für Geologie und Paläontologie der Universität Innsbruck (IGPUI)). This collection houses the majority of type material of the monographs of DREGER (1892, 1904). Additional molluscs collections derived from the Häring locality were consulted from the museums and public collections in Innsbruck (Tiroler Landesmuseum Ferdinandeum, Innsbruck (TLMFI)), Basle (Naturhistorisches Museum Basel (NMB)), Frankfurt am Main (Senckenberg Museum, Frankfurt a. M. (SMF)), Munich (Bayerische Staatssammlung für Paläontologie und Historische Geologie München (BSPM)) and Vienna (Geologische Bundesanstalt Wien (GBAW); Institut für Paläontologie der Universität Wien (IPUW); Naturhistorisches Museum in Wien (NHMW)). The cephalopods were revised by SCHULTZ (1976).

An open nomenclature was used in taxonomic identification by LÖFFLER (1999) when necessary diagnostic features (e.g., the hinge and the interior of bivalves; the apex and especially the aperture of gastropods) are not present. Poor preservation is due to aragonite dissolution (the majority of fossils are present as moulds respectively sculptured moulds) and to common tectonic deformation (compare RUTSCH, 1928, 1949; FANCK, 1929; HÖLZL, 1957; KELLER, 1989). Feeding strategies and substrate preferences of fossil mollusc taxa were assessed by actualistic comparison with Recent representatives of the respective mollusc families and genera (ABBOTT, 1974; ABBOTT & DANCE, 1986; MORTON, 1983; PONDER, 1983; RIEDL, 1983; GAGE & TYLER ,1991; POPPE & GOTO, 1991, 1993; MAXWELL, 1992; OLIVER, 1992; GRUNER et al., 1993; ROSENBERG, 1993; LINDNER, 1994; KILIAS, 1997; WELLE, 1998). These are summarised in Tab. 2. Interpretation of the bathymetry of the depositional environment was examined using the "Taxonomic Structure Method" (HICKMAN, 1974, 1984). This method is based on the comparison of the frequency of major taxonomic groups within the molluscs (Bivalvia: Protobranchia, Pteriomorphia, Heterodonta, Septibranchiata; Gastropoda: Archaeogastropoda, Mesogastropoda, Neogastropoda, Opisthobranchia) in Recent major regional faunas ranging from shallow water to bathyal and abyssal zones.

Microfacies analysis is based on the examination of thin sections (5 × 5 and 8 × 10 cm) cut perpendicular to bedding planes. These were obtained from both autochthonous carbonates of the Werlberg Member from the locality Bergpeterl Quarry-SW, Osterndorf and Kufsteinerwald (Fig. 2) as well as allochthonous debris flow deposits

CLASS	SUB-CLASS	ORDER	SUPERFAMILY	FAMILY	SPECIES
GASTROPODA					
	Prosobranchia				
		Archaeogastropoda	Pleurotomarioidea	Pleurotomariidae	*Perotrochus* cf. *sismondai* (GOLDFUSS, 1844)
			Fissurelloidea	Fissurellidae	*Emarginula kittli* DREGER, 1892
			Patelloidea	Patellidae	Patellidae gen. et spec. indet.
			Cocculinoidea		Cocculinoidea fam. et gen. et spec. indet.
			Trochoidea	Trochidae	*Lischkeia* sp.
				Turbinidae	*Turbo* (*Heteroninella*) *tuberculosus* DREGER, 1892
			Neritoidea	Neritidae	*Nerita* sp.
		Mesogastropoda	Cerithioidea	Cerithiidae	Cerithiidae gen. et spec. indet.
				Potamididae	*Granulolabium* sp.
			Stromboidea	Aporrhaidae	*Aporrhais haeringensis* (GÜMBEL, 1861)
					Aporrhaidae ? gen. et spec. indet.
				Strombidae	*Rimella* sp.
					Tibia (*Sulcogladius*) *haueri* (DREGER, 1892)
			Crepiduloidea	Crepidulidae [Calyptraeidae]	*Calyptraea striatella* NYST, 1845
			Xenophoroidea	Xenophoridae	*Xenophora* cf. *subextensa* (ORBIGNY, 1852)
			Cypraeoidea		Cypraeoidea fam. et gen. et spec. indet.
			Naticoidea	Naticidae	*Sinum* cf. *rotundatum* (KOENEN, 1891)
					Naticidae gen. et spec. indet.
			Tonnoidea	Ficidae	*Ficus* cf. *crassistria* (KOENEN, 1889)
				Cassidae	*Cassis* (*Morionella*) *fuchsi* DREGER, 1892
					Galeodea cf. *nodosa* (SOLANDER in BRANDER, 1766)
					Sconsia cf. *ambigua* (SOLANDER in BRANDER, 1766)
					Echinophoria haeringensis (DREGER, 1892)
				Ranellidae	*Ranella haeringensis* (DREGER, 1892)
					Charonia crassa (GRATELOUP, 1847)
					Sassia flandrica (KONINCK, 1838)
					Sassia sp.
					Ranellidae gen. et spec. indet.
			Epitonioidea	Epitoniidae	*Opalia rodleri* (DREGER, 1892)
					Turriscala subulata (DREGER, 1892)
					Epitoniidae gen. et spec. indet.
			Eulimoidea	Eulimidae	*Niso* sp.
		Neogastropoda	Muricoidea	Muricidae	"*Murex*" *guembeli* DREGER, 1892
					Pterynotus sp. 1
					Pterynotus sp. 2
				Buccinidae	*Neptunea* (s.l.) *mittereri* (DREGER, 1892)
					Buccinidae gen. et spec. indet. 1
					Buccinidae gen. et spec. indet. 2
				Fasciolariidae	*Streptodictyon* sp.
					Fasciolariidae gen. et spec. indet.
				Volutidae	*Athleta stromboides* (DREGER, 1892)
					Lyria sp. 1
					Lyria sp. 2
				Olividae	*Ancilla olivaeformis* (DREGER, 1892)
				Mitridae	Mitridae gen. et spec. indet.
				Costellariidae (Vexillidae)	*Vexillum* sp.
			Cancellarioidea	Cancellariidae	Cancellariidae gen. et spec. indet.
			Conoidea	Conidae	*Conus* sp.
				Turridae	*Turricula haeringensis* (DREGER, 1892)
					Acamptogenotia cf. *morreni* (KONINCK, 1838)
					Acamptogenotia sp.
					Bathytoma dregeri (BOUSSAC, 1911)
					Bathytoma sp.
					Turridae gen. et spec. indet.
	Heterobranchia				
			Architectonicoidea	Architectonicidae	*Architectonica dumontii* (NYST, 1845)
				Mathildidae	*Gegania* sp.
	Opisthobranchia				
		Cephalaspidea	Acteonoidea	Acteonidae	*Tornatellaea simulata* (SOLANDER in BRANDER, 1766)
				Scaphandridae (Cylichnidae ?)	*Scaphander* sp.
		Thecosomata			

Tab. 1: Molluscan taxa of the Lower Oligocene Paisslberg Formation (after LÖFFLER, 1999).

CLASS	SUB-CLASS	ORDER	SUPERFAMILY	FAMILY	SPECIES
BIVALVIA					
	Protobranchia				
		Solemyoida	Solemyoidea	Solemyidae	*Solemya* aff. *doderleini* (MAYER, 1861)
					Solemya haeringensis (DREGER, 1904)
					Solemya sp.
		Nuculoida	Nuculoidea	Nuculidae	*Nucula* cf. *comta* GOLDFUSS, 1837
					Nucula sp.
					Ennucula haeringensis (DREGER, 1904)
			Nuculanoidea	Nuculanidae	*Nuculana* sp.
	Pteriomorphia				
		Arcoida	Arcoidea	Arcidae	*Arca* sp.
					Barbatia sp.
					Barbatia (*Acar*) sp.
					Bathyarca deshayesana (MAYER & GÜMBEL in GÜMBEL, 1861)
					Bathyarca sp.
					Bentharca sp.
			Limopsoidea	Glycymerididae	*Glycymeris nobilis* (DREGER, 1904)
					Glycymeris spp.
		Mytiloida	Mytiloidea	Mytilidae	*Brachidontes* ? sp.
					Amygdalum sp.
					Arcoperna sp.
					Lithophaga sp. 1
					Lithophaga sp. 2
		Pterioida	Pterioidea	Pteriidae	*Pteria* sp.
				Isognomonidae	*Isognomon* (*Hippochaeta*) *sandbergeri* (DESHAYES, 1861)
			Pinnoidea	Pinnidae	*Pinna hungarica* HOFMANN, 1873
		Limoida	Limoidea	Limidae	*Acesta szabói* (HOFMANN, 1873)
					Acesta (*Plicacesta*) *mittereri* (DREGER, 1904)
					Limaria (*Limatulella*) *guembeli* (MAYER in GÜMBEL, 1861)
					Limaria sp.
					Kiscellima aff. *cancellata* (HOFMANN, 1873)
		Ostreoida	Ostreoidea		Ostreoidea fam. et gen. et spec. indet.
				Ostreidae	Ostreidae gen. et spec. indet.
				Gryphaeidae	*Pycnodonte brongniarti* (BRONN, 1831)
					Pycnodonte gigantica (SOLANDER in BRANDER, 1766)
			Plicatuloidea	Plicatulidae	Plicatulidae gen. et spec. indet.
			Pectinoidea	Pectinidae	*Lentipecten corneus* (SOWERBY, 1818)
					Chlamys (s.l.) cf. *telleri* (DENINGER, 1901)
					Chlamys (s.l.) sp. 1
					Chlamys (s.l.) sp. 2
					Chlamys (s.l.) sp. 3
					Cyclopecten sp.
				Propeamussiidae	*Propeamussium bronni* (MAYER, 1861)
					Propeamussium semiradiatum (MAYER, 1861)
				Spondylidae	*Spondylus* sp.
			Anomioidea	Anomiidae	*Anomia* ? sp.
	Heterodonta				
		Veneroida	Lucinoidea	Lucinidae	*Lucina* (s.l.) *mittereri* MAYER & GÜMBEL in GÜMBEL, 1861
					Lucina (s.l.) *rostralis* MAYER & GÜMBEL in GÜMBEL, 1861
					Lucina (s.l.) cf. *rostralis* MAYER & GÜMBEL in GÜMBEL, 1861
					Myrtea ? *heeri* (MAYER & GÜMBEL in GÜMBEL, 1861)
					Lucinidae gen. et spec. indet.
				Thyasiridae	*Thyasira rollei* (MAYER & GÜMBEL in GÜMBEL, 1861)
					Thyasira vara (KOROBKOV, 1939)
			Carditoidea	Carditidae	*Venericardia* aff. *laurae* BRONGNIART, 1823
					Venericardia sp.
					Venericardia (*Venericor*) sp.

Tab. 1: continued.

CLASS	SUB-CLASS	ORDER	SUPERFAMILY	FAMILY	SPECIES
			Crassatelloidea	Crassatellidae	*Crassatella* sp.
					Crassatellidae gen. et spec. indet.
			Cardioidea	Cardiidae	*Nemocardium haeringense* (DREGER, 1904)
					Nemocardium oenanum (GÜMBEL, 1861)
					Laevicardium (s.l.) *tirolense* (MAYER & GÜMBEL in GÜMBEL, 1861)
			Tellinoidea	Tellinidae	Tellinidae gen. et spec. indet.
				Semelidae (Scrobiculariidae)	*Abra* cf. *budensis* (HOFMANN, 1873)
					Abra sp. 1
					Abra sp. 2
					Abra sp. 3
			Arcticoidea	Arcticidae	*Arctica* sp.
			Glossoidea	Glossidae	*Glossus* sp.
			Veneroidea	Veneridae	*Macrocallista* sp.
					Cordiopsis ? sp.
					Veneridae gen. et spec. indet.
		Myoida	Hiatelloidea	Hiatellidae	*Panopea haeringensis* (DREGER, 1904)
	Anomalodesmata				
		Pholadomyoida	Pholadomyoidea	Pholadomyidae	*Pholadomya* cf. *puschii* GOLDFUSS, 1841
					Pholadomya rugosa HANTKEN, 1872
					Pholadomya subalpina DREGER, 1904
			Pandoroidea (Thracioidea)	Thraciidae	*Thracia karlguersi* LÖFFLER, 1999
				Lyonsiidae	*Lyonsia* ? sp.
			Poromyoidea	Cuspidariidae	*Cuspidaria scalarina* (MAYER & GÜMBEL in GÜMBEL, 1861)
					Cuspidaria sp. 1
					Cuspidaria sp. 2
					Cardiomya bicarinata (MAYER & GÜMBEL in GÜMBEL, 1861)
					Myonera sp.
				Verticordiidae	*Verticordia* sp.
					Pecchiolia sp.
SCAPHOPODA					
		Dentaliida		Dentaliidae	*Fissidentalium haeringense* (DREGER, 1892)
					Fissidentalium aff. *castellanense* (ORBIGNY, 1850)
				Laevidentaliidae	"*Laevidentalium*" sp.

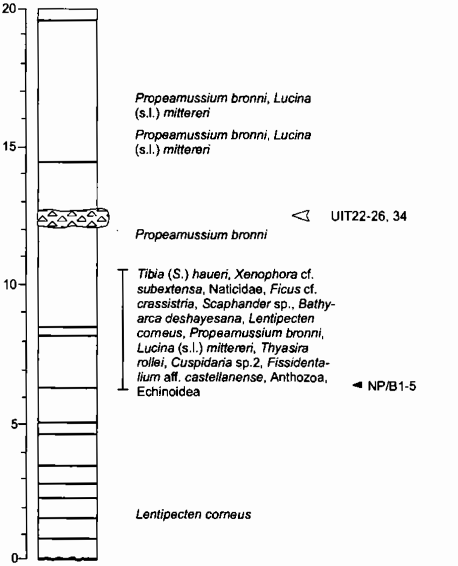
Tab. 1: continued.

within the marls of the Paisslberg Formation (Fig. 3). Multivariate statistical treatment (cluster analysis) of semi-quantitative component analysis as well as fabric comparison lead to the distinction of six facies: coralline algal facies, coralline algal – bryozoan facies, bryozoan facies, coral – coralline algal facies, foraminiferal facies, and bioclastic packstone facies (Nebelsick et al., 2001). The components are subdivided following trophic categories (Fig. 5) into photoautotrophs (coralline algae), symbiotrophs (larger foraminifers, corals), suspensivores (pectinids and oysters, bryozoans, brachiopods, serpulids), and polytrophs (smaller benthic foraminifers, echinoderms).

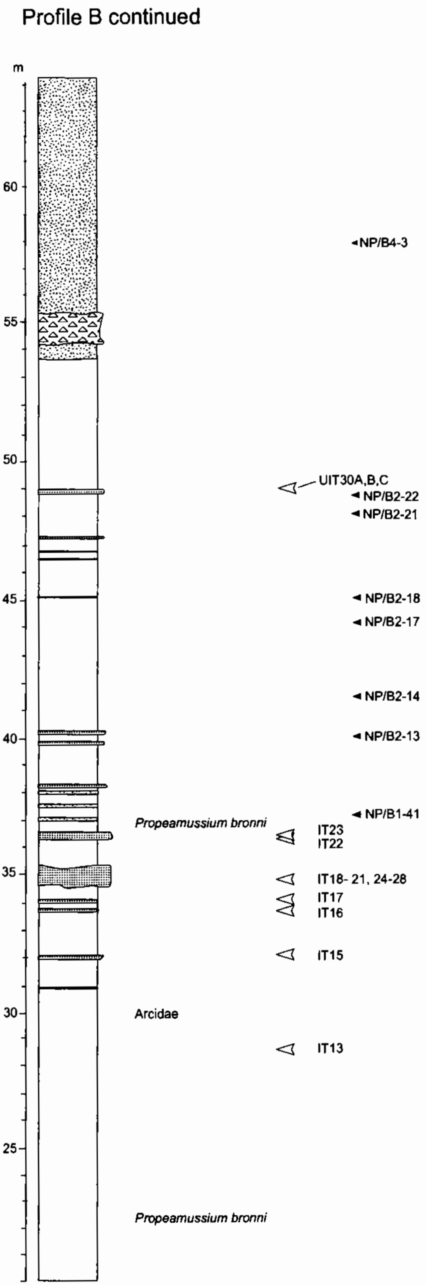
3. RESULTS

3.1. Bergpeterl quarry profile

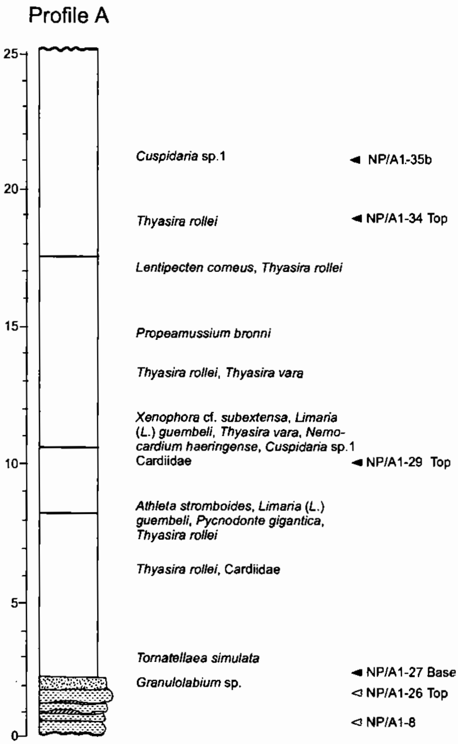
The profile is divided into three parts (Fig. 3): A and B are situated in the NE of the quarry, C in the SW. The exact stratigraphic position of the profiles relative to one another cannot be clearly determined, though it is obvious that they follow one another



Profile B



Profile B continued



Profile A

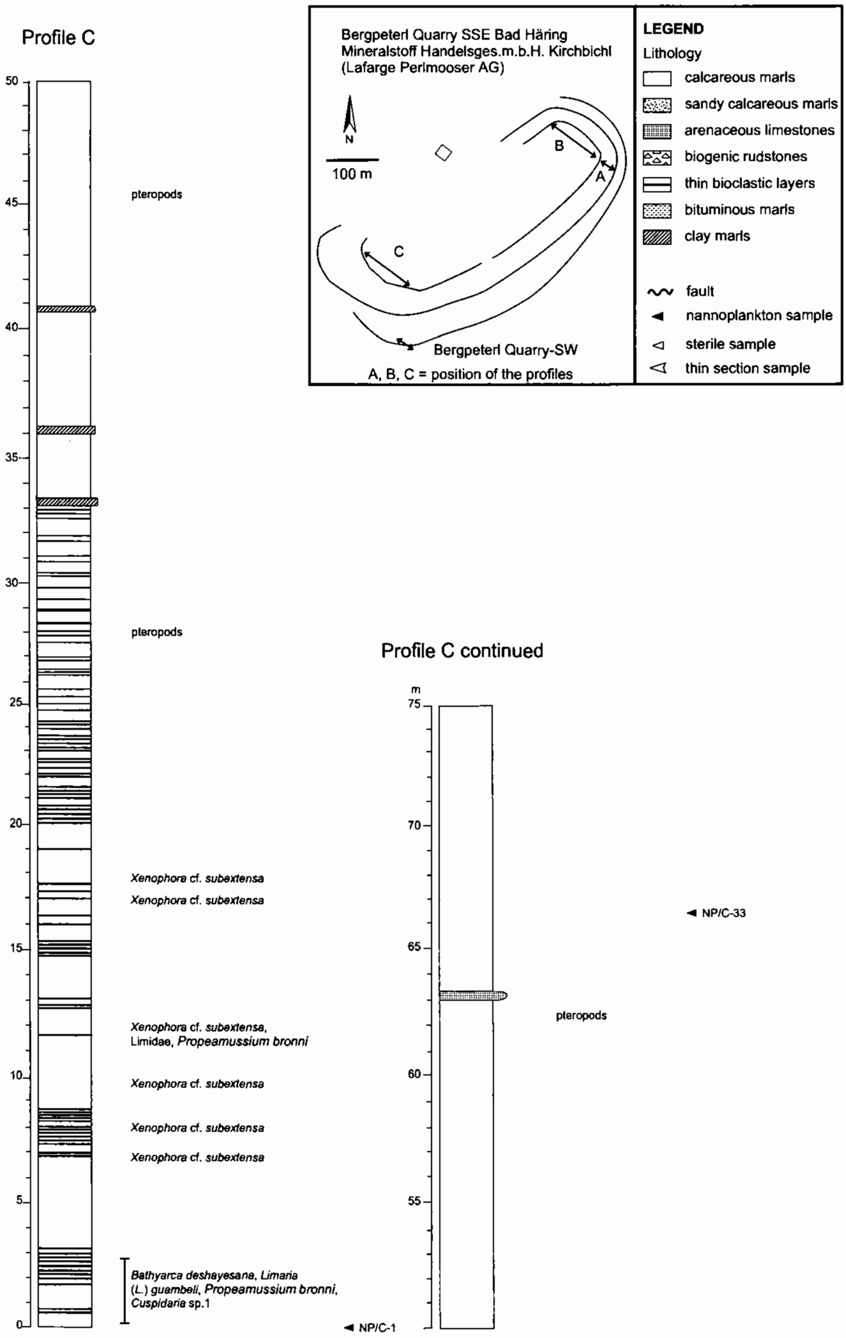


Fig. 3: Location and Profile of the Paisslberg Formation within the Bergpeterl Quarry SSE of Bad Häring.

stratigraphically. The thickness of the Paisslberg Formation in the quarry is at least 160 meters. The base of the formation is clear as it follows concordantly above the bituminous marls of the Bergpeterl Member (Häring Formation). The marls consist of massively bedded, hard, greenish dark grey calcareous marls. They are richer in carbonate at the base (A & B), and richer in clay towards the top (C) (for details see ORTNER 1996; ORTNER & STINGL, this volume). The marls are punctuated by debris flow beds and rare clayey marl layers. The debrites show different lithologies ranging from thick bioclastic limestones containing large lithoclasts to arenaceous limestones to very thin skeletal layers interpreted as distal debrites. There are few intercalations of debrites at the base of the profile A. In section B they become more common and are, in part, bundled. These are debris flow deposits showing widely differing lithologies and microfacies. The top of section B is characterized by a (poorly exposed) thicker layer of biogenic and sandy limestones. This may correspond to the so called "*Lithothamnium* breccia" of the older literature which is best exposed in the "Bridge Profile" along the Quarry Rd. to the North (see NEBELSICK et al., 2001). This consists of a ca. 8 metre thick amalgamation of debris flows containing biogenic debris and angular to rounded lithoclasts up to 30 cm in diameter. Section C shows numerous very thin bioclastic layers, which become rarer higher up in the section, and three distinctive, thin clayey marl layers. A prominent 30 cm thick arenaceous limestone layer occurs towards the top of the section.

3.2. Molluscs

The systematic revision of the mollusc fauna of the calcareous marls of the Paisslberg Formation (LÖFFLER, 1999) revealed 142 taxa comprising 58 gastropods, 81 bivalves and 3 scaphopods (Tab. 1; Pls. 1 & 2). A number of species were recovered from the Bergpeterl Quarry profile (Fig. 3). The gastropod *Granulolabium* sp. was found within the bituminous marls (Häring Formation). Some general trends can be seen in the distribution of molluscs. They are more common in profile A and at the base of profile B. The large oyster *Pycnodonte gigantica* (SOLANDER in BRANDER, 1766) is more common at the base of the marls. *Propeamussium bronni* (MAYER, 1861) (Pl. 2, Fig. 1) can be common throughout profiles A and B. *Xenophora* cf. *subextensa* (ORBIGNY, 1852) (Pl. 1, Fig. 3) is found throughout profiles A, B and C and is the only benthic taxon that dominates the latter. Mass occurrences of pteropods are found in several horizons in profile C. A number of other molluscan taxa were also found in the profiles including *Athleta stromboides* (DREGER, 1892) (Pl. 1, Fig. 1), *Tibia* (*S.*) *haueri* (DREGER, 1892) (Pl. 1, Fig. 2), *Fissidentalium* aff. *castellanense* (ORBIGNY, 1850) (Pl. 1, Fig. 5), *Limaria* (*L.*) *guembeli* (MAYER in GÜMBEL, 1861) (Pl. 2, Fig. 2), *Nemocardium haeringense* (DREGER, 1904) (Pl. 2, Fig. 3), *Lucina* (s.l.) *mittereri* MAYER & GÜMBEL in GÜMBEL, 1861 (Pl. 2, Fig. 4), *Thyasira rollei* (MAYER & GÜMBEL in GÜMBEL, 1861) (Pl. 2, Fig. 5), and *Bathyarca deshayesana* (MAYER & GÜMBEL in GÜMBEL, 1861) (Pl. 2, Fig. 6). The agglutinating *Xenophora* shells bear a wide variety of shelly material especially that of *Propeamussium bronni* (see Pl. 1, Fig. 3) and thin test fragments of spatangoid echinoids. More seldom ornaments are the scaphopod *Fissidentalium*, the bivalve *Limaria*, the gastropod taxa *Tornatellaea*, *Galeodea*, Turridae, and *Granulolabium* as well as bryozoan fragments.

3.3. Ecological analysis of molluscs

The analysis of the trophic structure (Tab. 2; Fig. 4) shows major differences among gastropods and bivalves. Gastropods are dominated by carnivores (76%) with the families Turridae, Ranellidae, Cassidae as well as Epitoniidae, Muricidae, Buccinidae, and Volutidae. Also present are detritivores (14%) represented by the Cerithiidae and Potamididae as well as herbivores (8%) represented by the Patellidae, Turbinidae and Neritidae. Suspensivores (2%) are very rare (Crepidulidae). The bivalves are dominated by suspensivores (69%) belonging to a number of families, e.g., the Solemyidae, Limidae, Lucinidae, Thyasiridae, Mytilidae, Isognomonidae, Ostreidae, and Gryphaeidae. Detritivores are also represented (19%) by members of the families Semelidae, Pholadomyidae, Nuculidae, and Nuculanidae (among others). Carnivores (12%) belonging to the families Cuspidariidae and Verticordiidae are also present. Special feeding strategies are found with chemosymbiotic relationships which are known to exist within Recent taxa of families Solemyidae, Lucinidae, Thyasiridae (these are included in the analysis within the suspensivores) and in the Eulimidae which can be parasitic on echinoids. The combined analysis of gastropods and bivalves reflects the respective dominance in each class with an almost equal percentage of suspensivores (41%) and carnivores (39%), the presence of detritivores (17%) and the rare occurrence of herbivores (2%).

A wide range of substrate relationships is present within the gastropods and bivalves (Tab. 2). The majority of gastropod taxa is epifaunal on both hard and soft substrates. A large number of families reported as occurring as both epi- and infaunal are associated with soft substrates. A few families are infaunal. Special substrate relationships are found again in the parasitic Eulimidae as well as the planktic pteropods (Thecosomata). Most bivalves are infaunal with both shallow and deeper burrowing forms. Epifaunal taxa are also well represented. Some taxa change strategies with ontogeny (e.g., Glycymeridae) and other families show a wide range of substrate relationships. This is especially obvious within the Mytilidae which include epifaunal byssate forms on hard substrates, infaunal byssate forms in soft substrates, nestlings as well as boring bivalves (*Lithophaga*).

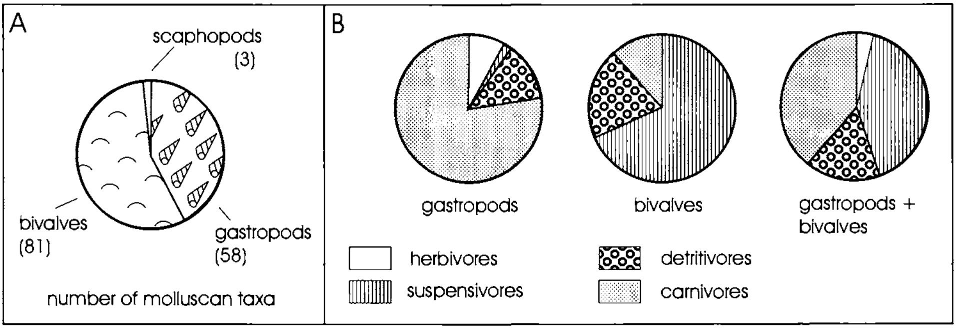


Fig. 4: Ecology of molluscs from the Lower Oligocene Paisslberg Formation: A) total number of molluscan taxa; B) trophic relationships within gastropods, bivalves and both combined.

CLASS	SUB-CLASS	ORDER	SUPERFAMILY	FAMILY	FEEDING STRATEGIES (WITHIN RECENT FAMILIES)	RELATION TO SUBSTRATE (WITHIN RECENT FAMILIES)
GASTROPODA						
	Prosobranchia					
		Archaeogastropoda	Pleurotomarioidea	Pleurotomariidae	carnivore	
			Fissurelloidea	Fissurellidae	carnivore, detritivore/ herbivore	epifaunal on hard substrates
			Patelloidea	Patellidae	detritivore/ herbivore	epifaunal on hard substrates
			Cocculinoidea		detritivore	ecology little known
			Trochoidea	Trochidae	carnivore, detritivore/ herbivore	epifaunal
				Turbinidae	herbivore	epifaunal on hard substrates
			Neritoidea	Neritidae	herbivore	epifaunal on hard substrates
		Mesogastropoda	Cerithioidea	Cerithiidae	detritivore	epifaunal on soft substrates
				Potamididae	detritivore	epifaunal on soft substrates
			Stromboidea	Aporrhaidae	detritivore	partly infaunal in soft substrates
				Strombidae	detritivore/ herbivore	epi-/infaunal on/in soft substrates
			Crepiduloidea	Crepidulidae [Calyptraeidae]	suspensivore	epifaunal on hard substrates
			Xenophoroidea	Xenophoridae	detritivore	epifaunal on soft substrates
			Cypraeoidea		carnivore, herbivore	epifaunal on hard substrates
			Naticoidea	Naticidae	carnivore	epi-/infaunal on/in soft substrates
			Tonnoidea	Ficidae	carnivore	epifaunal on soft substrates
				Cassidae	carnivore	epifaunal on soft substrates
				Ranellidae	carnivore	epi-/infaunal on/in soft substrates
			Epitonioidea	Epitoniidae	carnivore	epifaunal on soft substrates
			Eulimoidea	Eulimidae	carnivore/ parasitic	mostly vagile, partly sessile or endoparasitic
		Neogastropoda	Muricoidea	Muricidae	carnivore	epifaunal on soft and hard substrates
				Buccinidae	carnivore	epifaunal on soft substrates
				Fasciolariidae	carnivore	epifaunal on soft and hard substrates
				Volutidae	carnivore	infaunal in soft substrates
				Olividae	carnivore	infaunal in soft substrates
				Mitridae	carnivore	epi-/infaunal on/in soft substrates, epifaunal on hard substrates
				Costellariidae (Vexillidae)	carnivore	epi-/infaunal on/in soft substrates
			Cancellarioidea	Cancellariidae	carnivore	epi-/infaunal on/in soft substrates
			Conoidea	Conidae	carnivore	epi-/(semi-)infaunal on/in soft substrates, epifaunal on hard substrates
				Turridae	carnivore	epi-/infaunal on/in soft substrates, epifaunal on hard substrates
	Heterobranchia					
			Architectonicoidea	Architectonicidae	carnivore	epifaunal
				Mathildidae	carnivore	
	Opisthobranchia					
		Cephalaspidea	Acteonoidea	Acteonidae	carnivore	epifaunal on soft substrates
				Scaphandridae (Cylichnidae ?)	carnivore	infaunal in soft substrates
	Thecosomata				planktotroph	planktonic

Tab. 2: Feeding strategies and substrate relationships of mollusc families from the Lower Oligocene Paisslberg Formation following data of Recent molluscs.

CLASS	SUB-CLASS	ORDER	SUPERFAMILY	FAMILY	FEEDING STRATEGIES (WITHIN RECENT FAMILIES)	RELATION TO SUBSTRATE (WITHIN RECENT FAMILIES)
BIVALVIA						
	Protobranchia					
		Solemyoida	Solemyoidea	Solemyidae	suspensivore/ chemosymbiotic	infaunal in soft substrates
		Nuculoida	Nuculoidea	Nuculidae	detritivore	infaunal in soft substrates
			Nuculanoidea	Nuculanidae	detritivore	infaunal in soft substrates
	Pteriomorphia					
		Arcoida	Arcoidea	Arcidae	detritivore, suspensivore	epifaunal-byssate on hard substrates, vagile (semi-) infaunal
			Limopsoidea	Glycymerididae	suspensivore	juveniles epifaunal byssate and adults infaunal vagile on/in soft substrates
		Mytiloida	Mytiloidea	Mytilidae	suspensivore	epifaunal-byssate on hard substrates, (semi-) infaunal byssate in soft substrates; nestling; boring in hard sub strates
		Pterioida	Pterioidea	Pteriidae	suspensivore	epifaunal-byssate on hard substrates
				Isognomonidae	suspensivore	epifaunal-byssate on hard substrates
			Pinnoidea	Pinnidae	suspensivore	(semi-) infaunal (byssate) in soft substrates
		Limoida	Limoidea	Limidae	suspensivore	mostly epifaunal byssate on hard substrates, nestling; seldom vagile infaunal; swimming
		Ostreoida	Ostreoidea		suspensivore	epifaunal, juvenile byssate, adult cemented
				Ostreidae	suspensivore	epifaunal, cemented on hard substrate, seldom free lying
				Gryphaeidae	suspensivore	epifaunal, cemented on hard substrate, seldom free lying
			Plicatuloidea	Plicatulidae	suspensivore	epifaunal, sessile on hard substrates
			Pectinoidea	Pectinidae	suspensivore	epifaunal, vagile to byssate; swimming
				Propeamussiidae	carnivore	epifaunal, swimming
				Spondylidae	suspensivore	epifaunal, cemented on hard substrates
			Anomioidea	Anomiidae	suspensivore	epifaunal byssate on hard substrates
	Heterodonta					
		Veneroida	Lucinoidea	Lucinidae	suspensivore/ chemosymbiotic	deep infaunal in soft substrates
				Thyasiridae	suspensivore/ chemosymbiotic	deep infaunal in soft substrates
			Carditoidea	Carditidae	suspensivore	infaunal in soft substrates to epifaunal byssate on hard substrates
			Crassatelloidea	Crassatellidae	suspensivore	infaunal in soft substrates
			Cardioidea	Cardiidae	suspensivore	epi-/infaunal on/in soft substrates
			Tellinoidea	Tellinidae	detritivore	deep infaunal in soft substrates
				Semelidae (Scrobiculariidae)	detritivore	infaunal in soft substrates
			Arcticoidea	Arcticidae	suspensivore	infaunal in soft substrates
			Glossoidea	Glossidae	suspensivore	shallow infaunal in soft substrates
			Veneroidea	Veneridae	suspensivore	shallow infaunal in soft substrates

Tab. 2: continued.

CLASS	SUB-CLASS	ORDER	SUPERFAMILY	FAMILY	FEEDING STRATEGIES (WITHIN RECENT FAMILIES)	RELATION TO SUBSTRATE (WITHIN RECENT FAMILIES)
		Myoida	Hiatelloidea	Hiatellidae	suspensivore	deep infaunal in soft substrates
	Anomalodesmata	Pholadomyoida	Pholadomyoidea	Pholadomyidae	detritivore	deep infaunal in soft substrates
			Pandoroidea (Thracioidea)	Thraciidae	suspensivore	deep infaunal in soft substrates
				Lyonsiidae	suspensivore	infaunal byssate in soft substrates
			Poromyoidea	Cuspidariidae	carnivore	infaunal in soft substrates
				Verticordiidae	carnivore	infaunal in soft substrates
SCAPHOPODA		Dentaliida		Dentaliidae	detritivore	semi-infaunal in soft substates
				Laevidentaliidae	detritivore	semi-infaunal in soft substates

Tab. 2: continued.

The general molluscan fauna derived from museum collections shows a mixture of "shallow" and "deeper" water forms following the autecological distribution to Recent taxa. "Shallow water" gastropods are found within the Cerithiidae and Potamididae, Patellidae, Turbinidae, and Neritidae while corresponding "shallow water" bivalves are represented by the Mytilidae, Isognomonidae, Ostreidae, and Gryphaeidae. "Deeper water" bivalves are represented by the Solemyidae, Limidae, Lucinidae, Thyasiridae, Cuspidariidae, and Verticordiidae, Nuculanidae, and "deeper water" gastropods such as the Pleurotomariidae as well as some examples of the family Trochidae (e.g., *Lisckeia* sp.). This is confirmed by the taxonomic structure method (Hickman, 1974, 1984) which indicates a depositional environment ranging from the deeper sublittoral to upper bathyal zones.

3.4. Carbonates

A succession of facies patterns can be seen within the autochthonous carbonates especially in the Bergpeterl Quarry-SW profile. The carbonates, which follow a Triassic basement, show a transition from the coralline algal facies at the base through the coralline algal – bryozoan facies to the bryozoan facies at the top (Nebelsick et al., 2001). This transition is accompanied by the reduction of corals and lithoclasts (isolated, large, bioeroded boulders occur, however, throughout the section). Small benthic and large foraminifers occur throughout. There is an increase of muddy matrix toward the top of the section and the components become more distinctly orientated parallel to bedding. The carbonates in the other isolated autochthonous localities (Fig. 2) show the coral – coralline algal facies (Kaiserwald) and foraminiferal facies (Osterndorf). Both occurrences follow immediately above the Triassic basement and contain lithoclasts, but differ widely in component distribution (Fig. 5) and fabric. Minor components also show distinct distributions. Epifaunal brachiopods and serpulids are, for example, most common in the coral – coralline algal facies.

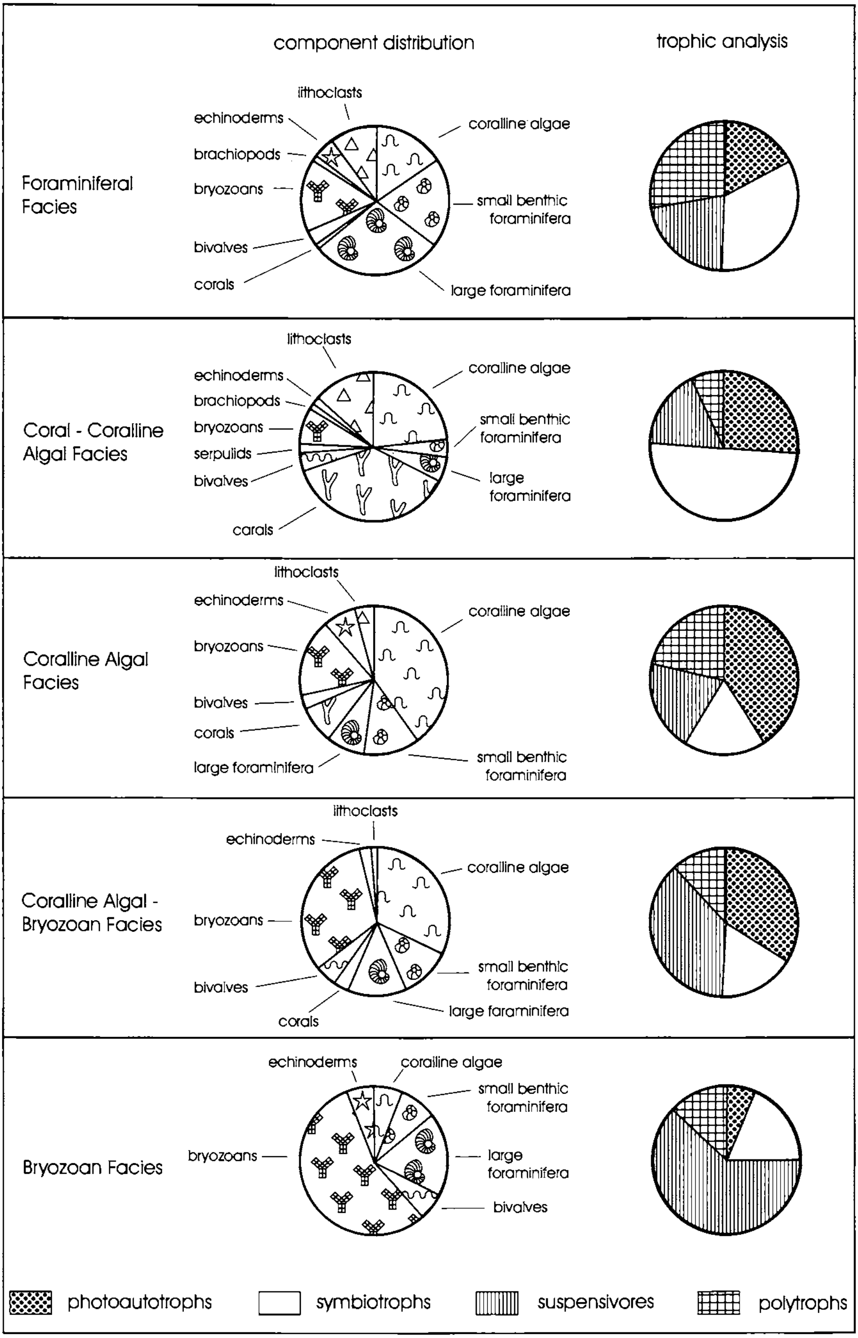


Fig. 5: Trophic analysis of component distribution (as determined by thin section analyses) within carbonate facies of the Lower Oligocene Paisslberg Formation.

The allochthonous carbonates recovered from the Bergpeterl Profile (Fig. 3) and the "Bridge Profile" to the NE (see NEBELSICK et al., 2001) show widely different facies types. All the facies types represented in the autochthonous carbonates are also represented in the allochthonous carbonates. The bioclastic packstone facies, however, is restricted to the debris flows. They can be dominated by various components including coralline algae and small benthic foraminifera, but most components cannot be identified.

The difficulties in applying trophic categories to components recognized in thin sections as seen in Fig. 5 lie in the high taxonomic level at which most can be identified. This is true for smaller benthic foraminifers which show very broad feeding strategies as well as echinoderms which include herbivores, carnivores and omnivores even within classes such as the echinoids (DE RIDDER & LAWRENCE, 1982). Other taxa have dual strategies (e. g., zooxanthellate corals as symbiotrophic suspensivores). Some taxonomic units discerned in thin section can, however, be readily referred to specific trophic categories including photoautotrophic organisms as well as suspension feeding bryozoans, brachiopods, serpulids and calcitic shelled pectinids and oysters. The organisms recognized in thin sections are totally dominated by epifaunal encrusters.

4. DISCUSSION

The conjectured deepening of depositional environment within the Oligocene sediments of the Bad Häring area as proposed for example by KROIS (1992) is clearly reflected in the mollusc fauna found *in situ* in the Bergpeterl Section (Fig. 3). This begins with the shallow water gastropod *Granulolabium* at the base of the section (still within the Häring Fm.), the reduction of taxonomic diversity within the Paisslberg Fm. (the fauna becomes less diverse towards the top), and mass occurrences of pelagic pteropods are found towards the top of the section. The fact that some taxa (*Xenophora*, *Propeamussium*) occur through much of the section suggests that dramatic changes of substrate conditions did not take place within the marls of the Paisslberg Formation. The deepening of depositional environment is also mirrored by debris flows with few occurrences in profile A; the presence of bundled thick proximal debris flows in Profile B and common thin distal debris flows at the base of profile C which eventually disappear towards the top of the section.

Differences in trophic patterns can be followed from the coralline algal through the coralline algal – bryozoan facies to the bryozoan facies which is interpreted as a depth related gradient (NEBELSICK et al., 2001). This comparison shows the expected decrease of photoautotrophic elements and increase of suspension feeders in keeping with a change from a shallow, well lit environment to a deeper, poorly lit environment. It is interesting that the percentage of symbiotrophic organisms remains the same with larger foraminifera replacing corals in deeper water (compare HOHENEGGER, 1994; HOHENEGGER et al., 1999). The three facies interpreted to represent shallow water facies (coral – coralline algal facies, coralline algal facies and foraminiferal facies) not only include a relatively higher percentage of lithoclasts, but also contain more than 50% photoautotrophic plus symbiotrophic organisms. An interpreted exposure gradient ranging from more highly exposed coral – coralline algal through the coralline algal facies to a less exposed foraminiferal facies (NEBELSICK et al., 2001) is, however, not reflected in trophic patterns.

Assessing substrate relationships of components in thin section is also hampered by variances of habit within higher taxonomic units as well. There are also problems of interpretation: although many bryozoans require initial hard substrates for encrustation, these need not be very large (see McKinney & Jackson, 1989). Upright growing bryozoans can thus utilise small skeletal remnants within "soft substrates". Faunal elements with specific substrate preferences show restricted distributions to specific facies. Epifaunal brachiopods and serpulids are thus most common in the coral – coralline algal facies where larger components (corals) offer ample opportunities for an encrusting mode of life (compare Taddei Ruggiero 1993, 1994).

5. CONCLUSIONS

1) A palaeoecological analysis of the Lower Oligocene Paisslberg Formation is based on the distribution of 142 molluscan taxa (comprising 58 gastropods, 81 bivalves, 3 scaphopods) and 6 carbonate facies (coralline algal, coralline algal – bryozoan, bryozoan, coral – coralline algal, foraminiferal, bioclastic packstone facies) present in both autochthonous limestones and allochthonous debrite flow deposits.
2) The molluscs show a wide range of feeding strategies and substrate relationships. Gastropods are dominated by carnivores with subordinate detritivores and herbivores and very rare suspensivores. Bivalves are dominated by suspensivores with subordinate detritivores and carnivores. The marls were deposited in a deeper sublittoral to upper bathyal depositional environment as demonstrated by the taxonomic structure method based on Recent distributions of subclasses respectively orders.
3) A trophic subdivision of carbonate components was made into photoautotrophs (coralline algae), symbiotrophs (larger foraminifers, corals), suspensivores (pectinids and oysters, bryozoans, brachiopods, serpulids), and polytrophs (small benthic foraminifers, echinoderms). These feeding strategies show distinct distribution among carbonate facies differentiated using standard microfacies techniques.
4) The trophic analysis of carbonate facies can be a useful additional tool in palaeoecological reconstructions based on thin-section analysis. Differences of feeding strategies are seen to reflect ecological gradients related to the availability of light with a marked dominance of photoautotrophic and symbiotrophic organisms in well lit, shallow water environments and suspensivores in poorly lit, deeper environments. There are, however, no clear trends which can be related to changes in exposure and substrate. This is, in part, due to the low resolution of trophic pattern recognition of components in thin sections.
5) The interpreted changes of feeding patterns both within the mollusc fauna and carbonate facies reflect the general basinal development within the studied sediments. This is especially true with respect to the deepening-up sequence which has been inferred from various other sedimentological and palaeontological data.

Acknowledgements: We would like to thank K. Gürs (Flintbek), R. Janssen (Frankfurt a. M.), E. Martini (Frankfurt a. M.), H. Ortner (Innsbruck), W. E. Piller (Graz), M. Rasser (Wien), V. Stingl (Innsbruck), J. Wilson (London) for help in the field and helpful discussions. We also thank T. Brachert (Mainz) and M. Harzhauser (Wien) for helpful reviews. W. Gerber (Tübingen) is thanked for the photographs of molluscs. We are especially indebted to H. Hriberschek and A. Landsteiner of the Mineralstoff Handelsges.m.b.H. in Kirchbichl (Lafarge Perlmooser AG) for permission to work in the active quarry. This study was supported by the Sonderforschungsbereich (SFB) 275 of the German Science Foundation (DFG).

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Plate 1

Gastropoda and Scaphopoda

Fig. 1: *Athleta stromboides* (DREGER, 1892), Lectotype, IGPUI: F.5129.

Fig. 2: *Tibia (Sulcogladius) haueri* (DREGER, 1892), IGPUI: F.36a.

Fig. 3: *Xenophora* cf. *subextensa* (ORBIGNY, 1852) with agglutinated *Propeamussium bronni*, IGPUI: P.2279a.

Fig. 4: *Aporrhais haeringensis* (GÜMBEL, 1861), BSPM: 1963 VI 180.

Fig. 5: *Fissidentalium* aff. *castellanense* (ORBIGNY, 1850), IGPUI: F.5181.

Plate 1


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Plate 2

Bivalvia

Fig. 1: *Propeamussium bronni* (MAYER, 1861), left valve, IGPUI: F.5047, scale bar = 2 mm.

Fig. 2: *Limaria* (*Limatulella*) *guembeli* (MAYER in GÜMBEL, 1861), IGPUI: P.2296b, scale bar = 5 mm.

Fig. 3: *Nemocardium haeringense* (DREGER, 1904), Lectotype, IGPUI: F.5033, scale bar = 5 mm.

Fig. 4: *Lucina* (s.l.) *mittereri* MAYER & GÜMBEL in GÜMBEL, 1861, Syntype ?, NMB: G 17398, scale bar = 2 mm.

Fig. 5: *Thyasira rollei* (MAYER & GÜMBEL in GÜMBEL, 1861), Neotype, IGPUI: F.5083, scale bar = 2 mm.

Fig. 6: *Bathyarca deshayesana* (MAYER & GÜMBEL in GÜMBEL, 1861), Neotype, left valve, IGPUI: P.9597, scale bar = 2 mm.

Plate 2


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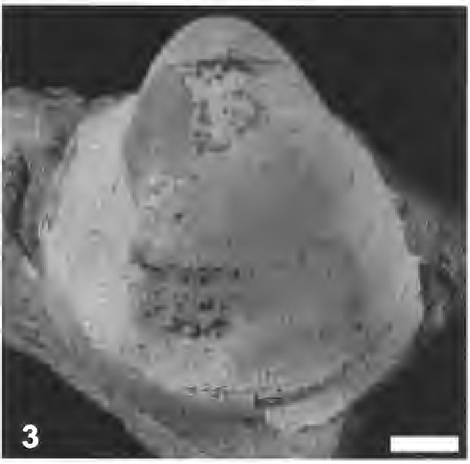
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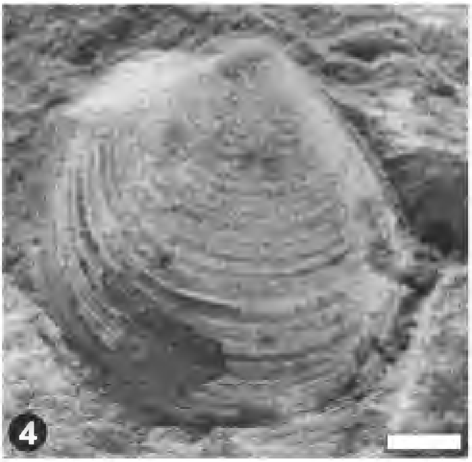
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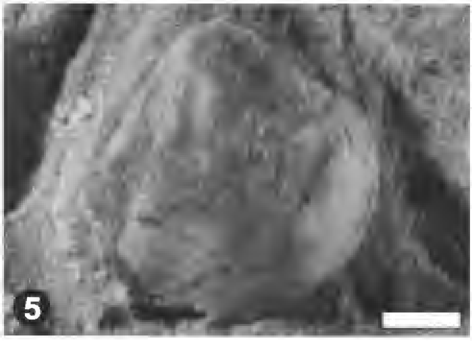
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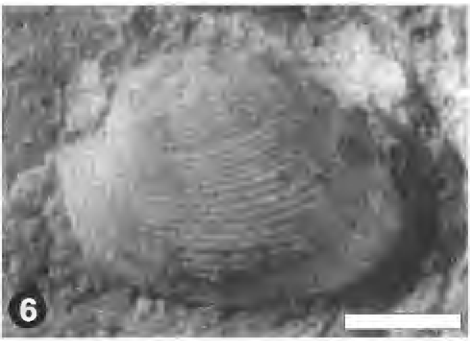
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Plate 3

Microfacies, scale bars = 2 mm

Fig. 1: Coralline algal facies; rudstone with packstone matrix, a number of calcite veins cut through the section; thin section: IT4.

Fig. 2: Coralline algal – bryozoan facies; rudstone with packstone matrix; thin section: IT7.

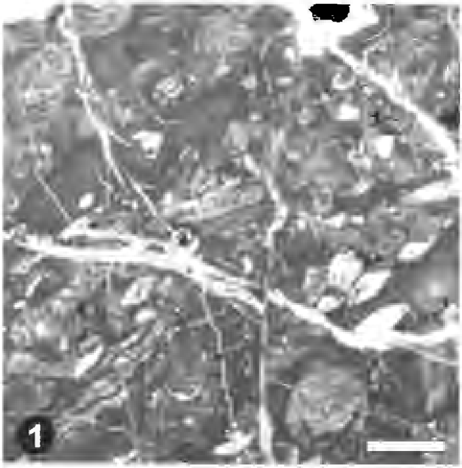
Fig. 3: Bryozoan facies, packstone with most components parallel to bedding; thin section: IT9.

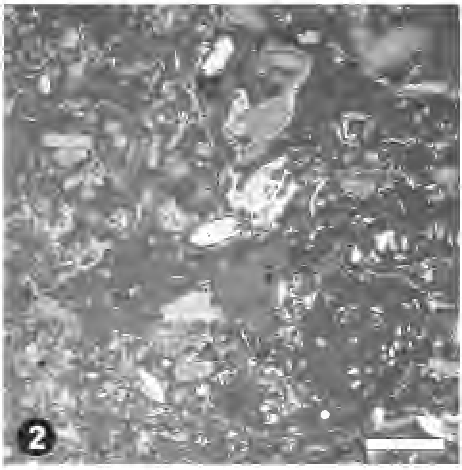
Fig. 4: Coral – coralline algal facies dominated by coral fragments showing "massive" growth form; thin section: UIT22.

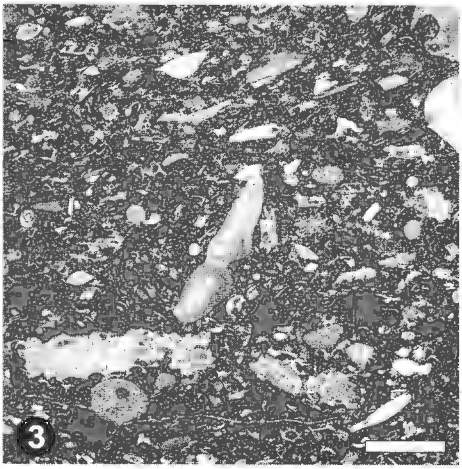
Fig. 5: Foraminiferal facies showing predominately *Amphistegina*; thin section: UIT1.

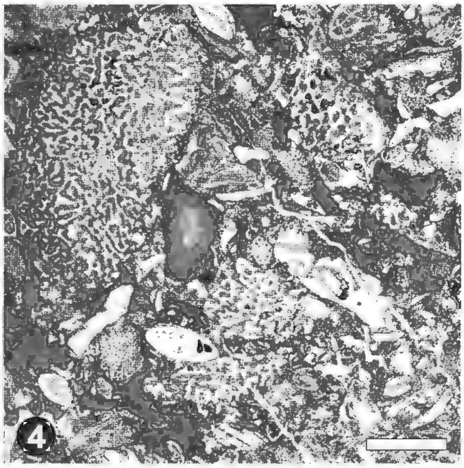
Fig. 6: Section showing very angular lithoclasts, a large oyster fragment as well as other bioclasts; thin section: UIT3.

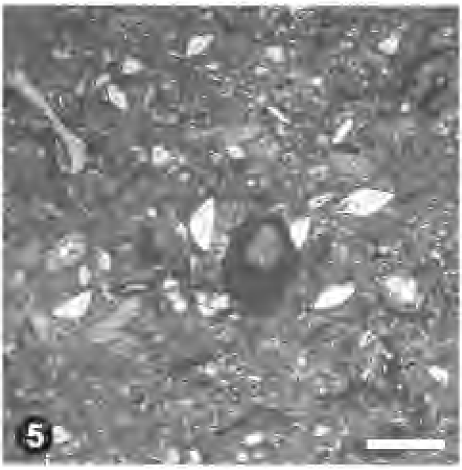
Plate 3











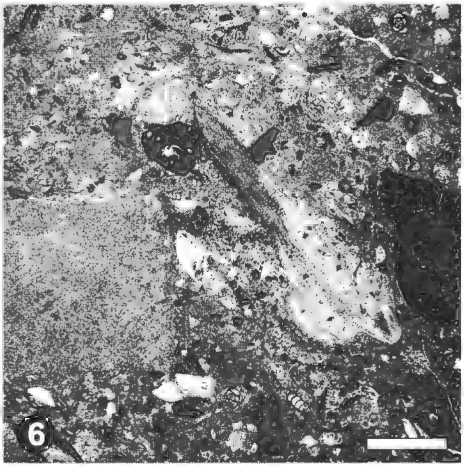


Plate 4

Biogenic components

Fig. 1: A prominent protuberance of the coralline algae *Lithothamnion* sp. 1 showing numerous conceptacles; thin section: UIT7B; (scale bar = 1 mm).

Fig. 2: The larger foraminifer *Nummulites* (centre) and *Amphistegina* (below); thin section: UIT24; (scale bar = 0.5 mm).

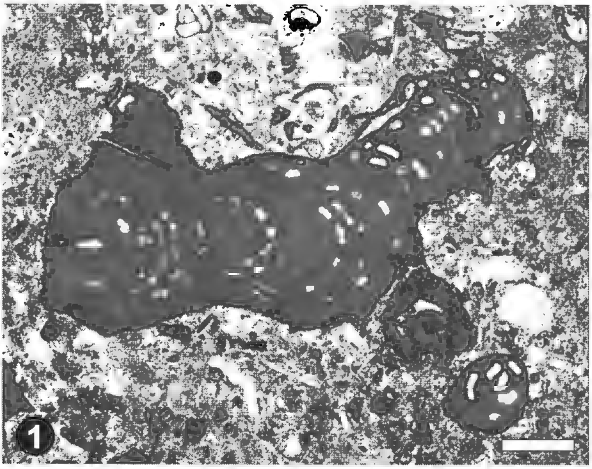
Fig. 3: Cross section through a single coral. The coral has been leached and replaced by calcite; thin section: UIT34B; (scale bar = 1 mm).

Fig. 4: Oblique section of an upright growing, bilaminate, cheilostome bryozoan; thin section: IT6; (scale bar = 1 mm).

Fig. 5: Cross section through a brachiopod. Note double wall structure and cross section of lophophore supports; thin section: UIT26; (scale bar = 0.5 mm).

Fig. 6: Slightly oblique section of a cidaroid, regular echinoid spine. Note the central medulla showing radial arrangement of beaded rays and sculptured, external cortex; thin section: IT5; (scale bar = 0.5 mm).

Plate 4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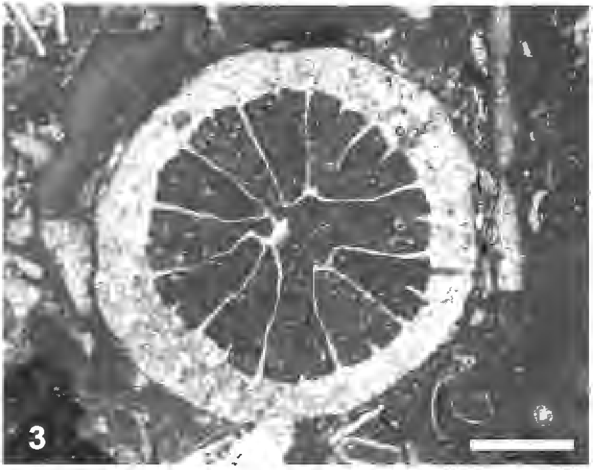
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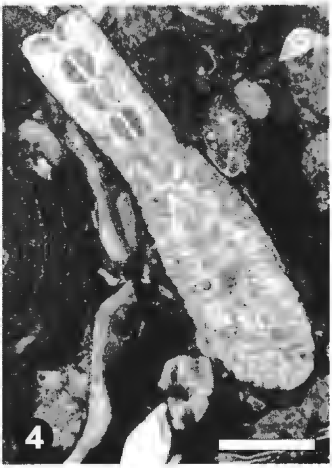
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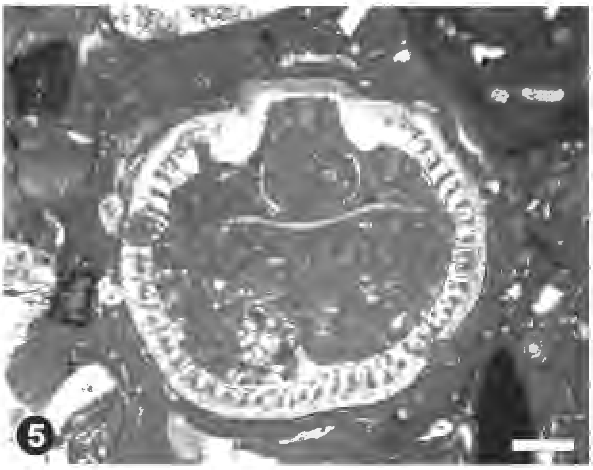
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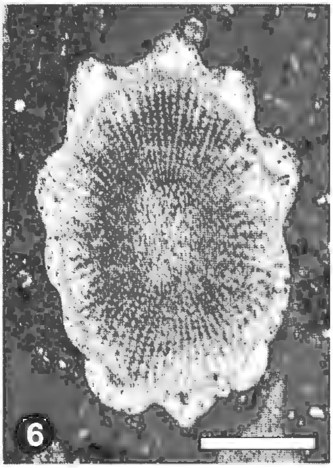
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