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Ewa Roniewicz

Triassic scleractinian corals of the  
Zlambach Beds, Northern Calcareous Alps,  
Austria

Mit 43 Tafeln

WIEN 1989  
IN KOMMISSION BEI SPRINGER-VERLAG, WIEN/NEW YORK





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## ABSTRACT

Sixty four species of Upper Rhaetian Scleractinia from Salzkammergut in Austria, mainly from the Fischerwiese site and the Gosaukamm region are described and their taxonomy revised in the present paper. Thanks to the fact that the original aragonitic skeleton has been preserved, the microstructure of septa and wall could be studied; special attention has been paid to distichophylliid and stylophyllid types of microstructure, new interpretations for which are put forward. Great morphological variability in stylophyllid species, as well as species diversity within the genera *Stylophyllum*, *Stylophylloidsis*, *Retiophyllia* and *Chondrocoenia* have been noted. Some features are indicated, i. e. the predominant types of skeletal microstructure, types of colony and growth forms in which Triassic Scleractinia differ from Recent corals.

New taxa, including 2 families (Cyclophylliidae and Gablonzeriidae), 2 subfamilies (Distichoflabellinae, Alpinophylliinae) and 10 genera have been described with the following type species: *Alpinophyllia*: *A. flexuosa* sp. n., *Alpinoseris*: *A. dendroidea* sp. n., *Anthostylis*: *Coccophyllum acanthophorum* FRECH, *Chondrocoenia*: *Prionastraea schafhaeutli* WINKLER, *Crassistella*: *Stephanocoenia juvavica* FRECH, *Cyclophyllia*: *Thecosmilia cyclica* SCHÄFER et SENOWBARI-DARYAN, *Distichoflabellum*: *D. zapfei* sp. n., *Kompsasteria*: *Isastraea oligocystis* FRECH, *Parastraeomorpha*: *P. minuscula* sp. n. and *Stuoresimorpha*: *Isastraea norica* FRECH. In addition to the taxa above, the following new species are described: *Cyclophyllia major*, *Parastraeomorpha similis*, *Retiophyllia frechi* sp. n. (= *Thecosmilia fenestrata* REUSS in FRECH 1890), *R. gephyrophora*, *R. gosaviensis*, *R. gracilis*, *R. multiramis*, *R. robusta*, *Seriastraea crassa*, *Stylophylloidsis ramosa*, *Stylophyllum vesiculatum*.

## INTRODUCTION

The coral fauna from the Zlambach Beds of the Salzkammergut region has been described in a series of papers by REUSS (1854, 1855, 1866) and in comprehensive monographs by FRECH (1890) and HAAS (1909). Great parts of the authors' original collections are still housed in the Geologische Bundesanstalt Wien (FRECH's and REUSS' collections), Bayerische Staatssammlung für Paläontologie und historische Geologie, München (FRECH's collection), Geiseltalmuseum, Universität Halle (FRECH's collection), Paläontologisches Institut der Universität Wien (HAAS' collection) and Naturhistorisches Museum Wien (one REUSS' holotype) as well as at the University of Wrocław (Breslau; Frech's collection).

The present paper revises taxa of these authors. It does not verify the taxa of other authors since the type material is dispersed and difficult to obtain for examination. The redescription has been made on the basis of the typical material preserved, as well as observation of thin sections made of neotype and topotype specimens which come from

recent collections. The synonymy has been limited to papers which contain reliable illustrations or discuss collections known to the author.

The material available, consisting of more than one thousand specimens, comes, first of all, from the collections of the Geologische Bundesanstalt Wien and Naturhistorisches Museum Wien. The collection from the Geologische Bundesanstalt, made mainly by Dr. H. LOBITZER, is representative of the coral fauna of Fischerwiese. A part of the collection, comprising specimens from Fischerwiese as well as from Zlambachgraben, Sommeraukogel, Hallstätter Salzberg and Schneckengraben, has been collected by Dr. U. PISTOTNIK, Dr. G. SCHÄFFER and others.

The collection of the Naturhistorisches Museum consists of specimens from Fischerwiese and the Gosaukamm region and is, mainly, representative of the fauna of the latter region, from the Schneckengraben site and the vicinity of Kesselwand. The latter site is known under various names: Kesselwand, Rohrmoos, Oedalm, Törleck, Hammer-tanger, Hammerkogel, Riedlkar, Zwieselalm (ZAPFE 1960). Here, the name Kesselwand-Rohrmoos has been adopted. The collection which has been built up over a hundred years contains specimens acquired from professional collectors (mainly L. GAPP) in the 19th and the beginning of the 20th century, as well as specimens collected by geologists and paleontologists (E. KITTL, O. HINTZE, H. CHLUPAČ, H. ZAPFE, E. FLÜGEL and others).

A small author's collection from Fischerwiese is kept at the Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Data on the age and facies characteristics of the Zlambach Beds at Fischerwiese and in the vicinity of Gosaukamm may be found in KRISTAN-TOLLMANN (1964), TOLLMANN & KRISTAN-TOLLMANN (1970), PISTOTNIK (1972), WURM (1982), SCHAUER (1983), MATZNER (1986) and in a general review by FLÜGEL (1982) on the coral buildups of the Alpine Triassic.

The last twenty years has seen a great increase of interest in Triassic corals. Of special importance are the pioneer researches on skeletal microstructure and contribution to the setting up of microstructural criteria for the systematics of Triassic corals by CUIF (1973, 1975 abc, 1976, 1977 b, 1981). The works of MONTANARO-GALLITELLI (1974 ab, 1975, 1980), and MONTANARO-GALLITELLI *et al.* (1974) have contributed much to our knowledge of skeletal microstructure and to the revision of the systematics of Carnian corals and other coelenterates. Microstructural criteria are an effective and order-bringing tool in the examination and classification of corals. Unfortunately, whole series of Triassic sediments contain recrystallized corals and for these less precise methods must suffice.

In addition to those contributions mentioned above, strictly taxonomic papers have been published, which are of real significance to our knowledge of corals although they were based on rather poorly preserved material. SCHÄFER & SENOWBARI-DARYAN (1978) described new taxa of Rhaetian corals of the Northern Calcareous Alps, TURNŠEK described Carnian corals from Slovenia (1985; TURNŠEK *et al.* 1982, RAMOVŠ & TURNŠEK 1984). FANTINI-SESTINI & MOTTA (1984) gave new data on Rhaetian corals from the Southern Alps (Lombardy), and MORYCOWA (1988) described new taxa from the Muschelkalk. During this period MELNIKOVA published a series of papers on the corals of Central and NE Asia (1967, 1968, 1971, 1972, 1975, 1983, 1984 ab, 1986), MONTANARO-GALLITELLI *et al.* (1979), and STANLEY (1979, 1986) on North American Triassic corals and WU (1975, 1977), LIAO WEIHUA (1982), DENG & KONG (1984), XIA JINBAO & LIAO WEIHUA (1986) and others on Chinese Triassic corals. SCHOLZ (1972)

presented Anisian coral buildups of the Carpathians and described new coral species. ZANKL (1969), KRISTAN-TOLLMANN *et al.* (1969, 1980), SCHÄFER (1979), SENOWBARI-DARYAN (1980), SADATI (1981), WURM (1982) and MATZNER (1986), describing Triassic coral-bearing sediments of Alps, gave short descriptions and clear illustrations of known coral species.

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Dr. WINFRIED WERNER (Bayerische Staatssammlung für Paläontologie und Historische Geologie, München) has kindly supplied me with information on collections and sent me holotypes and photographs of FRECH's originals (taken by Mr. F. HÖCK); a photograph of the holotype of *Thecosmilia cyathophylloides* is published here. Dr. DIETER WEYER informed me on FRECH's collection in the Geiseltalmuseum, Halle. Dr. CHRISTIAN MATZNER (Universität Erlangen-Nürnberg) has kindly made available corals from his collection as well as photographs of coral thin sections. Dr. JOHANN GÖLLNER (Karl-Franzens-Universität Graz) has sent me photographs of *Palaeastraea grandissima* (FRECH) and of the holotype of *P. grandistellata* KÜHN from KÜHN's collection, which are published here. The photographs of the type specimens of *Thecosmilia cyclica* SCHÄFER *et* SENOWBARI-DARYAN I have received from Dr. PRISKA SCHÄFER (Institut für Geologie, Marburg) and Dr. RUDOLF BIRENHEIDE (Forschungsinstitut Senckenberg, Frankfurt am Main), and sections for comparison from Dr. BABA SENOWBARI-DARYAN (Universität Erlangen-Nürnberg).

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### Terminology and abbreviations

Terminology, in general, follows the "Glossary" in MOORE (1956, F 245) and that of ALLOITEAU (1957). The following complementary terms or terms of restricted meaning concerning skeletal microstructure, corallite structural elements and colony type have also been used:

### A. Microstructure of septa

- bundles of fibres – here, elementary units of the skeletal organization in stylophyllids; when continuously growing the bundles of fibres resemble the minitraculae of distichophyllids (see trabecula);
- distichophyllid type of microstructure – for explanation see p. 36;
- fascicles of fibres – here, large units of the stereomal organization known in the distichophyllid lateral septal zone, growing perpendicularly to the mid-septal plane; an axis, when developed, gives them a trabecular character, hence – lateral trabeculae (CUIF 1975 a);
- median trabecula – see trabecula;
- meniane–lateral gallery on the septal flank formed by laterally fused expansions of trabeculae (after GILL 1967);
- minitracula – see trabecula;
- lateral trabecula – see fascicles of fibres and trabecula;
- pennula – collar-like expansion on an individual trabecula (after GILL 1967);
- septal spine – a spiny radial element of the stylophyllid corallite, composed of fibrous stereome (CUIF 1973); the fibres appear to be organized in bundles. The innermost, axial bundles may elongate in the form of minitraculae resembling those of distichophyllid type in shape and diameter (see bundles of fibres and trabecula);
- trabecula – continuously growing rod formed of fibres, provided with an axis and not divided into sclerodermites (after GILL 1967, 66). For descriptive purposes trabeculae are defined as (i) large (more than 50  $\mu\text{m}$  in diameter; the smallest trabeculae of this category, 50–90  $\mu\text{m}$  in diameter, are sometimes distinguished as medium sized), and minitraculae (usually 20–30  $\mu\text{m}$ , reaching up to 50  $\mu\text{m}$  in diameter, also called thin or small trabeculae); the latter are geometrically like large trabeculae but differ from them not only in size but also in their fine fibres; minitraculae are situated in the mid-zone of distichophyllid septa and, probably at the axes of stylophyllid septal spines (see bundles of fibres). Trabecular diameters are measured along the calicular radius. In distichophyllid microstructure, median trabeculae constituting a mid-septal zone, and lateral trabeculae subperpendicular to them, constituting a lateral septal stereome, have been distinguished;
- stereome – fibrous tissue usually organized in bundles and fascicles (see above);
- stylophyllid type of microstructure – for explanation see p. 117.

### B. Corallite

- endotheca and exotheca – dissepiments (vesicular, tabuloid) developed within and outside the zone of trabecular divergence, respectively;
- wall – in connection with its position in the corallite, the wall may be external, covering from the outside all skeletal elements (essential wall or derived from the development of other skeletal structures) or an internal, intracorallite wall (derived from the development of other skeletal structures); in connection with different structures the following wall types may be enumerated:
- bilaminar: fibrous, provided with a median fissure dividing it into two layers (ex. *Kompsasteria*, *Coccophyllum*, *Stylophyllum*, *Pinacophyllum*); known in cerioid colonies;
- palisaded: formed of a single row of vertical trabeculae (ex. *Kuhnastraea*, *Gablonzeria*); known in cerioid colonies;
- pellicular: formed of fibres of centripetal growth constituting an essential skeletal structure and functioning as an independent wall. This term is partly synonymous with “epitheca” which refers to all kinds of transversely folded outer coverings of corallites (colony); known in solitary and phaceloid corals.

### C. Colony

- kuhnasteroid – a colony plocoid in appearance in which corallite boundaries are defined by a palisaded trabecular wall, the calices at the same time being enclosed by their own internal walls; calices are elevated (ex. *Kuhnastraea*);
- phaceloid – a type of colony structure representing a separate growth form; owing to the composite morphology and genetic identity of individuals it is considered here as a colony although, from the point of view of integration of polyps, it represents a pseudo-colonial state (COATES & OLIVER 1974, COATES & JACKSON 1985);



## Abbreviations used and definitions of structural measurements:

- c-c – distance between calicular axes;
- c/mm – number of costae per millimeter, measured as s/mm (see below);
- d – diameter (= calicular diameter if not stated otherwise) measured between midpoints of the walls, or when the wall is lacking between the mid-points of boundaries which can be defined by other structures (troughs, fissures etc.);
- h – height of colony or corallite;
- men/mm – number of menianes per millimeter (density) measured on the septal surface in longitudinal section, in a vertical direction;
- s – number of septa in the corallite;
- s/calice – number of septa in a calice, when a difference exists between the total number of septa in the corallite and the number of septa limited to the calice;
- s/mm – septal density, number of septa per millimeter measured directly on the specimen (not calculated from other measurements) at the wall in cross section or on the wall surface;
- S1, S2 . . . – septa of succeeding size orders (which may or may not correspond to orders of appearance); 10 S1, 20 S2 . . . number of septa of particular size orders; number of septa in the corallite may be expressed as a sum of septa of succeeding septal orders, for example 52 (10 + 10 + 20 + 12);
- syn/mm – number of synapticalae per millimeter (density), measured as men/mm;
- t/mm – number of endothecal elements per millimeter measured as above.

## Symbols of collections:

BSP	Bayerische Staatssammlung für Paläontologie und historische Geologie, München
GBA	Geologische Bundesanstalt Wien
IGD	Institute of Geology, Tadshik Academy of Sciences, Dushanbe
IPWB	Institut für Paläontologie, Rheinische Friedrich-Wilhelms-Universität Bonn
NHMW	Naturhistorisches Museum Wien
PIUW	Paläontologisches Institut, Universität Wien
PSG	Paläontologische Sammlung, Universität Graz
SMF	Natur-Museum Senckenberg, Frankfurt am Main
ZPAL	Institute of Paleobiology, Polish Academy of Sciences, Warsaw

## Abbreviations used in synonymies:

<i>part.</i>	specific assignment accepted in part by the author (Lat. <i>partim</i> )
<i>v.</i>	originals seen and examined by the author (Lat. <i>vidimus</i> )
?	dubious assignment

## CORAL SITES AND PRESERVATIONAL STATE OF THE MATERIAL

Fischerwiese: Corals are found in alluvium and in rare outcrops in the bed and banks of the stream (MATZNER 1986). The rock sequence cannot be examined due to insufficient exposure of the profile (KRISTAN-TOLLMANN 1964, MATZNER 1986). Usually, matrix is preserved in depressions on the surface of the specimens. The corals come mainly from soft, grey and greenish-grey marls, less often from limestones. The corals from marls are either whole, isolated colonies attaining up to 20 cm in height and 30 cm in diameter, or fragments. It is principally phaceloid corals which are fragmentary.

The coral-bearing limestones are hard, poorly sorted organodetrital calcirudites, or well sorted calcarenites composed of peloids and fine detrital fragments. Most often corals coming from limestones have their microstructure altered and corallite structure blurred. Some of the specimens from limestones and marls have well-preserved aragonitic microstructure, at least in part of the skeleton. About 50 coral species are listed from Fischerwiese (Table 1).

Table 1. List of the examined species

No.	Species	Site				
		F	GK	HS	ZG	S
1.	<i>Alpinophyllia flexuosa</i> gen. et sp. n.		+			
2.	<i>Alpinoseris dendroidea</i> gen. et sp. n.		+			
3.	<i>Anthostylis acanthophora</i> (FRECH)	+				
4.	<i>Astraeomorpha confusa</i> (WINKLER)	+	+	+		+
5.	<i>Astraeomorpha crassisepta</i> REUSS	+	+	+	+	
6.	<i>Chondrocoenia ohmanni</i> (FRECH)	+	+			
7.	<i>Chondrocoenia schaffhaeutli</i> (WINKLER)	+	+			
8.	<i>Chondrocoenia waltheri</i> (FRECH)	+				
9.	<i>Chondrocoenia</i> sp. A.		+			
10.	<i>Chondrocoenia</i> sp. B					+
11.	<i>Coccophyllum sturi</i> REUSS	+	+	+		
12.	<i>Coryphyllia elliptica</i> (MELNIKOVA)		+			
13.	<i>Crassistella juvavica</i> (FRECH)	?	+			
14.	<i>Cuifastraea arthaberi</i> (HAAS)	+	+			
15.	<i>Cyclophyllia cyclica</i> (SCHÄFER et SENOWBARI-DARYAN)	+	+			
16.	<i>Cyclophyllia major</i> gen. et sp. n.		+	+		
17.	<i>Distichoflabellum zapfei</i> gen. et sp. n.		+			
18.	<i>Distichomeandra austriaca</i> (FRECH)	+	+			
19.	<i>Distichomeandra dieneri</i> (HAAS)	+	+			
20.	<i>Distichomeandra minor</i> (FRECH)	+	+			
21.	<i>Distichophyllia fritschi</i> (FRECH)	+				
22.	<i>Distichophyllia norica</i> (FRECH)	+	+	+	+	
23.	<i>Gablonzeria major</i> (FRECH)	+	+			
24.	<i>Gablonzeria profunda</i> (REUSS)	+	+	+		
25.	<i>Gigantostylis epigonus</i> FRECH	+	+	(?)		
26.	<i>Kompsasteria oligocystis</i> (FRECH)		+			
27.	<i>Kuhnastraea decussata</i> (REUSS)	+	+	+	+	
28.	<i>Kuhnastraea incrassata</i> (FRECH)	+	+	+		
29.	<i>Margarosmillia charlyana</i> (FRECH)	+	+	+	+	
30.	<i>Meandrostylis frechi</i> HAAS	+	+			
31.	<i>Meandrostylis irregularis</i> FRECH	+	+			
32.	? <i>Molukkia</i> sp.	+				
33.	<i>Oedalmia norica</i> (FRECH)	+	+			
34.	<i>Oedalmia</i> sp.	+				
35.	<i>Palaeastraea cyathophylloides</i> (FRECH)	+	+			
36.	<i>Palaeastraea grandissima</i> (FRECH)	+	+	+		
37.	<i>Pamiroseris rectilamellosa</i> (WINKLER)	+	+	+	+	
38.	<i>Parastraeomorpha minuscula</i> gen. et sp. n.	+	+			
39.	<i>Parastraeomorpha similis</i> gen. et sp. n.	+				
40.	<i>Pinacophyllum parallelum</i> FRECH	+	+			
41.	<i>Procyclolites triadicus</i> FRECH	+	+	+	+	
42.	<i>Retiophyllia caespitosa</i> (REUSS)	+	+	+		
43.	<i>Retiophyllia fenestrata</i> (REUSS)	+	+			

## List of the examined species (Continued)

No.	Species	Site				
		F	GK	HS	ZG	S
44.	<i>Retiophyllia frechi</i> sp. n.	+	+	+	+	
45.	<i>Retiophyllia gephyrophora</i> sp. n.		+			
46.	<i>Retiophyllia gosaviensis</i> sp. n.		+			
47.	<i>Retiophyllia gracilis</i> sp. n.	+	+			
48.	<i>Retiophyllia norica</i> (FRECH)	+	+	+	+	
49.	<i>Retiophyllia oppeli</i> (REUSS)	+	+	+	+	
50.	<i>Retiophyllia multiramis</i> sp. n.	+	+			
51.	<i>Retiophyllia robusta</i> sp. n.	+	+			
52.	<i>Retiophyllia</i> sp. A	+		+		
53.	<i>Seriastrea crassa</i> sp. n.		+			
54.	<i>Seriastrea multiphylla</i> SCHÄFER et SENOWBARI-DARYAN	+	+			
55.	<i>Stuoresimorpha norica</i> (FRECH)		+	+		
56.	<i>Stylophyllopsis lindstroemi</i> FRECH	+	+			
57.	<i>Stylophyllopsis polyactis</i> FRECH	+	+	+		
58.	<i>Stylophyllopsis ramosa</i> sp. n.	+				
59.	<i>Stylophyllopsis rudis</i> (EMMRICH)	+	+			
60.	<i>Stylophyllopsis zitteli</i> (FRECH)	+	+	+		
61.	<i>Stylophyllum paradoxum</i> FRECH	+	+			
62.	<i>Stylophyllum polyacanthum</i> REUSS	+	+			
63.	<i>Stylophyllum pygmaeum</i> (FRECH)				+	+
64.	<i>Stylophyllum vesiculatum</i> sp. n.	+	+			

F Fischerwiese

GK Gosaukamm vicinity (Kesselwand-Rohrmoos and Schneckengraben)

HS Hallstätter Salzberg

ZG Grosser Zlambachgraben

S Sommeraukogel

**Schneckengraben:** Fragments of a profile of well stratified marls and limestones are exposed here (TOLLMANN & KRISTAN-TOLLMANN 1970, MATZNER 1986). The scree from Schneckengraben has provided corals for dozens of years, some of them of great size (colonies up to 40 cm in diameter). However, corals do not occur *in situ* in great numbers. The corals often have clearly visible delicate calical structures and septal ornamentation. Some colonies come from fine-detrital rocks, crumbling due to weathering. Despite this, many colonies have the aragonitic skeleton preserved, at least in some parts.

**Kesselwand-Rohrmoos:** Only fragments of the profile are accessible in scattered exposures, in the vicinity of the Kesselwand rock (TOLLMANN & KRISTAN-TOLLMANN 1970, MATZNER 1986). The greatest collection of the Naturhistorisches Museum, including the majority of the large colonies, comes from this site. The corals have been collected for years from a weathered rock and scree covered by meadow. MATZNER (1986) has proved that in the presently accessible parts of the profile the corals are scattered in thin layers of detrital limestones (calcarenites and calcirudites).

In the collections, one's attention is attracted by colonies with fragments of a dense, black or dark grey micritic matrix preserved on the surface. These corals often have well-preserved aragonitic skeletons. Other well-preserved specimens come from marls or claystones with scattered biodetrital fragments a few mm in diameter. Outcrops of such rocks have not been identified in MATZNER's profile (1986). The large dimensions of the colonies from this site show that the coral-bearing strata might attain a thickness of several decimeters. At present beds of such a thickness are not exposed here either.

Kesselwand-Rohrmoos is the richest of all Zlambach Bed coral sites. This site and Schneckenengraben provided 55 coral species (Table 1).

Sommeraukogel, Hallstätter Salzberg and Kleiner Zlambachgraben: Marls provided poorly diversified corals with deeply recrystallized skeletons. In Sommeraukogel this fauna is rather dwarfish and represented by small-calicular morphotypes of the genera *Chondrocoenia*, *Astraeomorpha*, *Parastraeomorpha*, *Retiophyllia* and *Stylophyllum*. From Hallstätter Salzberg, a thin-branched *Retiophyllia* is known.

From the point of view of water depth, bottom stability, degree of turbidity and diversity of deposition environments, the conditions, in general, were similar in the whole region discussed. It is not obvious, however, that sedimentation of the coral-bearing deposits in question occurred simultaneously. It has been assumed that the coral deposits of Fischerwiese and Gosaukamm vicinity are approximately of the same age (WURM 1982).

Many corals from the claystones and marls of Fischerwiese and the other sites show considerable crushing and deformation. In *Distichophyllia norica* and *Procycololites triadicus* the corallum is often preserved as a rod consisting of a core and a cortex, which have been rotated in relation to each other. The core part has been rolled up to form a vortex. The septa are ripped along their whole length. In colonies of *Palaeastraea* and *Kuhnastraea*, the individual corallites, with strong skeletons, are relatively weakly linked with each other by thin-walled dissepimental exotheca. The corallites themselves, apart from their peripheral parts, are generally well-preserved though elements of the intercalicular zone are crushed into fine debris. In cerioid colonies of thin-septate corals, the inner ends of septa are torn and dislocated (*Gablonzeria*). Colonies with serial structure are frequently crushed along the axis of the series, for instance in *Alpinophyllia*. Apart from internal deformation, which is not always manifest on the surface, one observes single corals and branches of phaceloid corals which are severely flattened. Such corals are abundant in the siltstones of Fischerwiese. Those of them with delicate external walls are liable in addition to the destruction of their cortex through stream redeposition, as well as recent weathering.

As mentioned above, skeletal tissue in the Zlambach-Bed corals is often preserved in its original aragonitic form (ZAPFE 1936, CUIF 1972). In their preservational state, the corals from Zlambach Beds resemble those from the St. Cassian Beds (compare CUIF 1972, MONTANARO-GALLITELLI *et al.* 1974, SCHERER 1977). Thanks to this fact the skeletal microstructure of these corals could be studied (CUIF 1965, 1967, 1968, 1973, 1975 ac, 1976 and herein).

## REMARKS ON MORPHOLOGICAL VARIABILITY

The coral collections from the Zlambach Beds are excellent material for research on the diversity of skeletal structure. They also allow the measurement of the great taxo-

nomie variety and intraspecific variability of Rhaetian corals and make one realise how vague is the species range in this group of organisms. Unfortunately, it is impossible to start any studies of this problem because of limitations imposed by the material itself.

The extensive collections made over dozens of years comprise colonies, their fragments and simple corals only from a narrow time interval represented by a relatively small fragment of the Rhaetian profile. Each site provides corals from many different strata, however, the sequence of coral horizons is impossible to reconstruct in any of the sites. Thus, the collection from each locality represents a mixed sample of heterochronous populations. Such a sample, though it comes from a small interval of geological time, exhibits great morphological variability of the various ranks. The range of morphological differences between species representatives from individual sites is worth a separate detailed analysis.

Great morphological variability poses the problem of whether to treat the morphotypes as separate taxa or as a manifestation of intraspecific variability. Different groups of Rhaetian corals are variously treated in this respect in the literature. In the Stylophyllina, morphotypes with different thickness and density of radial elements are considered to be conspecific (for example the range of *S. paradoxum*, *S. polyacanthum* and *S. rudis*).

On the other hand, in corals with complex structures, morphotypes are considered as separate species. For example, within the genera *Palaeastraea*, *Gablonzeria* and *Retiophyllia* there are pairs or triads of morphotypes differing above all in diameters (*Palaeastraea grandissima* — *P. cyathophylloides*; *Gablonzeria major* — *G. profunda*; *Retiophyllia robusta* — *R. norica* — *R. caespitosa*; *Retiophyllia gephyrophora* — *R. fenestrata* — *R. gracilis*; *R. frechi* — *R. oppeli*). Treatment of such morphotypes as separate species seems to be justified by their different septal densities or endothecal structures. The status of morphotypes is still unclear in those series where distinguishing features, except for diameters, have not been defined.

The interpretation of this variability would be much easier if it could be established whether morphotypes coexisted within populations, belonged to different populations, or occurred in stratigraphical succession.

Regardless of one's approach to the variability of the coral fauna from the Zlambach Beds, it is clear that some of the corals were undergoing a sudden radiation. Unfortunately, inability to examine the whole profile makes it impossible to find how the coral fauna changed with time. The genus *Retiophyllia*, which is represented in the collection by as many as eleven species, may be quoted as an example of intense speciation. Apart from *norica* — *caespitosa* and certain cases of the series *fenestrata* — *gracilis*, the species distinctly differ morphologically and constitute the following groups (1) *oppei*—*frechi*—*caespitosa*—*norica*—*robusta*, (2) *gosaviensis*, (3) *multiramis* and (4) *gracilis*—*fenestrata*—*gephyrophora* (see p. 46).

In the Norian-Rhaetian of the Pamirs the variety is also great (*R. norica*, *R. dichotoma*, *R. multigranulata*, *R. minima*, *R. clathrata*, *R. cf. cyathophylloides*, *R. wanneri*), and the collection seems to differ from that of the Alps more than the list indicates (compare MELNIKOVA 1975).

Similarly, the Norian of Turkey contains forms which little resemble the Alpine species (CUIF 1975 a). This diversification is evidence of a particular expansion of this genus, much greater than that of the other Triassic genera, and comparable to the radiation of the Upper Jurassic genera *Pleurophyllia*, *Pseudocoenia*, or *Heliocoenia*.

# PECULIARITIES OF THE RHAETIAN CORAL FAUNA AND ITS RELATIONSHIP TO OTHER SCLERACTINIA

## 1. General characteristics

In spite of the homeomorphy that has characterized Scleractinia from the Triassic onwards, the coral faunas from each of the periods in which their full variability may be examined, clearly show their distinct features. Also in the whole of the Tethys area the Rhaetian coral fauna has its specific set of features. Its specific character consists in domination of a certain type of corallite and colony architecture as well as septal structure and ornamentation over the other types.

**Structure and ornamentation of septa:** Among Rhaetian corals the most common are those having fine and medium-sized trabeculae (see terminology) and non-trabecular corals with radial elements built of septal spines. As far as the septal microstructure is concerned, two homogeneous groups from among them attract special interest: (i) distichophylliid corals (family Reimaniphylliidae) and (ii) stylophyllid corals.

(i) Distichophylliid corals have minitrabecular microstructure of a special type (p. 36). Radial elements of costoseptal type can freely grow laterally and attain considerable thickness, though minitrabecular mid-septal zone remains always very thin. This type of structure is characteristic of over ten genera (over forty species) of the Rhaetian and Norian-Rhaetian corals (*Distichophyllia* CUIF, *Retiophyllia* CUIF, *Kuhnastraea* CUIF, *Oedalmia* CUIF, *Coryphyllia* CUIF, *Palaeastraea* KÜHN, *Toechastraea* VOLZ, *Alakiria* CUIF, *Distichoflabellum* gen. n., *Margarosmia* VOLZ, *Distichomeandra* CUIF).

(ii) Stylophyllids are non-trabecular Triassic corals. Their septal apparatus consists of septal spines, free or cemented by stereome; the stereome has characteristic fascicular structure (p. 117). Most often the spines are much thicker than any trabeculae. This type of septum, with isolated structural elements, is also repeated, though in exceptional cases and to a limited extent, by Rhaetian trabecular corals, e. g. *Kompsasteria* gen. n., or *Cyclophyllia* gen. n. Altogether six genera and over ten stylophyllid species are known in the Upper Triassic. In the Carnian, Stylophyllina were not diversified (*Stylophyllopsis* FRECH, *Pinacophyllum* FRECH). In the Rhaetian, numerous colonial and solitary species of *Stylophyllum* REUSS, *Stylophyllopsis* FRECH, or *Meandrostylis* FRECH, *Pinacophyllum* FRECH and *Coccophyllum* REUSS developed. The genera with the simplest structure, i. e. *Stylophyllum* and *Coccophyllum*, are known from the Rhaetian only, whilst *Stylophyllopsis*-like corals, with much more complex architecture, are known from the Anisian to the Lias (p. 123). The harmonious growth of all skeletal elements (wall, septa, dissepiments) has made *Stylophyllopsis*-like corals (*Stylophyllopsis* FRECH, *Meandrostylis* FRECH, *Anthostylis* gen. n.) resemble the corals of trabecular groups.

The remaining Triassic corals, including a large Rhaetian group, belong, first of all, to groups with septal blades built of small, coalesced trabeculae of non-distichophylliid type or medium-sized trabeculae. Although some of the corals (e. g., thamnasterioid forms) had trabeculae arranged in a divergent system, the genera with serial septal structure were more common. These are phaceloid corals, whose septal apparatus developed without any space limitations (*Cyclophyllia* gen. n.) as well as cerioid forms (*Gablonzeria* CUIF, *Kompsasteria* gen. n., *Stuoresimorpha* gen. n., *Alpinophyllia* gen. n., *Distichomeandra* CUIF, and some Carnian forms, as *Guembelastraea* CUIF, *Andrazella* CUIF, *Stuoresia* CUIF and others). This septal structure reappeared to a very limited

extent in the Jurassic, and was represented by *Isastraea* MILNE-EDWARDS et HAIME only. Also the vesicular endotheca in this genus was identical to that of the Triassic corals listed above, except for *Kompsasteria*. Due to this fact, for over a century the name *Isastraea* has been applied to species of those genera. The septal microstructure of *Isastraea*, analogous to that in Montlivaltiidae (GILL 1970, GILL & LAFUSTE 1971, RONIEWICZ 1983), does not allow this genus to be connected with any of the known Triassic corals (CUIF 1976).

It is striking that Rhaetian corals do not contain a certain type of septal structure known in the Carnian *Omphalophyllia* LAUBE, *Conophyllia* D'ORBIGNY, or in *Araiophyllum* CUIF. In describing the structure of *Omphalophyllia* and *Conophyllia*, CUIF (1975 c) pointed to the fact that the septa are composed of series of trabeculae, which are ordered like trabeculae in the costae, i. e. they are vertical near the corallite axis like axis of divergence and bend towards the periphery. This type of serial structure has not been found so far neither in Rhaetian nor in later corals.

The majority of thin-septal corals discussed here have a characteristic ornamentation – the septa covered either by menianes (i), or by sharp, sparse granules (ii).

(i) The menianes are long or short, with margins smooth or regularly indented. In the Carnian, these corals are represented by *Craspedophyllia* VOLZ, *Guembelastraea* CUIF, *Andrazella* CUIF, *Stuoresia* CUIF, *Tropiastraea* CUIF, and in the Norian-Rhaetian by *Procycolites* FRECH, *Alpinoseris* gen. n., *Alpinophyllia* gen. n., some *Retiophyllia* CUIF, *Stuoresimorpha* gen. n., *Thamnasteriamorpha* MELNIKOVA, *Karatchastraea* CUIF, *Cuifastraea* MELNIKOVA, *Gillastraea* MELNIKOVA, *Seriastraea* SCHÄFER et SENOWBARI-DARYAN, *Chevalieria* MELNIKOVA, *Astraeomorpha* REUSS, and *Stuoresia* CUIF which ranges from the Carnian to the Norian. With the exception of *Astraeomorpha* the meniane-bearing corals are thin-septal.

In Carnian *Omphalophyllia* LAUBE or *Rhopalophyllia* CUIF rows of nodes parallel to the distal margins of the septa function similarly to menianes, but they do not fuse into true menianes. The Jurassic pennular corals (Microsolenidae, Latomeandridae, Thamnasteriidae) differ from those of the Upper Triassic in having a skeleton consisting of relatively thick trabeculae and consequently, in wide, multifascicular pennulae (see GILL 1967, 1968, 1982, GILL & RUSSO 1980, RONIEWICZ 1983). Though they fuse into menianes, the pennulae do not lose their individuality completely as is the rule in the case of side trabecular offsets in the Triassic meniane corals.

(ii) *Gablonzeria* CUIF, *Kompsasteria* gen. n. and *Cyclophyllia* gen. n. are Rhaetian corals with medium-sized trabeculae and septa ornamented with granules. In *Gablonzeria* there is a tendency for granules to develop in the form of plates more or less regularly paralleling the distal septal edge. The granules or plates strongly protrude into interseptal spaces. Their arrangement is irregular, not resembling that of menianes. In *Kompsasteria*, at the inner margin carenes appear running along the trabeculae; the granules are not prominent here. In *Cyclophyllia*, on the contrary, the granules are sharp and strongly protruding.

The thick-trabecular corals were little diversified in the Rhaetian (*Pamiroseris* MELNIKOVA, *Crassistella* gen. n.), whereas in the Carnian-Norian the thick-trabecular genera were relatively numerous (*Beneckastraea* CUIF, *Margarastraea* FRECH, *Elysastraea* LAUBE, *Ampakabastraea* ALLOITEAU – see CUIF 1976). Their corallite structure does not have any particular features, the endotheca is vesicular, the ornamentation – granular.

**Corallite structure:** Two features of corallite structure seem characteristic of many Triassic corals: (i) a pellicular fibrous wall, and (ii) great skeletal density.

(i) All simple and phaceloid corals have a pellicular, transversely folded wall. It is always thin, with centripetally growing fibres (p. 28, 43, 62). It is an independent element – sometimes strengthened by centripetally growing, secondary stereome (*Cyclophyllia*). This wall may appear or disappear temporarily, according to circumstances (e. g., when phaceloid coral pass into kuhnastreoid form, as observed in *Retiophyllia*).

In Jurassic corals pellicular walls of this type are substituted by a wall of dissepimental origin (Montlivaltiidae and Dermosmiliidae: RONIEWICZ 1976), or a cover of pennular origin (Microsolenidae: GILL 1967). In the Palaeozoic, an independent element, analogous (? homologous) to the Triassic wall, is common in Rugosa under the name of epitheca. A similar structure occurs in some Recent corals (BARNES 1972, SORAUF 1972).

(ii) Skeletal density: Almost all trabecular corals of the Triassic, not only the Rhaetian, have endotheca built of fine vesicles (except for Protoheterastraeina, Stylophyllina and Pachytheclina) regardless of septal structure and ornamentation. Therefore, a type of structure dominated in the Triassic, which involved much mineral material per cm<sup>3</sup> of skeleton volume. In this feature Triassic corals differ as well from Recent scleractinians and are similar to rugosans.

**Colony structure:** In the Rhaetian, the most common among massive corals are cerioid colonies (i) and among branched are phaceloid ones (ii).

A colony type is characteristic of a genus, and therefore, as a rule, colony types occur discretely. In some genera, however, cerioid colony may transform into phaceloid one or *vice versa*, e. g., *Distichomeandra* CUIF is cerioid but phaceloid colony stages may be found occasionally (p. 82); *Retiophyllia* CUIF is phaceloid but in some species corallites fuse locally into a kuhnastreoid form (resembling cerioid, p. 47); in *Kuhnastrea* CUIF, corallites transform temporarily into phaceloid form; in *Stylophyllum* REUSS – phaceloid colonies grade into cerioid ones. In novel conditions corallites may preserve their walls (*Stylophyllum*) or acquire a wall of a new type (in *Kuhnastrea* – the usually trabecular palisaded wall transforms into a pellicular wall, and conversely in *Retiophyllia*: the pellicular wall transforms into a palisaded wall).

(i) In cerioid colonies, the wall is single (trabecular palisaded, septal or septo-synaptic) or a bilaminar, non-trabecular, fibrous wall with a median fissure. In contrast with this, phaceloid colonies have homogeneous fibrous wall (see above). Corals with bilaminar walls in many cases represent a temporary cerioid colony, in others, however, it is a more permanent form.

In phaceloid-cerioid colonies the bilaminar, temporary wall is formed when two individuals which join and separate during growth, touch with their pellicular fibrous walls; a separating fissure is well expressed here (*Stylophyllum* REUSS, *Pinacophyllum* FRECH). When the individuals separate, the two layers function as independent walls.

In corals which seem to be permanently cerioid, for example *Kompsasteria* gen. n., *Coccophyllum* REUSS, or *Heterastraea* TOMES, the wall is non-trabecular and of a homogeneous fibrous structure; its distal edge is thin and sharp, tectiform. A fissure is very narrow and this suggests that it may be of a diagenetic origin, analogical to that of the median septal fissure in astraeomorphids, procyclolitids or distichophylliid corals.

The bilaminar wall is correlated with a septal apparatus composed of septal spines (*Coccophyllum*, *Heterastraea*) or with isolated trabeculae (*Kompsasteria*). Corals with a



non-trabecular, tectiform wall with a fissure are known from the Carnian (*Cerioheterastraea* CUIF) to the Liassic (*Heterastraea* TOMES).

In other cerioid and cerio-meandroid corals one finds two types of single wall: (1) septal or septo-synapticular (*Distichomeandra* CUIF, *Meandrostylis* FRECH) – a type characteristic, primarily, of post-Triassic time; (2) trabecular palisaded (*Gablonzeria* CUIF, *Kuhnastraea* CUIF), which is extremely rare in the post-Triassic time (Jurassic *Pseudodiplocoenia* ALLOITEAU – see RONIEWICZ 1970).

(ii) Phaceloid growth form: In the Triassic it is a common growth form. In the Upper Rhaetian at least seven phaceloid coral genera are known: *Retiophyllia* CUIF, *Margarosmilia* VOLZ, *Cyclophyllia* gen. n., *Stylophyllum* REUSS, *Stylophyllopsis* FRECH, *Pinacophyllum* FRECH; in the Norian-Rhaetian additionally – *Gillastraea* MELNIKOVA and *Morycastraea* MELNIKOVA; and in the Carnian-Norian, apart from *Margarosmilia*, *Pinacophyllum* and *Stylophyllopsis*, there are in addition *Volzeia* CUIF, *Craspedophyllia* VOLZ, *Omphalophyllia* LAUBE, *Tropidendron* CUIF, *Protoheterastraea* WELLS, *Myriophyllum* CUIF, *Araiophyllum* CUIF, *Pachysolenia* CUIF and *Quenstedtiphyllia* MELNIKOVA. In *Stylophyllum* and *Stylophyllopsis* it is an alternative growth form to the simple corallum. Out of more than sixty species from the Rhaetian of the Alps, which are described here, thirty are phaceloid species rarely alternatively phaceloid-cerioid. The Carnian fauna is similar in this respect. This proportion is, therefore, characteristic of the whole of the Upper Triassic fauna. Phaceloid corals of this period are not only very diversified taxonomically but constitute a frequent element of organic assemblages and perform an important rock-building function. This growth form was equally abundant in the Upper Jurassic but later it disappeared almost completely (RONIEWICZ 1976). In the dominance of the phaceloid form, Triassic corals resemble the Rugosa of the late Palaeozoic.

The popularity of this growth form in Mesozoic organisms believed to have lived in very shallow water is difficult to explain from the point of view of recent coral requirements. First of all, it is the kind of structure which does not allow an organism to gain full advantage of the colonial way of life. No integration of individuals can be found within this type which is a pseudocolony, a clone of isolated individuals originating from the same planula, connected only by skeleton (compare COATES & OLIVER 1974). Despite that, however, this specific growth form was a particularly popular adaptive type – it occurs in different families and arose through different modes of increase: equivalent division with lamellar or trabecular linkages, lateral increase, "Taschenknospung", parricidal buds (compare the mode of increase in Triassic corals presented by CUIF 1975 a, b as well as in this paper). The Jurassic phaceloid corals are described in many papers and their mode of increase characterized (KOBY 1881–1889, RONIEWICZ 1976, MELNIKOVA & RONIEWICZ 1976, ELIÁŠOVÁ 1973, 1974, 1975, 1976 a–c and others).

Undoubtedly, this growth form prevailed because of its connection with specific environment which extended over large areas in the Mesozoic seas, beginning in the Middle Triassic up to the Tithonian, and which also developed in the Palaeozoic, especially in the Devonian, Carboniferous and Permian. In Triassic rocks such corals (when observed in life position) are associated with fine grained sediments such as marls and biomierites and pelmierites. Among the grain components there are reworked and micritized clasts of psammitic fraction; the sediment is autochthonous – the micrite not transported away. At the time of deposition the sediment was an ooze, the bottom unstable with the degree of consolidation difficult to assess. In no way can such a

substrate be considered as suitable for coral settlement, from the point of view of Recent hermatypic corals. On the other hand, it is comparable to substrates populated by many ahermatypic corals.

Rhaetian phaceloid colonies often have (many species of *Retiophyllia*) peculiar transverse skeletal bridges connecting the branches, whose function is impossible to determine, though strengthening cannot be ruled out. In general, however, thin-branched phaceloid corals were not resistant to turbulent water.

**Simple versus colonial corals:** The Rhaetian fauna contains numerous simple corals. Among the discussed assemblages from Fischerwiese and Kesselwand-Rohrmoos they are fairly common and taxonomically diversified. The Fischerwiese fauna contains: *Procycolites* FRECH (one species), *Distichophyllia* CUIF (one or two species), *Gigantostylis* FRECH (one species), ? *Molukia* JAWORSKI (one species), *Stylophyllum* REUSS (one simple species), *Stylophyllopsis* FRECH (four simple species). In Kesselwand-Rohrmoos the spectrum is a little different (*Coryphyllia* CUIF is present), but the number of species with a simple growth form is similar.

In the collections examined the ratio between the species with simple growth form and the colonial ones is 1 : 8, and two of them may, alternatively, occur in a colonial or simple form (*Stylophyllopsis zitteli* FRECH, *S. rudis* EMMRICH).

*Stylophyllum* and *Stylophyllopsis* are the genera with an unstable status: some species are simple and some are colonial, or, alternatively, simple or colonial (phaceloid or cerioid with a fissure). It should be noted at the same time that these genera display a strong specific diversification with regional differences between the Alpine and Pamirian regions. In the Rhaetian they were at the stage of intense speciation.

The simple growth form was common among corals of various families. The simple corals which needed a calm environment found favourable conditions in the Rhaetian. Their occurrence in marls and micrite limestones together with colonial (mainly phaceloid) corals shows that the environmental requirements of both groups were at least partially overlapping. Simple and phaceloid corals, that is, such forms which must not have come from high-energy waters, amount almost fifty per cent of all Rhaetian species in Europe and Asia, and the same is true for the Norian corals.

The geological literature of the last twenty years abounds in papers on Triassic coral buildups (for review see FLÜGEL 1982). These papers contain the results of detailed studies on organic assemblages as well as some interpretations of sedimentation conditions and palaeoecological reconstructions. The interpretations seem to be greatly inspired by the studies of the Recent coral reefs and tend to emphasize similarities between the fossil and Recent coral faunas. However, such interpretations could be much enriched by a detailed analysis of the differences between the faunas discussed.

The above resemblance in structure and mode of occurrence (skeleton density, growth form, rock matrix) typical of the Upper Triassic Scleractinia and Palaeozoic Rugosa suggest that their habitats were alike. It has been admitted (WELLS 1954) that rugose corals and modern deep-water scleractinians resemble each other in their ecological requirements. The same may be assumed as regards Triassic corals and Recent ahermatypes and this analogy cannot be neglected when considering the palaeoenvironmental conditions of the formation of the Triassic coral buildups.

## 2. Relationships between Rhaetian and Carnian corals

The Rhaetian coral fauna differs from the Carnian fauna in its microstructural types. As far as microstructures are concerned the Carnian abounds in corals with thick and medium-sized isometric trabeculae ornamented with granules, as well as with medium-sized trabeculae ornamented with menianes. Corals of a typical distichophylliid or stylophyllid microstructures are scarce here. The Rhaetian fauna, on the other hand, contains only few protoheterastraeid corals, so diversified in the Carnian (CUIF 1975 a, 1976, MELNIKOVA 1984 b) and is devoid of such a typical Carnian fauna as: *Myriophyllum* CUIF, *Omphalophyllia* LAUBE, *Craspedophyllia* VOLZ, and corals of a zardino-phyllid-pachytheccaliid group (MONTANARO-GALLITELLI 1974 a, b, CUIF 1975 b). Therefore, in comparison with the Carnian, the Rhaetian has just the reverse proportion of the coral groups. This is the result of environmental changes and the expression of new ecological conditions that appeared and to which some coral groups adapted. It should be added here that no lesser changes must have occurred between the Carnian and the coral developmental phase of the Anisian-Ladinian. This is proved by the differences between the dominating colony types of these periods (compare VOLZ 1896 – Carnian fauna, and ECK 1879, 1880, WEISSERMEL 1925–1928, ASSMANN 1937, MORYCOWA 1988 – fauna of the Muschelkalk). The oldest coral faunas, at least in the European Middle Triassic, seem to be dominated by corals with cerioid and thamnasterioid colonies. Their microstructure is unknown so far. However, in Chinese literature concerning the Anisian many phaceloid forms have been mentioned (QI WENTONG 1984, DENG & KONG 1984).

## 3. Remarks on microstructural evolution and phylogeny of some scleractinian groups originating in the Triassic

The palaeontological record potentially allows microstructural changes of the coral skeleton to be traced through geological time, thus enabling the reconstruction of evolution of skeletal structures and phylogeny of coral groups.

So far we possess considerable knowledge on Triassic coral microstructures (CUIF 1965, 1966, 1967, 1968, 1973, 1975 a, b, c, 1976, 1977 a, b, MONTANARO-GALLITELLI 1974 a, b, 1976, MONTANARO-GALLITELLI *et al.* 1974) which contrasts with that concerning the microstructures of other fossil Scleractinia.

As far as Jurassic Scleractinia are concerned, the observations are fortuitous, due to the scarcity of well preserved skeletal material. Relatively complete information on skeletal structures is very rare (GILL 1967, 1968, 1970, GILL & LAFUSTE 1971, RONIEWICZ 1983). Most frequently original microstructures are traceable in vestiges in individual, rare groups (RONIEWICZ 1970, 1976). There are better prospects for the examination of Cretaceous microstructures (compare MORYCOWA 1964, 1971, 1981, M. BEAUVAIS 1982). The same is true for Tertiary corals the structure of which have been described in detail in few papers so far (GILL & RUSSO 1973, RUSSO 1974, 1976).

The main bulk of information on recent microstructures we owe to CHEVALIER (1971, 1974, 1975) who endeavoured if possible to examine the entire skeleton in his taxonomic studies. Other authors whose works concern the structure of particular skeletal parts or the formation and arrangement of structural details have much enriched our knowledge (for example WELLS 1969, SORAUF 1972, SORAUF & JELL 1977, SORAUF &

PODOFF 1977, JELL 1974, JELL & HILL 1974, GILL 1981) not to mention biologists examining the mechanisms of skeleton growth. But all this does not change the fact that our recognition of scleractinian microstructures remains incomplete and random. It would be premature therefore to attempt to present general tendencies in coral evolution on the basis of microstructural succession. Observations made so far may concern only selected coral phylogenetic stocks.

One of the few stocks whose history, though imperfectly known, can be traced from the Triassic to the Recent is the group of corals of distichophylliid microstructure. According to existing evidence their development began in the Carnian and entered its main phase in the Norian-Rhaetian, when distichophylliids developed on a large scale. This group seems to be the ancestral group of the Caryophylliina VAUGHAN et WELLS (RONIEWICZ 1984). The mechanisms of formation of large trabeculae displayed by the Triassic distichophylliid corals (fusing of fine trabeculae, or diameter enlargement together with the reduction of the number of trabeculae in the septum) show the fine-trabecular microstructural transformations which may have accompanied the possible appearance of new related groups. At present, the basic fine-trabecular distichophylliid microstructure is continued only in the suborder Caryophylliina (*op. cit.*).

Meniane-bearing corals with fine- and medium-sized trabeculae did not survive the Triassic, if one may judge from the data available so far. The individualization of trabeculae within a homogeneous mid-septal zone and groupings of fine trabeculae into compound trabeculae (Astraeomorphidae) may illustrate how coral structures transformed into thick-trabecular pennular structures which developed in the Middle Jurassic and survive up to the Late Cretaceous (Microsolenidae, Latomeandridae, Thamnasteriidae and others) or even to the Eocene (GILL & RUSSO 1980).

When comparing the thin-trabecular microstructures of Triassic corals with the thick-trabecular microstructures of the Recent ones, one feature may be observed in both: the fusing of small trabeculae or their individualization within a mid-zone mentioned above. The compound trabeculae of Faviidae (CHEVALIER 1971, text-fig. 73) resemble the large trabeculae of Triassic distichophylliid corals and protoheterastraeids. Trabeculae with different diameters coexist frequently in the same septum in faviids (*op. cit.*). Individualization of trabeculae within the homogeneous septal median zone observed in Galaxeinae or Caryophylliinae (CHEVALIER 1971, text-fig. 11; 1975, text-fig. 46) resembles a similar phenomenon in Procycolitoidea. This mechanism, therefore, may be considered important in the formation of thick-trabecular microstructures.

Thick-trabecular corals were relatively diversified in the Triassic, though the development of this heterogeneous group was most intensive in later geological periods. The Pamiroseriidae – common Rhaetian corals – have all the features of Astraeoina. The family is well represented beginning with the Anisian (MORYCOWA 1988).

Stylophyllidae developed from the Anisian to the Lias. The group seems to be highly homogeneous in its microstructural pattern lacking true trabeculae (CUIF 1977 and herein). Due to the general scarcity of data on microstructure it is hardly possible to decide which of the known coral groups may be regarded as related to them. The only fossil corals having microstructural elements similar to the long and thin fibre bundles of Stylophyllidae are, primarily, distichophylliid corals, and then rhipidogyrids which developed in the Jurassic and Cretaceous (compare BEAUVAIS L. & M. 1975, RONIEWICZ 1976). Among recent corals some structural analogies are exhibited by the Mussidae, which have septa composed of very thin and long trabeculae grouped in larger units. This, however, does not necessarily prove the stylophyllid-mussid

relationship. There is a group in the Jurassic, the family Epismiliidae, which resembles stylophyllids in its skeletal features. Among other things, large lobes of distal septal edge and fine granulation distinctive for this group are similar to those of large *Stylophyllopsis* (compare BEAUVAIS 1976, text-figs. 3, 4, 7–11 and 31–32). Epismiliid microstructure is not known owing to recrystallization of the skeleton but the above mentioned external features point out to the stylophyllid microstructure.

Archaeocoeniina, represented by the family Actinastraeidae, appeared as early as in the Anisian. The following set of actinastraeid characters may be traced throughout the whole Mesozoic: peculiar septal arrangement, relatively large trabeculae and very small corallite diameters. These corals have never been important faunal components with the exception of the Early Cretaceous. The history and relationships of Archaeocoeniina are especially hardly traceable due to scarcity of data caused by recrystallization destroying fine skeletons in these small-corallite corals. For this reason they remain among the least known coral groups.

Outside the main trend of the Triassic, the Carnian-Norian corals developed of the well-defined pachythecaliid and protoheterastraeid groups (CUIF 1973, 1975 b, 1977 a, b, MONTANARO-GALLITELLI 1974 a, b, 1976, MELNIKOVA 1984). Transformation of septal fibres organization from apparently non-trabecular in zardinophyllids-pachythecaliids to trabecular in cyclophylliids, gablonzeriids and protoheterastraeids, exemplifies the same trend to trabeculization as that observed in other groups. This tendency is here correlated with gradual diminishing of the role of the fibrous wall (compare CUIF 1977 b). The first of them developed later as amphiastraeids and became important in the shallow-water coral assemblages as late as the Late Jurassic, especially at the turn of the period, and practically disappeared in the Lower Cretaceous (see ELIÁŠOVÁ 1975, 1978, MELNIKOVA & RONEWICZ 1976). Their microstructure and corallite architecture differ from the remaining Scleractinia to such a degree that MONTANARO-GALLITELLI (1976) decided to place the group in a separate order, Hexantiniaria, within the Zoantharia.

## REMARKS ON SYSTEMATICS

Scleractinian groups which follow one another in the stratigraphical column are morphologically similar. The following characteristics of the skeleton may be repeated from group to group: colony shape (massive, branched, lamellate), colony type (plocoid, astreoid, phaceloid, thamnasterioid, cerioid, etc.), corallite architecture (shape of radial elements, organization of endotheca, type of columella, etc.), type of budding (place of budding, kind of linkages). Skeletal microstructure, on the contrary, is a unique feature specific to each coral group.

In the late sixties it became apparent that Scleractinia examined microstructurally could not be classified according to the systematics based on the criteria other than those of microstructure. GILL (1967, 1977) and GILL & LAFUSTE (1971) discussing some Jurassic scleractinians have shown that these corals should be reclassified considering the specificity of their microstructure and ornamentation. The examination of some Tertiary corals (GILL & RUSSO 1973, 1980, RUSSO 1974, 1976) has proved that some of the Mesozoic patterns of the septal structure persist in the modern scleractinian faunas. The septal structures discriminated by these authors allow some structural groups to be recognized among Jurassic and Recent corals, namely the pennular corals (Pennulacae:

GILL 1967) and the montivaltioid-type corals (Montivaltioidea ALLOITEAU 1952 emend. GILL & LAFUSTE 1971); the corals provided with auriculae (GILL 1977), though probably representing a distinct group of Mesozoic corals, still cannot be taxonomically evaluated.

The microstructural criteria for the classification of the Triassic corals were first used in the second half of the seventies. MONTANARO-GALLITELLI (1975) was first to break with the traditional way of classification. She decided to form within Anthozoa a new order, Hexantiniaria, for the family of non-trabecular corals, thus stressing their unique skeleton structure which makes it difficult to place them in any of the existing suborders of the Scleractinia. It is worth of mention that recently thin trabeculae were noticed in this group of corals (ILJINA 1984).

A general outline of the classification of the Triassic Scleractinia has been given by CUIF (1977 b). He claimed that the existing systematic frameworks (VAUGHAN & WELLS 1943, ALLOITEAU 1952, WELLS 1956) cannot be applied to these corals and presented a general outline of the classification on the basis of microstructure of septa and ornamentation. He divided the Triassic corals into microstructural groups and subgroups arranged according to the increasing complication in the organization of the septal skeleton and diminishing role of the wall, and gave the larger groups the rank of families. They are:

A. Non-trabecular corals:

- Pachythecaliidae CUIF<sup>1</sup> — a group in which the development of the wall is prior to the development of septa; the wall is built of fibres growing centripetally; CUIF regards the septa as composed of fibres not organized into trabeculae.
- Stylophyllidae VOLZ (the correct authorship is: FRECH, 1890, see p. 116) — all the skeleton is fibrous; although it forms the wall as well as horizontal and vertical elements (septal spines), the fibrous skeleton is not differentiated microstructurally, and the individual architectural elements are in perfect continuity with each other. CUIF regards these corals as opposing to all other groups due to the regression of the septa.
- Distichophylliidae CUIF<sup>2</sup> — the septum has a trilaminar structure: it consists of left and right lateral layers separated by wavy middle zone which, according to CUIF, is homogeneous in structure (see Discussion p. 36). The side-layers are composed of fascicles of fibres evolving into rudimentary trabeculae with axes perpendicular to the mid-septal plane, or temporarily vertical and bending side-ways; the wall is an evolutionary novelty: it is not an independent element, but a septotheca.

B. Corals of trabecular structure<sup>3</sup> — a heterogeneous group consisting of all remaining corals with trabecular septa, including many independent developmental stocks.

Unfortunately, due to the fact that, generally, the skeletal microstructure of Recent and fossil corals is known only exceptionally, CUIF was not able to link these groups with other Scleractinia.

BEAUVAIS' attempt at the systematics of Mesozoic corals (1981) is a compilation of CUIF's systematic proposals (1977 b) and ALLOITEAU's system (1952), as well as some elements of other authors (MONTANARO-GALLITELLI 1975, ELIÁŠOVÁ 1978) and

<sup>1</sup> Notes on nomenclature, p. 24: Familia Pachythecaliidae.

<sup>2</sup> *Ibidem*: Familia Distichophylliidae.

<sup>3</sup> *Ibidem*: Trabecular corals.

her own proposals. The part which follows CUIF's ideas (pachythecaliid, distichophylliid and stylophyllid corals) is based on strictly microstructural criteria set by CUIF. The remaining part applies criteria that are not very clearly established and this makes the system more difficult to use. She distinguished the following suborders: Stylophyllina BEAUVAIS, 1981; Pachythecaliina ELIÁŠOVÁ, 1978; Distichophylliina BEAUVAIS, 1981; Archaeofungiina ALLOITEAU, 1952 (the correct authorship is: BEAUVAIS, 1981) and Archaeocoeniina ALLOITEAU, 1952.

Recently MELNIKOVA (1984 a, b) has been working on a classification of Triassic corals on the basis of her own studies of the materials with rather poorly preserved microstructure. She includes (1984 a) trabecular corals in the order Archaeocoeniida with two suborders: Archaeocoeniina ALLOITEAU, 1952 and Cuifastraeina MELNIKOVA, 1984. The latter comprises six families of trabecular Triassic corals having pennular ornamentation in different stages of development. In the order Hexantiniaria she (1984 b) distinguishes three suborders: Pachythecaliina ELIÁŠOVÁ, 1978, Protoheterastraeina MELNIKOVA, 1984 and Distichophylliina BEAUVAIS, 1981. While the protoheterastraeid and pachythecaliid corals are in some way related microstructurally (compare CUIF, 1977), such an assignment of the distichophylliid corals is difficult to corroborate.

In the present paper I accept criteria of the CUIF classification and a great deal of his systematic proposals. However, I interpret the skeletal structure of a distichophylliid type in a different way (as well as in the related coral groups – p. 36) and I supplement the interpretation of Stylophyllidae microstructure (p. 117). All this results in some systematic consequences which are discussed in the chapters concerning these groups.

I have classified some of the families determined here using ALLOITEAU's systematics (1952, 1957) as they refer to the microstructure. Other families have found their places in new suborders erected recently by ELIÁŠOVÁ (1978) or BEAUVAIS (1981).

The corals examined have been assigned to eleven families and six suborders according to their morphology and microstructure. A relatively credible relationship with other corals can be discerned in the cases of: the Pamiroseriidae – a position near to the family Faviidae, suborder Astraeoinea; an isolated genus *Chondrocoenia* nov. – family Actinastraeidae, suborder Archaeocoeniina; Reimaniphylliidae (= Distichophylliidae of CUIF) – position close to the family Caryophylliidae, suborder Caryophylliina. As regards the corals from the superfamily Procycololitoidea, it is not at all easy to recognize related groups, or to decide upon their position in one of the existing suborders. Because of analogies to the Microsolenidae I have decided to include the Procycololitoidea in the Fungiina, *faute de mieux*. However, microstructural similarities to distichophylliids may be proof of some phylogenetic affinities between those groups.

Stylophyllid corals have been assigned to the suborder Stylophyllina BEAUVAIS, 1981, a group of uncertain affinity. New families Cyclophylliidae and Gablonzeriidae have been considered as representatives of the suborder Pachythecaliina ELIÁŠOVÁ, the group believed to be limited to the Mesozoic.

The criteria for systematic discrimination adopted are:

- Suborder: Skeletal microstructure. Characteristics of septal apparatus. General type of increase (= budding).
- Family: Ornamentation of radial elements corresponding with microstructure. Skeleton architecture (presence of specific parts of the skeleton, organization of endotheca and peritheca). Mode of increase.

Genus: Mode of growth – simple or/and colonial; colony type; detailed pattern of colony increase. Wall structure. Characteristics of radial elements (costosepta – septa, details of ornamentation, etc.). Type of columella.

#### Notes on nomenclature:

For groups of genera CUIF (1977 b) indicated the type genera, defined their range and gave their microstructural diagnoses. From the point of view of ICZN (Art. 32 c) these are family-group taxa with incorrect original spelling. According to Art. 32 d I introduce the following corrections:

#### Familia Pachythecaliidae CUIF, 1975:

- 'groupe *Pachythecalis*': I change into subfamily Pachythecaliinae CUIF, 1977
- 'groupe *Protoheterastraea*': subfamily Protoheterastraeinae CUIF, 1977 (*non* BEAUVAIS, 1981)
- 'groupe *Volzeia*': subfamily Volzeiinae CUIF, 1977 (*non* BEAUVAIS, 1981)

#### Familia Distichophylliidae CUIF, 1977:

- 'groupe *Distichophyllia*': subfamily Distichophylliinae CUIF, 1977
- 'groupe *Retiophyllia*': subfamily Retiophylliinae CUIF, 1977
- 'groupe *Margarophyllia*': subfamily Margarophylliinae CUIF 1977 (*non* BEAUVAIS, 1981)
- 'groupe *Craspedophyllia-Procyclolites*': subfamily Craspedophylliinae CUIF, 1977 (*non* BEAUVAIS, 1981)

#### Trabecular corals:

- 'groupe *Conophyllia-Omphalophyllia*': corresponds to the family Conophylliidae ALLOITEAU, 1952
- 'groupe *Tropiastraea*': I change into family Tropiastraeidae CUIF, 1977 (*non* MELNIKOVA, 1984)
- 'groupe *Guembelastraea-Stuoresia-Gablonzeria*': family Guembelastraeidae CUIF, 1977 (*non* MELNIKOVA, 1984)



## DESCRIPTIONS

Ordo Scleractinia Bourne, 1900

Subordo Pachythecaliina ELIÁŠOVÁ, 1976

**Emended diagnosis:** Wall fibrous, developed prior to the septa. Septa fibrous, provided with straight median line, or trabecular. Colony increase of variable intracalicular (marginal, together with its extreme form – Taschenknospung; symmetrical corallite division by a dividing wall of septal origin) or extracalicular (lateral) types.

The group contains two sub-groups which have been distinguished at the familial or subfamilial level (CUIF 1975 b, 1977 b) and are transferred here to the super-familial category:

Superfamilia Pachythecaloidea CUIF, 1975: wall formed primarily of fibrous, centered, radially arranged units; septal microstructure fibrous or trabecular. Families: Triassic – Pachythecaliidae CUIF, 1975, Zardinophyllidae MONTANARO-GALLITELLI 1975; Jurassic – Amphiastraed groups.

Superfamilia Volzeioidea CUIF, 1977: wall formed of simple fibres of radial orientation, or of trabeculae. Radial elements of costoseptal or septal character, built of fibres disposed perpendicularly to the medioseptal plane, or a row of trabeculae. Families: Protoheterastraedidae CUIF, 1977<sup>4</sup>, Volzeiidae CUIF, 1977<sup>5</sup>, Cyclophylliidae fam. n. and Gablonzeriidae fam. n.

**Discussion:** The most striking features of the Pachythecaliina are: its microstructure transitional between fibrous and trabecular, and variable modes of budding resulting in peculiar types of corallite increase, among them septal division (bicentric or polycentric: Volzeioidea) and Taschenknospung (amphiastraeds), being rarely (the former) or never (the latter) observed in other corals.

Protoheterastraed septal structure has been interpreted by CUIF (1973, 1977 b) as non-trabecular, built of elongated elements shorter than trabeculae, and as trabecular by MELNIKOVA (1984 b). At any rate, an ability to form well centered microstructural elements in septa (true trabeculae or trabecula-like elements) in the protoheterastraed group speaks for its consideration as a model group showing all transitions, in microstructural and architectural features, leading from thick-walled, oligoseptate pachythecaliids to thin-walled, polyseptate and trabecular volzeioid corals, viz., cyclophylliids or gablonzeriids.

<sup>4</sup> Notes on nomenclature, p. 24: 'groupe *Protoheterastraea*' CUIF, 1977. Originally, protoheterastraed corals have been assigned into Pachythecaliidae CUIF, 1975.

<sup>5</sup> *Ibidem*: 'groupe *Volzeia*' CUIF, 1977.

Superfamilia Volzeioidea CUIF, 1977  
Familia Cyclophylliidae nov.

Genus typicus: *Cyclophyllia* nov.

Diagnosis: Septa built of a row of medium-sized trabeculae strongly inclined towards the axis; costae lacking; the internal septal edges in higher order septa separate into discrete trabeculae; the shortest septa are developed as rows of isolated trabeculae; septal lateral ornamentation in the form of coarse granules. Endotheca subtabular or large-vesicular. Budding intracalicular, chiefly marginal, producing inequable individuals. Wall fibrous.

Genera included: *Cyclophyllia* gen. n., *Kompsasteria* gen. n.

Discussion: General features allow *Cyclophyllia* and *Kompsasteria* to be placed close to the Volzeiidae or Protoheterastraeidae, but their unique combinations of features do not allow assignment to either family:

Spiniform ornamentation of septa, simple fibrous wall, corallite architecture and the mode of increase of cyclophylliids resemble those characteristics of the genus *Volzeia* CUIF, 1967 (compare CUIF 1975 a). However, perfect trabecular microstructure and the tendency for the septa to disintegrate differentiate cyclophylliids from that genus. When compared with *Protoheterastraea* (see CUIF 1973, text-fig. 26), cyclophylliids reveal the same trabecular dimensions and corallite architecture, differing at the same time in their type of wall built of simple fibres, septal blades discontinuous at the internal edges, as well as marginal budding dominating other possible types of increase.

Genus *Cyclophyllia* nov.

Species typica: *Thecosmilia cyclica* SCHÄFER et SENOWBARI-DARYAN, 1978.

Derivatio nominis: Greek *kyklos* – ring, from the dissepiments arranged in rings, and *phyllon* – leaf, a conventional ending of the names of corals; *femin.*

Diagnosis: Colony phaceloid. Budding marginal. Costae lacking. Septal faces ornamented with sharp granulation. Internal septal edges dissociated into thin trabecular projections. Dissepiments vesicular, large, crossing the lumen. Wall fibrous, thickened by peripheral stereozone. Microstructure small-trabecular to large-trabecular.

Species included: *Cyclophyllia cyclica* (SCHÄFER et SENOWBARI-DARYAN, 1978), *Cyclophyllia major* sp. n.

Stratigraphic and geographic ranges: Rhaetian of the Alpine region.

Discussion: Septal microstructure in *Cyclophyllia* resembles that of distichophylliids in its small-dimensional trabeculae marking slightly wavy mid-septal line. This microstructure, however, differs from that of distichophylliids in the lack of lateral septal zones built of densely packed lateral trabeculae or centered fascicles of fibres (p. 28). In *Cyclophyllia*, the thickening of septa proceeds by simple lateral thickening of trabeculae. In this way, peripherally, quite large-dimensional trabeculae may develop.

Externally *Cyclophyllia* gen. n. resembles not only *Volzeia* and *Protoheterastraea* (see above) but also *Retiophyllia* CUIF, 1967 differing from it in the following features: a lack of connecting processes, marginal budding producing inequivalent individuals, and such internal corallite features as: uniform endotheca composed of large dissepiments and septa provided with internal edge dissociated into trabeculae.

Corals of four genera: Triassic *Cyclophyllia* gen. n. and Jurassic *Helladophyllia* ALLOITEAU et DERCOURT, 1966, *Intersmilia* ELIÁŠOVÁ, 1974 and *Donacosmilia* DE FROMENTEL, 1861 show a similar pattern of corallite architecture in cross sections. Unfortunately, at present it is not clear which of them are structurally identical and synonymous, or at least closely related, and which are only superficially similar, homeomorphic. It is worth of mention here that the stratigraphy of beds with *Helladophyllia* is rather doubtful, as all corals contained (*Fasciseris*, ? *Procyclolites*) seem to be Upper Triassic in character.

Among mentioned genera, *Cyclophyllia* has many common features especially with *Helladophyllia*: septal arrangement and ornamentation, endotheca and mode of increase (compare ALLOITEAU & DERCOURT 1966, 306, Pl. 3, fig. 2). However, in *Cyclophyllia* external *Calamophylliopsis*-like "collerettes" are absent and no costae are developed, both features being enumerated in the generic diagnosis of *Helladophyllia*.

*Cyclophyllia cyclica* (SCHÄFER et SENOWBARI-DARYAN, 1978)

Pl. 1, figs. 1, 4–6, Pl. 2, fig. 1

- part. 1978 *Thecosmilia cyclica* – SCHÄFER et SENOWBARI-DARYAN, p. 125, Pl. 3, figs. 4 a, b, 5 (non Pl. 2, fig. 3, nec text-figs. 4, 5)  
 1979 *Thecosmilia cyclica* SCHÄFER et SENOWBARI-DARYAN – SCHÄFER, p. 44, Pl. 9, fig. 1  
 1980 "*Thecosmilia*" *cyclica* SCHÄFER et SENOWBARI-DARYAN – SENOWBARI-DARYAN, p. 34, Pl. 1, fig. 3  
 non 1982 "*Thecosmilia*" *cyclica* SCHÄFER et SENOWBARI-DARYAN – WURM, p. 218, Pl. 34, fig. 3  
 1984 "*Thecosmilia*" *cyclica* SCHÄFER et SENOWBARI-DARYAN – SCHÄFER, Pl. 1, fig. 2

Holotypus: SMP 30751 (o/54); SCHÄFER et SENOWBARI-DARYAN 1978, Pl. 3, fig. 4

Locus typicus: Röteland Reef

Stratum typicum: Upper Rhaetian

Material: Eight isolated corallites and seven colony fragments from Fischerwiese GBA 1982/12/146–152, 797, 798, NHMW 1982/57/14–16, 23, 53, 54. Generally, strongly recrystallized with the exception of the specimens NHMW 1982/57/15, 16, 54

Dimensions (in mm):

Specimen No.	d	s	s/5 mm
NHMW 1982/57/14	9	est. 60 (11 + 11 + 22 + est. 16)	
	9	42 (9 + 9 + 18 + 6)	
SMF 30751/o/54 (holotype)	8	57 (13 + 13 + 26 + 1)	
	10	71 (14 + 14 + 28 + 15)	11–13
	10	62 (12 + 12 + 24 + 14)	
	11	61 (11 + 11 + 22 + 17)	

Description: Colony phaceloid, corallites cylindrical, smooth. Budding marginal, producing corallites of very narrow diameters. The organization of the parental corallite seems to be undisturbed by the formation of new corallites.

Calices deep, with thin, sharp edges; corallite dimensions strongly variable within the colony due to the size difference between juveniles and adults (Pl. 1, figs. 1 a, b).

Radial elements non-exert, wedge-like. Septal apparatus differentiated into 4 orders, S1–S3 septa regularly distributed. The S1 septa reach nearly the radius in length, usually leaving a narrow axial cavity free, S3 septa thinner and shorter than S1; the length of S3 ranges between 1/3 and more than half the length of S1 within the same corallite. The S4 septa are very thin and short, variable in number; for example in 3 corallites examined there are 1–16 S4 at diameters of 8.5–9 mm. Lateral septal granules rare and sharply pointed. Inner septal edges dissociated into thin and short trabecular projections that may be visible in longitudinal and slightly oblique transverse sections (Pl. 1, figs. 4, 6).

Endotheca formed by large vesicles steeply inclined at the periphery and crossing the lumen, and deeply concave at the axis (Pl. 1, fig. 6).

Wall structure complex, composed of (i) primary, fibrous wall, (ii) septa and (iii) interseptal, peripheral stereome (Pl. 2, figs. 1 a, c, d).

Microstructure (Pl. 2, figs. 1 a–d): Septal microstructure has been observed in two corallites (NHMW 1982/57/54). Trabecular septal tissue is variably developed, resembling in this respect some *Retiophyllia*. In some septa, or in some septal portions seen in transverse sections, the fibres are subparallel, slightly convergent to the axes of small trabeculae (20–30 µm in diameter). In others, they are arranged into large trabeculae (60–90 µm/diameter). The mid-zone is straight, wavy, or even zigzag. Small trabeculae follow each other in a single row or alternate and decline from the mid-line. In longitudinal radial section, the course of trabeculae is clearly visible and their diameters distinguishable. Peripherally, trabeculae are subvertical. Thus, wedge-like radial elements seem to represent simple septa or costo-septa with extremely reduced costal portion. At the rest of the blade the trabeculae are usually subhorizontal with the exception of the adaxial trabeculae of S1 and S2 septa which may be directed subvertically.

The primary wall is thin and formed of fasciculated fibres growing centripetally, and with peripheral septal edges embedded. Secondly, it is thickened by stereome. The wall stereome is formed by fascicles of fibres founded either directly on the internal thecal surface, and growing epitaxially with wall fibres, or on septa.

Discussion: Diameters of specimens from Röteland and Feichtenstein Reefs, in original description, are between 7 and 13 mm, usually, 9–12, number of septa is 49–90 (SCHÄFER & SENOWBARI-DARYAN 1978). Corallites examined here are of the same diameter range as those of the holotype colony (see Dimensions). A variability of this parameter among the specimens described from the Feichtenstein and Gruber Reefs by SENOWBARI-DARYAN (1980) is far larger (up to 16 mm) whilst a variability of number of septa is narrower (26–60). The morphotype of larger corallites represents *C. major* sp. n.

Budding has not been observed in the sections examined. A good example of marginal budding in *C. cyclica*, with a characteristic isolation of small daughter from far larger parent individual, was presented by WURM (1982, Pl. 34, fig. 3). One of FRECH's specimens of *Thecosmilia defilippi* (1890, Pl. 4, fig. 15 b) shows budding that more closely resembles *Cyclophyllia*-like increase than the bifurcation of *Retiophyllia* giving equivalent individuals.

Distribution: Rhaetian of the Northern Calcareous Alps; known in the Zlam-bach Beds at Kesselwand-Rohrmoos and Fischerwiese, and in the Rhaetian of the Röteland, Feichtenstein and Gruber Reefs near Salzburg.

*Cyclophyllia major* sp. n.

Pl. 1, figs. 2, 3

part., v. 1890 *Thecosmilia caespitosa* REUSS – FRECH, Pl. 1, fig. 13 (non Pl. 1, figs. 1–12)

part. 1978 *Thecosmilia cyclica* – SCHÄFER & SENOWBARI-DARYAN, Pl. 2, fig. 3, text-figs. 4, 5 (non Pl. 3, figs. 4 a, b)

1980 *Thecosmilia cyclica* SCHÄFER et SENOWBARI-DARYAN – SENOWBARI-DARYAN, p. 34, Pl. 1, fig. 3

Holotypus: NHMW 1982/56/26<sub>2</sub>; Pl. 1, figs. 3 a–c

Locus typicus: Schneckengraben

Stratum typicum: Zlambach Beds

Derivatio nominis: Latin *major* – larger, from the corallites larger than in *C. cyclica* SCHÄFER et SENOWBARI-DARYAN, 1978.

Diagnosis: *Cyclophyllia* of mean diameter of adult corallites between 12 and 18 mm and number of septa ranging from 40 to 60.

Material: Two colonies from Gosaukamm region: NHMW 1982/56/26<sub>3</sub> from Schneckengraben (holotype) with well preserved skeleton and NHMW 1982/56/26<sub>1</sub> from Kesselwand-Rohrmoos with calices preserved and skeleton entirely recrystallized; three thin sections

## Dimensions (in mm):

Specimen No.	d	s	s/5 mm
NHMW 1982/56/26 <sub>2</sub>	11 × 15	72 (12 + 12 + 24 + 26)	10–11
	12 × 15	69 (13 + 13 + 26 + 17)	
NHMW 1982/56/26 <sub>1</sub>	8 × 14		
	11 × 16		
	17 × 19		
SMF 3075 a/o/58			
adults	14 × 15	62	8–12
	15 × 17	ca. 74	

Description: Colony phaceloid, dense (Pl. 1, figs. 2, 3). Budding marginal, producing single corallites strongly differing in diameters from parent corallite. Corallites cylindrical. Calices deep, edges thin, sharp, septa non-exsert.

Corallite surface transversely wrinkled. Septa thin, differentiated into four size orders. S1 and S2 septa subequal, S1 approaching the axis. S3 septa more than one-third the length of S1, regularly distributed. S4 septa abundant, but rarely more than three septa per system. Adaxial septal portion straight or zigzag in shape. Septal faces with sharply pointed, large granules. Internal edges provided with thin trabecular projections (Pl. 1, fig. 2 b).

Endotheca abundant, formed by large dissepiments obliquely disposed at the periphery of the calice and concave at the axial cavity. Wall relatively thin.

Microstructure as in type species.

Discussion: The new species resembling the type species in septal differentiation and arrangement differs from it in having far larger corallites and smaller septal density. FRECH's specimen from Hallstätter Salzberg figured as *Thecosmilia caespitosa* (1890, Pl. 1, fig. 13), exhibits features of the species considered: calices sharply rimmed,

septa straight, budding producing inequivalent individuals, colony dense with corallites up to  $11 \times 15$  mm in diameter.

Direct comparison with the material from Feichtenstein Reef (kindly sent to me by Dr. BABA SENOWBARI-DARYAN) proved that a large-corallite morphotype of *C. cyclica* known in the Gruber and Feichtenstein Reefs is conspecific with the here described species.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Schneckengraben and Kesselwand-Rohrmoos in the Gosaukamm region, Hallstätter Salzberg; Rhaetian limestones of the Gruber and Feichtenstein Reefs near Salzburg.

### Genus *Kompsasteria* nov.

Species typica: *Isastraea oligocystis* FRECH, 1890

Derivatio nominis: Greek *kompsos* – delicate, and *aster* – star; *femin.*

Diagnosis: Cerioid; wall bilaminar, fibrous. Septal trabeculae nearly normal to the wall. The smallest septa are developed as septal spines, in other septa only internal edge dissociated into trabeculae. Ornamentation granular. Granules short, pointed. Endotheca constituted of rare, subhorizontal elements. Budding intracalicular, marginal.

Species included: The genus is monotypic.

Stratigraphic and geographic ranges: As for the type species.

Discussion: Due to the architecture and microstructure of its corallites the new genus is assigned to the family Cyclophylliidae. With its colony type (cerioid; double wall with a fissure) and general pattern of corallite morphology, the genus has a counterpart in *Cerioheterastraea* CUIF, 1976. They differ from each other, above all in septal microstructure and type of budding (in the latter genus the microstructure is of imperfect trabecular type with an intermediate zone close to the wall, and calices divided by the wall founded on septa).

### *Kompsasteria oligocystis* (FRECH, 1890)

Pl. 2, figs. 2, 3, Pl. 3, figs. 1–5

1890 *Isastraea oligocystis* – FRECH, p. 24, Pl. 5, figs. 8, 8 A, 8 b, 8 B

Holotypus: BSP AS XII 17; figured by FRECH 1890, Pl. 5, figs. 8–8 B

Locus typicus: Hammerkogel, Gosaukamm

Stratum typicum: Zlambach Beds

Material: Six specimens from the Gosaukamm region: NHMW 1959/361/45 and 1982/56/4, from Schneckengraben, NHMW 1903 XII 86 from Riedelkar, NHMW 1982/56/4,–4, from Kesselwand-Rohrmoos; fifteen thin sections. The species is also represented in the NHMW collections by other specimens from the same region.

### Dimensions:

Specimen No.	d	s	s/3 mm
NHMW 1959/361/45	7	41	7–8
	$6.5 \times 9$	46	
	6	38 (10 + 10 + 18)	
	$5 \times 6.5$	42 (11 + 10 + 18 + 3)	
	$6.5 \times 8$	51 (12 + 13 + 25 + 1)	

Description: Colony lamellate with lower surface costulate and upper surface covered with polygonal shallow calices (Pl. 3, figs. 1 e, 2–5). Calicular edges very sharp,

thin. Septa thin, differentiated into regularly distributed septa of 3 size orders and rare S4. The S1 septa of 300  $\mu\text{m}$  at the base, tapering to 50  $\mu\text{m}$  at the axis, penetrate the axial cavity where some of them can fuse with their internal edges, especially those from the opposite sides. The S2 septa, usually about 60  $\mu\text{m}$  in thickness, vary in length but are always shorter than S1 septa. The S3 septa, regularly distributed between the former, vary in length from very short up to half the radius or slightly more. The S4 septa are developed as rows of short septal spines (5–6 per 500  $\mu\text{m}$  in longitudinal section). The details of the distal septal ornamentation have been obliterated. The very edge of S1–S3 septa is disintegrated into free trabeculae. The septal faces are ornamented with short, sharply pointed granules, relatively large at their base.

The endotheca is poor. It consists of thin-walled, large, horizontal, tabuloid elements 1.5–1.8 mm high (Pl. 3, fig. 1 b).

The wall is between 200  $\mu\text{m}$  and 1 mm thick, provided with a straight or strongly wavy intramural line or a narrow fissure, usually filled with a transparent calcite. Weathered specimens easily separate from each other along the intramural fissure and show internal, intramural surfaces which display delicate growth lines (Pl. 3, fig. 3). The intramural surfaces resemble the internal septal surfaces of distichophylliids in appearance (ex. *Retiphyllia* and *Coryphyllia* in CUIF 1975 a, text-figs. 33 a, 37 c, d). The intramural fissure is interpreted here as an artefact produced by differential leaching of skeleton analogical to that observed in distichophylliid septa.

Budding intracalicular marginal resembling amphiastreaeid "Taschenknospung" and producing small corallites from the beginning separated from the parent corallite. At the corner of the parent, the wall splits and rapidly a new individual enlarges, originally growing on the expense of the parental calicular space. Initially, the peripheral portion of parental septal apparatus constitutes the septa of a new individual. Its own septa arise from the wall separating it from the parent (Pl. 3, fig. 4).

Microstructure: The septa are trabecular, the wall is fibrous and both seem to be in a structural continuation of each other. The septa initiate in the wall tissue with large bases which narrow abruptly and continue into septal blades. The wall fibres grow centripetally (Pl. 2, figs. 2, 3, Pl. 3, fig. 1 a). In cross section one can see very oblique sections of trabeculae, at most 3–5 per septum. In longitudinal section normal to the septal blade the trabecular structure is much more visible. Trabeculae are isometric, the largest of them are 120–150  $\mu\text{m}$  in diameter (Pl. 3, figs. 1 c, 1 d, 3). Trabeculae sometimes emerge on the septal surface in form of longitudinal thickenings. No traces of axial organization have been observed in lateral granules.

Remarks: The species is remarkable for its morphology and microstructure. The microstructure needs further examination with respect to, e. g., relations between the septa and the wall and the structure of the septal granules.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Schneckengraben and Kesselwand-Rohrmoos.

#### Familia Gablonzeriidae nov.

Genus typicus: *Gablonzeria* CUIF, 1976

Diagnosis: Trabeculae well defined, ranging from small to medium sized. Ornamentation in the form of strongly protruding granules varying in shape from spines

to thin blades. Endotheca vesicular. Colony increase through subequal division of calices into 2 or more individuals; dividing wall trabecular, originating from septa.

The family comprises one genus only, *Gablonzeria* CUIF, 1976.

**Discussion:** The family has been included in the suborder Pachythecaliina, superfamily Volzeioidea, due to such combination of features as: medium-sized trabeculae, prominent granulation, relatively large dissepiments and corallite increase by division. In gablonzeriids, as in cyclophylliids, radial elements are septal in character and are formed of a single series of trabeculae vertical at the wall and strongly inclined adaxially. The wall, which develops from the septa dividing the parental corallite, is formed of a single row of vertical trabeculae. The latter feature differentiates essentially gablonzeriids from other groups included in the superfamily.

#### Genus *Gablonzeria* CUIF, 1976

**Species typica:** *Isastraea profunda major* FRECH, 1890

**Diagnosis** (after CUIF 1976, 118): Colonies cerioid. Septa compact, formed of perfect trabeculae in monolinear series. The trabeculae, vertical at the periphery, becoming progressively inclined adaxially toward the axis of the corallite. Lateral ornamentation of granules more or less differentiated morphologically: rounded, spinate, or sometimes with tendency to pennular character. Wall in microstructural continuity with septa and displaying identical microstructure: vertical, centered elements ordered in monolinear series.

**Species included:** Norian — *Gablonzeria reussi* CUIF, 1976 and *G. meandriiformis* CUIF, 1976; Rhaetian — *G. major* (FRECH, 1890) and *G. profunda* (REUSS, 1854).

**Stratigraphie and geographic ranges:** Norian-Rhaetian of the Alps and Taurus.

#### *Gablonzeria major* (FRECH, 1890)

Pl. 4, figs. 2, 3, 4, Pl. 5, figs. 1, 2

1890 *Isastraea profunda* REUSS var. *major* — FRECH, p. 22, Pl. 5, figs. 4, 5

1976 *Isastraea profunda major* FRECH — CUIF, p. 114, text-fig. 13, Pl. 11, fig. 1, Pl. 12, figs. 4, 5

1986 *Gablonzeria major* (FRECH) — MATZNER, Pl. 9, fig. 8

**Lectotypus** (here chosen): BSP AS XII 14; FRECH 1890, Pl. 5, fig. 5, CUIF 1976, Pl. 11, fig. 1 (see Remarks p. 33).

**Locus typicus:** Hammerkogel (= Kesselwand-Rohrmoos)

**Stratum typicum:** Zlambach Beds

**Material:** Six specimens from Kesselwand and Schneckengraben, NHMW 1836 XII 1106, NHMW 1959/365/21, NHMW 1982/56/31<sub>1</sub>–31<sub>3</sub>, GBA 1982/12/ 803, and two colony fragments from Fischerwiese, GBA 1982/12/396, 802; seventeen thin sections. Common in the GBA and NHMW collections.

#### Dimensions (in mm):

Specimen No.	d	s
NHMW 1836 XII 1106	6 × 7	est. 90 (13 + 17 + 27 + est. 38 S4)
	6 × 8	119 (18 + 22 + 35 + 44)
	6	est. 88 (12 + 12 + 21 + est. 44 S4)
NHMW 1959/365/21	6 × 7	128 (17 + 18 + 29 + 64 + rudimentary S4)
NHMW 1982/56/31 <sub>2</sub>	4 × 8	76 (12 + 13 + 23 + 28)



**Description:** Upper colony surface flattened. Calices depressed, with sharp edges. Increase through the division of a parent corallite into 2–3 (rarely 4) individuals. Short series of budding corallites can be seen. The dividing wall is founded on opposing septa which meet at the axis.

Septa rather thin, well differentiated into 4 orders. S1 septa thickest, reaching the axis, S2 septa thinner, in general shorter than S1. S3 septa variable in length from about a quarter to three-fourths of the length of S1. The S4 septa have a well defined septal blade in some portions of the colony, in others they remain underdeveloped and traceable only in the wall structure, regularly distributed. The thickness of the wall attains 500–1500  $\mu\text{m}$  (Pl. 4, figs. 2 a, b, 3, Pl. 5, fig. 1 a).

Endotheca composed of large, thin-walled vesicles, steeply inclined from the periphery adaxially. Septal faces covered with abundant, protruding granules varying in shape and arranged in poorly defined rows, about 140  $\mu\text{m}$  apart, parallel to the endothecal vesicles (Pl. 4, figs. 3, 4).

**Microstructure:** The wall is formed of a straight or zigzag row of vertical trabeculae, every second or third one giving rise to series of septal trabecular sets (Pl. 5, fig. 1 b, see also CUIF 1976, text-fig. 13). The septal and wall trabeculae are of identical diameters. The wall trabeculae are isometric, 65–70  $\mu\text{m}$  in diameter, rarely less. The wall attains a thickness of 550  $\mu\text{m}$  up to 1500  $\mu\text{m}$  due to enlargement of the volume of stereome growing epitaxially on the wall and septal (peripheral) trabeculae. The septa are formed of numerous trabeculae, subvertical peripherally and strongly inclined adaxially (Pl. 5, fig. 2). The radial trabecular diameters of S1 and S2 septa are from 50  $\mu\text{m}$  (rarely 30) up to 100  $\mu\text{m}$  at the periphery; the transverse septal (i. e. transverse trabecular) diameter is from 60  $\mu\text{m}$ , midway from the wall to the axis, to 180  $\mu\text{m}$  at the wall, and 60–90  $\mu\text{m}$  in the free septal blades of S1 septa. The thinnest S3 are about 24  $\mu\text{m}$  in section (in GBA 1982/12/396 even less than 20  $\mu\text{m}$ ). This implies that unthickened trabeculae have very small diameters similar to the diameters of small trabeculae in the distichophylliid corals and procyclolitids. Trabeculae give long lateral offsets which constitute a form of granulation on the septal faces. The granules are round or flattened in section, their edges ornamented. They may coalesce to form short, list-like, protruding structures frequently lacerated at the edge.

**Remarks:** The only preserved specimen of two originals figured by FRECH has been chosen herein as lectotype. It was re-figured by CUIF (1976, Pl. 11, fig. 1), who erroneously stated that the specimen represents the REUSS original of *Isastraea profunda*.

**Distribution:** Rhaetian of the Northern Calcareous Alps; common in the Zlam-bach Beds of the Gosauklamm region and in Fischerwiese.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Gablonzeria profunda* (REUSS, 1854)

Pl. 4, fig. 1, Pl. 5, fig. 3

1854 *Isastraea profunda* – REUSS, p. 116, Pl. 9, figs. 5, 6

1890 *Isastraea profunda* REUSS – FRECH, p. 21, Pl. 5, figs. 1–3 A

part. 1976 *Isastraea profunda* REUSS – CUIF, p. 113, text-fig. 12, Pl. 11, figs. 2–6 (non fig. 1, presenting FRECH's specimen No. BSP AS XII 14, designated herein lectotype of *G. major*)

**Holotypus:** lost; REUSS 1854, Pl. 9, fig. 5; FRECH 1890, Pl. 5, figs. 1, 1 A

**Locus typicus:** after REUSS: "Gosauschichten, Gosau" after FRECH's supposition: Oedalm (= Kesselwand-Rohrmoos)

**Neotypus** (here chosen): NHMW 1851 XII 1898; Pl. 4, figs. 1 a–e, Pl. 5, figs. 3 a–c

**Locus typicus:** Kesselwand-Rohrmoos

**Stratum typicus:** Zlambach Beds

**Material:** Seventeen specimens from Fischerwiese, GBA 1982/12/384–395, NHMW 1982/57/7–9, 65, and the neotype specimen, from the type locality; seventeen thin sections; common in the GBA and NHMW collections

#### Dimensions (in mm):

Specimen No.	d	s
NHMW 1891 XXI 1898	3 × 3.5	51 (10 + 10 + 14 + 17)
	3 × 3.5	62 (10 + 8 + 15 + 29)
	3.5 × 4	62 (9 + 10 + 19 + 24)
	3.5 × 4	68 (10 + 10 + 17 + 31)
	3 × 5	76 (11 + 12 + 22 + 31)
	4 × 5	64 (12 + 12 + 20 + 20)
	4 × 5	73 (13 + 14 + 17 + 29)
	5	66 (10 + 11 + 20 + 25)

**Description:** Colonies massive or lamellate, unifacial or bifacial. Calices variable in shape and diameter depending on where they are placed in the colony (Pl. 4, fig. 1 a). Calicular edges sharp, cavities deep. Increase by division of the calice into 2–3 individuals. Dividing wall based on two opposing septa (Pl. 5, fig. 3 a).

Septa differentiated into 4 orders. Incomplete systems are frequent. The interpretation of orders in the incomplete systems is tentative due to their untypical lengths. S1 septa reaching the axis, S2 septa rather regularly distributed, shorter and thinner than S1, S3 usually attaining more than half the length of S1, lacking in some systems, S4 reaching one-third of the length of S1 and lacking in some systems. Septal faces covered with strongly protruding spiniform granules or listlike structures. Rows of granules are strongly inclined from the wall adaxially.

Endotheca strongly depressed at the calicular axis, formed by thin-walled vesicles (Pl. 4, fig. 1 b).

**Microstructure:** The septa are in microstructural continuity with the wall. Both are formed of trabeculae of the same dimensions (compare CUIF 1976, text-fig. 12). The septal trabeculae may be strongly anisometric, e. g. 40 µm × 120 µm, 50 µm × 120 µm (the radial diameter is 40–60 µm, the transverse one may reach 120 µm). The wall trabeculae are vertical and arranged in a straight or zigzag row. The wall trabeculae facing the septal trabecular rows alternate with single trabeculae that have no continuation into the septal blades. The wall, usually 150 µm–200 µm in thickness, may be thickened up to 500 µm. The fibres of the wall stereome grow centripetally in the interseptal space beginning with the wall trabeculae. The septal trabeculae are vertical peripherally and inclined adaxially in the remaining portion of the blade. In transverse section of the septa, trabeculae are usually disposed in a single straight row, or, they may alternate in parts (Pl. 5, fig. 3 b). The lateral trabecular offsets have their own axes (Pl. 5, fig. 3 c). The ornamentation they constitute is irregular, some of them being free and some being

fused to form thin sheets with uneven edges. Isolated granules are sharp, spiniform or pennula-like strongly protruding and denticulate at the edge (Pl. 4, figs. 1 c–e).

The thickening of the septa is due to stereome growing epitaxially on the trabecular fibres.

**Remarks:** The neotype represents a fragment of a very well preserved specimen. As a rule, the state of preservation of the material is poor.

**Distribution:** Rhaetian of the Northern Calcareous Alps; known in the Zlam-bach Beds of Fischerwiese and Gosaukamm region; FRECH noted it in Hallstätter Salz-berg and SCHÄFER (1979) in Upper Rhaetian coral limestones.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

### Subordo Caryophylliina VAUGHAN et WELLS, 1943

**Emended diagnosis:** Radial elements built of a medially situated row of small, densely packed trabeculae forming a thin, straight or zigzagged zone when observed in cross section, and bordered on each side by a thick layer of fibrous tissue. The latter is organized in large fascicles densely packed, perpendicular to the median zone. Fascicles may be provided with their own axes of convergence and form lateral, short trabeculae. Some of them protrude as ornamentation on the septal faces. Known from the Triassic to Recent.

**Discussion:** The group differs from other Scleractinia in the peculiar microstruc-ture of the radial elements. It contains corals of the superfamily Reimaniphyllioidea MELNIKOVA, 1975, as well a majority of corals of the suborder Caryophylliina *sensu* VAUGHAN et WELLS, 1943, here redefined as a superfamily. The superfamilies repre-sent different adaptations in their corallite architecture:

(1) Caryophyllioidea GRAY, 1847: Radial elements of "septal" (median trabeculae arranged in simple series) or "costo-septal" type (median trabeculae arranged in a water-jet pattern) depending on family. In some families pali are present; the endotheca is developed or rudimentary. Granulated stereome may cover the corallite outer surface. Deep- and shallow water corals, known from the Liassic to Recent.

(2) Reimaniphyllioidea MELNIKOVA, 1975: Radial elements of the costo-septal type. Endotheca abundant, vesicular. Transversely wrinkled pellicular fibrous wall forms the corallite outer surface. Shallow-water corals limited to the Upper Triassic. *Familiae:* Reimaniphyllidae MELNIKOVA 1975 (= Distichophyllidae CUIF, 1977), Margarophylliidae CUIF, 1977.

### Superfamilia Reimaniphyllioidea MELNIKOVA, 1975

*Familia* Reimaniphyllidae MELNIKOVA, 1975 (= Distichophyllidae CUIF, 1977)

**Genus typicus:** *Distichophyllia* CUIF, 1975 (= senior subjective synonym of *Reimaniphyllia* MELNIKOVA, 1975)

**Emended diagnosis:** Small trabeculae ordered in a single, straight, wavy or zigzagged row and forming a mid-septal zone. The fascicles of fibres or lateral trabeculae constitute the lateral portions of radial elements. Lateral ornamentation granular; menianes rare. Endotheca vesicular. Pellicular, fibrous wall present. Stereozonal wall may be developed. Columella papillar, if present. Intracalicular budding with indirect linkages; additionally extracalicular b. in thamnasterioid and kuhnastreoid colony types.

Genera included: *Distichophyllia* CUIF, 1975, *Paradistichophyllum* MELNIKOVA, 1975, *Retiophyllia* CUIF, 1967, *Oedalmia* CUIF, 1976, *Coryphyllia* CUIF, 1975, *Palaeastraea* KÜHN, 1936, *Kuhnastraea* CUIF, 1976, *Alakiria* CUIF, 1976 and *Distichoflabellum* gen. n.

Discussion: The works of CUIF (1966, 1967, 1968, 1975 a, 1976) gave a profound insight into the nature of this peculiar coral group and introduced a general systematic order into it (1977 b). In 1975 CUIF and nearly simultaneously MELNIKOVA published their considerations on this group (CUIF: 1975 a, issued on April 1975; MELNIKOVA: 1975, date of publishing lacking); MELNIKOVA gave diagnosis and family name – Reimaniphylliidae – to these corals. CUIF determined here several groups of genera basing on microstructural criteria: (1) 'groupe *Retiophyllia*', (2) 'groupe *Distichophyllia*', diverging into (2 a) corals of granular ornamentation and (2 b) those of penular ornamentation, and (3) 'groupe *Margarophyllia*'<sup>6</sup>.

The family name Distichophylliidae was not given to them until 1977 (CUIF 1977 b). This name, a junior subjective synonym of Reimaniphylliidae MELNIKOVA, 1975, has already been accepted in the literature (MONTANARO-GALLITELLI 1978, BEAUVAIS 1981, RONIEWICZ 1984).

The emendation concerns the diagnosis (characteristics of the septal microstructure and nature of the wall – originally recognized as epicostal paratheca and septotheca), and the family range.

The family range is enlarged here in comparison to the original one and that of CUIF (1977 b) by including genera *Alakiria* and *Distichoflabellum* and excluding *Pamirastraea* MELNIKOVA, 1975. *Alakiria* CUIF 1976 reveals features seemingly common with distichophylliid corals: a tendency towards concentration of fibres in relation to centres in the mid-zone (CUIF 1976, text-fig. 30 b), and an ability to develop lonsdaleoid septa with which it corresponds to *Kuhnastraea*, *Palaeastraea* and *Coryphyllia*. As to the genus *Distichoflabellum* gen. n. it is assigned here on the basis of the most general resemblance of its septal structure to the distichophylliid one. The architecture of the corallites, however, does not fit exactly within the familial diagnosis, as in this genus the dissepiments are very low and extended laterally in contrast with the vesicular ones typical of the remaining genera. Genus *Pamirastraea* seems to represent family Margarophylliidae (p. 75).

Because of the differences in corallite structure we may distinguish three subfamilies here: Reimaniphylliinae MELNIKOVA, 1975, Coryphylliinae BEAUVAIS, 1981 and Distichoflabellinae subfam. n.

Discussion on the microstructure in the family Reimaniphylliidae: As the microstructure of this group has been exemplified by the genus *Distichophyllia* I call this type of microstructure a "distichophylliid type", and Reimaniphylliidae – corals which have this feature – distichophylliid corals.

The distichophylliid type of microstructure was described (CUIF 1966, 1967, 1968, 1975 a, 1976) and interpreted (CUIF 1975 a, 1977 b, 1981) on the basis of material which seemed well preserved in detail. Unfortunately, the skeleton had been altered by diagenesis at its most critical point, the small-trabecular mid-septal zone (see pls. 13, 14, 17). Thus was overlooked the most striking of the distichophylliid features, small trabeculae measuring between 20 and 50  $\mu\text{m}$  (RONIEWICZ 1984).

<sup>6</sup> This primary classification and its more developed version (CUIF 1977 b) were later used by BEAUVAIS (1981) as the basis for distinguishing family-group taxa (see Notes p. 24).

The mid-septal zone of distichophylliid corals is built of a row of trabeculae closely apposed to each other; laterally a stereome develops in the form of fascicles of fibres growing out epitaxially from the trabeculae. The boundary between the crystallites of the mid-zone and those of the stereome is rarely visible. In general, the septal structure resembles that of the family Caryophylliidae.

This, briefly diagnosed, basic structure developed multidirectionally, giving different structural patterns, each diagnostic of a group of species or genera. There is a general tendency observed in the family, for the complexity of the septal structure to increase. The simplest of all is the structure with the mid-septal zone formed by small trabeculae, 20–50  $\mu\text{m}$  (or slightly more) in diameter, from which well defined fibres run laterally subparallel to each other, with a slightly marked fascicular arrangement. The structure of the trabeculae is rarely preserved, their fibres being extremely narrow. It is a type met within many species of *Retiophyllia*.

The extremities of thin fibre bundles may be visible on the septal surface as micro-ornamentational elements (for example in *Palaestraea*). In tangential sections of the septa, lateral fibre fascicles of the stereome can be observed in cross section (CUIF 1966, 1975 a, 1977 b). In more simple cases, they are devoid of axes (partly *Retiophyllia*) whilst with more advanced tissue organization, they are organized around the axes of convergence (*Distichophyllia*, partly *Retiophyllia*).

This organization of the stereome is the special caryophylliid-distichophylliid contribution to the septal structure. The microstructure based on the formation of lateral axes, i. e. lateral trabeculae, has been described in details and illustrated by CUIF (1975 a). The genus *Distichophyllia* served as an excellent example for him. In brief, lateral trabeculae of large diameter (150–200  $\mu\text{m}$ ) are formed on both sides of the zigzag mid-septal zone. Their axes, being in continuity with the mid-septal zone, are built of delicate fibres. Densely and regularly distributed, lateral trabeculae constitute the main structural element of the septa. In practice, the septal blade consists of two thick layers of lateral trabeculae diverging from a mid-zone of insignificant thickness. When observed from the septal surface, the tops of the lateral trabeculae are disposed in subvertical rows, with those in neighbouring rows situated on the same level (CUIF 1975 a). The same structural pattern can be observed in many species of *Retiophyllia*, in some as the dominant pattern in the costal portion of the radial elements. Some lateral trabeculae being overgrown may penetrate the interseptal space in form of lateral septal projections (= synapticalae).

Apart from the usual structure with fine-trabecular middle zone, distichophylliid corals show a tendency towards a thick-trabecular microstructure formation. This tendency is realised by: (i) fusing of fine trabeculae into compound units, which results in formation of thick trabeculae on the corallite periphery (*Retiophyllia*, *Kuhnastraea*); (ii) expanding of diameters and reducing of the number of trabeculae in the septum – in Margarophylliidae (*Margarosmilia*).

(i) In some species examined of the genus *Retiophyllia* (*R. gephyrophora*, *R. fenestrata*, *R. gracilis*), relatively large trabeculae (50–90  $\mu\text{m}$ , and slightly more) co-exist with small trabeculae in the median zone; in one of them even being dominant in some septa (*R. gephyrophora*). In *Kuhnastraea* perfectly developed trabeculae form the intercorallite, pallisaded wall, as well as peripheral, costal portions of some septa (Pls. 14, 17).

(ii) The most advanced stage on the way to a large-trabecular septal structure is seen in a related group of the genera *Margarophyllia*-*Margarosmilia*. There, the septum

is practically formed by relatively thick trabeculae assymmetrically developed in relation to the geometrical median plane, and slightly alternating in position. In those genera lateral trabeculae regularly diverge from the median trabeculae, and, as observed on the septal surface, they alternate in position in neighbouring rows (for illustrations see CUIF 1975 a, text-figs. 11, 12 and herein Pl. 22).

The transformation of small trabeculae into large trabeculae proceeds through the separation of the dense rows of small trabeculae at points where the distance between them allows for a reorientation of the thick outer stereomal fibres from subparallel to a concentric one. The fibres converge to particular small trabeculae, which become their axes of convergence. Trabecular borders become well defined when crystallites, growing from opposite directions and not parallel as previously, compete for space. In some large trabeculae, the axis seems to be composed of several thin axes, if one can judge from its outline in a cross section. A similar process of "trabeculization" is observed in other coral groups: in cyclophylliids (p. 28), astraeomorphids (Pl. 29) and procyclolitids (Pls. 31, 32).

**Microstructural affinity with other corals:** The small-trabecular distichophylliid type of microstructure of reimaniphylliids is comparable to that in the Recent ahermatypic family Caryophylliidae (RONIEWICZ 1984). SORAUF & PODOFF (1977) and SORAUF & JELL (1977) gave SEM documentation of details of the Recent caryophylliid septal structure, and RUSSO (1976) gave the same of Eocene corals. Its essential character consists in the extremely thin-fiber structure of mid-septal small trabeculae contrasted with epitaxially growing lateral crystallites that form a thick-fibrous tissue. As a result, the thin-fibred and small-dimensional trabeculae form a very thin internal blade (corresponding to Urseptum of early authors) differing in structure from the external thick-fibrous stereome which practically forms the whole of the septal blade.

Based on the close microstructural resemblance of reimaniphylliids and caryophylliids one can consider them phylogenetically allied (RONIEWICZ 1984).

**Diagenetic influence on the clarity of the distichophylliid microstructure:** The thin- and thick-fibrous septal portions have been unequally influenced by diagenesis. At the very beginning of the diagenetic process, the finest aragonitic fibres were subject to dissolution and recrystallization. When the calcium carbonate had been dissolved, it either recrystallized in place or was removed from the septum. As a result, a homogeneous recrystallized zone appeared in the middle of the septum, or a fissure which eventually collapsed. In this way, the small trabeculae disappeared from the septal structure and the median trabecular zone has reduced to a mid-septal contact zone between two septal halves. At the same time, the stereomal portions of the septa could preserve intact their thick-fibred structure, being misleading as an indicator of a good state of preservation of the original skeletal structure (Pls. 13, 14).

#### Subfamilia Reimaniphylliinae MELNIKOVA, 1975

Genus typicus: *Distichophyllia* CUIF, 1975

Diagnosis: Radial elements vertically continuous. Endotheca vesicular at least in some zones.

Genera included: *Distichophyllia* CUIF, 1975, *Paradistichophyllum* MELNIKOVA, 1975, *Retiophyllia* CUIF, 1967, *Oedalmia* CUIF, 1976.

**Discussion:** The range of the subfamily has been changed in comparison with 'groupe *Distichophyllia*' s. s. CUIF 1977 by adding *Retiophyllia* and excluding *Distichomeandra* and *Toechastraea*. The microstructural variability of *Retiophyllia* comprises the microstructural type of *Distichophyllia*. The microstructures of *Distichomeandra* and *Toechastraea* differ from that of *Distichophyllia* but are related to the margarophylliid one (compare CUIF 1976, Pls. 15 and 16, text-figs. 20, 24–26, and presented herein microstructure of *Margarosmilia*, Pl. 22, figs. 3, 4).

The taxon *Distichophyllum* CUIF, 1967, which used to be included here, is to be found in the synonymy of *Retiophyllia* (p. 42).

### Genus *Distichophyllia* CUIF, 1975

**Species typica:** *Montlivaltia norica* FRECH, 1890

**Emended diagnosis:** Solitary. Surface covered with pellicular wall. Radial elements costoseptal; median septal zone zigzag-shaped; lateral axes of convergence regularly contributing to the septal structure; lateral ornamentation granular. Dissepiments small, vesicular, abundant.

**Species included:** The genus was derived from Triassic *Montlivaltia*. It is represented by the following species from the Alpine Rhaetian: *Distichophyllia norica* (FRECH, 1890) and *Distichophyllia fritschi* (FRECH, 1890), and perhaps, by species that have not yet been revised, i. e. *M. marmorea* FRECH.

A Carnian representative of the genus was reported by CUIF (1975 a). Norian forms from North America were reported by STANLEY (1986).

**Stratigraphic and geographic ranges:** Carnian-Rhaetian of the Tethyan realm.

**Discussion:** The taxon *Distichophyllia* CUIF 1975 has the priority over the synonymous *Reimaniphyllia* MELNIKOVA 1975 (see p. 35). *Reimaniphyllia* MELNIKOVA is based on *Montlivaltia gosaviensis* FRECH, which is synonymous to *M. norica* FRECH (see also p. 41).

The type species has been thoroughly described and figured by previous authors (FRECH 1890, CUIF 1975 a). Aspects of its septal structure and ontogenetical structural transformations have been analyzed by CUIF (1975 a).

The interpretation of distichophylliid type of septal microstructure and a discussion of the CUIF thesis is presented above.

### *Distichophyllia norica* (FRECH, 1890)

Pl. 6, figs. 2–4

- 1854 *Montlivaltia cupuliformis* – REUSS, p. 102, Pl. 6, figs. 16, 17
- 1890 *Montlivaltia norica* – FRECH, p. 39, Pl. 3, figs. 8, 9, Pl. 10, figs. 1–5, Pl. 18, fig. 17
- 1890 *Montlivaltia gosaviensis* – FRECH, p. 41, Pl. 11, fig. 7
- 1966 *Montlivaltia norica* FRECH – CUIF, p. 535, Pl. 11, figs. 3–5
- 1975 a *Montlivaltia norica*, *Distichophyllia* (*Montlivaltia*) *norica* (FRECH) – CUIF, p. 304, text-figs. 2–6
- part. 1975 *Reimaniphyllia gosaviensis* (FRECH) – MELNIKOVA, p. 87, Pl. 15, fig. 1 (non fig. 2)
- 1977 b *Distichophyllia norica* (FRECH) – CUIF, Pl. 4, figs. 5–7
- 1979 *Montlivaltia norica* FRECH – SCHÄFER, p. 44, Pl. 10, fig. 1, Pl. 11, fig. 2

**Series typica:** BSP AS XII 46, 48 — specimens the details of which have been figured by FRECH 1890, Pl. 13, figs. 1 and 4; the second of them re-figured by CUIF 1975, text-fig. 2 a; see also herein, Note on p. 146

**Locus typicus:** Grosser Zlambachgraben

**Stratum typicum:** Zlambach Beds

**Material:** About seventy specimens from Fischerwiese, GBA 1982/12/286–330, 344–349, 355–367, NHMW 1982/57/63, 64; four specimens from Kesselwand-Rohrmoos, NHMW 1959/365/2, 1982/56/29<sub>2,3</sub>, 4L<sub>2</sub>; one specimen from Schneckengraben, NHMW 1982/56/29<sub>1</sub>; thirty thin sections

**Dimensions (in mm):**

Specimen No.	d	f	s	s/10 mm
GBA 1982/12/294	12 × 14	6	65 (6 + 6 + 12 + 24 + 17)	
GBA 1982/12/293	18 × e. 22	6	126 (8 + 10 + 18 + 35 + 54)	
GBA 1982/12/291	20 × 30		137 (12 + 13 + 25 + 40 + 47)	
NHMW 1982/56/29 <sub>2</sub>	20 × 24		110	20
NHMW 1959/365/2	20 × 30	14	e. 130 (48 S1–S3)	
NHMW 1982/56/29 <sub>1</sub>	40 × 50		186 (132 S1–S4)	18

**Description:** A full description of the species by FRECH (1890) includes remarks on the variability of the corallum shape, and the development of columella and septa. This complimentary description gives an alternative interpretation of septal orders, five in all, as well as some details on the columella, endotheca and wall.

In a young individual (for example GBA 1982/12/294) at a diameter of about 10 mm with 65 septa, there are 6 systems comprising regularly distributed S1–S4 septa and an incomplete ring of S5. An axial fissure with well marked sulci at its ends may be developed at this stage. The S1 septa are the thickest and reach the axis or axial fissure. The S2 septa, equal in length, are thinner than S1. The S3 septa are of variable length: those disposed along the sides of the axial fissure are subequal to S1 in length, others situated at the sulci are markedly shorter. The S4 septa reach at least half the length of S1 in normally developed systems. The S5 septa usually reach 1/5–1/4 the length of the neighbouring S1–2 (Pl. 6, fig. 2).

In adult individuals, the number of systems is variable: often 7–9, it can reach 14. The S1 and S2 septa, equal in length and thickness, thickened all along their length to the axis. S3 septa are thickened somewhat outside the periaxial portion. Some corallites show a tendency to a club-shaped thickening of the internal edges of S1–2 (rarely S3). Thick internal edges may be provided with strong spines. S4 and S5 septa thin. At the distal constriction of diameter in adults, rejuvenescence takes place: the S5 septa disappear, whilst S3 assume the shape of young corallites.

The columella, if present, is very variable in structure: usually it is feeble, papillar, rarely lamellar, and discontinuous. It may happen that septa of the one side of the axial fissure fuse together, or septa from both sides fuse among themselves chaotically. In any case, the columella seems to be parietal in origin rather than developed as an essential skeletal element. CUIF (1975 a) was of the opposite opinion.

The endotheca is vesicular, abundant, and slightly concave at the axis (Pl. 6, fig. 3).

The pellicular wall is extremely thin, preserved only occasionally (GBA 1982/12/325).

**Microstructure:** The microstructure of the septa, its modification during ontogeny, deviations from the normal septal microstructure, and modifications of the wall and



columella appearing during ontogeny, have been described by CUIF (1975 a). In the material examined, septal microstructure is observable only in some specimens.

Trabecular orientation in the median zone is variable. In radial elements of the first and second orders in the specimen examined (NHMW 1982/56/29, Pl. 6, fig. 4), the trabeculae are subvertical in the majority of the blade and become inclined adaxially near the internal edge. In elements of higher orders, trabeculae are subvertical in the peripheral portion and steeply inclined adaxially in the rest of the blade. The diameter of small trabeculae is variable between 20 and 50  $\mu\text{m}$  depending on the septum. From the median zone, lateral axes diverge. Lateral tissue may be organized in respect to them to form lateral trabeculae, or may be organized into fascicles which are oriented perpendicularly to the median zone. In the adaxial portion, the boundary between the median and lateral fascicular zones may be sharply delimited. The lateral trabeculae are 200 to 300  $\mu\text{m}$  in diameter.

The interpretation of distichophylliid type of microstructure and a discussion of the CUIF thesis is presented on pages 36–38.

**Discussion:** — In the synonymy of *D. norica* I include *D. gosaviensis* FRECH, the species described from the Zlambach Beds of Oedalm (= Kesselwand-Rohrmoos) on the basis of one specimen (FRECH 1890, 41, Pl. 11, figs. 7–7 A). This specimen, housed in BSP, has been lost. Its description and illustrations suggest the form of relatively thin septa and subcylindrical shape of the corallum. Such specimens are to be found in the collection NHMW (1982/56/29<sub>2,3</sub>). Their features fall within the variability of *D. norica* observed in the collections GBA and NHMW, it is not a common morphotype, however.

MELNIKOVA (1975) chose *Montlivaltia gosaviensis* FRECH as the type species of *Reimaniphyllia*. However, the specimens she illustrated do not resemble the morphotype discussed above and identifiable with *M. gosaviensis* FRECH. One of the two Pamirian specimens determined by MELNIKOVA as *R. gosaviensis*, represents a common morphotype within *D. norica* (MELNIKOVA 1975, Pl. 15, fig. 1). The other one (*l. c.*, Pl. 15, fig. 2) has a very dense endotheca, composed of very numerous, low and largely extending dissepiments, which are not to be found in *Distichophyllia* known from the Alps.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese, Kesselwand-Rohrmoos and Schneckengraben; FRECH mentioned this species from Grosser Zlambachgraben (holotype), Hallstätter Salzberg and Scharitzkehlalp. Species common in the European and Asiatic parts of Tethys.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Distichophyllia fritschi* (FRECH, 1890)

Pl. 6, fig. 1

1890 *Montlivaltia Fritschi* — FRECH, p. 40, Pl. 11, figs. 2–5, Pl. 13, fig. 8

**Lectotypus** (here chosen): BSP AS XII 49; FRECH 1890, Pl. 11, fig. 5

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Material:** One specimen from Fischerwiese broken proximally and distally, GBA 1982/12/801; two thin sections

**Dimensions (in mm):**

h	d	s	s/3 mm
e. 22	12	58 (12 + 12 + 22 + 12)	7–9

**Description:** The species was briefly described by FRECH on the basis of damaged specimens. Unfortunately, in the specimen here examined its proximal and distal ends are lacking as well. The corallum is slender, with circular calice and apparently narrow basis. The proximal broken end is 5 mm in diameter. Septal faces are covered with strongly protruding granulation, especially well distinct at the internal edges. Septa are differentiated into four size orders. The S1 septa, the strongest of all, six at the proximal and twelve at the distal end, are subequal, reaching the axis and fusi-form. The S2 septa are slightly shorter and thinner. The S3 septa exceed half the radius in length and S4 are very thin and variable in length.

The dissepiments are thin-walled, vesicular, abundant. Wall pellicular, lying on strong costae.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds at Fischerwiese.

### Genus *Retiophyllia* CUIF, 1967

**Species typica:** *Thecosmilia fenestrata* REUSS, 1854 in FRECH, 1890 (*non* REUSS, 1854) = *Retiophyllia frechi* sp. n.

**Emended diagnosis:** Colony phaceloid. Budding intratentacular with trabecular linkages, corallites symmetrically bifurcating (or trifurcating) with a simple division of septal apparatus. Processes connecting corallites present. Radial elements costoseptal; trabeculae arranged in the water-jet pattern. Small trabeculae disposed along the straight, wavy or zigzag septal mid-line. Peripherally, lateral axes of convergence may contribute regularly to the septal structure, in the rest of septum stereome organized in more or less expressed fibre fascicles. A tendency is present to transform peripheral small trabeculae into large trabeculae. Lateral ornamentation in form of granules or menianes. Endotheca composed of small marginal and larger internal dissepiments. Wall pellicular or double, pellicular-stereozonal.

**Synonymy:** *Distichophyllum* CUIF, 1967 (type species: *Thecosmilia caespitosa* REUSS, 1854), *Desmocoenia* ALLOITEAU et DERCOURT, 1966 (type species: *D. helladensis* ALLOITEAU et DERCOURT, 1966), *Parathecosmilia* RONIEWICZ, 1974 (type species: *Thecosmilia sellae* STOPPANI, 1862), *part. Paradistichophyllum* MELNIKOVA, 1975 (type species: *Thecosmilia norica* FRECH, 1890).

**Species included:** *R. caespitosa* (REUSS, 1854) = *Distichophyllum caespitosum* (REUSS, 1865) in CUIF 1975 a, *R. clathrata* (EMMRICH, 1853), *R. defilippi* (STOPPANI, 1862), *R. dichotoma* (MELNIKOVA, 1975), *R. fenestrata* (REUSS, 1854), *R. frechi* sp. n. = *Thecosmilia fenestrata* REUSS, 1854 in FRECH 1890, *R. gephyrophora* sp. n., *R. gosaviensis* sp. n., *R. gracilis* sp. n., *R. minima* (MELNIKOVA, 1975), *R. multigranulata* (MELNIKOVA, 1975), *R. norica* (FRECH, 1890), *R. oppeli* (REUSS, 1865), *R. paraclathrata* RONIEWICZ, 1974, *R. multiramis* sp. n., *R. robusta* sp. n., *R. sellae* (STOPPANI, 1862), *R. wanneri* (VINASSA DE REGNY, 1915), *R. helladensis* (ALLOITEAU et DERCOURT, 1966).

In the Upper Triassic of Turkey four different morphotypes of *Retiophyllia* were reported (CUIF, 1975 a) that represent separate species. The same concerns the Alpine form described here — *Retiophyllia* sp. A and North American forms (STANLEY 1986).

**Stratigraphic and geographic ranges:** Norian-Rhaetian of the Tethyan realm, Norian of North America.

**Discussion:** The genus was erected and largely discussed by CUIF (1967; 1975 a). This emendation concerns the microstructure of the radial elements (see Discussion p. 36) and the species content of the genus.

From the two synonymous taxa established simultaneously by CUIF (1967): *Distichophyllum* and *Retiophyllia*, the priority has been given here to the latter as *Distichophyllum* displays a peculiar set from among the diagnostic features of *Retiophyllia* (see also Discussion, p. 52). Competing in priority is also *Desmocoenia* ALLOITEAU et DERCOURT. Both, *Retiophyllia* and *Desmocoenia*, have been known in literature as established in 1966. In reality, the CUIF paper issued in February 1967, thus, *Retiophyllia* should fall into the synonymy of *Desmocoenia*. However, the exact date of publication of ALLOITEAU and DERCOURT's paper being unknown to me, I decide to maintain the name *Retiophyllia*.

As for *Parathecospimia* RONIEWICZ, it falls into synonymy of *Retiophyllia* CUIF, their type species having similar corallite architecture (FANTINI-SESTINI & MOTTA, 1984).

Some of the corals described by MELNIKOVA as *Paradistichophyllum* (*P. dichotomum*, *P. multigranulatum*, *P. minimum*, *P. clathratum*, *P. cf. cyathophylloides*) belong to *Retiophyllia*; the coral described as *Paradistichophyllum noricum* (FRECH, 1890), however, has different features than those of the mentioned nominal species and even seem to belong to a different genus (compare MELNIKOVA 1975, and Discussion p. 54).

**Remarks on morphological and microstructural variability:** Corals of the genus *Retiophyllia* are most frequent in the Upper Triassic fauna, represented by many species differing from each other, apart from dimensions, in details of their corallite structure and the microstructure of the radial elements. The mosaic character of their resemblance does not allow different genera to be distinguished amongst them (Table 2). The most constant generic features are (i) the structure of the pellicular wall and (ii) the mode of budding.

(i) The pellicular wall, an essential skeletal element, is invariably developed as a thin layer increasing centripetally and composed of more or less clearly fasciculated fibres. Its surface is minutely horizontally wrinkled. The wall primarily covers all the corallite but is rarely preserved because of its fragility.

(ii) The budding is intratentacular with indirect linkages between individuals, distinguished by the way the parent divides into two (bifurcation), rarely more, subequivalent individuals. A rapid elongation of one of the calicular diameters of the parent calice is noticeable in the initial stage of bifurcation; constriction at the perimeter is not observed. Division takes place after the dividing wall has been established. The dividing wall is based on two opposite septa and it transforms subsequently into pellicular wall; subsequent development gives equal corallites.

Such features as (1) microstructure and arrangement of radial elements, (2) complexity of the wall structure, (3) size and shape of endothecal vesicles, as well as (4) intercorallite relations, vary in the intra- as well as interspecific plans:

(1) Radial elements. The radial elements are formed by trabeculae arranged in the water-jet pattern (CUIF 1975 a, text-fig. 37 d), with the axis of divergence shifted more or less peripherally, depending on the species. This results in a greater or smaller development of the costal portion, for example, in *R. caespitosa* it is strongly reduced, whilst in *R. gephyrophora* it equals  $\frac{1}{5}$ – $\frac{1}{3}$  of the total septal length. Septa are fusiform in transverse section, with their maximum width at the axis of trabecular divergence. Such corallite features as the position of the wall and the development of the exotheca are correlated to some extent with the position of the axis of trabecular divergence (see below).

The range of microstructural variability of the septa in *Retiophyllia* includes both simple, small-trabecular and large-trabecular skeleton organization, as well as the more

Table 2. Comparison of some specific features of the examined species of *Retiophyllia* CUIF, 1967

Species	adults		costae	connecting processes	endotheca	angle of bifurcation	ornamentation
	d	s					
<i>R. oppeli</i> REUSS	3.5 – 4.5	40 – 60	thin	frequent, narrow	concave, abundant	acute	granular
<i>R. frechi</i> sp. n.	5 – 6	40 – 50	unequal	frequent, narrow	concave, abundant	acute	granular
<i>R. caespitosa</i> REUSS	10 – 11	40 – 50	thick	rare, large	horizontal, rare	obtuse	granular
<i>R. norica</i> FRECH	11 – 13	50 – 70	thin	rare, large	horizontal, rare	obtuse	granular
<i>R. robusta</i> sp. n.	13 – 16	40 – 50	thick	?	concave, rare	obtuse	granular
<i>R. gosaviensis</i> sp. n.	9 – 11	110 – 120	thin	frequent, large	concave, abundant	acute	granular
<i>R. gracilis</i> sp. n.	3.5 – 4.5	40 – 50	?	frequent, narrow	convex, abundant	acute	granular
<i>R. fenestrata</i> REUSS	5.5 – 6	40 – 50	thick	frequent, narrow	convex, abundant	acute	granular
<i>R. gephyrophora</i> sp. n.	10 – 12	60 – 70	?	frequent, large	convex, abundant	acute	granular
<i>R. multiramis</i> sp. n.	4.5 – 5.5	60 – 80	thin	frequent, narrow	concave, abundant	acute	menianes
<i>R.</i> sp. A.	3.5 – 4	30 – 40	thin	?	? ?	obtuse	menianes

complex organization of small trabeculae with lateral axes of convergence. As seen in transverse sections of the S1 and S2 septa, the structure of the septal portion is simpler than that of the costal part. In the septa, there are small trabeculae densely packed, expanded laterally, with their lateral fascicles of thick fibres disposed subparallel to each other. Dimensions of the small trabeculae are very constant in all species, despite the difference in their septal dimensions, and reach 20–30  $\mu\text{m}$  (measured in the radial plane). In some species, the peripheral trabeculae of the median plane show a tendency to enlarge isometrically their dimensions. In *R. multiramis*, *R. fenestrata* or in *R. gracilis*, this tendency is marked by the occasional widening of the trabeculae up to 60–90  $\mu\text{m}$  or more. In *R. gephyrophora*, the large isometric trabeculae form the costal portion in many septa or even the entire blades of some S4 septa, the trabecular diameters attaining between 75 and 150  $\mu\text{m}$  or more. In peripheral septal portions, the overgrown lateral trabeculae may appear as long lateral septal projections, initiated inside the septum and developed as rods or short plates protruding into the interseptal space. They can reach neighbouring septa and form a kind of synapticulae. Lateral septal projections were stated in *R. frechi* (see CUIF 1967), *R. caespitosa*, *R. norica*, *R. multiramis*, *R. fenestrata*, *R. gephyrophora*, and *Retiophyllia* sp. A.

Lateral septal ornamentation is granular or in form of menianes. Granules are circular in section (*R. norica*, *R. caespitosa*, *R. frechi*) or more or less flattened (*R. multiramis*, *R. paraclathrata* — see RONIEWICZ 1974, and *Retiophyllia* sp. A). In the last group the granules are very prominent and menianes may develop as well (*R. multiramis*).

It is important taxonomically to give an account of the intraspecific variability in septal size and morphology. In the following group of related species: *R. oppeli*, *R. frechi*, *R. caespitosa*, *R. norica* and *R. robusta*, there can be distinguished corallites with two different modes of septal development: (i) multiseptate, having numerous fully developed systems composed of septa of four well expressed orders, costal and septal portions well developed, costae thin and sharp; (ii) pauciseptate, having irregular systems composed mostly of septa of no more than 3 or even 2 orders, septa thick, often club-shaped, and costae relatively thick and obtuse. This observation caused HAAS (1909) to create subspecies in several species. An alternation of superposed zones of thin and thick costae can be observed on the corallite surface, reflecting the alternation of these two modes of septal development mentioned above. In *R. caespitosa*, the difference in septal thickness results in the existence of two corallite forms: thin-septate, with well ornamented faces, and thick-septate with smooth septal faces, the latter exemplified by specimens figured by CUIF (1967, Pl. 4, fig. 3 and 1975 a, text-fig. 35 b). In both, the septa are differentiated into 3 or 2 orders. Transverse section of the thick-septate *R. caespitosa* form strongly resembles pauciseptate *R. norica*. They differ only in diameters.

Some irregularity seen in the development of the septal apparatus results from the way in which septal number is augmented with increase of corallite diameter. The daughter corallite obtains a majority of its septal apparatus from the parent corallite and its development is accomplished by the transformation of some existing S2 and S3 septa into the categories of longer septa and by an appearance of new S4 septa. Due to the transformation of some septa from a lower into a higher size category, some systems in the corallite contain septa of atypical size or number for the order they represent.

(2) Wall structure. Inter-specific differences in the wall structure of the genus *Retiophyllia* were illustrated by CUIF (1975 a, text-figs. 39–43). In this genus, two types of wall develop: (i) a simple pellicular wall (*R. gosaviensis* sp. n. and *Retiophyllia* type I and *R.* type IV of CUIF 1975 a), and, (ii) a double wall, composed of peripheral or internal

stereozone associated with a pellicular wall or with pellicular wall and thickened septa. A peripheral stereozone is known in majority of species, for example, *R. norica*, *R. caespitosa*, *R. frechi*, *R. fenestrata*, and *R. type II* of CUIF (1975 a). A ring of internal stereozone (internal wall) may be observed in *R. gosaviensis*, *R. gephyrophora*, *R. sellae* (STOPPANI), and *R. type II* of CUIF (1975 a). In the case when a stereozone is developed, interseptal spaces are narrowed by laterally widened septa, and penetrated by lateral septal projections. The rest of the free space may be filled with fibrous, centripetally growing stereome, a tissue formed by long fibres deposited on the dissepiments. Here, some sort of trabeculae formation in that tissue may be observed, resulting in the appearance of short, upwardly directed trabecular axes on the dissepimental surface. The deposition of a stereozonal wall depends on the rate of skeletal deposition. When the rate of deposition diminished, corallites were temporarily devoid of stereozonal walls. In transverse sections of a colony fragment, all transitions between the wall types can be observed; nevertheless, one of them prevails.

(3) Endotheca. The interseptal skeleton in its fullest development is formed by dissepiments of three categories: (i) large dissepiments lying internally to the zone of trabecular divergence, more or less concave in the majority of species, rarely convex (*R. gephyrophora*, *R. fenestrata*, *R. gracilis*); (ii) small dissepiments lying at the zone of trabecular divergence, distributed in a few irregular rings; those lying outside the axis of divergence (exotheca), especially abundant and small in *R. gephyrophora* and *R. gosaviensis*, whilst rare in *R. caespitosa*; (iii) small vesicles (a) leaning against the septa, more frequent at the internal edge and in its vicinity, observed in *R. norica*, *R. caespitosa* and, rarely, in *R. frechi*, mainly in corallites involved in the process of budding; (b) filling the axial region in *R. multiramis*.

(4) As a rule, colonies in the genus *Retiophyllia* are phaceloid. In some species, however, the lateral fusion of corallites embraces some corallites or a whole colony. The phenomenon may repeat many times during the colony growth. As a result, a mixed, phaceloid-kuhnastreoid colony develops (*R. oppeli*). For comparison see *Kuhnastraea*, page 71.

Contacts among phaceloid corallites take place through connecting processes, common in *Retiophyllia*. The corallite connecting processes are blind, external corallite expansions comprising septa and endotheca, covered entirely with pellicular wall, and varying in shape and frequency. They are numerous, leaning against corallites in *Retiophyllia frechi*, *R. fenestrata* and, especially, in *R. gephyrophora*, and rare, reduced to sub-horizontal folds overhanging the corallite surface at irregular intervals in *R. norica*.

In the *Retiophyllia* four groups may be distinguished among the species considered: (1) *norica*-group, in which the endotheca is concave at the calicular axis, septal apparatus is composed of septa of 2–3 orders and the septa are ornamented with round granules (*R. oppeli*, *R. frechi*, *R. caespitosa*, *R. norica*, *R. robusta*); (2) *gosaviensis*-group, comprising one species only, *R. gosaviensis*, in which the endotheca and septal ornamentation resembles those of the *norica*-group but septal apparatus shows an extraordinary development of septa of the fourth order; (3) *multiramis*-group, in which the endotheca is concave at the axis, septal apparatus composed of septa of 3–4 orders and septa are ornamented with menianes (*R. multiramis*, *Retiophyllia* sp. A.); (4) *fenestrata*-group, in which the endotheca is convex at the axis and the septa are rather feebly ornamented with round granules (*R. fenestrata*, *R. gracilis*, *R. gephyrophora*).

1. *Retiophyllia norica* group (in all groups species are ordered according to growing corallite diameters)

*Retiophyllia oppeli* (REUSS, 1865)

Pl. 9, figs. 7, 8, Pl. 10, figs. 3, 4

v. 1865 *Calamophyllia Oppeli* — REUSS, p. 160, Pl. 4, fig. 1

part., v. 1890 *Thecosmilia Oppeli* REUSS — FRECH, p. 10, Pl. 2, figs., 18–20, 24, Pl. 3, figs. 4 A–E (non Pl. 2, figs. 21–23)

Holotypus: GBA type collection, No. 2805; REUSS 1865, Pl. 4, fig. 1

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: Fourteen specimens (complete and fragmentary colonies) from Fischerwiese, GBA 1982/12/134, 135, 137, 139–144, 769, 774, NHMW 1982/57/57–59; five colonies from Kesselwand-Rohrmoos, NHMW 1982/56/1, 3<sub>1</sub>–3<sub>4</sub>; fifteen thin sections

Dimensions (in mm):

Specimen No.	d	s	c/3 mm
GBA 1982/12/137	3.5 × 5	43 (7 + 7 + 10 + 19)	11–13
	3.5 × 6	58 (8 + 8 + 14 + 28)	
GBA 1982/12/773	3	38 (7 + 7 + 14 + 10)	12
	3.5 × 4.5	46 (8 + 8 + 16 + 14)	
	3.5 × 4	57 (11 + 11 + 22 + 13)	

Description: Colonies up to 100 mm in height. In typical, phaceloid colonies, apart from lateral connecting processes another form of contact may be developed, i. e. a complete fusion of corallites embracing some individuals or larger colony parts, and repeating at some intervals in the colony; the structure of fused colony portions is of kuhnastreoid type (Pl. 10, fig. 4). Bifurcation frequent. New individuals grow slowly in diameter. Budding of the protocorallite is multiple, taking place simultaneously on the whole calicular circumference. Connecting processes narrow. Corallite surface costulate.

In cross section, corallites oval or angular in shape. Radial elements strongly fusiform, ornamented with abundant, large and protruding granules. Multiseptate and pauciseptate forms may be distinguished. In the multiseptate type the septal apparatus is ordered in regular systems consisting of septa of four orders. The S1 and S2 septa are subequal in length, but S1 are twice or three times as thick as the others. The S3 septa are about  $\frac{2}{3}$  the length of S1; the S4 septa are thin and at least  $\frac{1}{3}$  the length of S1. Costae of the three first orders are strongly developed, equal, prominent and sharp. In pauciseptate type the S4 septa are lacking.

A thin pellicular wall rests on the costae. A peripheral stereozone is usually developed (Pl. 10, fig. 3). In kuhnastreoid parts isolated trabeculae appear in the intercorallite mural zone, constituting rudimentary palisaded wall.

Endotheca deeply depressed at the axial cavity, composed of numerous vesicles variable in size at the axis and small at the periphery (Pl. 9, figs. 7, 8).

Discussion and Remarks: The species is remarkable for its strong inequality in the size of its septa and in surprisingly equal costae. In corallite dimensions it resembles *R. minima* (MELNIKOVA, 1975) and differs from this species in its strong S1–S2 septa.

Specimens of the LOBITZER collections agree with the holotype and specimens of the FRECH collection (GBA, No. 2751). In some colonies with typically developed septa and wall, the corallite diameters are much smaller than usually observed in the species (GBA 1982/12/144), reaching between 2.5 and 3.5 mm, at the colony diameter about 20 mm.

Some specimens figured by FRECH (1890, Pl. 2, figs. 21 and 22) show a feature unusual in *Retiophyllia*: single buds of the original "twins" remaining as underdeveloped individuals with their calices at the level of the initial maternal calices. This poorly known morphotype, additionally showing meniane-like ornamentation, I separate as *Retiophyllia* sp. A (p. 58).

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds from Fischerwiese, Hallstätter Salzberg, Grosser Zlambachgraben and Kesselwand-Rohrmoos. Known from the Triassic of Indonesia (VINASSA DE REGNY 1915).

According to STANLEY (1986, 27: a list of verified species) present in the Norian of North America.

*Retiophyllia frechi* sp. n.

Pl. 7, figs. 1–8, Pl. 9, fig. 5, Pl. 13, fig. 2

- part., v.* 1890 *Thecosmilia fenestrata* REUSS – FRECH, p. 9, Pl. 1, figs. 25–27, Pl. 2, figs. 1–11, 13–17 (*non* fig. 12)
- 1965 *Calamophyllia fenestrata* REUSS – CUIF, p. 533, text-fig. 2 A
- 1967 *Retiophyllia fenestrata* (REUSS) – CUIF, p. 130, text-fig. 4 A, B, Pl. 4, fig. 4
- 1975 a *Retiophyllia fenestrata* (REUSS) – CUIF, p. 369, text-figs. 33–35

**Holotypus:** GBA Frech's type collection, No. 2750; FRECH 1890, Pl. 2, fig. 7

**Paratypi:** No. 2750 bis, No. 2748 (two specimens); *ibidem*. Pl. 2, fig. 10, Pl. 1, figs. 25 and 27, respectively; see also herein p. 146

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Derivatio nominis:** In honour of FRITZ FRECH (1861–1917), geologist and palaeontologist, to whom we owe the framework of knowledge on the Alpine Rhaetian corals.

**Diagnosis:** Corallites bifurcating at sharp angle. Connecting processes present. Mean diameter 8–9 mm with 40–60 septa. S1 and S2 septa thick. Pellicular wall thin; costae visible. Endotheca abundant, concave at the axis. Internal stereozonal wall present.

**Material:** Fragmentary corallites and nine fragmentary colonies from Fischerwiese, GBA 1982/12/1–68, 736–763, ZPAL H VIII/1–6, NHMW 1982/57/196; three colony fragments from Kesselwand-Rohrmoos, NHMW 1982/56/15<sub>4,5</sub>, NHMW 1851 XXI 1889; one corallite from Kleiner Zlambachgraben, GBA 1982/12/647; forty thin sections



## Dimensions in mm:

Specimens No.	d	s	c/3 mm
ZPAL H VIII/1	7 × 9	36 (9 + 9 + 15 + 6)	6–9
GBA 1982/12/15	7 × 9	43 (12 + 12 + 15 + 4)	
GBA 1982/12/26	6.5 × 11	50 (11 + 12 + 23 + 4)	6–7
GBA 1982/12/24	8 × 10	52 (17 + 16 + 19)	
GBA 1982/12/9	7.5 × 10	59 (15 + 15 + 28 + 1)	
GBA 1982/12/749	6.5 × 7	53 (8 + 8 + 16 + 21)	
GBA 1982/12/748	5.5 × 8	48 (8 + 8 + 16 + 14)	
	7 × 9	55 (9 + 9 + 18 + 19)	
CUIF 1975 a, text-fig. 35 a	e. 5 × 6	70 (15 + 15 + 30 + 10)	

**Description:** Connecting processes appear irregularly – on some corallites lacking, but on others – up to 5 in a series, spaced 10 mm apart. Corallite surface with costal ridges well marked, covered by a delicate, pellicular theca which is very rarely preserved. Colony increase by fission, producing two, rarely three subequal individuals (Pl. 7, fig. 1: budding, figs. 6–8: pellicular wall).

Radial elements fusiform with lateral granulation large but scarce. Septa are thickest at  $\frac{1}{4}$  to  $\frac{1}{3}$  of their length from the periphery, i. e. at the trabecular divergence zone. The septal apparatus is differentiated into three orders with sporadic fourth order septa. S1 septa subequal, variable in number, approaching the axis. At the axis, there is a marked tendency for their internal edges to meet. S2 septa conspicuously thinner and usually shorter than S1. S3 septa thin and reach at least half the length of S1. The S4 septa are rudimentary and can alternately disappear and reappear during corallite growth (Pl. 7, figs. 2, 6 b).

Among the groups of specimens examined there are corallites showing some septal features atypical of the species: three specimens (GBA 1982/12/63–65) have club-shaped S1; two others (GBA 1982/12/67, 68) much resemble *caespitosa* in their septal development – but their skeletons are much more delicate in structure than in that species; in colonies GBA 1982/12/748, 749 there are numerous S4 septa per corallite; in colonies from Kesselwand-Rohrmoos S4 septa are usually long and permanent.

In transverse section, few dissepiments are seen. In longitudinal section, zoning of the endotheca can be observed: peripherally there are numerous small dissepiments, including one ring of marginal (exothecal) ones, axially – subhorizontal or concave, large dissepiments traverse the lumen (Pl. 9, fig. 5).

On the corroded corallite surface one can observe alternating zones, of different width, of more or less well developed marginal dissepiments (Pl. 7, fig. 6 b). The internal wall is developed in the zone of fusiform thickening of septa, as a secondary thickening of the dissepiments and septal blades in the form of variably expressed stereozonal coatings (para-septotheca of CUIF 1975 a, 373).

**Microstructure:** The septal mid-zone is more or less undulating depending on septal size. In fully developed septa of the first order, it can be zigzagged (Pl. 13, fig. 2).

The septal mid-zone is formed by a single row of small trabeculae, 15–30  $\mu$ m apart (measured between the centres). The thick fibres which are founded laterally on the trabeculae are organized into fascicles. The latter may be provided with their own axes.

The pellicular wall shows centripetal growth of fibres.

**Discussion and Remarks:** The species described by FRECH from Fischerwiese as *Thecosmilia fenestrata* (REUSS) has been re-named as *R. frechi*, because it differs from

REUSS' species, described originally as *Calamophyllia fenestrata*, in the following features: larger diameters, septa more abundant and strongly differentiated in thickness, faint pellicular wall, and abundant dissepiments, concave at the axial cavity (compare *R. fenestrata*, p. 59). FRECH (1890) illustrated REUSS' type specimen (NHMW, No. 148) in Pl. 2, fig. 12.

Specimens from Kesselwand-Rohrmoos differ from those of Fischerwiese in having larger diameters and S4 septa usually well developed.

A form from Fischerwiese described by CUIF (1975 a), due to its unusually high number of S4 septa, differs from typically developed *R. fenestrata* (REUSS) *sensu* FRECH (= *R. frechi* sp. n.). It has a counterpart in a morphotype represented in GBA collection by colonies No. 1982/12/748 and 749.

The HAAS collection contains material of moderate value for microscopic observations.

**Distribution:** Rhaetian of the Northern Calcareous Alps; known from Zlambach Beds of Fischerwiese, Hallstätter Salzberg, Zlambachgraben and Kesselwand-Rohrmoos.

*Retiophyllia caespitosa* (REUSS, 1865)

Pl. 8, figs. 2, 4, 9; Pl. 9, fig. 3

- |                |   |
|----------------|---|
| 1865           | <i>Thecosmilia caespitosa</i> — REUSS, p. 159, Pl. 3, fig. 3                                |
| part., v. 1890 | <i>Thecosmilia caespitosa</i> REUSS — FRECH, p. 7, Pl. 1, figs. 1–12, non fig. 13           |
| v. 1909        | <i>Thecosmilia caespitosa</i> REUSS n. v. <i>pauciseptata</i> — HAAS, p. 144, Pl. 5, fig. 1 |
| 1966           | <i>Thecosmilia caespitosa</i> REUSS — CUIF, p. 534, text-fig. 2 B                           |
| 1967           | <i>Distichophyllum caespitosum</i> (REUSS) — CUIF, p. 129, text-fig. 3, Pl. 4, fig. 3       |
| 1975 a         | <i>Distichophyllum caespitosum</i> (REUSS) — CUIF, p. 375, text-figs. 35 b and 36           |
| 1986           | <i>Distichophyllum caespitosum</i> (REUSS) — MELNIKOVA, p. 47, Pl. 13, fig. 2               |

**Holotypus:** Lost

**Neotypus** (here chosen): GBA, FRECH's type collection, No. 2753; FRECH 1890, Pl. 1, fig. 4

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Diagnosis:** Colony caespitose, offsets bifurcating at an obtuse angle. Corallite diameter 10 mm. Pellicular wall present. Costae subequal, thin. Connecting processes flat. Radial elements differentiated into 3 (rarely 4) orders; costal portion very short. Ornamentation scarce. Endotheca of large and sparse dissepiments.

**Material:** About thirty corallite fragments from Fischerwiese, GBA 1982/12/69–90, 92, 93, NHMW 1982/57/46–50, 67 and two complete colonies, GBA 1982/12/764, 765; one corallite fragment from Kleiner Zlambachgraben, GBA 1982/12/648; more than twenty thin sections

## Dimensions (in mm):

Specimen No.	d	s	c/3 mm	Remarks
GBA 1982/12/70	9 × 11	50 (13 + 13 + 19 + 5)		before bifurcation
70 A	8	28 (7 + 5 + 12 + 4)		juvenile A
70 B	9	35 (9 + 11 + 15)		juvenile B
GBA 1982/12/84	8 × 15	46 (12 + 11 + 23)		before bifurcation
84 A	11	40 (12 + 12 + 16)		juvenile A
GBA 1982/12/76	10 × 11	42 (10 + 11 + 21)		
GBA 1982/12/764	9 × 11	45 (14 + 14 + 17)	4–6	
	8 × 13	61 (17 + 17 + 27)	4–8	before bifurcation
	8 × 12	65 (16 + 16 + 31 + 2)	5–8	before bifurcation

**Description:** Corallites bifurcate frequently and at an obtuse angle. Corallite surface costulate and covered with a thin pellicular wall (Pl. 8, figs. 2, 9). The number of costae and their thickness depend on the stage of the septal apparatus development: in corallites with short S3 septa the costae are denser and thinner than in those having S3 septa fully developed. A tendency towards uniform thickening of all radial elements is observed (Pl. 8, fig. 4).

Septa of 3 (temporarily 4) size ranges differing in length. In corallites with non-thickened skeleton, septa are thin and ornamented with large, protruding granules. In corallites with thickened skeleton, all septa are subequal in thickness, their internal edges being club- or wedge-shaped. The S1 septa are often shorter than the radius, leaving the axial cavity free. The S2 septa are distinctly shorter than S1; the S3 septa are variable in length and can reach half the length of S1. S4 septa rare, transitional and representing the initial stages of development of septa of a higher order.

Endotheca formed of variable elements: (i) sparse and large dissepiments crossing the lumen, (ii) few vesicles leaning against the wall, and (iii) small vesicles leaning against the septal blades, abundant at the stage immediately preceding division of a corallite (Pl. 9, fig. 3).

Septotheca well developed.

**Microstructure:** In S1 and S2 septa, the median septal zone is undulating or zigzagged; peripherally, the lateral portions of septal blades are formed of closely spaced lateral trabeculae. In other portions of S1 and S2 septa and in young septa, fibre fascicles are devoid of an axis.

**Discussion:** The description has been completed with species diagnosis as originally the taxon was very briefly diagnosed.

*Retiophyllia caespitosa* differs from *R. frechi* and *R. norica* in its less numerous dissepiments and relatively few and poorly ornamented septa of subequal thickness. However, there are specimens known with well ornamented septa fitting well within the diagnosis. Corallite size of *R. caespitosa* is intermediate between *R. frechi* and *R. norica*.

In the GBA collection of types there are four specimens in the Fischerwiese illustrated collection of FRECH (1890, Pl. 1, figs. 1–4, GBA No. 2753) and a specimen from Hallstätter Salzberg (*op. cit.* Pl. 1, fig. 13, No. 2754) labelled *Th. caespitosa*. The latter specimen is a pseudo-ceriod colony fragment of a calicular surface with numerous young individuals of a diameter equal to one-quarter the diameter of adults. It has nothing in common with the genus *Retiophyllia* nor any related genus. In all probability this form represents *Cyclophyllia major* (p. 29). As to other figured specimens preserved in the collection, they have a typically developed septal apparatus, corallite surface obliterated or

with costae covered by pellicular wall (specimens figured by FRECH 1890, Pl. 1, figs. 1 and 4).

In the collection examined, the nature of the corallite surface is difficult to ascertain as the majority of specimens collected is represented by corallite fragments with corroded surfaces. Only four fragments of corallites from thirty examined here have a pellicular covering fragmentarily preserved on subequal, slightly protruding costae. The pellicular wall is well preserved in the colony embedded in the rock (GBA 1982/12/764: Pl. 8, fig. 9).

The species has been chosen by CUIF (1967) as type species of a new genus, *Distichophyllum*. He emphasized the microstructure as a diagnostic feature distinguishing it from *Retiophyllia* CUIF, 1967. He interpreted the structure of radial elements as devoid of a costal portion and this representing simple septa, not costosepta typical of *Retiophyllia*. The zigzag mid-line of *Distichophyllum* he contrasted with the undulating one in *Retiophyllia*, and stressed that synapticulae are absent in *Distichophyllum*. These distinguishing features are considered in turn: (i) in the case of septum *versus* costoseptum, it is apparent that in this species, the zone of trabecular divergence is strongly displaced peripherally. Nevertheless, the costal portions are developed and, on well preserved corallite surfaces, thick, short costae may be observed (Pl. 8, figs. 2 a, b, 9); (ii) the lack of synapticular structure in *R. caespitosa* could be considered to be a simple consequence of a very close septal arrangement; (iii) zigzag mid-lines, identical to that in *caespitosa*, are known in *R. norica* and *R. frechi* (Pl. 13, fig. 2 and Pl. 14, fig. 2), both possessing typically developed radial elements of a costoseptal type. On the basis of the material examined, it is difficult to support CUIF's view that *R. caespitosa* represents a separate genus.

Distribution: Rhaetian of the Northern Calcareous Alps; known in Zlambach Beds from Fischerwiese and Zlambachgraben. Norian of the Caucasus and Central and NE Asia.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Retiophyllia norica* (FRECH, 1890)

Pl. 8, figs. 5–8; Pl. 9, fig. 2; Pl. 14, figs. 1, 2

part., v. 1890 *Thecosmilia norica* – FRECH, p. 9, Pl. 1, figs. 14–24 (non Pl. 10, fig. 6)

v. 1909 *Thecosmilia norica* FRECH nov. var. *densiseptata* and nov. var. *lobatiseptata* – HAAS, p. 145, Pl. 5, figs. 3 and 4

non 1975 *Paradistichophyllum noricum* (FRECH) – MELNIKOVA, p. 90, Pl. 15, figs. 3, 4

Lectotypus (here chosen): GBA FRECH's type collection, No. 2744; FRECH 1890, Pl. 1, fig. 19

Paralectotypus: The only originals preserved are those presented in FRECH 1890, Pl. 1, figs. 19 and 20 (both GBA No. 2744), the second of them has been here chosen as paralectotypus

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: About forty fragmentary corallites from Fischerwiese, GBA 1982/12/91, 94–129, NHMW 1982/57/41, 45; one fragment from Kleiner Zlambachgraben, GBA 1982/12/649; about twenty thin sections

## Dimensions (in mm):

Specimen No.	d	s	c/3 mm	Remarks
GBA 1982/12/112	11	50	5–6	
GBA 1982/12/113	11 × 13	72 (13 + 9 + 16 + 34)	5–7	before bifurcation
113 A	12	56 (14 + 12 + 14 + 28)	5–7	juvenile A
113 B	14	74 (11 + 19 + 16 + 37)	5–7	juvenile B
GBA 1982/12/115	10 × 15	78		before bifurcation
115 A	12	53	7–8	juvenile A
115 B	13	66	7–8	juvenile B
NHMW 1982/57/41	11 × 15	85 (14 + 14 + 27 + 30)	7–8	before bifurcation
41 A	8 × 11	56	7–8	juvenile A

**Description:** Corallites bifurcating at an obtuse angle. On the corallite surface, there may be developed rare overhanging folds, homologues of the connecting processes (Pl. 8, fig. 6 a). Pellicular wall very thin (preserved in fragments), failing to mask the costae. Septo-synapticular wall may develop.

Septa fusiform, the largest in the zone of trabecular divergence. Internal septal edges with a tendency to thicken and to incorporate dissepiments into their structure (Pl. 8, fig. 6 b, Pl. 9, fig. 2). Thickening of septal skeletal elements reduces the lumen.

Septal apparatus formed by septa of 3–4 orders. The S1 septa are the longest and thickest and reach the centre; the S2 septa are subequal in length or shorter than S1; the S3 septa are roughly half the length of S1; the S4 septa are of variable length between  $\frac{1}{4}$  and  $\frac{1}{3}$  the length of S1. Costae subequal, thin (Pl. 8, figs. 5 a, b).

S1 and S2 septa provided with lateral projections in their costal portions. The projections, developed as spines or short ledges directed upward, meet the opposite septal blades and form synapticulae. The synapticulae are ordered in 1–3 incomplete rings (Pl. 14, fig. 1 b). On the eroded corallite surface, there are lateral septal projections visible reaching the adjacent septal blades (GBA 1982/12/109: Pl. 8, fig. 7).

In corallites in which the number of septa increases, lower order septa are promoted to a higher order and the shortest, new septa appear at the wall. New septa grow in pairs, each diverging from the S3 septum (Pl. 8, fig. 7).

The endotheca is composed of the following kinds of dissepiments: (i) subhorizontal ones crossing the lumen, (ii) small, vesicular, peripheral dissepiments convex adaxially, (iii) dissepiments variable in number, irregular in size, based as a group against the septal faces. The latter are most frequent at the centre, in the zone below the level of corallite bifurcation. Transverse sections show that the endotheca, in general, is depressed in the centre. However, an elevation at the centre can appear sporadically. Exothecal, i. e. small marginal vesicles, external to the zone of divergence, are convex abaxially (Pl. 14, fig. 1 a).

**Microstructure:** The mid-septal zone is straight or undulating in the *Distichophyllia* pattern (Pl. 14, figs. 1 b, 2, compare CUIF 1975 a, text-fig. 4). In the zone of trabecular divergence, the S1 septal blade is built of closely packed lateral trabeculae, each provided with an axis. Fascicles of fibres may attain a conspicuous length and transform into synapticulae (Pl. 14, fig. 1 b). Trabeculae in the mid-zone are 20–30  $\mu$ m in diameter. Rare septal granules are large and circular in section. The skeleton is thickened by the overgrowth of septa and dissepiments by successive continuous layers of fibrous stereome. The pellicular wall is fibrous in structure and shows centripetal growth. Septal external edges are embedded in wall tissue (Pl. 14, fig. 1 a).

**Discussion:** The species is well characterized in the original description and figures. Specimens from the LOBITZER and HAAS collections, although fragmentary, have well preserved microstructure and such fragile details as pellicular wall. Two specimens from the FRECH type collection which are stored at GBA (FRECH 1890, Pl. 1, figs. 19 and 20, No. 2744) much resemble *R. caespitosa*. In reality, specimens of *R. norica* having small diameter corallites are hardly distinguishable from *R. caespitosa*. Specimen figured by FRECH *op. cit.*, Pl. 10, fig. 6 represents rather *R. robusta* than *R. norica*.

Corals described from Pamirs by MELNIKOVA (1975) as *Paradistichophyllum noricum* (FRECH, 1890) differ from the Alpine form and from other species of *Retiophyllia* in having numerous low, largely extending dissepiments, as well as narrow and long axial fissure.

**Distribution:** Rhaetian of the Northern Calcareous Alps; known in Zlambach Beds of Fischerwiese and Zlambachgraben. Frequently described in the literature concerning the Tethyan Upper Triassic.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Retiophyllia robusta* sp. n.

Pl. 8, figs. 1, 3, 10

? 1890 *Thecosmilia norica* — FRECH, Pl. 10, fig. 6

**Syntypi:** GBA 1982/12/435, 766, 767; Pl. 8, figs. 3, 10

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Derivatio nominis:** Latin *robustus* — strong, from a thick structure of the skeleton.

**Diagnosis:** Colonies built of a few corallites. Corallites about 15–20 mm in diameter with 40–50 septa. Radial elements very strong, costae protruding.

**Material:** Twelve colony fragments from Fischerwiese, GBA 1982/12/430–435, 766, 767, NHMW 1982/57/42, 51, 52, 55; one nearly complete colony from Kesselwand-Rohrmoos, and two fragments, NHMW 1982/56/15<sub>1</sub>–15<sub>3</sub>; eight thin sections

**Dimensions (in mm):**

Specimen No.	d	s	c/3 mm	Remarks
NHMW 1982/57/51	15 × 20			before bifurcation
51 A	11 × 13	34		juvenile A
51 B	11 × 13	35		juvenile B
NHMW 1982/57/52	10 × 18	52	3–4	before bifurcation
52 A	13	32	3	juvenile A
NHMW 1982/57/55	16 × 18	51		before bifurcation
55 A	13	30		juvenile A
55 B	10	23		juvenile B
NHMW 1982/56/15 <sub>1</sub>	18	52	4–5	
GBA 1982/12/434	16	51		before bifurcation
434 A	13 × 15	46		juvenile A
434 B	14	39		juvenile B

**Description:** Colonies small, composed of 2–6 corallites (Pl. 8, fig. 1). Bifurcation at small intervals. Protocorallite tall. Connecting processes reduced to feebly

marked folds. Corallite surface strongly costulate, at least in the calicular region. Costae of the two first orders thick, protruding (Pl. 8, fig. 3). Pellicular wall does not mask the costae.

Radial elements fusiform, often strongly thickened (Pl. 8, fig. 10). Lateral ornamentation granular, thick, scarce. Septa are differentiated into 3–4 orders. The S1 septa approach the axis, often club-shaped, S2 are thinner and shorter than S1, S3 are  $\frac{1}{4}$ – $\frac{1}{2}$  the length of S1, regularly distributed. The S4 septa are developed in corallites of increasing diameter, as an initial stage of S3. Septal mid-line in S1 and S2 septa fine, undulating or zigzagged in the costal portion.

Endotheca of large, low dissepiments, sloping at the periphery and subhorizontal at the axial cavity.

Stereozone peripheral, if developed.

**Discussion and Remarks:** Large corallite diameters, large dissepiments, strong costae of the first two orders and relatively low number of septa differentiate this species from others. The same characters may be observed in the illustration in FRECH 1890, Pl. 10, fig. 6, representing a specimen determined as *Thecosmilia norica*.

The specimens examined are strongly abraded. The pellicular wall is preserved only on one fragmentary corallite.

**Distribution:** Rhaetian of the Northern Calcareous Alps; known from the Zlam-bach Beds of Fischerwiese and Kesselwand-Rohrmoos.

## 2. *Retiophyllia gosaviensis* group

### *Retiophyllia gosaviensis* sp. n. Pl. 9, fig. 1, Pl. 11, figs. 4, 5

**Holotypus:** NHMW 1903 XII 17; Pl. 9, fig. 1, Pl. 11, figs. 4 a–c

**Locus typicus:** Kesselwand-Rohrmoos

**Stratum typicum:** Zlam-bach Beds

**Derivatio nominis:** From the locality name – Gosau in Alps.

**Diagnosis:** Corallites more frequently oval in cross section than circular. Diameters of adult corallites about  $8 \times 10$  mm, with more than 100 septa; septal density 10–12/3 mm.

**Material:** Three specimens from Kesselwand-Rohrmoos, NHMW 1903 XII 17, 95, NHMW 1982/56/13; five thin sections

**Dimensions (in mm):**

Specimen No.	d	s	s/3 mm
NHMW 1903 XII 17	$8 \times 11$	121 (20 S1 in it)	12
	$8 \times 10$	109	11–12
NHMW 1903 XII 95			10

**Description:** Colony phaceloid, dense. Connecting processes frequent. Corallite surface covered with thin pellicula. When the latter is abraded, the corallite surface shows thin, even, densely packed costae (Pl. 11, figs. 5 a, b).

The process of budding is longlasting; corallites remain not separated for a long time after their septal apparatuses have been reorganized in relation to new calicular centres and definitely separated (Pl. 11, fig. 5 a).

Radial elements fusiform, with long and delicate costal portion. Septa in four size orders. Systems uneven — some of them fully developed but some with very short S4 or even with S4 lacking. The S1 septa are strongest and reach the axis; S2 may attain the same length but usually are shorter and thinner than S1; S3 usually longer than  $\frac{2}{3}$  of the length of S1; S4 rather regularly distributed, short or attaining one-third of the radius in length depending on a system (Pl. 11, figs. 4 b, c). Thickened internal edges of S1–S2 septa form a sort of columella. Lateral edges covered with strong granules.

Endotheca formed of rather large dissepiments in the periaxial region and smaller ones peripherally. At the corallite circumference one ring of rather small dissepiments is developed which may be completed by some vesicles of the exotheca (Pl. 9, fig. 1).

Microstructure: The mid-septal line is straight or zigzag. The lateral trabeculae are well developed in thick septa. No tendency to form lateral septal projections is observed. Upper dissepimental layer may be thick. The steromal internal wall develops at about  $\frac{1}{4}$ – $\frac{1}{3}$  the way from the wall axialwards.

Discussion: The species differs from other known *Retiophyllia* species in its numerous septa, equal, thin and dense costae, in septal apparatus with well developed S4 septa, and in its longlasting process of division of corallites.

Distribution: Rhaetian of the Northern Calcareous Alps: known only in the type locality.

### 3. *Retiophyllia multiramis* group

*Retiophyllia multiramis* sp. n.

Pl. 9, fig. 4, Pl. 11, figs. 1–3, Pl. 12, fig. 1

Holotypus: NHMW 1982/56/7; Pl. 11, fig. 2

Paratypi: NHMW 1959/361/9; Pl. 11, figs. 1 a–b

NHMW 1982/56/10; Pl. 12, figs. 1 a–h

Locus typicus: Kesselwand-Rohrmoos

Stratum typicum: Zlambach Beds

Derivatio nominis: Latin *multi* — many, *ramus* — branch, from ramose colony shape.

Diagnosis: Corallite bifurcating at a sharp angle. Connecting processes present. Mean diameter 4.5–5.5 mm, with 50–85 septa. Septal apparatus composed of S1–S4 septa, with sporadic S5; S1 septa thickest and reaching the axis. Costae thin, equal, covered with pellicular wall. Septal ornamentation in form of menianes and isolated granules. Endotheca concave, with numerous, small vesicles at the axial cavity.

Material: Five specimens from Kesselwand-Rohrmoos, NHMW 182/56/7<sub>1</sub>, 7<sub>2</sub>, 8, 10, NHMW 1959/361/9 and two from Fischerwiese, NHMW 1982/57/97 and GBA 1982/12/768; ten thin sections. The species well represented in NHMW collections from Kesselwand-Rohrmoos.

#### Dimensions (in mm):

Specimen No.	d	s	c/3 mm
NHMW 1982/56/7 <sub>1</sub>	4.5	54 (14 S1/S2 + 14 + 26)	11–14
	4 × 6	72 (19 S1/S2 + 20 + 33)	
	4.5 × 6	65 (10 + 10 + 19 + 26)	
	5.5	52 (14 S1/S2 + 13 + 25)	
	5.5	85 (27 S1/S2 + 21 + 33 + 4)	
NHMW 1982/56/8	5.5	85 (27 S1/S2 + 21 + 33 + 4)	
	4.5 × 6	70	



**Description:** Corallites densely distributed in the colony (Pl. 11, figs. 1, 3). Connecting processes abundant. Bifurcations and trifurcations (NHMW 1982/56/8) frequent.

Radial elements fusiform, especially S1 and S2, differentiated into four orders; S5 septa sporadic. Ornamentation conspicuous, in the form of protruding menianes of variable length as well as isolated, flattened granules (Pl. 11, fig. 2, Pl. 12, figs. 1 a–e, 1 h). The S1 septa reach the axis; S1 and S2 subequal in length but S2 usually thinner than S1; S1 and S2 meet at the axis with their internal edges. S3 variable in length, reaching  $\frac{1}{2}$ – $\frac{4}{5}$  the length of S1. The S4 septa are very variable in length: when normally developed they equal  $\frac{1}{3}$  the length of S1 but in other cases they can be either longer or rudimentary. The systems are usually disturbed by an overgrowth of the S2 septa. The axial cavity is filled with the internal edges of S1 and S2 septa, as well as dissepiments (Pl. 11, fig. 2). An internal stereozonal ring appears irregularly.

Endotheca is formed by (i) small peripheral vesicles, disposed in 1–3 rings, (ii) larger ones, situated axialwards and (iii) very small ones at the axial cavity (Pl. 9, fig. 4, Pl. 12, fig. 1 b).

The pellicular wall masks the costae which are thin and equal.

**Variability:** The specimens examined differ from each other in some individual features: NHMW 1982/56/8 bifurcates and trifurcates frequently; the mid-lines of S1 and S2 are straight or weakly undulating. NHMW 1982/56/7<sub>1</sub> has very long S4, even longer than  $\frac{1}{3}$  the length of S1; the mid-line is undulating and zigzagged, trabeculae rather thinner than in other specimens, and vesicles abundant. NHMW 1982/56/10 has the strongest menianes of all, especially well expressed in the juvenile corallite figured in Pl. 12, fig. 1 a.

**Microstructure:** Trabeculae clearly visible. There is a pronounced tendency to individualize trabeculae of a diameter 2–3 times larger than the smallest ones (Pl. 12, figs. 1 d, f). The trabeculae in S1 septa are 60–90  $\mu$ m in radial and 150–220  $\mu$ m in transverse diameter. In S2 and S3 septa trabeculae are mostly isometric, 24–40  $\mu$ m (usually 30–40  $\mu$ m) in diameter. Thick trabeculae are well delimited, often alternating along the mid-line. Small trabeculae may be well delimited or fused in the mid-line. Median septal line is straight, sinuous or zigzagged. In thick trabeculae, many axes may be seen in the centre. This implies that they are formed by the fusion of small trabeculae.

In the wall region, the thick trabeculae may form lateral trabecular axes which protrude into the interseptal space in the form of lateral projections and reach neighbouring septa as strong synapticalae (Pl. 12, fig. 1 g).

Menianes are formed as lateral enlargements of the trabeculae. Their edges are thin and smooth. Fibres in the menianes are subparallel (Pl. 12, fig. 1 d).

**Discussion:** The species seems to be closely related to the *R. clathrata* group of species as it has numerous and strongly ornamented septa. It resembles *R. paraclathrata* RONIEWICZ, 1974 in corallite diameters and prominent septal ornamentation. However, it differs from that species in more abundant septa and dissepiments. A question arises whether it is conspecific with the Alpine coral described by ZANKL (1969) as *Thecosmilia clathrata* forma A, as the corallite diameters of both species are the same, but the number of septa in the second is not known. The coral described from Pamirs by MELNIKOVA as *Paradistichophyllum clathratum* (EMMRICH) shows an analogous fine structure of septal apparatus and abundant endotheca, but its diameters are about twice as large as in the new species (1975). Unfortunately, any valuable comparison with *R. clathrata* (EMMRICH) is practically impossible to make as the type material of this species has not

been re-examined. In such a situation, I prefer to introduce a new name to avoid further confusion.

Other similar species, known so far, are: *Retiophyllia minima* (MELNIKOVA, 1975) and *R. multigranulata* (MELNIKOVA, 1975), from which the new species differs in corallite diameters and in strong development of the pseudo-columellar structure.

Distribution: Rhaetian of the Northern Calcareous Alps; abundant in Zlambach Beds of Kesselwand-Rohrmoos, rare in Fischerwiese.

*Retiophyllia* sp. A.

Pl. 7, fig. 9

part., v. 1890 *Thecosmilia oppeli* REUSS – FRECH, Pl. 2, fig. 21, 22 (non Pl. 2, figs. 18, 19, 23, 24)

Material: Four fragmentary branches from Hallstätter Salzberg, GBA 1982/12/792–794, 797; one fragment from Schneckengraben, NHMW 1982/56/10<sub>2</sub>; six thin sections

Dimensions (in mm):

Specimen No.	d	s	s/1 mm
GBA 1982/12/793	3.5 × 4	e. 34 (7 + 7 + 14 + e. 6 S4)	5
GBA 1982/12/796	3.5		5

Description: Branches diverging at very irregular distances and at rather obtuse angles. At the top of the branch equivalent forking takes place which is usually followed by subsequent uneven growth of "twins", one of them remaining as short, underdeveloped individual. A series of short individuals may occupy one side of the branch. External corallite surface smooth or minutely granulated. Connecting processes have not been observed.

Septa differentiated into four orders, S1 being strongest and long and S4 rather rare. Distribution of S1–S3 septa is very irregular. Septal ornamentation in the form of large, flattened, strongly protruding granules. Lateral septal projections may be developed. Microstructure preserved in vestiges.

Discussion and Remarks: The form is remarkable for its colony growth form and granular corallite surface. Both features distinguish it from other species of *Retiophyllia*. Scarce and strongly recrystallized material does not allow for detailed characteristics of the species to be made.

The figured specimens of FRECH (see synonymy) are kept in GBA FRECH's collection, box No. 2751 with *R. oppeli* specimens.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Hallstätter Salzberg and Schneckengraben.

4. *Retiophyllia fenestrata* group

*Retiophyllia gracilis* sp. n.

Pl. 9, fig. 9, Pl. 10, fig. 2, Pl. 13, fig. 3

Holotypus: NHMW 1982/56/9, original label *Thecosmilia charlyana*; Pl. 10, fig. 2, Pl. 13, fig. 3

Locus typicus: Kesselwand-Rohrmoos

**Stratum typicum: Zlambach Beds**

**Derivatio nominis:** Latin *gracilis* – slim, for its narrow corallite diameters.

**Diagnosis:** Corallites 3–5 mm in diameter, with relatively thin and abundant septa between 40 and 60 in number. Pellicular wall relatively thick. Endotheca convex at the centre.

**Material:** Colonies and isolated corallites from Fischerwiese, GBA 1982/12/145, 776, 782–785 and from Kesselwand-Rohrmoos, NHMW 1982/56/2<sub>1</sub>, 2<sub>2</sub>, 9, 11; eight thin sections. The species is well represented in the NHMW collections from Kesselwand-Rohrmoos.

**Dimensions (in mm):**

Specimen No.	d	s	c/3 mm
NHMW 1982/56/9	3	44 (6 + 6 + 10 + 22)	8–12
	3.5 × 4	39 (7 + 6 + 11 + 15)	
	3.5 × 4.5	50 (12 + 13 + 23 + 3)	
	3.5	51 (9 + 8 + 17 + 17)	
	3.5 × 5.5	62 (10 + 10 + 15 + 27)	
	4.5 × 4	56 (12 + 11 + 23 + 10)	

**Description:** Colonies 50–60 mm in height. Branching frequent. Connecting processes large, abundant. In cross section, corallites sub-circular in shape (Pl. 10, fig. 2).

Radial elements are subequal in thickness and rather thin. Ornamentation is scanty, granular. The septal apparatus is differentiated into septa of four orders. The S1 and S2 septa are subequal in length, approaching the axis. The S3 septa between  $\frac{1}{2}$  and  $\frac{2}{3}$  the length of S1. The S4 septa frequently appear as rudiments on the internal surface of the pellicular wall. When well developed, they reach  $\frac{1}{4}$  the length of S1. Costae thin, undifferentiated in size. In peripheral septal parts a tendency is observed to develop well defined trabeculae up to 90 µm in radial diameter (Pl. 13, fig. 3).

Endotheca at the centre formed of a small number of large and convex dissepiments (Pl. 9, fig. 9). Peripheral ring, if developed, is formed of small dissepiments.

Pellicular wall relatively thick, transversely wrinkled, masking the costae. An internal or peripheral wall stereozone is developed.

**Microstructure:** See p. 45.

**Discussion:** In its internal corallite structure, the species resembles the following species: *R. sellae* (STOPPANI) in FRECH (1890) and RONIEWICZ (1974), *R. wanneri* (VINASSA DE REGNY) in MELNIKOVA (1975), *Retiophyllia* type IV of CUIF (1975 a) and *R. fenestrata* (REUSS). It differs from all of them in its narrower corallite diameter.

Some illustrations of *R. oppeli* given by FRECH (1890, Pl. 3, figs. 4 A–D) show a form resembling this species in its corallite cross-section. The dissepiments in cross section of corallites of *R. oppeli* are much more abundant, however, than those in *R. gracilis*.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Kesselwand-Rohrmoos and Fischerwiese.

*Retiophyllia fenestrata* REUSS, 1854

Pl. 9, fig. 6, Pl. 10, fig. 1, Pl. 13, fig. 1

- v. 1854 *Calamophyllia fenestrata* – REUSS, p. 105, Pl. 5, fig. 20, non 21  
 part. 1890 *Thecosmillia fenestrata* REUSS – FRECH, Pl. 2, figs. 12, 12 A, non description, nec other illustrations

- non 1966 *Thecosmilia fenestrata* REUSS – CUIF, 533, text-fig. 2  
 non 1967 *Retiophyllia fenestrata* REUSS – CUIF, 130, text-fig. 4, Pl. 4, fig. 4  
 1973 *Archaeophyllia fenestrata* REUSS – BEAUVAIS, p. 311, Pl. 4, figs. 8, 9, 10  
 non 1975 a *Retiophyllia fenestrata* REUSS – CUIF, p. 369, figs. 33–35 a  
 1986 *Retiophyllia fenestrata* (REUSS) – MATZNER, Pl. 9, fig. 5, Pl. 10, fig. 4  
 non 1986 *Retiophyllia fenestrata* (REUSS) – MELNIKOVA, p. 48, Pl. 14, fig. 4

Holotypus: NHMW type collection, No. 148; figured by REUSS 1854, Pl. 5, fig. 20; refigured by FRECH 1890, Pl. 2, figs. 12, 12 A, BEAUVAIS 1972, Pl. 4, figs. 8–10 and herein Pl. 9, fig. 6, Pl. 10, figs. 1 a, b, Pl. 13, figs. 1 a–c

Locus typicus: Zlambach near Altaussee

Stratum typicum: Zlambach Beds

Diagnosis: Corallites bifurcating at a sharp angle. Connecting processes abundant. Adult diameters are between 5.5 and 6 mm with 28–34 S1–S3 septa and a variable number up to 20 of rudimentary S4. Septa thickened. Dissepiments large, rare, convex at the centre. Pellicular wall relatively thick<sup>7</sup>.

Material: Two colonies from the vicinity of Altaussee: the holotype from Zlambach and one colony from Fischerwiese, GBA 1982/12/775; one colony from Kesselwand-Rohrmoos, NHMW 1982/56/7<sub>2</sub>; six thin sections

#### Dimensions (in mm):

holotype	d	s	Remarks
	5	29 (9 + 9 + 11)	juvenile
	5 × 6	39 (8 + 8 + 16 + 7)	adult
	5 × 6	38 (7 + 7 + 14 + 10)	
	5 × 6	46 (7 + 7 + 14 + 18)	
	6	50 (9 + 8 + 17 + 16)	

Description: Corallites densely packed in the colony, connected to each other by abundant, large processes. In cross section corallites are subcircular. Pellicular wall masks details of the internal corallite structure.

Septa thick, fusiform, differentiated into four orders (Pl. 10, figs. 1 a, b). S1 septa approach the centre, where a narrow space remains free. S2 septa distinctly shorter and thinner than S1, whilst S3 septa reach roughly half the length of S1. S4 septa relatively numerous, rudimentary. Stereozonal wall thick, formed by lateral septal processes.

Endotheca differentiated into two zones: the peripheral one formed by vesicles convex outward, and the internal zone formed by large convex vesicles, constituting a central elevation (Pl. 9, fig. 6).

Microstructure: Small trabeculae are disposed along the straight or zigzagged mid-septal line (Pl. 13, figs. 1 a–c). Trabeculae grow in diameter peripherally (p. 45). Lateral axes are developed, and at the zone of trabecular divergence lateral septal projections are observed.

Discussion: *R. fenestrata* belongs to the group of species characterized by a median zone of elevated dissepiments, together with *R. gracilis* and *R. gephyrophora*. In the structure of the septal apparatus it much resembles *R. gracilis*. *R. fenestrata* is known

<sup>7</sup> The diagnosis of this, so far, poorly known species has been given to facilitate comparisons with other species.

as a species typical of Fischerwiese, whereas *R. gracilis* is especially abundant in the Gosaukamm vicinity, although observed in both.

A form described by MELNIKOVA (1986) differs from the Alpine species in its endotheca built of numerous small dissepiments.

**Distribution:** Rhaetian of the Northern Calcareous Alps; known in Zlambach, Fischerwiese and in the Gosaukamm vicinity.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Retiophyllia gephyrophora* sp. n.

Pl. 9, fig. 10, Pl. 10, fig. 5

**Holotypus:** NHMW 1982/56/14; Pl. 9, figs. 10 a, b, Pl. 10, figs. 5 a, b

**Locus typicus:** Kesselwand-Rohrmoos

**Stratum typicum:** Zlambach Beds

**Derivatio nominis:** Greek *gephyros* – bridge, *phoros* – bearing, from the connecting processes abundantly developed.

**Diagnosis:** Corallites subcylindrical, irregular in transverse section; connecting processes abundant and thick; septa differentiated into 3 orders, about 55 in number at a diameter of 9–10 mm; wall internal; pellicular wall strong.

**Material:** Holotype colony; fourteen thin sections

**Dimensions (in mm):**

d	s	Remarks
9	55	internal
10 × 11	58	parts of the
9 × 15	60	corallites are
11 × 13	72	recrystallized

**Description:** Colony phaceloid, dense, formed by corallites irregular in shape in cross section. Connecting processes thick and numerous, 5–8 mm apart (Pl. 10, fig. 5 a, Pl. 9, figs. 10 a, b). Bifurcation occurs at a sharp angle, producing equivalent-sized individuals. Corallite surface covered with pellicular wall (60–90 µm thick).

Radial elements fusiform (Pl. 10, fig. 5 b) with the costal part well developed: in the longest septa, the ratio of the costal to the septal portion is 1 : 4 or 1 : 3. Septa differentiated into 3 orders: S1 approach the axis, thin at their internal edge, S2 shorter than S1 and S3 very variable in length – from rudimentary up to half the length of S1. Ornamentation has not been noticed. In the zone of trabecular divergence, there are thick lateral septal projections provided with their own axes, oblique to the septal blade in cross section and directed slightly upward. An internal wall develops in the zone of trabecular divergence. Its structure is composite: fusiform thickened septa, lateral septal projections and stereozone developed on dissepiments. Usually, costae are embedded in the pellicular wall tissue but in places these two skeletal elements are not in contact.

Endotheca is formed (i) at the centre with large, convex or subhorizontal dissepiments crossing the lumen, (ii) at the internal wall, with smaller dissepiments and (iii) outside the internal wall region, with small dissepiments covered with the pellicular wall (Pl. 9, figs. 10 a, b).

**Microstructure:** The microstructure of the radial elements is composite: the costal portion is formed by relatively large trabeculae, the septal portion is small-trabecular and

between them trabeculae of transitional dimensions are observed. Costal trabeculae are 90  $\mu\text{m}$  in diameter with their centres disposed in the mid-line. Towards the corallite axis, their dimensions become smaller and frequently they are disposed alternately in relation to the mid-line. Adaxially, the septa are uniformly small-trabecular. The midline is straight or slightly wavy and the lateral fibres become palisaded or slightly centered into fascicles. In better preserved fragments the original small trabeculae are visible or their easily recognized vestiges, their diameters being between 20 and 30 (rarely 60)  $\mu\text{m}$ . The smallest, rudimentary septa nearly all show well developed trabeculae of rather large diameters.

The pellicular wall is formed by fascicles of fibres growing centripetally. Seen in longitudinal section, fascicles are directed slightly upwards (about 55°).

**Discussion:** The new species differs sharply from other retiophylliids of the same corallite diameter in the low septal number, the large endothecal dissepiments and relatively thick pellicular wall.

**Distribution:** Rhaetian of the Northern Calcareous Alps. The species is known from the type locality only.

### Genus *Oedalmia* CUIF, 1976

**Species typica:** *Thamnastraea norica* FRECH, 1890

**Emended diagnosis:** Colonies thamnasterioid, calices in meandroid series. Distal and internal septal edges smooth. Lateral septal stereome organized into fascicles of fibres; lateral axes may develop; septal ornamentation granular. Endotheca abundant, small-vesicular.

**Species included:** The type species only.

In the GBA collection a thamnasterioid form is known (p. 63) which may represent another species of *Oedalmia*.

**Stratigraphie and geographic ranges:** Rhaetian of the Alpine region.

**Remarks:** The above diagnosis differs essentially from the original one (CUIF 1976, 159) in the characteristics of the endotheca (see p. 63).

### *Oedalmia norica* FRECH, 1890

Pl. 15, figs. 3, 4, 6

v. 1890 *Thamnastraea norica* nov. sp. — FRECH, p. 63, Pl. 17, figs. 1–6

**Lectotypus** (here chosen): GBA FRECH's collection of types, No. 2787; FRECH 1890, Pl. 17, fig. 3

**Paralectotypi:** BSP AS XII 121–124; *ibidem*, figs. 1, 2, 5, 6; GBA FRECH's type collection, No. 2787, *ibidem* fig. 4; the specimen chosen as lectotype shows a well preserved, characteristic calicular surface of the colony.

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Material:** Twenty fragmentary colonies from Fischerwiese, GBA 1982/12/231–239, 241–247, 799; Kesselwand-Rohrmoos, NHMW 1982/56/27, 28; Schneckenengraben, NHMW 1959/365/43; twenty two thin sections

## Dimensions (in mm):

Specimen No.	c-c	d	s
NHMW 1959/365/43		8	21 ( 7 S1 reach the axis)
		11	30 (8 + 8 + 13)
NHMW 1982/56/28	5-8	9	28 (10 S1 reach the axis)
		8 × 13	38 (10 + 10 + 18)

**Description:** Colony laminar, from a few millimeters to about one decimeter thick. Calices ordered in simple series paralleling a colonial margin and diverging in places. Collines more or less sharply profiled distally. In the series, the calices are well defined and provided with a narrow calicular or fissure-like axial cavity (Pl. 15, fig. 3). Calices linked by simple bisepetal blades or by intermediate combined T-shaped or L-shaped septa. Series appear at the colonial margin as a result of extracalicular marginal budding. At the middle of the colony, the same phenomenon of serial budding is observed along the tops of the collines. Simple calices situated between the series frequent, as well as calices diverging from the series.

Septal apparatus is differentiated into septa of three orders, S1 septa being the thickest and approaching the axis. Regularly distributed S2 septa are thinner and usually shorter than S1. The S3 septa are thin, short and tending to reach the S2 septal faces with their internal edges. The septal faces are ornamented with sharp, numerous granules. The internal edges of the septa are smooth, distal edges are smooth or provided with few irregularly distributed nodular thickenings.

Endotheca is slightly depressed axially and elevated peripherally, formed by very small, abundant, vesicular dissepiments (Pl. 15, fig. 4).

**Microstructure:** The material examined is strongly recrystallized, but a wavy septal mid-line can be distinguished. In some colonies, stereome covers septa and dissepiments closing up all free interskeletal spaces.

**Discussion:** FRECH (1890) interpreted the septal structure in the type species as being originally regularly porous and thickened secondarily by stereome. He was also convinced that synapticulae here are developed. In turn, CUIF (1976) stated that the development of dissepiments in this species is impossible from the structural point of view. The examination of FRECH's originals, as well as other material from the type locality, does not confirm either of these opinions.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos.

*Oedalmia* sp.

**Material:** One specimen from Fischerwiese, GBA 1982/12/240.

**Description:** A colonial, patellate, thamnasterioid distichophylliid coral with thick septa. The colony, measuring 35 mm in diameter and 15 mm in height, is composed of a central corallite and two daughter ones. Budding circumoral in proximity of the protocorallite axis (at a distance of 10 mm). The number of septa in the protocorallite is about 40. The coral has far larger corallites than *Oedalmia norica*.

## Subfamilia Coryphyllinae BEAUVAIS, 1981

**Genus typicus:** *Coryphyllia* CUIF, 1975

**Emended diagnosis:** Typical distichophylliid corals with radial elements of higher order vertically discontinuous (lonsdaleoid). Endotheca vesicular.

Genera included: *Coryphyllia* CUIF, 1975, *Palaeastraea* KÜHN, 1936, *Kuhnastraea* CUIF, 1976, *Alakiria* CUIF, 1976, *Axotrochus* BEAUVAIS, 1986.

Discussion: The emendation concerns this part of the original diagnosis which negated the typical development of distichophylliid microstructure in this group of corals. The new diagnosis points to the presence of lonsdaleoid septa.

The original range of the subfamily included (BEAUVAIS 1981, 352), apart from the mentioned ones, *Retiophyllia* CUIF, 1967 and *Parathecosmilia* RONIEWICZ, 1974. I consider *Parathecosmilia* as the junior subjective synonym of *Retiophyllia* CUIF and I include the latter genus in the subfamily Reimaniphylliinae due to the structure of the radial elements (no tendency to develop lonsdaleoid septa).

### Genus *Coryphyllia* CUIF, 1975

Species typica: *Coryphyllia regularis* CUIF, 1975

Emended diagnosis: Simple. Pellicular wall present. Radial elements costoseptal; lonsdaleoid elements present. Dissepiments vesicular, abundant. The microstructure of the midseptal zone is small-trabecular; mid-line straight or undulated. Lateral, stereozonal septal portions built of fascicles of fibres or relatively thin lateral trabeculae. Ornamentation granular.

Species included: *C. regularis* CUIF, 1975, *C. elliptica* (MELNIKOVA, 1975), *C. frechi* (HAAS, 1909).

Stratigraphic and geographic ranges: Norian and Rhaetian of the Tethyan realm.

Discussion: The emendation of the diagnosis concerns two points: presence of lonsdaleoid septa and trabecular character of septal microstructure.

The genus, in its general morphological features resembles *Distichophyllia* CUIF, 1975. It differs from the latter in having lonsdaleoid radial elements and in a tendency to maintain the septal lateral stereome weakly organized in fascicles. Nevertheless, fascicles and even the well axed lateral trabeculae may be developed in thick septa. The Rhaetian forms (specimens of the Alps and Pamirs of *C. elliptica*) have the microstructure much more complex than the Norian species of Taurus (*C. regularis*). But, also in the Rhaetian representatives, a weakly organized stereome prevails when septa are observed in cross sections.

Lonsdaleoid septa were observed by MELNIKOVA in *C. elliptica* (MELNIKOVA, 1975), but not mentioned by CUIF (1975 a) in the description of the type species of *Coryphyllia*. Nevertheless, small (initial) lonsdaleoid septa are seen on the dissepimental surface in *C. regularis*, in the original figure given by CUIF (1975 a, text-fig. 37 b).

The genus has much in common with *Palaeastraea* KÜHN, 1936, *Kuhnastraea* CUIF, 1976 and, presumably, *Alakiria* CUIF, 1976 (lonsdaleoid septa, rather straight course of the septal mid-line, weakly marked tendency towards the trabecular organization of the lateral septal stereome).

BEAUVAIS (1981) defined a new family Coryphyllidae for the genus in question. However, the features differentiating this genus (and some similar genera just mentioned) from *Distichophyllia* and *Retiophyllia*, i. e. the ability to lonsdaleoid septa formation, and a prevailing straight course of the mid-septal line, seem to be insufficient as a basis for a taxon of the familial rank to be discriminated.



*Coryphyllia elliptica* (MELNIKOVA, 1975)

Pl. 15, figs. 1, 2, 7

1975 *Cuifia elliptica* — MELNIKOVA, p. 84, Pl. 14, figs. 3–5

Holotypus: IGD 505/277/4; MELNIKOVA 1975, Pl. 14, fig. 3

Locus typicus: Por-Dzilga, SE Pamirs

Stratum typicum: Norian-Rhaetian

Material: Four specimens of the Gosaukamm region (three of them originally labelled *Montlivaltia fritschii*), NHMW 1982/56/39<sub>1</sub>–39<sub>4</sub>; six thin sections

## Dimensions (in mm):

Specimen No.	Remarks	d	s	s/10 mm
NHMW 1982/56/39 <sub>1</sub>	at ca. 140 from the base	50 × 55	e. 155	9
	at ca. 40 from the base	40	110 (24 S1/2 + 24 + 48 + 14)	
NHMW 1980/56/39 <sub>4</sub>	h ca. 70	40 × 50	e. 148 (21 S1/2)	9
NHMW 1982/56/39 <sub>2</sub>	h ca. 50	45 × 50	151 (26 S1/2 + 26 + e. 48 + e. 5)	
	at 25 from the base	45 × 50	152	

**Description:** Corallum cylindrical or slightly flattened, attaining remarkable height and diameter, sharply narrowing proximally. Calice shallow, with a short fissure. Wall surface transversely wrinkled.

Radial elements differentiated into five size orders (Pl. 15, figs. 2 a, b). Septa of the first two orders reach the axis. The S1 septa are very thick, up to 10 times thicker than S4 or S5, their distal edges, however, being very thin and sharp. The S3 septa can reach the axis, but usually are shorter. The S4 septa, rather regularly distributed, are more than half the radius in length. Septa S5 develop in large corallites, very thin and commonly discontinuous vertically. Lonsdaleoid S6 occasionally can develop (Pl. 15, figs. 1 b, 2 a). Distal septal edge smooth. Lateral faces covered with small, abundant granules (Pl. 15, fig. 1 a). Corallite symmetry initially is hexametral or so. The systems are rather regular. The number of septa rises during the corallum growth from 48 (12 S1) at the diameter of 10 mm up to 150 (ca. 24 S1) at the diameter of 50 mm.

The corallum attains the ultimate calicular diameter and number of septa early in its ontogenetic growth (see Dimensions). The proximal end of the specimen NHMW 1982/56/39<sub>3</sub> is bent, relatively slender, of an initial diameter smaller than 10 mm. Beginning with 15 mm from the base, the corallum starts to grow in diameter and at the height of 40 mm it attains 30 × 40 mm in diameter. Other specimen (NHMW 1982/56/39<sub>1</sub>) is stout at the beginning: the base is around 5 mm in diameter; at the distance of 12 mm from the base, corallum diameter reaches 30 mm and at the height of 40 mm it has 45 mm; the whole corallum height is 130–140 mm and the calicular diameter maximum 50 mm.

Endotheca of short, adaxially inclined dissepiments rather large in size (compare with *D. norica*, Pl. 6, fig. 3).

**Microstructure:** The median septal zone is straight or wavy or zigzag in cross section, and it is built of thin trabeculae 30–70  $\mu\text{m}$  in diameter. The lateral portions of septal blades are built of fascicles of fibres organized in distinct lateral trabeculae.

The pellicular wall is built of centripetally arranged fibres and may attain 2 mm in thickness.

**Variability:** Large morphological and microstructural variability is observed among 4 examined specimens. Individuals are short or tall, elongated at the proximal end or enlarging abruptly from the base. Septa of the lonsdaleoid type in one specimen are frequent while in other are rare. The wall was rather well developed in three of them, and in the fourth (NHMW 1982/56/39<sub>2</sub>) it must have been thin and especially friable, because no traces of it are preserved (Pl. 15, fig. 7). Lateral fascicles of fibres or lateral trabeculae are individualized in different degree and are of different size, causing differentiation of shape and dimensions of septal granules in specimens.

**Discussion:** The species has been excluded from the genus *Cuifia* MELNIKOVA, 1975 and introduced to *Coryphyllia* CUIF, 1975 due to characteristics of its septal apparatus (a tendency to develop the last order septa in the form of discontinuous blades; thin abundant granulation) and endotheca (relatively large vesicles).

*C. elliptica* is well represented in the NHMW collection. The Alpine representatives from Kesselwand-Rohrmoos fit well within the original description. In the collection from Fischerwiese only one very poorly preserved specimen may be assigned to this species with reservation. Another form externally close to *C. elliptica*, originally named *Montlivaltia frechi* was stated by HAAS in this site (1909). The latter morphotype differs from *C. elliptica* (MELNIKOVA) in having a smaller number of septa. A similar form was described by VINASSA DE REGNY as *Montlivaltia stylophylloides* (1915, 100, Pl. 68, figs. 3–6). This author drew the attention to the resemblance of this species to *Phyllocoenia grandissima* FRECH or *Thecosmilia cyathophylloides* FRECH (= *Palaeastraea cyathophylloides*). Judging from the low number of septa (ca. 48 at the diameter of 22  $\times$  35 mm) the form described by VINASSA DE REGNY is not conspecific with *C. elliptica*.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Gosaukamm region (Kesselwand-Rohrmoos, Schneckengraben) and ? Fischerwiese; Norian-Rhaetian of the Pamirs and Central Iran.

### Genus *Palaeastraea* KÜHN, 1936

**Species typica:** *Thecosmilia cyathophylloides* FRECH, 1890 [= *Palaeastraea grandissima* (FRECH) in KÜHN 1936]

**Emended diagnosis:** Colony of astreoid type and massive form. Calices strongly convex and separated from each other by a narrow depression of variable depth. Budding intratentacular with trabecular linkages. Wall lacking. Radial elements strongly exsert, nonconfluent or subconfluent. Septal apparatus composed of fusiform costosepta; lonsdaleoid septa developed. Dissepiments small, vesicular, abundant. There is a tendency for the septa to thicken by the incorporation of dissepiments resting entirely against the septal faces. Septal microstructure small-trabecular, mid-septal line straight, wavy or zigzag; septal stereome intensely developed.

**Species included:** *Palaeastraea cyathophylloides* (FRECH, 1890), *P. kokeni* (FRECH, 1890), *P. grandissima* (FRECH, 1890), *P. iljinae* MELNIKOVA, 1975, *P. minima* CUIF, 1976, *P. granulata* CUIF, 1976

Stratigraphic and geographic ranges: Norian-Rhaetian of Eurasia.

Discussion: KÜHN (1936) and CUIF (1976) have contributed a great deal to the knowledge of the genus; the microstructure has been described by the latter author.

There is a need to correct the type species name, from the original *Palaeastraea grandissima* (FRECH, 1890) in KÜHN (1936) to *Thecosmilia cyathophylloides* FRECH, 1890, resulting from their synonymy. KÜHN limited *P. grandissima* (FRECH, 1890), the species originally defined by FRECH very broadly (see p. 69), to forms which have calice diameters between 5 and 14 mm with more than 36 septa. However, another of FRECH's species has these characteristics: *Thecosmilia cyathophylloides* (see below) which becomes a senior subjective synonym of *Palaeastraea grandissima* (FRECH) *sensu* KÜHN 1936.

Colonies in this genus were submissive to fragmentation due to different mechanical resistance of their components: robust corallites and linking them delicate, extracalicular dissepiments. Isolated corallites (frequent in Fischerwiese) might be considered as fragments of phaceloid colonies of *Retiophyllia*. However, they differ from retiophylliid corallites in thick-septal blades ornamented with abundant, delicate granulation, the presence of lonsdaleoid septa, and endotheca of equal, small vesicles.

From *Kuhnastraea* CUIF, the genus differs, first of all, in the lack of an intercorallite wall (further discussion on p. 70).

Distribution: The Carnian and Rhaetian of the Tethyan realm.

*Palaeastraea cyathophylloides* (FRECH, 1890)

Pl. 16, figs. 2–4, Pl. 18, fig. 7

part. 1890 *Thecosmilia* (?) *cyathophylloides* – FRECH, p. 12, Pl. 3, figs. 6 A–6 D (non figs. 7–7 A)

part., v. 1890 *Phyllocoenia grandissima* – FRECH, p. 31, Pl. 9, figs. 3, 5 (non figs. 1, 2, 4, 6, 7)

1936 *Palaeastraea grandissima* (FRECH) – KÜHN, p. 26, Pl. 1, fig. 1

Lectotypus (here chosen): BSP AS XII 7; FRECH 1890, pl. 3, figs. 6 B–6 C, herein Pl. 16, figs. 4 a–c, Pl. 18, fig. 7

Material: One fragmentary colony and 8 isolated corallites, GBA 1982/12/284, 339–343, 857, NHMW 1982/57/62; two thin sections

Dimensions (in mm):

Specimen No.	d	s	Remarks
NHMW 1982/57/62	11	24 (8 + 7 + 9)	– juvenile A
	11	30 (9 + 8 + 8 + 5)	– juvenile B
BSP AS XII 7	12	36 (11 + 11 + 13 + 1)	measured from a photograph
	11 × 18	42 (12 + 12 + 16 + 2)	

Description: Colonies massive. Septal apparatus regularly developed, differentiated into septa of 4 orders. The S1 septa are the longest and the thickest, the S2 septa are thin and  $\frac{1}{4}$  the length of S1, the S3 and S4 septa are very thin, the latter being rarely and temporarily developed. Septal faces granulated.

Endotheca small-vesicular, abundant (Pl. 18, fig. 7). Dissepimental contributions to the structure of the septal blade can be observed.

Discussion and Remarks: FRECH (1890) hesitated in assigning this species to the genus *Thecosmilia* and stressed its unequivocal resemblance to his other species,

*Phyllocoenia grandissima*. Colonies massive in type, having corallites of the same diameters as *Thecosmilia cyathophylloides*, he attributed to *Phyllocoenia grandissima*.

Lectotype represents a colony fragment in which corallites are isolated or, in some places, connected to each other by their subconfluent septa. The lack of contact between corallites has evidently resulted from the destructive activity of endolithic organisms which occupied an intercalicular space (Pl. 16, fig. 4, Pl. 18, fig. 7). KÜHN's specimen (1936, Pl. 1, fig. 1) is the best preserved of all the figured specimens of the species. KÜHN considered it to be a representative of *P. grandissima* (FRECH). The specimen is close to the lectotype of *P. cyathophylloides* (FRECH) in its corallite diameters and number of septa (compare Pl. 16, fig. 2).

FRECH's specimen named *Thecosmilia* cf. *cyathophylloides* (FRECH 1890, Pl. 3, figs. 7–7 A, GBA No. 2755) represents a species of *Retiophyllia* with a very large corallite diameter, having nothing in common with the species under discussion.

Distribution: Rhaetian of the Northern Calcareous Alps: Fischerwiese. Also, a colony found as a boulder in the massif of Plabutsch near Graz.

*Palaeastraea grandissima* (FRECH, 1890)

Pl. 16, fig. 1, Pl. 17, fig. 2

- 1826 *Astraea rosacea* — GOLDFUSS, p. 66, Pl. 22, fig. 6  
 part., v. 1891 *Phyllocoenia grandissima* — FRECH, p. 31, Pl. 3, figs. 10, 11; Pl. 9, figs. 2, 4, 6, 7 (non figs. 1, 3, 5)  
 1936 *Palaeastraea grandistellata* — KÜHN, p. 27, Pl. 1, fig. 2  
 non 1936 *Palaeastraea grandissima* (FRECH) — KÜHN, p. 26, Pl. 1, fig. 1  
 1976 *Palaeastraea grandissima* (FRECH) — CUIF, p. 74, text-fig. 2, Pl. 2, figs. 1–7

Lectotypus (here chosen): BSP AS XII 28; FRECH 1890, Pl. 9, fig. 2

Other FRECH's originals — see Remarks, p. 70

Locus typicus: ? Fischerwiese

Stratum typicum: Zlambach Beds

Material: Two fragmentary colonies and 4 isolated corallites from Fischerwiese, GBA 1982/12/283, 331–334, NHMW 1982/57/61; three thin sections

Dimensions (in mm):

Specimen No.	d	s	septal thickness	
			min.	max.
GBA 1982/12/283	16	20 (7 + 6 + 7)		
	13 × 18	27 (7 + 7 + 11 + 1)	0.09	2.0
BSP AS XII 28	15 × 20	32 (10 + 10 + 12)		
	25 × 35	28 (9 + 9 + 10)		
	14 × 18	31 (11 + 12 + 8)		

Description: Corallites large. Radial elements fusiform. Septal apparatus strongly differentiated. S1 septa approaching the axis, thick, enlarged by small dissepiments which, developed along the septal faces, become incorporated into the blades (Pl. 16, fig. 1 b, Pl. 17, fig. 2 a). S2 septa significantly thinner than S1, reaching  $\frac{3}{4}$ – $\frac{4}{5}$  the length of the latter and regularly distributed. S3 septa very thin, usually short, lacking in many systems. Septal faces abundantly granulated.

Endotheca depressed at the axial cavity, consisting of abundant vesicular dissepiments, small at the periphery and larger at the axial cavity. Stereomal thickening of the wall of dissepiments may be observed. In the intercalicular region, dissepiments are oriented convex upwards; thus, their subcircular sections are frequent. Lonsdaleoid dissepiments present (Pl. 17, fig. 2 b).

Microstructure: The median septal zone is frequently well delimited and reaches a thickness of about 50  $\mu\text{m}$ . It is built of one straight, wavy and zigzag row of small trabeculae of about 35–50  $\mu\text{m}$  diameter. Its slight thickness contrasts with that of the rest of the blade, especially in S1 septa (Pl. 17, figs. 2 c, d). Stereomal skeleton is strongly developed. Long, very narrow fascicles of delicate fibres are discernible in the septal and dissepimental stereome as well. Their course is straight or slightly wavy. Their distal portions can be seen on the skeletal surface as a microornamentation, a minute granulation consisting of elements of about 20  $\mu\text{m}$  in diameter.

Lateral trabeculae are embedded in the fasciculate tissue, their heads protruding as prominent granules on the septal faces.

Discussion: The species is very well defined by its peculiar morphological features. Fischerwiese appears to be the only locality where it has been found *in situ* (collections of FRECH, CUIF, and LOBITZER).

The three synonymous names, *Astraea rosacaea* GOLDFUSS, 1826, *Phyllocoenia grandissima* FRECH, 1890 and *Palaeastraea grandistellata* KÜHN, 1936 are, in a sense, invalid, all being represented by well figured type specimens, but each coming from an unknown type locality: (1) *Astraea rosacaea* GOLDFUSS (holotype: IPUB GOLDFUSS collection No. 220) was said to come from the vicinity of Basel: the information is erroneous as in this region coralliferous Upper Triassic is lacking, or it suggests that the specimen was found in some secondary bed; (2) *Phyllocoenia grandissima* FRECH: the most typical specimen (FRECH 1890, Pl. 9, fig. 2: BSP AS XII 28) comes from an unknown locality; (3) The holotype of *Palaeastraea grandistellata* KÜHN (PSG, KÜHN collection) comes from a secondary deposit (? alluvial, ? glacial) in the vicinity of Graz. From these GOLDFUSS' name falls into the category of names rejected due to the fact that it has never been in usage, in contrast to FRECH's name which is well established in the Alpine literature.

FRECH (1890, and then CUIF, 1976) admitted the conspecificity of some specimens characterized by large corallites with *Astraea rosacaea* GOLDFUSS. However, having no opportunity to examine the holotype of GOLDFUSS' species, FRECH decided to create a new taxon, *Phyllocoenia grandissima*.

Unfortunately, in the original meaning, *Phyllocoenia grandissima* FRECH contained a series of morphotypes with different corallite dimensions. The lack of a precise definition resulted later in diverse interpretations of the species. The structure of the septal apparatus and differences in corallite size enable two species to be distinguished from among these morphotypes: (1) *Palaeastraea grandissima* FRECH s. s. with large calices and relatively few septa displaying a strong tendency to thicken through the incorporation of dissepiments into the septal blades; KÜHN's re-interpretation of the morphological range of *Phyllocoenia grandissima* FRECH has been discussed (p. 67); (2) *P. cyathophylloides* (FRECH) [= *Palaeastraea grandissima* (FRECH) in KÜHN 1936] of medium-sized corallites with normally developed numerous septa. In addition, the original FRECH's series contains a small-calicular morphotype which has been here assigned to *K. incrassata* (specimen figured by FRECH 1890, Pl. 9, fig. 1).

Abundant septa (30–40) at a diameter of 20–30 mm differentiate the specimens from Röteland limestones (SCHÄFER 1979) from those here described.

**Remarks:** The following original specimens of *Phyllocoenia grandissima* figured by FRECH are housed in the GBA type collections: specimens from Donnerkogel (1890, Pl. 3, fig. 10) – in the box lacking the catalogue number; specimen from Oedalm (*ibid.*, Pl. 9, fig. 4) – No. 2765; specimen from Fischerwiese (figs. 6–6 A) and another one from unknown locality resembling lectotype (fig. 2), as well as two specimens from Fischerwiese ascribed by the present author to *P. cyathophylloides* and *Kuhnastraea incrassata* (figs. 5 and 1, respectively; see synonymies on pages 67 and 72) – in box No. 2795. In the BSP collection two specimens are stored (*ibid.*, Pl. 9, figs. 4 and 5) one of them determined herein as *P. cyathophylloides* (fig. 5).

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds at Fischerwiese, Kesselwand-Rohrmoos. Hauptdolomit of Donnerkogel. Found among boulders in the massif of Plabutsch near Graz.

The species frequently described from the Tethyan Upper Triassic (ZANKL 1969, SCHÄFER 1979, FANTINI-SESTINI & MOTTA 1984, MELNIKOVA 1986, and others).

### Genus *Kuhnastraea* CUIF, 1976

**Species typica:** *Phyllocoenia decussata* REUSS, 1854

**Emended diagnosis:** Colony of kuhnaestreoid or astreoid type and massive or subphaceloid growth form. Budding intratentacular with trabecular linkages, rarely extratentacular, intercorallite. Calices separated from each other by a depression of differentiated depth; in places, it is very deep causing subphaceloid colony formation. Intercorallite trabecular-palisaded wall marked as a thin line at the middle of the intercorallite depression. Internal stereomal wall at the zone of trabecular divergence. Dissepiments vesicular. Costosepta fusiform, exsert. Lonsdaleoid septa present. Median zone straight, wavy or zigzag; septal stereome varying in organization from simple, fibrous to organized in lateral trabeculae. Pellicular wall present on phaceloid corallites.

**Species included:** *Kuhnastraea decussata* (REUSS, 1854), *K. incrassata* (FRECH, 1890). *Kuhnastraea cowichanensis* (CLAPP et SHIMMER, 1911) in MELNIKOVA & BYCHKOV 1986.

**Stratigraphic and geographic ranges:** Norian-Rhaetian of the Tethyan realm.

**Discussion:** The above diagnosis summarizes the information on the genus given by CUIF (1976) in his description of *K. decussata* and *K. incrassata*, and is completed by data obtained by present author (budding, lonsdaleoid septa). It differs essentially from the original diagnosis (CUIF 1976, 83) only in the interpretation of the distichophylliid septal microstructure (compare Discussion p. 36).

The genus, like *Palaeastraea*, has lonsdaleoid septa, a feature observed in few distichophylliids only. In the macro- and microstructural details *Kuhnastraea* resembles much *Distichophyllia* and *Retiophyllia*, whereas *Palaeastraea* is rather close to *Coryphyllia*.

As for the *Kuhnastraea* and *Palaeastraea*, these genera differ in the structure of skeleton in the intercalicular zone (lack of trabecular wall in *Palaeastraea*), as well as in the septal structure (usually the dissepiments join the septal blade in *Palaeastraea*, whereas in *Kuhnastraea* this has not been observed). *K. incrassata* gives evidence that the relationship between the two genera in question is very close. The peripheral

parts of costae in the form of wall rudiments, observed in this species, suggest the way in which kuhnastreoid corals might originate from *Palaeastraea* group and *vice versa*.

There is a structural resemblance between colonies of *Kuhnastraea* and those portions of colonies of some *Retiophyllia* in which massive and phaceloid stages of growth repeat and superpose. There, in kuhnastreoid stages of colony growth, a rudimentary palisaded wall may develop (p. 47).

*Kuhnastraea decussata* (REUSS, 1854)

Pl. 14, fig. 3, Pl. 17, fig. 1, Pl. 18, figs. 1, 2

1854 *Phyllocoenia decussata* — REUSS, p. 99, Pl. 13, figs. 2, 3

part. 1890 *Phyllocoenia decussata* REUSS — FRECH, p. 28, Pl. 7, figs. 1–7, 9, 10 (non fig. 8)

v. 1909 *Phyllocoenia decussata* REUSS mut. spec. (+ *Phyllocoenia incrassata* FRECH) — HAAS, p. 146, Pl. 5, fig. 6

1976 *Phyllocoenia decussata* REUSS — CUIF, p. 78, text-fig. 3, Pl. 3, figs. 1–6

Holotypus: Lost, originated from Zlambach Beds of the vicinity of Aussee

Neotypus (here chosen): GBA 1982/12/787; Pl. 18, figs. 2 a–b

Locus typicus: Fischerwiese near Aussee

Stratum typicum: Zlambach Beds

Material: Sixteen colony fragments from Fischerwiese, GBA 1982/12/240, 252, 259–261, 263, 278–282, 787, 859–861, NHMW 1982/57/118, three colonies from Kesselwand-Rohrmoos, NHMW 1908 XII 84, NHMW 1959/361/2, 6; more than twenty thin sections

Dimensions (in mm):

Specimen No.	d	s	s/3 mm
GBA 1982/12/282	6.5 × 7	38 (10 + 10 + 18)	
	6 × 7.5	36 (12 + 12 + 12)	
GBA 1982/12/259	6 × 7	49 (14 + 14 + 21 + S4)	
	5 × 8	60 (15 + 15 + 30 + S4)	
	4.5 × 5	31 (10 + 10 + 11)	
GBA 1982/12/787	5.5 × 7	49 (8 + 8 + 14 + 19)	
	5 × 6	37 (9 + 9 + 16 + 9)	7–9
NHMW 1903 XII 84	3.5 × 4.5	36 (9 + 9 + 17 + 2)	7–10
	3.5 × 4	35 (9 + 10 + 17)	
NHMW 1959/361/6	4 × 6	46 (9 + 9 + 14 + 14)	6–8
	4.5 × 6.5	52 (12 + 12 + 20 + 8)	
	4.5 × 6	37 (9 + 9 + 15 + 4)	

Description: Colonies massive (Pl. 18, fig. 2 a) convex or platy: unifacial with the lower side costulate, or bifacial. Partially, colony structure may be subphaceloid (Pl. 18, fig. 1). In the latter case, the corallites are isolated from each other and covered with a pellicular epitheca. Calices convex, delimited from each other by an ambulacrum giving the surface the appearance of a plocoid colony. Budding of two types: (i) intra-tentacular, by simple subequal division of the septal apparatus between 2 or 3 new individuals; the dividing plane passes through opposite septa; a constriction is marked prior to the wall formation; incompletely divided calices may form long series; (ii) extra-

tentacular intercalicular, in which the foundation of new individuals takes place on the extremities of radial elements of 3–4 neighbouring corallites.

Radial elements fusiform. Lateral ornamentation in the form of large granules. Septal apparatus differentiated into septa of 3 orders: S1 septa numerous, strongly enlarged at the middle of their length and reaching the axis, S2 septa thinner and attaining about  $\frac{1}{6}$  the length of S1, S3 septa of variable length between rudimentary, resting on the wall, and those reaching more than half the length of the S1 septa and often being developed as vertically discontinuous lonsdaleoid blades. In large corallites, S1 septa are twice as numerous as in small ones. Their number rises by the transformation of S2 into S1. This means that the ultimate ring of septa of the first order of magnitude (= cycle) is composed of septa of two succeeding orders of appearance.

A polygonal intercorallite wall is thin. There is a marked tendency to develop an internal wall: a stereozone founded on septa and on one ring of dissepiments, both rather slightly thickened (Pl. 18, fig. 2 a).

Dissepiments relatively large. Those disposed internally to the internal wall (endothecal) are small in number, inclined adaxially at the periphery and subtabuloid at the axis. Others (exothecal) are vesicular, disposed subhorizontally (Pl. 18, fig. 2 b).

In some parts of colonies a thickening of all skeletal elements by stereome may be observed.

Microstructure: In the S3 septa and in internal portions of S1 and S2, the median septal zone is straight; in peripheral portions of S1 and S2 it may be straight, wavy or zigzag. Lateral trabeculae are developed in the peripheral portions of S1 and S2 (Pl. 14, fig. 3, Pl. 17, fig. 1). The stereomal thickening of dissepiments is observed often in the zone of the internal wall. Intercorallite wall continuous, formed of trabeculae in a single row; trabecular axes ca. 50  $\mu$ m distant from each other (Pl. 14, fig. 3, Pl. 17, fig. 1).

Remarks: The illustrated REUSS original has been lost; reference to the type locality was imprecise (REUSS, 1854, 99: "Fundort: Selten und schlecht erhalten in der Gosau und am Zlambach bei Aussee"). The illustrated REUSS specimen resembles in its general state of preservation the corals from the vicinity of Aussee rather than those of Kesselwand (= Gosau). The Fischerwiese material being close to topotypic, the neotype I have chosen from among the specimens of that locality. FRECH's originals: p. 146.

The specimens from Kesselwand-Rohrmoos represent a morphotype with small corallites.

Comparison with *K. incrassata* see p. 73.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese, Kesselwand-Rohrmoos, Hallstätter Salzberg, Zlambachgraben and Scharitzkehralp (the latter three sites after REUSS 1854 and FRECH 1890).

*Kuhnastraea incrassata* (FRECH, 1890)

Pl. 18, figs. 3–6

- v. 1890 *Phyllocoenia incrassata* – FRECH, p. 30, Pl. 8, figs. 1–14
- part., v. 1890 *Phyllocoenia grandissima* – FRECH, Pl. 9, fig. 1, non figs. 2–7
- 1976 *Kuhnastraea incrassata* – CUIF, p. 82, text-fig. 4
- 1979 *Phyllocoenia incrassata* FRECH – SCHÄFER, p. 46, Pl. 11, fig. 8
- 1986 *Kuehnastraea incrassata* (FRECH) – MATZNER, Pl. 9, fig. 6

Lectotypus (here chosen): GBA FRECH's type collection, No. 2792; FRECH 1890, Pl. 8, fig. 3



Paralectotypi: GBA No. 2792, figured *ibidem*, figs. 7 and 13; BSP AS XII 26 and 27, *ibidem*, figs. 10 and 14; Geiseltal Museum Halle, *ibidem*, fig. 9

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: About twenty fragmentary colonies from Fischerwiese, GBA 1982/12/136, 255–257, 262, 266–270, 273, 274, 277, 285, 863, NHMW 1982/57/1, 11, 12; twenty four thin sections

Dimensions (in mm):

Specimen No.	d of calice	s	Remarks
GBA 1982/12/257	3.5	32 (5 + 5 + 10 + 12)	
	4	31 (5 + 5 + 10 + 11)	
NHMW 1982/57/11	3.5 × 5.5	38 (10 + 10 + 18)	
	4	31 (8 + 8 + 13 + 2)	
GBA 1982/12/285	est. 6	32 (7 + 7 + 12 + 6)	} internal wall lacking
	est. 4.5 × 7	40 (7 + 7 + 12 + 14)	
GBA 1982/12/863	5	37 (9 + 9 + 18 + 1)	

Description: Colonies platy, unifacial or digitiform. Calices elevated, separated by a groove of variable depth. Prolonged costae of neighbouring corallites meet in the intercorallite depression or are divided by a zone of delicate granulation. Astreoid condition more frequent than kuhnastreoid.

Radial elements fusiform. S1 septa sometimes very thick, approaching the axis; S2 thinner and shorter than S1; S3 more than half the length of S1; S4 thin, long, not abundant, often lonsdaleoid. Intercorallite wall incomplete, formed by scattered trabeculae and prolongations of costae bending peripherally. Calicular (= internal) wall of a stereomal-septothecal type, or lacking (Pl. 18, fig. 4 a).

Endotheca of small, very abundant dissepiments sloping down from the internal wall adaxially. Exotheca of small, subhorizontal dissepiments (Pl. 18, figs. 4 b, 6 b).

In some colonies the zones of unthickened and thickened skeleton superpose. The thickening concerns radial elements as well as dissepiments. The cross sections of thickened skeleton differ very much from those of unthickened ones. In the unthickened zones calicular walls are lacking and rudiments of the trabecular wall are hardly noticeable. Their *Palaeastraea*-like appearance is contrasted with that of the thickened zones where calicular walls are strongly developed, the S1 septa robust and the intercorallite space filled with stereome or, at least, showing incomplete trabecular walls (Pl. 18, figs. 6 a and 5). The thick-skeletal colonies are frequent in the material examined.

Microstructure: Septal mid-line straight or wavy, formed by very thin trabeculae, spaced a minimum of 30 µm apart (measured between the trabecular axes). Stereome thick, especially that of S1 and S2 septa, rather weakly organized into fascicles. Trabeculae of 60 µm diameter form an incomplete intercorallite wall.

Discussion and Remarks: FRECH (1890) and later CUIF (1976) stressed the role of stereome in strengthening the colony skeleton in this species. Colony growth form, the structure of the theca and number of septa, which according to FRECH differentiate *decussata* from *incrassata*, were considered by HAAS (1909) as extremely variable features in different parts of the colony.

The material examined permits to indicate the following features differentiating this species from *K. decussata*: endotheca and intercalicular exotheca formed of small dissepiments; exothecal dissepiments distributed at random; S1 septa usually thickened, S4

septa frequently well developed; stereomal and dissepimental zones alternating in the exotheca; colony from lamellate to branching. Stereomal thickening of skeleton may be found in both species. However, in *K. incrassata* it developed much more frequently than in *K. decussata* and changed completely colony structure.

Thin-skeletal forms of *K. incrassata* are surprisingly similar to small-calicular species of *Palaeastraea* (compare CUIF 1976). The only difference between them consists in a tendency to form a wall in the first of them.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese; FRECH (1890) mentioned it from Hallstätter Salzberg, and SCHÄFER (1979) from Röteland reef limestone.

### Subfamilia *Distichoflabellinae* nov.

Genus typicus: *Distichoflabellum* nov.

Diagnosis: Distichophylliids with low and subtabuloid dissepiments and with radial elements vertically continuous.

The subfamily is monotypic.

### Genus *Distichoflabellum* nov.

Species typica: *D. zapfei* sp. n.

Derivatio nominis: *Distichoflabellum* – distichophylliid with a flabellate corallum; *neutr.*

Diagnosis: Corallites in a single series, forming a flabellate, platy corallum; calices poorly differentiated. Radial elements costoseptal in type, thick, with mid-line marked, granulated. Endotheca of very large, deep dissepiments. Columella lacking. Budding intramural with indirect linkages.

Species included: Type species only.

Stratigraphic and geographic ranges: Upper Rhaetian of the Northern Calcareous Alps.

Discussion: The assignment of the genus *Distichoflabellum* into the family Reimaniphyllidae is tentative due to scarce information on the microstructure, obtained from examination of the material. The type species shows thick costo-septa with a granular ornamentation and thin mid-line. In these features the genus resembles that family, while in the structure of the endotheca (large, low, tabuloid dissepiments) it differs from other genera here ascribed in such a degree that it may be considered as a representative of a separate subfamily.

### *Distichoflabellum zapfei* gen. et sp. n.

Pl. 6, fig. 5

? 1969 *Margarophyllia* sp. – ZANKL, p. 37, text-fig. 36, Pl. 2, fig. 9

Holotypus: Private collection of Prof. Dr. H. ZAPFE; Pl. 6, figs. 5 a–d

Locus typicus: Schneckengraben

Stratum typicum: Upper Rhaetian

Derivatio nominis: *zapfei* – in honour of Professor Dr. HELMUTH ZAPFE, an eminent Austrian student of the Alpine Triassic.

**Diagnosis:** Corallum 80 mm wide, 20 mm thick and 80 mm high, composed of a few poorly individualized corallites; septal density  $10/10$  mm; septa differentiated into two orders.

**Material:** Holotype colony with abraded surface, and 3 colony fragments from Kesselwand-Rohrmoos, NHMW 1982/56/78, 1903 XII 133<sub>1,2</sub>; three thin sections

**Description:** Corallum plate-like, flabellate, calicular surface subhorizontal. Budding intramural with indirect linkages between corallites. Calices 6–7 in number, poorly individualized. Radial elements exsert, fusiform, differentiated into two orders strongly differing in thickness. S1 septa thick and reaching the axial fissure, their internal edges thick and frequently T-shaped. The S2 septa are very thin and appear irregularly. Septal faces covered with abundant, small granules. Endotheca dense, concave at the axial part, steeply mounting peripherally up to the mural line (i. e., trabecular divergence zone) and sloping down peripherally. Dissepiments large, deep, crossing the lumen.

**Microstructure:** In the recrystallized septa, a straight or wavy thin median line of distichophylliid type is visible. In fragments, the original fibrous structure of the septal tissue can be observed.

**Discussion:** ZANKL's (1969) *Margarophyllia* sp. which has flabelloid-meandroid shape seems to be conspecific with the form described here.

**Distribution:** Rhaetian of the Northern Calcareous Alps; Zlambach Beds of Schneckengraben and Kesselwand-Rohrmoos.

#### Familia Margarophylliidae CUIF, 1977 (as "groupe *Margarophyllia*")<sup>8</sup>

Genus typicus: *Margarophyllia* VOLZ, 1896

**Emended diagnosis:** Median septal zone formed of a row of relatively thick vertical trabeculae with long lateral trabeculae diverging alternatively toward opposite septal faces and constituting lateral parts of the septal blade. Ornamentation spiniform. Endotheca abundant, formed of small vesicles. Pellicular wall present in phaceloid forms.

**Genera included:** *Margarophyllia* VOLZ, 1896, *Margarosmilia* VOLZ, 1896, *Distichomeandra* CUIF, 1976, *Pamirastraea* MELNIKOVA, 1975.

**Discussion:** The emendation concerns microstructural characteristics and family range.

The margarophylliid septal structure was interpreted by VOLZ (1896) as trabecular and by CUIF (1975 a, 1977 b) as nontrabecular. According to CUIF, margarophylliid septa are composed of large sclerodermites the axes of which run at a smaller or greater angle to the septal plane and constitute granules on the septal faces. He pointed to the alternate position of lateral sclerodermites when the septa were seen in side view (1975 a, text-figs. 11 d, 12).

In the light of the latest observations such an interpretation may be only partially acceptable. In contrast with it and in accordance with VOLZ's opinion, vertical trabeculae have been recognized in the mid-line of the septa (Pl. 22, figs. 1 b, 3, 4 a, b). Their dimensions vary depending on the genus; for example in *Margarosmilia charlyana* (FRECH) the vertical trabeculae are thinner than in *Distichomeandra dieneri* (HAAS) or *D. austriaca* (FRECH). Their lateral axes seen in transverse septal section run alternately

<sup>8</sup> See Notes on nomenclature p. 24.

towards opposite septal faces. Lateral axes formed by neighbouring trabeculae, when observed on the septal faces, alternate in position (Pl. 22, fig. 2). The pattern of the septal microstructure in the family Margarophylliidae resembles that described by VOLZ (1896) in the structure of the median septal portion and that of CUIF (1975 a) in the structure of the septal sides. The lateral trabeculae, as in Reimaniphylliidae, are recognized here as a constituent element of the septal blade. The peculiarity of the margarosmiliid type of microstructure lies in the development of well established, relatively thick median trabeculae and decidedly trabecular lateral expansions (Pl. 22, figs. 1 b, 3, 4 a, b, and MELNIKOVA 1975, Pl. 19, fig. 1 a).

The median vertical trabeculae seen in cross section seem to be initiated with very narrow vertical axes, though they are sometimes conspicuously larger in diameter in comparison with the average diameters in the *Distichophyllia* group. In some sections a few thin axes equivalent to distichophylliid thin trabeculae may be discerned in the centres of median (vertical) trabeculae. Thus the relatively thick margarosmiliid vertical trabeculae disclose their complex nature. When septa are thickened and vertical trabeculae are densely packed, a typical margarosmiliid pattern can hardly be observed. Most of them, setting off lateral axes simultaneously towards both septal faces, become symmetrical in cross section. It is therefore more useful to study the structure in thinner septa.

### Genus *Margarosmilia* VOLZ, 1896

Species typica: *Montlivaltia zietenii* KLIPSTEIN, 1843

Emended diagnosis: Phaceloid, mono- to polycentric. Septa numerous, ornamented with prominent sharp spines. Endotheca vesicular. Wall pellicular. Gemmation intracalicular with indirect linkages.

Species included: Carnian — *Margarosmilia zietenii* (KLIPSTEIN, 1843), *Margarosmilia confluens* VOLZ, 1896, *M. richthofeni* VOLZ, 1896; Rhaetian — *Margarosmilia charlyana* (FRECH, 1890).

Stratigraphie and geographic ranges: Rhaetian of the Alps.

Discussion: The type species and *M. confluens* have been analysed by CUIF (1975 a) from the microstructural and morphological point of view. In accordance with VOLZ's and FRECH's opinions (1896) and contrary of CUIF's view, I consider the septal structure in this genus to be trabecular (see above).

The species from the Zlambach Beds, i. e. *M. charlyana* FRECH, appears to be the first Rhaetian *Margarosmilia* and reveals a structural peculiarity, viz., high trabecular density in the costal parts of the radial elements.

FRECH and VOLZ (in VOLZ 1896) assumed the presence of the genus in the Rhaetian. Unfortunately, they wrongly considered the genus *Margarosmilia* as close to Triassic *Phyllocoenia* (= *Palaeastraea* KÜHN), for example, *P. grandissima* which, in reality, reveals the simplest distichophylliid type of microstructure (p. 69). The same is true of *Thecosmilia cyathophylloides* FRECH (compare herein p. 67), the species which was assigned to *Margarosmilia* (VOLZ 1896, 33). FRECH and VOLZ believed the thick septa of the two species to have a complex margarosmiliid structure.

*Margarosmilia charlyana* (FRECH, 1890)

Pl. 19, figs. 1–4, Pl. 22, figs. 3, 4

1890 *Thecosmilia Charlyana* – FRECH, p. 11, Pl. 3, figs. 5–5 B, Pl. 5, figs. 6–7 A

Series typica: Lost

Neotypus (here chosen): NHMW 1982/57/2; Pl. 19, fig. 3

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Diagnosis: *Margarosmilia* of permanently phaceloid corallites, 5.5–7.5 mm in average diameter, with 80–100 septa strongly granulated.

Material: Five isolated corallites, GBA 1982/12/351–353, 436, NHMW 1982/57/22 and six fragmentary colonies from Fischerwiese, GBA 1982/12/354, NHMW 1982/57/2–6, 66, and two fragmentary colonies from Kesselwand-Rohrmoos, NHMW 1982/56/5, 6; 23 thin sections. With a few exceptions, the material is recrystallized. In the NHMW collection fragments of large colonies from Kesselwand-Rohrmoos are deposited.

## Dimensions (in mm):

Specimen No.	d	s	c/3 mm
GBA 1982/12/354	5.5 × 6.5	107 (17 + 14 + 26 + 50)	14–15
NHMW 1982/57/2	6 × 9	80 (11 + 12 + 17 + 39)	10–14
	6	92 (13 + 13 + 24 + 42)	
NHMW 1982/57/3	5 × 6	74 (13 + 12 + 22 + 26)	
	8	88 (11 + 11 + 20 + 41 + 5)	
	7 × 8.5	99 (17 + 16 + 23 + 39 + 4)	
	7 × 9	102	
	6.5 × 9.5	105	

Description: Phaceloid colony composed of densely spaced and frequently branching corallites. Corallites cylindrical, of a diameter alternately widening and diminishing during their growth. Rudimentary connecting processes may be observed. Pellicular wall thin, having no traces of the internal corallite structure on its surface.

Corallites generally bi- or trifurcating. New individuals subequal. At the first stage of increase two parent septa oppose each other and fuse to form a solid partition between the daughter individuals. After the septal apparatus has been divided, the new individuals remain connected with each other by the partition which becomes their common wall. The course of the septa in the partition zone is very variable because they are founded on the partition itself or on parallel septa. They run subperpendicularly or obliquely to the partition before bending sharply towards the axes of new corallites.

Radial elements numerous, thin, differentiated into four size orders. S1 septa, generally thickest, extend to the corallite axis where their thin internal edges may meet. S1 and S2 septa are slightly different in length in young individuals, whilst subequal in adults. S3 septa are hardly half the length of S1 in young individuals and about the length of S1 in adults. S4 septa attain half the length of S1 in adults and are abundant, alternating with the septa of the other orders. S5 septa are sporadic, short. External septal edges merge into thin pellicular wall. In some specimens, S4 septa are strongly enlarged and become contiguous with the peripheral portions of the adjacent septa, causing a septotheca to develop. Septal faces covered with strongly protruding granules.

Endotheca convex at the periphery and concave at the axis, composed of vesicular thin-walled dissepiments filling up all interseptal and axial spaces. Axial dissepiments somewhat larger than peripheral (Pl. 19, fig. 4 b).

**Microstructure:** The microstructure is trabecular. Primary structure is, generally, considerably changed and traceable only partially. However, in some specimens it is well preserved (GBA 1982/12/353, NHMW 1982/57/6, NHMW 1982/56/5). The vertical trabeculae have variable dimensions. The lateral trabecular axes are not equal in all specimens examined; for example in NHMW 1982/57/4 and NHMW 1982/56/5 they are numerous and densely spaced, whilst in others they seem sparse. The septal mid-line may be well marked. A slight alternation of the vertical trabeculae results in a weakly zigzag line. The septal granules are slightly flattened, with a finely ornamented edge. The pellicular wall is fibrous, growing centripetally. Septal microstructure is presented in Pl. 22.

**Discussion:** In view of the absence of FRECH's originals from type collections, I have chosen a neotype from the specimens belonging to the collection of the Naturhistorisches Museum Wien. The neotype is a colony fragment with very well preserved morphological features. Vestiges of the characteristic features of the microstructure are traceable.

The original description and figures point to the differences between this species and all others assigned by FRECH (1890) to the genus *Thecosmilia*, namely, its high septal density, rich septal ornamentation and abundant endotheca. The original illustrations show the peculiarities of budding: its high frequency and mode of dividing the corallites (1890, Pl. 3, fig. 5 and Pl. 5, fig. 6).

The septal apparatus of *M. charlyana* resembles that of *M. zietenii* figured by CUIF (1975 a, text-fig. 29 b). In the adult individual ( $13 \times 16$  mm in diameter: measurements taken from the photo) of *M. zietenii*, the septal arrangement is similar ( $16 + 15 + 30 + 50 + 6$ ) to that of a small individual of *M. charlyana* (GBA 1982/12/354 – see Dimensions). Unfortunately, it is impossible to make any detailed comparisons between this species and *M. confluens* (which has approximately the same corallite size) as the original description of the latter is very brief.

**Distribution:** Rhaetian of the Northern Calcareous Alps; Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos; FRECH (1890) mentioned its occurrence in Hallstätter Salzberg and Zlambachgraben.

### Genus *Distichomeandra* CUIF, 1976

**Species typica:** *Distichomeandra spinosa* CUIF, 1976

**Emended diagnosis:** Colony cerioid or meandroid. Septa nonconfluent or subconfluent, differentiated into three permanent sizes. Wall septothecal-synapticular or septothecal, if present. Septal ornamentation granular. Columella feeble, parietal, if present. Endotheca abundant, vesicular. Microstructure of margarophylliid type. Budding intratentacular with indirect linkages.

**Species included:** Norian – *D. spinosa* CUIF 1976; Rhaetian – *D. dieneri* (HAAS, 1909), *D. austriaca* (FRECH 1890), *D. minor* (FRECH, 1890).

**Stratigraphic and geographic ranges:** The Norian-Rhaetian of the Alps and Taurus.

**Discussion:** The genus is the only representative of the margarophylliids of cerioid, grading into meandroid, colony type. Three of the species included in the genus

(*D. dieneri*, *D. austriaca* and *D. minor*) are of a cerioid, *Isastraea*-like colony structure, whilst *D. spinosa* is a typical meandroid species with permanent long, monolinear series of corallites. In colonies of the latter type one can find isolated, monocentric corallites. The transition from the cerioid into the meandroid colony type in *Distichomeandra* may be observed in the expanding, peripheral portions of cerioid colonies where series of rapidly dividing corallites are formed. Because of morphological resemblance, *D. austriaca* and *D. minor* may be considered as a natural group of related species.

Three of the Rhaetian species were originally assigned to the genus *Isastraea* (FRECH, 1890). Such a classification cannot be maintained because these corals, although very similar to *Isastraea* in morphology, differ essentially from this genus in their microstructure. *Isastraea* has typical montlivaltioid large-trabecular microstructure (RONIEWICZ 1983), representing an advanced phylogenetic stage, unknown in the Triassic.

The budding in the genus follows the common pattern; *D. dieneri* exemplifies this type of increase (p. 82).

CUIF (1977 b) included the genus *Distichomeandra* in the family Distichophylliidae. In my opinion, however, the microstructure in *Distichomeandra* has much more in common with that of *Margarosmia* than with *Distichophyllia* (compare descriptions of the microstructure).

*Distichomeandra austriaca* FRECH, 1890

Pl. 20, figs. 1, 6, Pl. 21, figs. 5, 6, Pl. 22, fig. 1

part., v. 1890 *Isastraea austriaca* — FRECH, p. 23, Pl. 6, figs. 1–3, 5, 6, non Pl. 6, fig. 4

part., v. 1890 *Isastraea eucystis* — FRECH, p. 26, Pl. 6, figs. 10, 10 A, non Pl. 7, figs. 11, 11 a, 12, 12 A

1886 "*Isastraea*" *eucystis* FRECH — MATZNER, Pl. 9, fig. 7

Lectotypus (here chosen): BSP AS XII 16; FRECH 1890, Pl. 6, fig. 5; the specimen is recrystallized

Locus typicus: Oedalm (= Kesselwand-Rohrmoos)

Stratum typicum: Zlambach Beds

Material: Two colonies from Fischerwiese, GBA 1982/12/397, 402, and four from Kesselwand-Rohrmoos NHMW 1981/56/24<sub>1</sub>–24<sub>4</sub>; eleven thin sections; many specimens from Kesselwand-Rohrmoos in NHMW collection examined externally

Dimensions (in mm):

Specimen No.	d	s	s/3 m
GBA 1982/12/397	6.5	50	
	7 × 9	59	7–9
	6 × 7.5	50	
NHMW 1982/56/24 <sub>1</sub>	7	52	
	7 × 7.5	60	8–9
	6.5 × 7		
BSP AS XII 16	7 × 10	ca. 50	7

Description: Colonies cerioid. Budding intratentacular with indirect linkages, usually bicentric, rarely triscentric. Calices polygonal, deep with sharp and high edges. Axial cavity small, filled with thickened inner edges of S1 septa that form a rudimentary columella.

Septa differentiated into 3–4 sizes. The first two sizes thickest, S1 septa reaching the axial cavity, S2 shorter than S1, S3 septa about half the length of S1, S4 short and sparse. Septal systems usually formed of regularly developed S1, S2 and S3 septa. Moreover, there are ca. 1–3 incomplete systems per calice. The septal faces of the lecto-type specimen are covered with granules. The granules are scattered or arranged in rows, depending on the septum. Peripherally in the calice they are rather round, and resemble short menianes near the inner edge. In specimen NHMW 1982/56/24, another modification is observed, i. e. a vertical elongation of granules in the perimural zone. In the same specimen, one can see a wavy internal septal edge with thickened denticles.

Wall thin, septothecal with few synapticalae (Pl. 21, figs. 5 a, 6).

Endotheca abundant, formed of small vesicles.

Microstructure: The microstructure may be observed in specimen NHMW 1982/56/24. The thinnest septa are 24  $\mu\text{m}$  thick, the thickest ones ca. 240–300  $\mu\text{m}$ . This range demonstrates the ratio between the thickness of essential structural elements, and of septal blades formed of recombined or thickened trabeculae. In the periaxial zone, the septa are formed of well developed isometric trabeculae 60–90  $\mu\text{m}$  in diameter with alternating small and sparse lateral axes. Toward the periphery the septa are thickened by lateral thickening of the trabeculae, their centres being about 90  $\mu\text{m}$  distant from each other.

An alternation of trabecular positions in mid-line is observed. In the thickest part (at the external edge), laterally symmetrical extensions arise from the median trabeculae (Pl. 22, fig. 1 b). The granules exhibit a tendency to vertical elongation (Pl. 22, fig. 1 a: lower left corner). As a result, thin ridges paralleling the trabeculae may develop. The wall is formed of the external edges of radial elements and sparse synapticalae (Pl. 21, figs. 5 a, 6).

The axial parts of trabeculae are often leached and filled with clear calcite. Thus, the mid-line of the septa acquires a characteristic zigzag appearance in cross section.

This microstructure resembles the typical margarophylliid pattern only generally. Nevertheless, it shows the following features of the latter: asymmetry in development of some lateral extensions and alternation of positions of some vertical trabeculae, as well as strong development of lateral axes which causes peripheral thickening of the septal blades.

Discussion: The specimen of FRECH (1890) figured on Pl. 6, fig. 4 belongs to *Kuhnastraea incrassata* (FRECH). Another FRECH's species, *Isastraea eucystis*, represents a morphotype corresponding to early astogenic stages of colonies of *D. austriaca* (FRECH). However, of the three specimens figured by FRECH as *I. eucystis* (1890, Pl. 6, figs. 10–10 A, Pl. 7, figs. 11–11 A, 12–12 A) only the first represents genus *Distichomeandra*. Its straight series are enlarged at calices and lack septes-de-vallée (herein, Pl. 20, figs. 1 a, b); abundant endotheca is formed of thin vesicles. The other specimens represent another of FRECH's species, *Meandrostylis irregularis* (compare p. 131).

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of the Gosaukamm region and Fischerwiese.



*Distichomeandra minor* (FRECH, 1890)

Pl. 20, figs. 2–5, Pl. 21, figs. 1, 2

v. 1890 *Isastraea norica* var. *minor* — FRECH, p. 26, Pl. 6, fig. 9

Holotypus: GBA FRECH's type collection, No. 2786; FRECH 1890, Pl. 6, figs. 9, 9 A, 9 B; herein Pl. 20, figs. 3 a, b; the skeleton is recrystallized.

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: Three specimens from Fischerwiese: the holotype colony and GBA 1982/12/804, 805; eight specimens from Kesselwand-Rohrmoos: NHMW 1982/56/25<sub>1-4</sub>, NHMW 1959/365/36<sub>1-3</sub>, NHMW 1903 XII 130; nine thin sections

## Dimensions (in mm):

Specimen No.	d	s	s/3 mm
GBA No. 2786	5 × 8	60	11
(holotype)	4.5 × 6.5	e. 50	
NHMW 1982/56/25	5.5 (hexagonal)	52 (13 + 13 + 36)	
	5.5	56 (13 + 13 + 26 + 4)	
	5 × 7	48 (12 + 12 + 21 + 4)	
	5 × 8	54	10
	6 × 8	60 (15 + 13 + 28 + 4)	11

Description: Colony meandroid-ceriod or ceriod (Pl. 20, figs. 2–4, Pl. 21, figs. 1 a, 2), massive or lamellate. Budding intracalicular with indirect linkages. Holotheca present. Series short. Isolated calices isometric or lobate. Axial cavity small. Wall tectiform.

Septa of subequal thickness, differentiated into 3–4 sizes. The S1 septa reach the axis, S2 are shorter, S3 are about half the length of S1 and distally very thin, S4 appear in developing systems. Septal faces covered by thick, strongly projecting, round granules. Septal inner edge with projections which form a rudimentary, parietal columella.

Endotheca abundant, composed of relatively large vesicles (Pl. 21, fig. 1 b).

Microstructure: Observations have been made in thin sections of specimen NHMW 1982/56/25<sub>1</sub>. The thinnest septa are about 25 µm, the S1 septa are usually 200–220 µm thick or thicker. Median trabeculae in S1 septa are 50–70 µm in diameter. They have alternating extensions in the periaxial zone and symmetrical ones in the wall region. Median trabeculae frequently alternate in their positions. In tangential sections of septal faces one observes sections of thick lateral trabeculae more than 50 µm in diameter, typical of margarophylliids. Wall thick, septo-synapticulothecal with sporadic trabecular elements independent of septa.

Discussion: This form was defined by FRECH as a subspecies (varietas) of *Isastraea norica*. However, it does not show structural characters in common with that species (compare p. 89, Pl. 25) but resembles in this respect *Distichomeandra austriaca*. From the latter it differs in smaller and lobate calices, more abundant septa subequal in thickness, larger dissepiments and in septal microstructure. The trabeculae of the examined specimen of *D. minor* are thinner and their lateral axes are more abundant than in *D. austriaca*. No vertical elongation of septal granules is observed.

**Remarks:** The holotype represents a young lamellate colony ( $40 \times 55$  mm large and 20 mm thick) with expanding, thin margins. Some calices are disposed in short series subperpendicular to the colony margin and some are isolated. Budding is frequent. The wall is only slightly marked on the calicular surface. Septa thin.

Among the examined specimens a massive growth form is common. Massive colonies have polygonal, well isolated, deep, rarely budding corallites. Massive colonies can desintegrate temporarily into phaceloid corallites provided with pellicular walls (Pl. 29, fig. 5).

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos.

*Distichomeandra dieneri* (HAAS, 1909)

Pl. 21, figs. 3, 4, Pl. 22, fig. 2

v. 1909 *Thamnastraea Dieneri* — HAAS, p. 151, Pl. 5, fig. 12

non 1975 *Pamiroseris dieneri* (HAAS) — MELNIKOVA, p. 132, Pl. 30, fig. 6, Pl. 36, figs. 1–2

**Holotypus:** PIUW HAAS's collection No. 50; HAAS 1909, Pl. 5, fig. 12

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Material:** One specimen from Fischerwiese, GBA 1982/12/437 and eight from Gosaukamm region, NHMW 1959/365/7, 9, 15, 18<sub>1,2</sub>, 49, NHMW 1982/56/30<sub>1,2</sub>; seventeen thin sections; numerous specimens in NHMW collection examined externally

**Dimensions (in mm):**

Specimen No.	d	s
GBA 1982/12/437	$7 \times 11$	42
	$11 \times 15$	56
	$7 \times 10$	46
NHMW 1959/365/15	$6 \times 12$	68 (17 + 17 + 30 + 4)
	$10 \times 12$	52 (13 + 12 + 25 + 2)
	12	64 (14 + 14 + 28 + 8)
	12	76
NHMW 1959/365/18	12	70 (18 + 17 + 31 + 4)
	12	

**Description:** Calices polygonal, shallow, permanently monocentric or forming monolinear series in expanding parts of the colony (Pl. 21, figs. 3 a, 4). Central cavity very small, circular. Budding intratentacular with indirect linkages, usually bi- rarely tri-centric. A new individual is initiated with the appearance of a new axis in a lobate extension of an adult. The septa of the parent corallite are directed towards the new axis with their internal edges deflected abruptly. The new axis is relatively distant from the original. Halfway between the axes, one or two opposing septa delimit a partition zone between two individuals. The septa do not coalesce.

Septa nonconfluent or subconfluent, thin, differentiated into three or four sizes. S1 septa thickest, reaching the axis, S2 subequal to S1 in some calices or shorter in others, S3 half the length of S1 or slightly longer, S4 shorter than S3, developed in some systems or lacking. Internal edges of S1 provided with a few trabecular projections which constitute a feeble parietal columella. External edges, with sparse synapticulae, directed toward external edges of radial elements of neighbouring corallites to form a

rudimentary, incomplete wall, zigzag when seen in transverse section (Pl. 21, fig. 3 b). Septal faces ornamented with abundant granules. The granules rounded or transversely elongated. In some cases they fuse into short bars resembling short menianes. Endotheca vesicular, abundant. Endothecal surface rising peripherally and concave, or sub-horizontal axially. In transverse section the boundary between axial and peripheral endothecal zones often is sharply marked.

**Microstructure:** The septa are formed of relatively thick trabeculae arranged in an asymmetrical fan, with the costal portion short or completely reduced. Well developed trabeculae are 100–180 µm in diameter when measured along the midline. In some parts, the septa have closely spaced trabecular axes (45–80 µm apart) with well marked boundaries between them. In such cases the line connecting the axes may be zigzag. The lateral axes spring off symmetrically or asymmetrically from the main trabeculae. They are connected with each other and constitute lateral portions of the septal blade (Pl. 22, fig. 2). Their protruding tips, narrower than the body, form the septal granulation. When observed in transverse sections, the main trabeculae of the thick septa with their more or less symmetrical lateral extensions may be regarded as large, flattened trabeculae of non-distichophylliid type.

**Remarks and Discussion:** This species is well represented in NHMW collections from Kesselwand-Rohrmoos and Schneckengraben, and is rather rare in collections from Fischerwiese (a few specimens in the GBA collection, one specimen in the PIUW HAAS type collection). In old collections it has been determined as *Thamnastraea dieneri*, but more frequently as *Phyllocoenia grandissima* or *P. kokeni*.

A thamnasterioid form described by MELNIKOVA (1975) as *Pamiroseris dieneri* (HAAS) is not congeneric with the Alpine form and reveals structure typical of *Pamiroseris*.

**Distribution:** Rhaetian of the Northern Alps: Zlambach Beds of Fischerwiese and the Gosaukamm region.

Subordo Fungiina VERRILL, 1865, *faute de mieux*

Superfamilia Procyclolitoidea VAUGHAN et WELLS, 1943

**Diagnosis:** Corals with compact radial elements and vesicular endotheca. The septa are built of poorly individualized trabeculae in the wavy mid-septal zone and/or medium sized, well defined trabeculae. The trabeculae give rise to lateral bundles of fibres to form menianes. Extracalicular increase prevails.

The following families will be discussed here: Procycloitidae VAUGHAN et WELLS, 1943, emend., Cuifastraeidae MELNIKOVA, 1983, and Astraeomorphidae FRECH, 1890. Their tentative assignment into the heterogeneous suborder Fungiina is based on their resemblance in meniane development to some of the coral groups included here up to now, viz., Microsolenidae KOBAY, 1890 and Latomeandridae ALLOITEAU, 1952 which have, however, porous radial elements; microsolenid corals have been considered by GILL (1967) as representative of a new superfamily Pennulacae.

Recently, MELNIKOVA (1984) has erected suborder Cuifastraeina partially overlapping the range of the here discussed superfamily.

Familia Procyclolitidae VAUGHAN et WELLS, 1943

Genus typicus: *Procyclolites* FRECH, 1890

**Emended diagnosis:** Median septal zone continuous or formed of relatively small and weakly delimited trabeculae. Menianes composed of bundles of fibres having

their own axes. Edges of menianes smooth. Columella absent. Endotheca composed of small vesicles. Fibrous, pellicular wall present.

Genera included: Two groups may be here discriminated: subfamily *Procyclolitinae* with a single genus *Procyclolites* FRECH, 1890 and subfamily *Alpinophylliinae* nov. with *Alpinophyllia* gen. n., *Stuoresimorpha* gen. n. and *Alpinoseris* gen. n.

Discussion: VAUGHAN and WELLS (1943) and WELLS (1956) included ten genera in the family on the basis of their morphological resemblance. ALLOITEAU (1952) has introduced changes to the original concept, erecting the separate family *Conophylliidae* (with the genera *Conophyllia*, *Craspedophyllia* and others).

Microstructural investigations (CUIF 1967, 1975 a, c) have made it possible to delimit a new range for the family (CUIF 1977 b). From the original list of genera, only *Craspedophyllia* has common microstructural features with *Procyclolites*: that is a continuous straight or zigzag median septal line and menianes. The genera *Gigantostylis* FRECH, 1890, *Margarophyllia* VOLZ, 1896, *Margarosmia* VOLZ, 1896 and *Conophyllia* D'ORBIGNY, 1849 represent three microstructurally independent groups. The other four genera included by VAUGHAN and WELLS (1943), i. e. *Triadophyllum* WEISSERMEL, 1925, *Thecoseris* FROMENTEL et FERRY, 1869, *Tricycloseris* TOMES, 1878 and *Phylloseris* TOMES, 1882, have not yet been investigated microstructurally. Nevertheless, the details of their morphology are not similar to those of *Procyclolites* and their relationship seems dubious.

Because of the presence of a continuous mid-septal line, CUIF (1975 a, c) regarded the group *Craspedophyllia-Procyclolites* as close to the *Distichophylliidae* CUIF (= *Reimaniphylliidae* MELNIKOVA, 1975). However, as new observations indicate, the continuous line is produced by the diagenesis of densely spaced, fine trabeculae, and is not caused by septal growth essentially different from that of other corals (compare CUIF 1977 b, 45). In fact, the structure of the septal blade differentiates *reimaniphylliids* from *procyclolitids* as in the latter the specific lateral septal increase, caused by development of side fascicles of fibres, is lacking. Because of this, I do not consider the *Craspedophyllia-Procyclolites* group as directly connected with the *Reimaniphylliidae*. Nevertheless, due to a common tendency in both groups to form septa of small or feebly individualized trabeculae, their relationship cannot be ruled out.

As far as the genera *Procyclolites* and *Craspedophyllia* are concerned, I consider them as representatives of two closely related families, the *Procyclolitidae* VAUGHAN et WELLS and *Conophylliidae* ALLOITEAU, which differ in corallite architecture: the *Conophylliidae* have a large, essential columella and symmetrical menianes, whereas the *Procyclolitidae* have no axial structures (columella) and menianes alternating on both septal faces.

New genera introduced to the family *Procyclolitidae*, together with *Procyclolites*, form a uniform morphogenetic series — from solitary corals to different colonial growth forms — having a common pattern of corallite architecture. In this series the individual genera show different stages of individualization of the trabeculae, from *Procyclolites*, where the tendency to form trabeculae is obscure, to *Alpinophyllia*, where clearly discernible trabeculae are most often found. The individualisation of trabeculae results in the fragmentation of menianes and even in the formation of isolated granules. In this respect these genera resemble the *Omphalophyllia-Conophyllia* group. They differ from this group, however, in their type of radial elements and corallite architecture.

The family, from the microstructural point of view, is diversified and may be divided into two subfamilies: *Procyclolitinae* and *Alpinophylliinae*.

Subfamilia *Procycolitinae* VAUGHAN et WELLS, 1943Genus typicus: *Procycolites* FRECH, 1890

Diagnosis: Septal blades thin, built of poorly discernible trabeculae. Menianes continuous, long.

The subfamily is monotypic.

Genus *Procycolites* FRECH, 1890Species typica: *Procycolites triadicus* FRECH, 1890

Emended diagnosis: Simple or forming incipient thamnasterioid colonies; budding intratentacular with direct linkages. Septa laminar, internal edge with projections; lateral faces covered by continuous, subhorizontal, smooth menianes. Dissepiments vesicular, small, numerous. Columella lacking or rudimentary, parietal. Septal tissue weakly differentiated into trabeculae.

Species included: The genus is monotypic.

Stratigraphic and geographic ranges: Norian-Rhaetian of the Tethyan realm.

Discussion: Although only one well established species has been described in the genus up to now (with a large intraspecific variability), there is an indication in the literature (ZANKL 1969, text-fig. 22) that species of branching growth form may be expected here.

*Procycolites triadicus* FRECH, 1890

Pl. 23, figs. 1–3, Pl. 24, figs. 1, 2

v. 1890 *Procycolites triadicus* – FRECH, p. 64, Pl. 18, figs. 1–16, text-fig. on p. 65

1909 *Procycolites clipeiformis* – HAAS, p. 153, Pl. 5, fig. 14

v. 1909 *Procycolites depressus* – HAAS, p. 153, Pl. 5, fig. 15

1975 Genus *Procycolites* FRECH – CUIF, p. 85, text-fig. 11, Pl. 9, figs. 1, 2, Pl. 10, figs. 1–8

1986 *Procycolites triadicus* FRECH – MATZNER, Pl. 10, fig. 7

Syntypi: GBA FRECH's type collection No. 2785; FRECH 1890, Pl. 18, figs. 5, 11, 15

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: Seventy five specimens, GBA 1982/12/153–227; twenty thin sections

Dimensions (in mm):

Specimen No.	h	d	s
High profile specimens:			
GBA 1982/12/153		55 × 80	
GBA 1982/12/179	40	40 × 55	250
GBA 1982/12/168	30	20 × 30	184
GBA 1982/12/163	20	10 × 23	148 (36 + 36 + 71 + 5)
GBA 1982/12/161	15	10 × 20	106 (26 + 26 + 52 + 2)
GBA 1982/12/165	13	10 × 10	63 (15 + 15 + 28 + 5)
Low profile specimens:			
GBA 1982/12/157	30	45 × 50	250
GBA 1982/12/158	10	28 × 33	234
GBA 1982/12/159	8	14 × 18	
GBA 1982/12/160	4	14 × 14	95

**Description:** Corallites discoid, patellate, trochoid or subcylindrical (with pointed apex) in shape. Calices circular or lobate, slightly depressed at the axial fissure, with a sharp edge. Apex free, pointed or enlarged when fastened to detrital fragments. Corallite surface covered with pellicular wall.

Septa very thin and abundant, closely spaced (Pl. 23, fig. 1). At the circumference of the corallite their density is 7–11 (14)/3 mm. Septal apparatus differentiated into 3 orders of well developed septa plus rather sporadic S4, S1 septa usually reaching the axial fissure, and frequently intertwined to form a parietal columella. S2 septa long, but much shorter than S1, regularly distributed. S3 septa regularly distributed, very variable in length, developed as short blades at the circumference of the calice up to half the length (and more) of S1. Septal faces with menianes variable in length, spaced 0.3–0.6 mm. The menianes alternate on both sides of the septum (Pl. 23, fig. 3). They are parallel to the septal distal edge and are more or less inclined adaxially depending on the shape of the corallite. The menianes of neighbouring septa may reach each other. The edges of menianes are usually smooth (Pl. 24, fig. 1 a).

Endotheca built of thin-walled, small, vesicular dissepiments (Pl. 23, fig. 2).

Intratentacular budding with lamellar linkages between corallites, circumoral in type, produces initial, bi- or tri-corallite colonies. New individuals do not attain a normal adult size. The original lamellar linkages between the centres of corallites may be interrupted in the early stages and a dividing wall may be developed. Rejuvenescence present. Both budding and rejuvenescence occur rarely.

**Microstructure:** In cross section, the mid-septal zone is well delimited and slightly zigzagged or straight (Pl. 24, figs. 1 a, 2 a). It is either fibrous, uniform in structure or displays incipient differentiation into trabeculae measuring from 30 up to 90  $\mu\text{m}$  in diameter (Pl. 24, figs. 1 b–c). The menianes show diverse stages of arrangement of fibres into fascicles. At the edge of the slightly protruding menianes, about 9 tops of fascicles per 1 mm may be discerned (Pl. 24, fig. 1 d).

The surface of the septal blade and edges of the menianes may be covered with very small, sharply pointed microgranules (13–15  $\mu\text{m}$  in height and 18  $\mu\text{m}$  wide at their base: Pl. 24, fig. 2 b).

**Remarks:** A detailed description of morphological variation and microstructural observations is given by CUIF (1975 c). He shows, in a tangential longitudinal section of the septum, a meniane with multiple axes arranged in one row (1975 c, text-fig. 11 c).

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos; reported from Hallstätter Salzberg and Zlambachgraben by FRECH (1890).

### Subfamilia Alpinophyllinae nov.

**Genus typicus:** *Alpinophyllia* gen. n.

**Diagnosis:** Trabeculae of medium size (see terminology). Thickening of septa through lateral increase of trabecular diameter. Menianes short, formed of lateral prolongations of main trabeculae, provided with axes. Wall septothecal or septo-synapticulothecal. Synapticulae rare, exclusively in the wall, if present. Columella lacking.

**Genera included:** *Alpinophyllia* gen. n., *Stuoresimorpha* gen. n., *Alpinoseris* gen. n.

**Discussion:** A group distinguished by septa built of rather well delimited trabeculae, short menianes and presence of synapticulae in the wall of septothecal character.

Genus *Alpinophyllia* nov.

Type species: *Alpinophyllia flexuosa* sp. n.

Derivatio nominis: from the Alps and Greek *phyllon*-leaf, a conventional ending for coral taxa; *femin.*

Diagnosis: Cerio-meandroid, series open, septes-de-vallée present. Budding intratentacular with direct linkages. Permanent septal ornamentation in form of short menianes. Menianes axiferous. Wall primarily septothecal, changing into septal-synapticulothecal during ontogeny. Trabeculae small to medium sized. Endotheca vesicular.

Species included: The genus is monotypic.

Stratigraphic and geographic ranges: Rhaetian of the Alpine region.

Discussion: The genus has been distinguished from among other *Isastraea*-like genera, first of all, on the basis of septal microstructure, ornamentation, a type of wall structure and mode of budding. In the Alpine Triassic, similar genera with menianes (or pennules) and septotheca are known to occur: *Stuoresia* CUIF, 1976, *Guembelastraea* CUIF, 1976, *Stuoresimorpha* gen. n., *Andrazella* CUIF, 1976. However, from the first two genera it differs in having menianes provided with axes. From *Andrazella* it differs, primarily, in having a wall, the structure of which is originally septothecal but becomes septo-synapticulothecal during ontogeny, while in *Andrazella* it remains septothecal (see CUIF 1976, text-figs. 9, 10). Secondly, it is distinguished from *Andrazella* by its type of budding with lamellar linkages between individuals.

From the very closely related *Stuoresimorpha* gen. n., it differs in having budding with direct, lamellar linkages between individuals whilst in that genus only indirect, trabecular linkages occur.

*Alpinophyllia flexuosa* sp. n.

Pl. 25, figs. 1–3, Pl. 26, figs. 1, 2

Holotypus: NHMW 1982/56/21<sub>1</sub>; Pl. 25, figs. 1 a–c; Pl. 26, figs. 1 a–d

Paratypus: NHMW 1982/56/21<sub>2</sub>; Pl. 25, figs. 2 a–d

Locus typicus: Kesselwand-Rohrmoos

Stratum typicum: Zlambach Beds

Derivatio nominis: Latin *flexus*-bent, from the flexuous course of series.

Diagnosis: Long, open monolinear series, varying in course and width (commonly 8–15 mm wide); in places corallites monocentric. Calices well distinguished, linked with each other by septes-de-vallée. In series, septa 60–80 per calice, in monocentric corallites up to 120 per calice. Septal density in the wall 10–13/5 mm.

Material: Three fragmentary colonies from the Gosaukamm region, NHMW 1982/56/21<sub>1,2</sub>, 58; eight thin sections

## Dimensions (in mm):

NHMW 1982/56/21<sub>1</sub>

corallites in series

d	s
ca. 11	55
11	63
9 × 13	65
15 × 20	85

NHMW 1982/56/21<sub>2</sub>

monocentric corallites

d	s
10	70
13.5	102
13 × 16	110
13 × 16	125

**Description:** Colony lamellate or massive. Monocentric corallites regularly polygonal (Pl. 25, fig. 2 d). Series open, monolinear, bifurcating, flexuous and strongly varying in width (Pl. 25, figs. 1 a, c). Collines tectiform. In series, calices 5–15 mm apart and linked by varying numbers of compact septes-de-vallée. Calicular fossa oval, very small.

Septa subparallel in collines and varying in thickness, abruptly bent adaxially in valleys. In the wall, septa nonconfluent. Septa of 4 size orders. S1 septa approaching the center, S2 septa usually shorter. As a rule, S1 thickened in their internal half whilst S2 in the middle of their length. S3 septa thin, reaching more than half the length of S1 and distributed regularly between S1 and S2. S4 septa very thin and variable in length, regularly developed in some systems, accidental or lacking in others.

Generally, distal septal edge smooth, but in thickened septal portions lateral thin ridges marking the course of the trabeculae are prolonged up to the edge. Lateral ornamentation changes depending on the growth stage of septa. In newly formed septal parts, just below the distal edge, only trabecular ridges (see above) are seen, on which lateral granules appear and grow in size when descending the septum toward the older septal parts. Downwards, simple granules become sparse, and large, flattened granules and then menianes appear (Pl. 25, fig. 3, Pl. 26, figs. 1 c–d, 2 b). Mixed ornamentation composed of granules and short menianes can be met all over the septum with the exception of the most distal zone 1–2 mm wide, close to the distal edge. The menianes are arranged in rows steeply inclined from the periphery toward the fossa.

Endotheca formed of small, abundant vesicles, sloping adaxially from the periphery (Pl. 25, fig. 1 b).

Wall thin, well marked on the calicular colony surface.

Budding with direct linkages (Pl. 25, fig. 1 c). New individuals appear at the periphery of the parent. In series, new centres develop at the end, or in their mid-length. In the latter case a new series is initiated. The septa of the parent are interrupted about halfway from the centre to the wall. The point of interruption becomes a new centre. The new individual takes over most of its septa from the parent. Complementary septa appear on the flanks of the septa which run in the vicinity of a new centre and are not included in its septal apparatus.

**Microstructure:** The septa are built of trabeculae which are subvertical at the wall and inclined adaxially in the rest of the blade; exceptions are observed in this rule. In the septes-de-vallée, the trabeculae are mostly subvertical as well as in the periaxial, thickened portions of S1 septa. Menianes are composed of lateral extensions of 4–6 trabeculae (Pl. 26, fig. 1 b). The edges of the menianes are smooth (Pl. 26, fig. 2 b). Lateral extensions exhibit their axes when they are observed in longitudinal sections (Pl. 26, figs. 1 a, d). Thin septal blades are built of isometric trabeculae of 50–90 µm diameter. Peripherally, in the wall region, the septa are built of thickened trabeculae of 100–200 µm (measured along the radius). Thick septa are up to 300 µm, the thinnest are 70–100 µm wide. In transverse section, a recrystallized zigzag mid-line may be observed (Pl. 25, fig. 2 c, Pl. 26, figs. 2 a, c).

The wall structure is complex. In the simplest case it is septothecal, formed of thickened alternating external edges of septa. A tendency is observed to form the structure by development of lateral trabecular axes, synapticular in character, at the external septal edge (Pl. 25, figs. 2 a, b). Primarily lateral, they change their position into subvertical at the mature stage of wall development and play the role of euthecal wall portions (see also *Stuoresimorpha norica*, p. 90). All stages of development of wall structure may



be observed in a single thin section cutting a colony fragment with monocentric corallites (NHMW 1982/56/21<sub>2</sub>). In portions where series prevail, the early stages of wall structure development are observed.

**Discussion:** Macroscopically, colonies of *A. flexuosa* sp. n. resemble those of *Stuoresimorpha norica* (FRECH) in their cerioid-meandroid type of corallite arrangement. However, they differ essentially in the mode of budding, with direct linkages in *A. flexuosa* and indirect in *S. norica*, and besides, in the shapes of monocentric corallites and series. In *A. flexuosa*, series are open, polycentric, and serpentine; isolated calices are shallow and regularly shaped. In *S. norica* series are strongly lobate, closed, only exceptionally more than bicentric, and calices are deep and irregularly lobate. The other features as well as microstructural details are strikingly similar in both. The mode of budding appears here as a factor controlling the shape of corallites and series.

**Distribution:** As for the type specimens.

### Genus *Stuoresimorpha* nov.

**Species typica:** *Isastraea norica* FRECH, 1890

**Derivatio nominis:** a name referring to the morphological similarity of this genus to the Carnian genus *Stuoresia* CUIF, 1976; *femin.*

**Diagnosis:** Cerio-meandroid, series closed. Budding intratentacular with indirect linkages. Septal ornamentation of short, axiferous menianes. Wall structure varies in ontogeny from septothecal to septo-synapticulothecal. Endotheca vesicular.

**Species included:** The genus is monotypic.

**Stratigraphic and geographic ranges:** Rhaetian of the Alpine region.

**Discussion:** The genus belongs to the large *Isastraea*-like group of genera characterized by the presence of short menianes, comprising *Alpinophyllia* gen. n., *Adrazella* CUIF, 1976, *Guembalastraea* CUIF, 1976, and *Stuoresia* CUIF 1976. In septal and wall microstructure it most closely resembles *Alpinophyllia* gen. n., differing in type of budding and the shape and arrangement of corallites (compare p. 88). Macroscopically, in the arrangement of corallites resulting from the same mode of budding, it resembles *Stuoresia* CUIF, 1976, from which it differs, above all, in having axiferous menianes and lobate corallites. The latter feature distinguishes it from *Guembalastraea*. From *Adrazella*, with axiferous pennules and menianes, it differs in wall structure (compare p. 90) and in the lack of any pennular bridges or platforms (compare CUIF 1976, 102) in the interseptal space.

### *Stuoresimorpha norica* (FRECH, 1890)

Pl. 25, figs. 4–6, Pl. 27, fig. 2

1890 *Isastraea norica* – FRECH, p. 25, text-fig. on p. 25, Pl. 6, figs. 7, 8

1976 *Isastraea norica* FRECH – CUIF, p. 116, text-fig. 14, Pl. 11, figs. 7, 8

**Series typica:** Lost

**Neotypus** (here chosen) NHMW 1959/361/1; Pl. 25, fig. 4, Pl. 27, fig. 2

**Locus typicus:** Kesselwand-Rohrmoos

**Stratum typicum:** Zlambach Beds

**Material:** Four fragmentary colonies from the Gosaukamm region, NHMW 1959/361/1, NHMW 1982/56/38<sub>1-3</sub>; eight thin sections; numerous specimens from Kesselwand-Rohrmoos in NHMW collection examined externally.

## Dimensions (in mm):

Specimen No.	d	s	s/3 mm
NHMW 1959/361/1	5 × 8	e. 69	8–10
	6 × 9	e. 65	
	6 × 7	e. 66	

**Description:** Colony thick, lamellate or massive. Calices deep, multilobate, permanently monocentric or in short bicentric series which are very elongated and irregular in shape; wall tectiform (Pl. 25, figs. 5, 6, Pl. 27, fig. 2).

Septa differentiated into 3–4 size orders. S1 septa reaching the axis, thickened adaxially except for the internal edge. S2 septa rather thin and long. S3 attaining more than half the length of S1. S4 sporadic, underdeveloped, very thin and short. Septal faces ornamented with short menianes parallel to the distal edge.

Endotheca abundant, consisting of small vesicles. Wall from 250 up to 800 µm in thickness (Pl. 25, fig. 4).

Budding peripheral. A new individual develops from a small portion of the parent, limited by two septa strongly bent towards the parental centre. A dividing wall develops very slowly as a continuation of the wall of a parent. It encloses the new individual when it attains nearly normal adult size.

**Microstructure:** The septa consist of monolinear series of trabeculae, which are vertical at the wall and inclined adaxially. The trabeculae vary in diameter. In thin septa or in their thin adaxial portions they are 40–60 µm along the radius, and up to 110 µm when measured perpendicularly to the septal plane. In thick septa, the trabeculae are up to 100–130 µm and 175 µm respectively. When differential diagenesis separates the primary skeleton from the secondary stereomal layer, in the middle of the septum there is a primary blade composed of trabeculae of 60–90 µm, coated secondarily with stereome up to 150 µm in total thickness. Leaching of trabecular axes may produce a continuous line along the middle of the septa. The wall is formed of the external edges of radial elements. At their simplest, the external edges of alternating septa from neighbouring corallites fuse (CUIF 1976, text-fig. 14). Generally, however, more complex wall structure develops, i. e. additional binding of the external edges is formed of short synapticulae that diverge from the very end of the septa. In addition, in some places the septa are interposed by large centres resembling euthecal elements. Auxilliary septa may develop on the basis of these elements. See also the wall structure in *A. flexuosa* p. 88.

**Remarks:** The colonies examined have slightly smaller corallites than FRECH's specimens (those are 10–15 mm in diameter). The neotype specimen fits the form figured by FRECH (1890) in Pl. 6, fig. 7, the others resemble a colony figured in the text-fig. on p. 25 (*op. cit.*) in the shape of its calices.

**Distribution:** Rhaetian of the Northern Calcareous Alps: known in Zlambach Beds of Kesselwand-Rohrmoos and Schneckengraben. In addition, FRECH (1890) reported it from Hallstätter Salzberg.

Genus *Alpinoseris* nov.

**Species typica:** *Alpinoseris dendroidea* sp. n.

**Derivatio nominis:** from the Alps and Latin *serere* – join, indicating serial disposition of individuals; *femin.*

**Diagnosis:** Colony thamnasterioid, composed of corallites arranged in short series producing leaf-like branches. Budding with direct linkages. Menianes long, oriented upwards. Dissepiments small, vesicular. Columella lacking. Epitheca present.

The genus is monotypic.

**Stratigraphic and geographic ranges:** Rhaetian of the Alpine region.

**Discussion:** *Alpinoseris* gen. n. differs from other genera of the family in its thamnasterioid-branching colony growth form, mode of budding and menianes strongly oriented upwards.

*Alpinoseris dendroidea* sp. n.

Pl. 27, fig. 1

? 1969 *Procyclolites* sp. 1 – ZANKL, p. 32, text-fig. 24

**Holotypus:** GBA 1982/12/806; Pl. 27, figs. 1 a–h

**Locus typicus:** Schneckengraben

**Stratum typicum:** Zlambach Beds

**Derivatio nominis:** Greek *dendron* – tree, from the colony form.

**Diagnosis:** Monocentric branches up to  $15 \times 20$  mm in diameter at a septal number of about 150; polycentric branches thicker. Septal density 15 per 5 mm.

**Material:** Fragment of a colony measuring  $50 \times 50 \times 60$  mm, collected by Dr. G. SCHÄFFER, GBA 1982/12/806; four thin sections. The specimen is embedded in dark biopelmicrite.

**Dimensions (in mm):**

d	s
$7 \times 10$	80
$8 \times 15$	110
$15 \times 20$	155 (104 S1–S4)

**Description:** Colony branched. Branches leaf-like, monocalicular or formed of series of corallites. The newly formed branches are monocalicular, oval in cross section, with an eccentric axis. Series irregular. Calicular centres linked by 3–5 radial elements. New branches arise from the upper surface of the older ones (Pl. 27, figs. 1 a–d).

The axial calicular cavities are extremely narrow. The septa are thin, dense, differentiated into 5 size orders: the S1 septa reach the centre and number about 10–14; the S2 septa are subequal to S1; the S3 septa are usually two-thirds to four-fifths the radius in length; the S4 may reach half the radius but usually are shorter; the S5 are thin, variable in length, often rudimentary. Peripherally, the septa become contiguous to form a thin septotheca. A thin pellicular wall covers the surface of branches. The septal faces are provided with long menianes, their edges smooth and oriented upwards. Dissepiments vesicular, abundant. Peripherally, a zone consisting of a single layer of small, often thickwalled vesicles is developed.

**Microstructure:** The septa are built of trabeculae  $60 \mu\text{m}$  in diameter (measured radially; Pl. 27, fig. 1 h). The trabeculae are disposed in a straight or zigzag line. The septa of higher orders are very thin (about  $70 \mu\text{m}$ ), those of the first order are thickened. The menianes are built of lateral trabecular extensions provided with axes (Pl. 27, figs. 1 e–g).

**Discussion:** A form described by ZANKL (1969, 32) as *Procyclolites* sp. 1 has some features common with the here described new taxon, i. e. irregular form of

branches, eccentric calices, peripheral budding. However, in lack of data concerning internal structure, no determination is here possible.

Distribution: As for the type specimen.

### Familia Cuifastraeidae MELNIKOVA, 1983

Genus typicus: *Cuifastraea* MELNIKOVA, 1983

Diagnosis (after MELNIKOVA 1983, 47): Solitary or colonial. Radial elements perfectly compact, formed by a row of vertical trabeculae. Lateral sides ornamented with regularly distributed, more or less extended, subhorizontal, wavy menianes, granulated at the edge.

Genera included: *Tropiphyllum* CUIF, 1975, *Gillastraea* MELNIKOVA, 1983, *Cuifastraea* MELNIKOVA, 1983.

Remarks: Basing on general structural pattern of the meniane-bearing corals, MELNIKOVA (1984) has erected a new suborder Cuifastraeina with the following, heterogeneous, familial content: Cuifastraeidae MELNIKOVA, 1983, Conophylliidae ALLOITEAU, 1952, Tropiastreaeidae MELNIKOVA, 1984, Guembelastraeidae MELNIKOVA, 1984, Andrazellidae MELNIKOVA, 1984 and Pamiroseriidae MELNIKOVA, 1984. I prefer, however, to retain the family Cuifastraeidae, due to their resemblance to microsolenid and latomeandrid corals, in the heterogeneous order Fungiina.

### Genus *Cuifastraea* MELNIKOVA, 1983

Species typica: *Cuifastraea granulata* MELNIKOVA, 1983

Diagnosis (after MELNIKOVA, 1983, 47, slightly shortened): Thamnasterioid colonies. Budding intracalicular. Distal septal edge covered with rounded denticles. Edges of menianes finely granulated. Endotheca vesicular. Columella trabecular, rarely lamellar or styliform.

Species included: Norian — *C. granulata* MELNIKOVA, 1983 and *C. tenuiseptata* (MELNIKOVA, 1967); Rhaetian — *C. incurva* MELNIKOVA, 1983 and *C. arthaberi* (HAAS, 1909).

Stratigraphic and geographic ranges: Norian and Rhaetian of the Tethyan realm.

Discussion: The genus resembles Carnian *Karatchastraea* CUIF, 1976 from which it differs in having perfectly confluent radial elements and ornamented meniane edges.

### *Cuifastraea arthaberi* (HAAS, 1909)

Pl. 23, fig. 4

v. 1909 *Thamnastraea* ? *Arthaberi* — HAAS, p. 151, Pl. 5, fig. 13

Holotypus: PIUW, HAAS collection No. 52; HAAS 1909, Pl. 5, fig. 13

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: Three specimens from Fischerwiese, GBA 1982/12/228, 229, 230 with seven thin sections; one colony from Kesselwand-Rohrmoos collection examined externally.

## Dimensions (in mm):

Specimen No.	c-c	s	s/3 mm
GBA 1982/12/228	5-10	28-40 (11-12 S1 reach the axis)	7-8
GBA 1982/12/229	5-10	28-32 (11-12 S1 reach the axis)	8
GBA 1982/12/330	7-11	22-30	

**Description:** Colonies laminar and 10-20 mm thick. Lower colony surface covered with thin epitheca (holotheca).

Intercalicular surface horizontal, calices slightly depressed. Budding intercalicular. Axial cavity small. Radial elements perfectly confluent, differentiated into 2-3 size orders (Pl. 23, fig. 4 a). S1 septa thickest and reaching the axis. In adults, the S1 and S2 septa differ slightly in length, while in young corallites the S2 septa are markedly shorter. The S3 septa may appear more or less regularly and reach from a half to two-thirds the radius in length. Internal septal edge slightly dissociated into trabeculae. Menianes continuous, strongly protruding, distributed alternately or symmetrically on both septal faces, their edges directed upwards. Density of menianes 3 per 1 mm measured in longitudinal sections. Menianes of neighbouring septa may meet in the interseptal space. The menianes reach the middle of the interseptal space along their course, or they narrow slightly between the trabeculae, and have a tendency to divide into pennules. The edges of the menianes are delicately and regularly ornamented with small granules (9 per 240  $\mu$ m). Columella rudimentary, parietal in the form of 2-3 trabecular projections penetrating the axial cavity.

Dissepiments abundant, vesicular. Dissepiments and menianes disposed sub-horizontally in the intercalicular zone and inclined adaxially (Pl. 23, fig. 4 e).

**Microstructure:** When observed in cross section, the trabeculae of S1 septa are strongly anisometric measuring 90-120  $\mu$ m in the smaller, radial diameter and up to 240  $\mu$ m in the transverse diameter (Pl. 23, figs. 4 d, f). The thinnest septa are 60-90  $\mu$ m thick at the periphery and 35-50  $\mu$ m at the internal edge. The trabeculae of thin septa are nearly isometric. The differences in trabecular diameter prove that originally the trabeculae are very thin and become thicker only by lateral increase. The septal mid-line may be zigzagged. In the menianes, lateral fascicles composed of subparallel fibres may be observed. Their tops, 25-30  $\mu$ m wide, can be seen as granules at the edge of the menianes (Pl. 23, figs. 4 b, c).

**Discussion:** The species has relatively large calices and small septal density in comparison with those of the three species described by MELNIKOVA (1983).

**Distribution:** Rhaetian of the Northern Calcareous Alps; known in the Zlam-bach Beds of Fischerwiese and Gosaukamm vicinity.

## Familia Astraeomorphidae FRECH, 1890

Genus typicus: *Astraeomorpha* REUSS, 1854

Emended diagnosis: Thamnasterioid, small-calicular. Septa with menianes and/or synapticalae. Columella styliiform. Endotheca dissepimental. Microstructure non trabecular developing into trabecular; the process of forming large trabeculae advanced.

Genera included: *Astraeomorpha* REUSS, 1854, *Parastraeomorpha* gen. n., *Seriastraea* SCHÄFER et SENOWBARI-DARYAN, 1978.

**Discussion:** The small-calicular, thamnasterioid type of colony in this family results in a striking homeomorphy with the quite different in microstructure family Thamnasteriidae. This caused the original assignment of astraeomorphids to the Tham-

nasteriidae. An apparent microstructural similarity links astraeomorphids and spongiomorphids. The nature of this resemblance and a possible relationship of both groups are worth further examination.

Three genera included here represent in the corallite structure three variations of the common architectural pattern: 1) *Astraeomorpha* has continuous menianes, simple, rudimentary columella, and synapticalae dependent on menianes, 2) *Seriastraea* has continuous menianes, thick, compound columella and thin synapticalae (the structure of which remains unknown in detail), and 3) *Parastraeomorpha* has thick synapticalae independent of other elements, simple, thin columella, and rudimentary pennulae. It is highly probable that astraeomorphids represent a natural, phylogenetically related group of genera.

The common microstructural characteristics observed in the genera of the family is their basic thin-trabecular or non-trabecular septal structure which shows a tendency to change into the large-trabecular one.

#### Genus *Astraeomorpha* REUSS, 1854

Species typica: *Astraeomorpha crassisepta* REUSS, 1854

Emended diagnosis: Thamnasterioid, budding intercalicular. Septa solid; distal edge smooth, lateral faces with menianes and synapticalae. Internal edge with regularly distributed projections. Columella styliform, thin. Dissepiments thin-walled, vesicular. Septal mid-line continuous or differentiated into small, densely arranged trabeculae. Menianes axiferous.

Species included: Carnian: ? *A. pratzi* VOLZ, 1896; Norian-Rhaetian: *A. crassisepta* REUSS, 1854, *A. confusa* (WINKLER, 1861), *A. minor* FRECH, 1890, *A. reimani* MELNIKOVA, 1967, *A. multisepta* MELNIKOVA, 1971, *A. major* VINASSA DE REGNY, 1915.

Stratigraphie and geographic ranges: ? Carnian, Norian-Rhaetian of the Tethyan realm.

Discussion: In the genus two different morphological trends can be seen: (i) in *A. crassisepta*, *A. minor*, *A. reimani* and *A. multisepta* calices are so densely packed that no perithecal zone develops and only single synapticalae mark the limits between corallites; (ii) in *A. confusa*, the perithecal zone develops with parallel septa and abundant synapticalae.

The microstructure shows a tendency to decompose the structurally uniform septal plates into relatively large trabeculae — the process attaining its acme in the Pamirian *A. multisepta* in which rhythmical narrowing of solid plates starts a septal fragmentation into smaller portions — individual trabeculae (compare MELNIKOVA 1971, Pl. 1, fig. 3). In other species, especially in *A. crassisepta*, this tendency is very weakly expressed.

#### *Astraeomorpha crassisepta* REUSS, 1854

Pl. 28, figs. 3–5

- 1854 *Astraeomorpha crassisepta* — REUSS, p. 127, Pl. 16, figs. 4–7
- 1854 *Astraeomorpha Goldfussi* — REUSS, p. 127, Pl. 16, figs. 8, 9
- 1882 *Astraeomorpha crassisepta* REUSS — PRATZ, p. 102, Pl. 1, figs. 13–15
- v. 1890 *Astraeomorpha crassisepta* REUSS — FRECH, p. 66, text-fig. on p. 70, Pl. 19, figs. 14–18
- 1964 *Astraeomorpha crassisepta* REUSS — KRISTAN-TOLLMANN & TOLLMANN, p. 559, Pl. 7, figs. 2, 7–9

- 1969 *Astraeomorpha crassisepta* REUSS — KRISTAN-TOLLMANN *et al.*, p. 15, Pl. 2, figs. 3, 4
- ? part. 1971 *Astraeomorpha crassisepta* REUSS — MELNIKOVA, p. 29, Pl. 1, figs. 1, 2
- non, v. 1974 *Astraeomorpha crassisepta* REUSS — RONIEWICZ, p. 113, Pl. 9, figs. 4, 5
- ? part. 1975 *Astraeomorpha crassisepta* REUSS — MELNIKOVA, p. 116, Pl. 23, figs. 1–6, Pl. 24, figs. 1–3, Pl. 25, fig. 1, Pl. 26, fig. 3
- 1975 c *Astraeomorpha crassisepta* REUSS — CUIF, p. 117, text-fig. 19, Pl. 17, figs. 1–7
- 1980 *Astraeomorpha crassisepta* REUSS — SENOWBARI-DARYAN, p. 38, Pl. 2, fig. 3
- 1984 *Astraeomorpha crassisepta* REUSS — FANTINI-SESTINI & MOTTA, p. 351, Pl. 29, fig. 4
- 1986 *Astraeomorpha crassisepta* REUSS — MATZNER, Pl. 9, fig. 1
- 1986 *Astraeomorpha crassisepta* REUSS — MELNIKOVA, p. 56, Pl. 20, figs. 1–3, Pl. 21, fig. 2

Holotypus: Lost

Neotypus (here chosen): NHMW 1982/56/37<sub>2</sub>; Pl. 28, fig. 5

Locus typicus: Gosau (= Kesselwand-Rohrmoos)

Stratum typicum: Zlambach Beds

FRECH's originals: GBA FRECH's collection No. 2813 (unfigured); BSP AS XII 131, figured by FRECH 1890, text-fig. on p. 67

Material: Three specimens from Kesselwand-Rohrmoos, NHMW 1903 XII 103, NHMW 1982/56/36<sub>1</sub>, 36<sub>2</sub>; nine specimens from Fischerwiese, GBA 1982/12/421–427, NHMW 1982/57/98, 99; specimens from Sommeraukogel, GBA 1982/12/428, 885 and Zlambachgraben, GBA 1982/12/886, 887; eight thin sections

Dimensions (in mm):

Specimen No.	c-c	s	m/1 mm
NHMW 1903 XII 103	1.5–3	11–13	3
NHMW 1982/56/36 <sub>1</sub>	2.5–3	15–17	2.5–3
NHMW 1982/56/36 <sub>2</sub>	2 –3	9–11	2.5–3
NHMW 1982/57/99	2 –3.5	9–11	2 –2.5

Description: Colonies massive, mostly hemispheric or columnar in shape. Calices distributed densely and disorderly (Pl. 28, fig. 3). Septa not abundant (up to 18), usually thick, in hexameral order, S1 and S2 subequal. Internal edges with regular projections of meniane or synapticular origin, those of S1 septa reaching the columella. Menianes strong (Pl. 28, fig. 5), with edge oriented upwards and thickened as a lip. Their density low, from 2 to 2.5, rarely 3 per 1 mm. Solitary, rare synapticulæ are developed at the internal septal edge and at the periphery of the calices. The synapticulæ origin at the edge of the meniane and direct slightly upwards in their way to the opposite septum, to reach it, most frequently, just at the base of the meniane. The synapticulæ are distributed regularly in vertical rows (Pl. 28, fig. 5).

Columella styliform. Endotheca formed of numerous, extremely thin, vesicular dissepiments.

Microstructure: The septal mid-line continuous or formed of a row of densely packed small trabeculae (Pl. 28, fig. 4). The mid-line continues throughout the septum or is divided into 2–3 portions. In the menianes, the fascicles of fibres are more or less con-

spicuous. In the vertical sections of menianes, the lateral axes may be observed which prolongs from the vertical ones. Synapticulae are relatively thin, circular in section and provided with axes. The contact line (suture) between synapticula and the neighbouring septum is sharp. The position of synapticulae (observed in longitudinal section) suggests that they origin on shorter septa, probably of the second order, and direct to the surface of the pre-existing first-order ones.

Microstructure of *A. crassisepta* compares with that of *A. confusa*.

Discussion: *A. crassisepta* was the first Triassic coral to be examined microstructurally: its fibrous structure was illustrated for the first time by PRATZ (1882). CUIF (1975 c) has given a microstructural characteristics of *A. crassisepta* based on moderately preserved specimens from Fischerwiese showing no traces of trabeculae. His interpretation of the microstructure of *Astraeomorpha*, as a non-trabecular one has not been accepted here in the light of the data obtained from a differently preserved skeleton.

As far as the synonymy of the species is concerned, I share the opinion of FANTINI-SESTINI & MOTTA (1984) that the range given by MELNIKOVA (1971, 1975) and RONIEWICZ (1974) for *A. crassisepta* is very large and overlaps that of *A. confusa* (WINKLER).

In species determination in *Astraeomorpha* the meniane index appears very useful. It indicates the number of menianes per 1 mm, relatively easy to be measured in longitudinal thin sections.

Distribution: Common in the Norian and Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese, vicinity of Gosaukamm, Zlambachgraben, Hallstätter Salzberg and Scharitzkehlalp; dolomites of the Gosaukamm; Rhaetian limestones of Tyrol and Salzburg vicinity. Rhaetian of the Southern Alps (Lombardy). Norian-Rhaetian of the Caucasus, Central Asia, Timor and NE Asia.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Astraeomorpha confusa* (WINKLER, 1861)

Pl. 28, figs. 1, 2, Pl. 29, figs. 1-3

- 1861 *Thamnastraea confusa* — WINKLER, p. 488, Pl. 8, fig. 10
- v. 1890 *Astraeomorpha confusa* WINKLER — FRECH, p. 67, Pl. 19, figs. 2, 3, 5, 6, 8, 10, 13
- 1915 *Astraeomorpha confusa* WINKLER *major* — VINASSA DE REGNY, p. 103, Pl. 68, figs. 13-15
- 1969 *Astraeomorpha confusa* (WINKLER) FORM B and C — ZANKL, p. 26, text-figs. 15, 16
- ? part. 1971 *Astraeomorpha crassisepta* REUSS — MELNIKOVA, p. 29, Pl. 1, figs. 1, 2
- v. 1974 *Astraeomorpha crassisepta* REUSS — RONIEWICZ, p. 113, Pl. 9, figs. 4, 5
- ? part. 1975 *Astraeomorpha crassisepta* REUSS — MELNIKOVA, p. 116, Pl. 23, figs. 1-6, Pl. 24, figs. 1-3, Pl. 25, fig. 1, Pl. 26, fig. 3
- 1979 *Astraeomorpha confusa* (WINKLER) — SCHÄFER, p. 46, Pl. 10, fig. 3
- 1980 *Astraeomorpha confusa minor* FRECH — SENOWBARI-DARYAN, p. 38, Pl. 5, fig. 4
- 1980 *Astraeomorpha confusa confusa* (WINKLER) — KRISTAN-TOLLMANN *et al.*, p. 171, Pl. 4, fig. 3
- ? 1984 *Astraeomorpha confusa* (WINKLER) — FANTINI-SESTINI & MOTTA, p. 352, Pl. 29, fig. 5



1986 *Astraeomorpha confusa* (WINKLER) — MATZNER, Pl. 9, fig. 2

1986 *Astraeomorpha confusa* (WINKLER) — MELNIKOVA, p. 57, Pl. 20, fig. 4,  
Pl. 21, fig. 1

? Holotypus: BSP AS XII 133; WINKLER 1861, Pl. 8, fig. 10; FRECH 1890, Pl. 19,  
fig. 3<sup>9</sup>

Locus typicus: Kothalp

Stratum typicum: Upper Rhaetian, Kössen Beds

FRECH's originals: BSP AS XII 132, 134, 135, figured by FRECH 1890, Pl. 19, figs. 2,  
8, 10 and BSP AS XII 136 — unfigured specimen

Material: Seventeen specimens of Fischerwiese, GBA 1982/12/415–418, 876–  
884, NHMW 1982/57/69–72; one specimen of Kesselwand-Rohrmoos, NHMW 1982/  
56/20; eight thin sections

Dimensions (in mm):

Specimen No.	c-c	s	m/1 mm
NHMW 1982/57/71	2 – 3	12–16	4
NHMW 1982/57/69	2 – 2.5	18–20	6
NHMW 1982/57/72	1.5–2	16	5–6

Description: Colonies flat, lying on the sediment or ramose. Calices in slightly  
marked series, centres distant (Pl. 28, fig. 1). In the calice, septa differentiated into  
3 size orders, two first of them subequal. The symmetry is hexameral. The septa are paral-  
lel and slightly wavy in the perithecal zone. Menianes densely spaced. Synapticulae  
numerous in the perithecal zone (Pl. 29, fig. 2). Dissepiments thin. Columella thin.

Microstructure: In the specimen NHMW 1982/56/20, the microstructure is well pre-  
served. The septa are composed of more or less differentiated trabeculae, the centra of  
which are more or less closely spaced (Pl. 29, figs. 1 b–d, 3). Synapticulae, when diage-  
nized, show their axes prolonging from the axes of menianes (Pl. 28, fig. 2, Pl. 29,  
fig. 1 a). The majority of the interseptal space filled with fibrous stereome, the fibres  
growing epitaxially on those of the septal tissue.

Discussion: *Astraeomorpha confusa* resembles *A. crassisepta* in the number of  
septae, differing from this species in smaller corallites, thinner septa and more densely  
spaced menianes. Both species seem to be closely related. It is very difficult to judge  
from the descriptions in the literature which of the species the author has in mind. Thus,  
the synonymy included here is much reduced.

The taxonomic identification of the ramose morphotype presented by ZANKL (1969:  
Form A) and FANTINI-SESTINI & MOTTA (1984) is difficult, because at least four species  
from among Alpine corals have comparable either growth forms or corallite diameters:  
*A. confusa* (WINKLER), *A. minor* FRECH, *P. similis* sp. n. and *P. minuscula* sp. n. In such  
a situation only internal structure and exactly measured corallite diameters may be deci-  
sive in species determination.

Distribution: Norian-Rhaetian of the Alps, Caucasus, Central Asia and Timor.  
The detailed list of Alpine ancient sites has been given by FRECH (1890). In addition to

<sup>9</sup> Specimens AS XII 133 and 134 are supposed to be WINKLER's originals (FRECH 1890, explanations to  
Pl. 19). The first of them shows colony surface conform with that presented on WINKLER's original illustration.

positions included in the synonymy the species has been cited by KRISTAN-TOLLMANN *et al.* (1969) from Tirol and by SADATI (1981) from the Hohe Wand.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

### Genus *Parastraeomorpha* nov.

Species typica: *Parastraeomorpha minuscula* sp. n.

Derivatio nominis: Greek *para* – near, to indicate morphological likeness to *Astraeomorpha* REUSS, 1854; *femin.*

Diagnosis: Colony thamnasterioid. Septa laminar, thin-trabecular. Columella styliform. Septal faces smooth or with rudimentary pennular expansions. Synapticules large, independent of other structures. Dissepiments thin, rare.

Species assigned: *P. minuscula* sp. n., *P. similis* sp. n.

Stratigraphic and geographic ranges: Rhaetian of the Northern Calcareous Alps.

Discussion: The genus is close morphologically and microstructurally to *Astraeomorpha* REUSS. The lack of menianes and development of thick synapticulae distinguish this genus from that of REUSS. Synapticular axes in *Parastraeomorpha* are horizontal, whilst oblique in *Astraeomorpha*.

### *Parastraeomorpha minuscula* sp. n.

Pl. 30, figs. 1, 2

*part.* 1890 *Astraeomorpha confusa* WINKLER forma *minor* – FRECH, p. 68, Pl. 19, figs. 4, 11, 12 (*non* fig. 1, *nec* 7)

Holotypus: NHMW 1982/57/17; Pl. 30, fig. 1

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Derivatio nominis: Latin *minusculus* – small, from small corallite dimensions.

Diagnosis: Corallites densely spaced, c–c from 1 mm to 1.3 mm (rarely 1.5), septes differentiated into 2–3 orders, columella small, synapticulae large, four per 1 mm in number when measured in longitudinal section.

Material: Twenty fragments of colonies from Fischerwiese, GBA 1982/12/406–413, 724, NHMW 1982/57/17–21, 24–28, five from Sommeraukogel, GBA 1984/12/871–875; four thin sections

Dimensions (in mm):

Specimen No.	c–c	s	syn/1 mm
NHMW 1982/57/20	1–1.3 (1.5)	14–18	4
NHMW 1982/57/17	1–1.3 (1.5)	14–16	4

Description: Colonies columnar or lamellate bifacial. Corallites dense and distributed disorderly. Calices slightly depressed. Septa wavy, differentiated into 2–3 size orders: usually 6 S1 septa alternating with shorter S2 septa; S3 septa rare. The S1 septa reach the columella with their regularly distributed synapticular projections. Adaxial synapticulae of the S3 septa usually meet the faces of S2 septa. Septal faces smooth or with faint pennular ornamentation. The synapticulae, when observed in longitudinal colony sections, are circular or oval, their longer diameter oriented vertically.

Their diameters are from 60  $\mu\text{m}$  to 200  $\mu\text{m}$  in circular and up to 150  $\times$  300  $\mu\text{m}$  in oval ones. Columella small. Dissepiments rare, thin.

**Microstructure:** A mid-septal line is well expressed. When the septa are fractured along this line, an internal septal surface exposes the skeletal growth lines, similar to those observed in distichophylliid corals (comp. CUIF 1975 a, text-figs. 37 c, d). Synapticular axes are horizontal. Synapticalae are mostly formed of projections growing out from two opposite septa and meeting each other in the interseptal spaces; the sutures are well marked.

**Discussion:** The species resembles another small-calicular coral, *A. confusa minor* FRECH, in corallite diameters and colony growth form differing from it in thinner septa, large synapticalae and lack of menianes. From *P. similis* sp. n. it differs in considerably smaller corallites.

The species is represented in the literature by specimens from Fischerwiese determined by FRECH as *A. confusa minor* (see synonymy). FRECH described two forms under this name: the first, represented by specimens from the Kössen beds (Kothalp) and the second – by specimens from the Zlambach Beds (Fischerwiese). The first of them exhibits strong menianes typical of *Astraeomorpha* (observed on the colony broken section in the specimens BSP AS XII 137 and 138, specimens figured by FRECH 1890, Pl. 19, figs. 1 and 7<sup>10</sup>), whilst the second, lacking menianes and having large synapticalae (compare *op. cit.*, Pl. 19, fig. 4) represents the genus *Parastraeomorpha*.

As to other small-calicular corals described in the literature (viz., *A. confusa* Form A – in ZANKL 1969, *A. confusa* Form A – in SENOWBARI-DARYAN 1890, *A. confusa minor* FRECH in KRISTAN-TOLLMANN *et. al.* 1980) it is difficult to say, while observing their illustrations, which of them belongs to the new species, or represents FRECH's species.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Sommeraukogel.

*Parastraeomorpha similis* sp. n.

Pl. 30, fig. 3

**Holotypus:** GBA 1982/12/420; Pl. 30, figs. 3 a, b

**Paratypus:** GBA 1982/12/419

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Derivatio nominis:** Latin *similis* – indicating its similarity to other corals.

**Diagnosis:** Colony lamellate. Calicular centres distant 1.8–3.5 mm, septa up to 19 in number arranged in 2–3 orders. Synapticalae strong, 2–3/1 mm.

**Material:** Two colonies from Fischerwiese, GBA 1982/12/419, 420; one fragmentary colony from Kesselwand-Rohrmoos, NHMW 1982/56/95; two thin sections

**Dimensions (in mm):**

Specimen No.	c-c	s	syn/1 mm
GBA 1982/12/420	2.0–3.5	15–19	3
GBA 1982/12/419	1.8–3.0	14–18	2–3

<sup>10</sup> Lectotype of *A. c. minor* FRECH (1890, Pl. 19, fig. 7) has the following characteristics: c-c 1.5–2 mm, s 12–16, 3–4 m/1 mm.

**Description:** Colonies lamellate unifacial or bifacial. Corallites distributed disorderly (Pl. 30, fig. 3 a). Septa wavy, in 2–3 size orders. About six S1 meet the columella with synapticular projections. S2 alternating with S1, S3 septa sporadic. Columella small. The synapticular numerous, especially at periphery. The synapticular are circular or oval when observed in longitudinal section (Pl. 30, fig. 3 b). Circular ones are about 100–200  $\mu\text{m}$ , and oval ones up to  $300 \times 500 \mu\text{m}$  in diameters. Synapticular projections of the S1 septa regularly distributed. Synapticular axes horizontal. In longitudinal septal sections some structures resembling weak pennulae may be observed.

Microstructure is poorly preserved.

**Discussion:** The species resembles *P. minuscula* sp. n. in all structural details differing from it in larger diameters of corallites, robust skeletal elements and lamellate (not thin-branched) colony growth form. Externally – the colonies of this species are not distinguishable from those of *A. confusa* (WINKLER).

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos.

#### Genus *Seriastraea* SCHÄFER et SENOWBARI-DARYAN, 1978

**Species typica:** *Seriastraea multiphylla* SCHÄFER et SENOWBARI-DARYAN, 1978.

**Emended diagnosis:** Thamnasterioid. Budding circumoral. Septa long, solid or porous; S1 reaching the axis, S3 developed in the intercalicular zone. Menianes continuous or interrupted, smooth. Synapticular numerous in the intercalicular zone. Columella styliform, thick and complex in structure. Dissepiments vesicular. In septa, large complex trabeculae develop, basing on original thin-trabecular structure.

**Species included:** *Seriastraea multiphylla* SCHÄFER et SENOWBARI-DARYAN 1978, *S. crassa* sp. n., ? *S. furukawai* (KANMERA, 1964).

**Stratigraphic and geographic ranges:** (? Norian) Rhaetian of the Tethyan realm.

**Discussion:** The diagnosis presented above is completed (in relation to the original one) with details enabling to distinguish this genus from similar, synapticular and meniane-bearing, thamnasterioid genera.

The authors of the taxon made large morphological analysis of its resemblances and differences with thamnasterioid genera *Oedalmia* CUIF, 1976, *Lupitschia* CUIF, 1976 (= *Pamiroseris* MELNIKOVA, 1971) and *Thamnasteria* LESAUVAGE 1821. But only the microstructural characteristics of each of them (for the first two – see CUIF 1976 and herein p. 63 and p. 112, for *Thamnasteria* – see RONIEWICZ 1983) may show clearly differences in their structure. Externally, their microstructural features are expressed in different septal ornamentation, observable even in sections of poorly preserved specimens.

The species assigned to *Seriastraea* differ from species of *Astraeomorpha* REUSS with serially arranged corallites in: (i) circumoral budding, (ii) large intercalicular zone, (iii) S3 septa restricted to the intercalicular zone, (iv) development of a thick columella complex in structure, (v) strongly expressed tendency to develop large trabeculae, (vi) development of perforated septa. The ornamentation of septa in *Seriastraea* and *Astraeomorpha* (menianes) and presence of synapticular make alike the longitudinal sections of their colonies.

*Seriastraea multiphylla* SCHÄFER et SENOWBARI-DARYAN, 1978

Pl. 31, figs. 2, 3

1969 Kalkschwammenlamellen – ZANKL, pp. 23, 60, Pl. 5

1978 *Seriastraea multiphylla* – SCHÄFER & SENOWBARI-DARYAN, p. 119, text-figs. 1, 2, Pl. 1, fig. 1, Pl. 2, fig. 2**Holotypus:** SMF 30748; SCHÄFER & SENOWBARI-DARYAN 1978, text-fig. 2, Pl. 1, fig. 1, Pl. 2, fig. 2**Locus typicus:** Gruber Reef**Stratum typicum:** Rhaetian**Material:** Three small, fragmentary colonies, NHMW 1982/56/18, GBA 1982/12/746, 747; one thin section**Dimensions (in mm):**

Specimen No.	s/corallite	s/calice	s/5 mm	m/1 mm
GBA 1982/12/747	ca. 50–60	25, 27	20	6
NHMW 1982/56/18	70 (central one)	ca. 25	20	

**Description:** Colonies 3–5 mm thick, lamellate. Upper surface smooth or with rudiments of lamellae of next colony generation. Lower surface costulate. Budding circumoral; primary corallite central or eccentric (Pl. 31, figs. 2, 3).

Septa differentiated into 3 size orders distributed irregularly. S1, about 15 in number, reach the columella with their synapticular projections of the internal edge; S2 attain the border of the calice; S3 are developed in the perithecal zone. Internal edges of the short septa coalesce the side of the neighbouring long septa. Synapticulariae numerous. Columella thick. Menianes continuous.

**Remarks:** The specimens here presented have the septal density in the peritheca lower than the holotype, if one can judge from a photograph of this specimen (SCHÄFER & SENOWBARI-DARYAN, 1978, Pl. 1, fig. 1 b).**Distribution:** Rhaetian of the Northern Calcareous Alps; common in limestones of Hohe Göll, Gruber Reef and rare in Zlambach Beds of Kesselwand-Rohrmoos and Fischerwiese.*Seriastraea crassa* sp. n.

Pl. 31, figs. 1, 4, Pl. 32, fig. 1

*Thamnastraea felixi* KITTL – NHMW in collection**Holotypus:** NHMW 1982/56/17<sub>2</sub>; Pl. 31, fig. 1, Pl. 32, fig. 1**Paratypus:** NHMW 1982/56/17<sub>1</sub>; Pl. 31, fig. 4**Locus typicus:** Kesselwand-Rohrmoos**Stratum typicum:** Zlambach Beds**Derivatio nominis:** Latin *crassus* – thick, from its strong septa.**Diagnosis:** Colony lamellate. In primary corallite about 70 septa, in daughter ones about 25; about 12 septa per calice; septal density in the peritheca 12/5 mm; density of menianes 4/1 mm.**Material:** Two small specimens enumerated above; two thin sections

## Dimensions (in mm):

Specimen No.	s/central corallite	s/daughter corallite	s/calice	s/5 mm	m/1 mm
NHMW 1982/56/17 <sub>2</sub>	ca. 70	ca. 25	ca. 12	12	4–5
NHMW 1982/56/17 <sub>1</sub>	ca. 70	ca. 25	ca. 12	12	4

**Description:** Thin, lamellate colonies of small diameters (20 × 30 mm) growing from a small central point of fixation to the substrate and abruptly expanding laterally (Pl. 31, figs. 1 a, 4). Budding circumoral.

Septa relatively thick, continuous or porous, differentiated into 3 size orders (Pl. 31, fig. 1 a). The S1 septa, 10–12 in number, reach the columella; the S2 septa attain a border of the calice; the S3 septa are distributed in the pericalicular space. Synapticulae numerous. Menianes subhorizontal, smooth-edged (Pl. 31, figs. 1 b, 1 d). Columella thick, styliform. Dissepiments vesicular, thin.

**Microstructure:** The mid-septal line is divided into unequal portions – some circular, other oval, elongated when observed in cross section (Pl. 31, fig. 1 d). The septa become porous, disintegrated into the portions (Pl. 31, fig. 1 c, Pl. 32, fig. 1 a). Diameters of the portions begin with 100–200 µm. Depending on the shape of the portions, circular or elongated, axes or line are seen in their middle. In the mid-line, traces of small-trabecular structure are discernible, the axes show the multicentered structure as well (Pl. 31, fig. 1 c, Pl. 32, figs. 1 a–c).

Such septal structure is considered here as incipient large-trabecular one, being developed in the process of the “trabeculisation”. In this process the following structural stages may be distinguished: (1) primary blade with a continuous median line composed of thin trabeculae more or less individualized, (2) the primary septal blade disintegrated into portions; the fragments of primary mid-line are elongated or rod-like; thickening of portions takes place radially, their axes or median lamella retaining a complex structure, (3) the primary blade disrupted into isolated fragments leading to formation of perforated septa.

Continuous menianes show a tendency to divide into shorter segments – pennulae. Well-centered lateral fascicles growing out from the trabeculae are visible in the menianes (Pl. 32, figs. 1 c, d). Menianes observed in longitudinal section are provided with axes. Small quantity of material makes it impossible to examine the microstructure of synapticulae.

**Discussion:** The new species differs from the type species in its thick skeleton and smaller number of septa per calice.

**Distribution:** As for the type specimen.

Subordo Archaeocoeniina ALLOITEAU, 1952 (as Archaeocaenida ALLOITEAU, 1952)

**Emended diagnosis:** Trabeculae thick in relation to septum dimensions, in septum inclined adaxially whilst vertical at the external edge, ornamented with pointed granules. Radial elements of septal type. Increase by extracalicular budding.

**Families included:** Mesozoic family Actinastraeidae ALLOITEAU, 1952; Recent families Stylophoridae MILNE-EDWARDS et HAIME, 1847; Seriatoporidae MILNE-EDWARDS et HAIME, 1849 and, tentatively, Acroporidae VERRILL, 1902.

**Remarks:** The emendation concerns the original family content of the suborder. On the basis of microstructural data two families have been excluded from there: Pinaco-

phyllidae VAUGHAN et WELLS, 1943 and Stylophyllidae FRECH, 1890 (*in* ALLOITEAU 1952, erroneously, VOLZ, 1896) and considered as representative of a separat suborder Stylophyllina BEAUVAIS, 1981 (herein, p. 115). As to the family Acroporidae, the recent data concerning their microstructure (GLADFELTER 1986) evidence for their rather non-trabecular structure of skeleton, thus, a separate systematic position.

### Familia Actinastraeidae ALLOITEAU, 1952

Genus typicus: *Actinastraea* D'ORBIGNY, 1849

FRECH (1890) has distinguished seven species among corals having small corallites and an *Astrocoenia*- or *Stephanocoenia*-like septal organization. In the NHMW and GBA collections, the group is abundantly represented, but is, nevertheless, difficult to examine in detail. The skeleton has undergone recrystallization and its external and internal morphological features and microstructure have been severely destroyed. However, when examined in thin sections, some specimens reveal well preserved fragments of skeleton.

For this group of corals new generic names are proposed: *Chondrocoenia* for *Astrocoenia ohmanni* FRECH, 1890, *A. waltheri* FRECH, 1890 and *Stephanocoenia schafhaeutli* (WINKLER, 1861), and *Crassistella* gen. n. for the single species, *S. juvavica* FRECH, 1890 (syn. *Astrocoenia* sp. nov. in FRECH 1890). The genus *Crassistella* has been assigned to the family Pamiroseriidae (Astraeoinea).

The diagnosis of the family and the discussion of the genera considered by ALLOITEAU as related to *Actinastraea* D'ORBIGNY have given an idea of the range and characteristics of the family (ALLOITEAU 1952, 602; 1957, 53, 54). When comparing such Jurassic genera of the family as *Actinastraea* D'ORBIGNY (compare MORYCOWA 1971), *Stephanastraea* ETALLON, and *Allocoenia* ETALLON (compare RONIEWICZ 1976, 34) the following features can be considered, first of all, as diagnostic of the family: small number of trabeculae per septum, regularly denticulated, internal septal edge, septal anastomosis of *Actinastraea*-like pattern and very small corallite size. This definition allows the Triassic genus *Chondrocoenia* nov. to be included in this family, which was previously known only from the Jurassic – Cretaceous.

### Genus *Chondrocoenia* nov.

Species typica: *Prionastraea schafhaeutli* WINKLER, 1861

Derivatio nominis: Greek *chondros* – a grain-shaped object, and *koinos* – common, from the granulated appearance of the coenosteal surface; *femin.*

Diagnosis: Plocoid to cerioid. Costae solid or discontinuous. Septa solid. Single paliform projections adaxially of S1 septa. Anastomosis between septa takes place by the internal edge of smaller septa abutting with the lateral faces of neighbouring, larger septa. Internal edges regularly denticulate with trabecular projections. Columella styli-form, monotrabecular. Endotheca of tabuloid dissepiments. Exothecal dissepiments vesicular. Septal trabeculae thinner than those of the costae. Trabeculae laterally ornamented with pointed granules.

Species included: *Chondrocoenia schafhaeutli* (WINKLER, 1861), *Ch. ohmanni* (FRECH, 1890), *Ch. waltheri* (FRECH 1890), *Ch. paradoxa* (MELNIKOVA, 1975).

Moreover, at least some forms from among Liassic corals determined as *Allocoeniopsis* ALLOITEAU (BEAUVAIS 1976, 1986).

Stratigraphic and geographic ranges: Norian-Rhaetian of the Tethyan realm. Liassic of European epicontinental and Tethyan regions.

Discussion: Among Mesozoic corals having an *Astrocoenia*- or *Actinastraea*-like arrangement of septa, this genus is the only one displaying an ability to develop peritheca (coenosteum) and having trabeculae strongly differentiated into small septal, and large costal ones.

The species included in the genus *Chondrocoenia* nov. have been assigned by various authors to the following different genera: *Astrocoenia* MILNE-EDWARDS et HAIME, *Prionastraea* MILNE-EDWARDS et HAIME, *Stephanocoenia* MILNE-EDWARDS et HAIME, *Cyathocoenia* DUNCAN and *Allocoeniopsis* ALLOITEAU. The first three genera (*Prionastraea* being a synonym of *Favites* LINK) are modern Tertiary-Recent cerioid corals having a microstructure different from that of the Triassic corals (compare ALLOITEAU 1957). As for the genus *Cyathocoenia* DUNCAN, 1867, a columella is lacking and the septa are free, so differing from these Triassic corals. Poorly known genus *Allocoeniopsis* is diagnosed by perfectly cerioid colonies.

*Chondrocoenia schafhaeutli* (WINKLER, 1861)

Pl. 33, figs. 1–3, 5

- 1861 *Prionastraea* ? *Schafhäutli* – WINKLER, p. 488, Pl. 8, fig. 11
- 1865 *Isastraea Süssi* – REUSS, p. 162, Pl. 2, fig. 4
- v. 1890 *Stephanocoenia Schafhäutli* WINKLER – FRECH, p. 37, text-fig. on p. 36 (A, B) and two text-figs. on p. 37
- part. 1890 *Stephanocoenia juvavica* – FRECH, p. 38, right text-fig. on p. 38 (specimen from Fischerwiese)
- 1968 *Cyathocoenia schafhaeutli* (WINKLER) – MELNIKOVA, p. 14, Pl. 3, figs. 3–4
- v. 1974 *Cyathocoenia alpina* GÜMBEL – RONEWICZ, p. 103, text-figs. 3 a, b, Pl. 1, figs. 3, 4
- 1975 *Cyathocoenia schafhaeutli* (WINKLER) – MELNIKOVA, p. 59, text-fig. 8, Pl. 2, figs. 4, 5, Pl. 4, figs. 1, 2
- 1980 *Stephanocoenia schafhaeutli* FRECH – SENOWBARI-DARYAN, p. 41, Pl. 5, fig. 1
- 1980 *Astrocoenia schafhaeutli* (WINKLER) – KRISTAN-TOLLMANN *et. al.*, p. 169, Pl. 1, figs. 1–4
- 1982 *Actinastraea juvavica* (FRECH) – WURM, p. 218, Pl. 34, fig. 6
- 1984 *Cyathocoenia schafhaeutli* (WINKLER) – FANTINI-SESTINI & MOTTA, p. 350, Pl. 28, fig. 3, Pl. 29, fig. 2

Holotypus: BSP AS XV 1; WINKLER 1861, Pl. 8, fig. 11

Locus typicus: Kothalp

Stratum typicum: Kössen Beds

FRECH's originals: Specimens from Kothalp am Wendelstein, Kössen Beds, BSP AS XII 40–44; see also herein p. 146

Material: Fourteen colonies from Fischerwiese: GBA 1982/12/717–724, NHMW 1982/57/73–78 and seven specimens from the Gosaukamm region, NHMW 1982/56/36<sub>1–7</sub>; ten thin sections



## Dimensions (in mm):

Specimen No.	c-c	d of calice	s
GBA 1982/12/721	2.0–2.2	2.0 rarely 2.2	24–26
NHMW 1982/56/36 <sub>a</sub>	1.6–1.8	1.5–1.8	20–24
BSP AS XII 40	2.5–3.0	2.2	20–22
BSP AS XII 41	1.5–2.0/2.5	1.3–1.5	16–20
BSP AS XII 44	2.5–3.0	2.0–2.3	24–26

**Description:** Colony lamellate or hemispherical, rarely branching. Diameters of hemispherical colonies up to 30 mm; lamellate colonies can be very large; a fragment of a large branching colony (NHMW 1982/56/60) has branches up to 20 mm in diameter and more than 70 mm in length. Budding perithecial; in addition, rare symmetrical division of corallites is observed. Peritheca lacking or rudimentary (Pl. 33, figs. 1, 3, 5).

Calices polygonal, roundish, usually shallow. Thin, styliform, slightly oval columella is surrounded in calices by a crown of paliform projections. A deep notch separates each projection from the rest of the septum.

Septa are usually thin, minutely and abundantly granulated laterally (4 granules per 200  $\mu$ m, in cross section), and differentiated into two size orders: 12 or 10 (rarely up to 16 or 18) S1 septa reaching the columella, and markedly shorter S2 septa. In regularly developed corallites alternate S1 septa are involved in anastomosis with a pair of neighbouring S2 septa to form 5, 6, 7 or more, radially distributed, triads (Pl. 33, fig. 11). In some colonies, corallites with regular triads are abundant, in others, irregularly developed corallites are more frequent. Usually, in densely growing colonies, with frequent budding, corallites are much more irregular in this respect.

Endotheca of tabular, thin-walled dissepiments, 4 per 1 mm in longitudinal section (Pl. 33, fig. 2).

**Microstructure:** Six or seven trabeculae form each S1 septum. In the septal portion, trabeculae are obliquely inclined and thin, 30–50  $\mu$ m in diameter (measured perpendicularly to the radius). In the costal portion of the same radial element, the trabeculae measure 120  $\mu$ m. Costal trabeculae are vertical. The columella, essentially monotrabecular, forms a complex structure with adjoining trabecular projections from S1 septa, and the horizontal elements of endotheca. Anastomosis of S1 septa is effected by sclerenchymal connections between S2 and an S1 septal flank. Numerous, thin, pointed granules are developed on trabecular sides.

**Discussion:** The species displays a great variability in corallite size and in colony growth form. It can be assumed that corallites in colonies of flat growth forms, with infrequent budding, attain maximum diameters while the calices which remain crowded in hemispherical, densely growing colonies are smaller. The colonies under study from the Zlambach Beds (Fischerwiese and Kesselwand-Rohrmoos) are small, hemispherical (diameters around 20–30 mm) with the exception of a branched colony (NHMW 1982/56/36<sub>a</sub>) which was several decimeters in height (Pl. 33, fig. 3). Their calices are of medium size (see Dimensions).

A series of FRECH's specimens from the Kössen Beds (Kothalpe) attributed to this species contains colonies of calicular diameters from 1.3 up to 2.2 mm. Among specimens of the diverse, delicately branching species from Sommeraukogel (GBA), there is a *Chondrocoenia* having corallites even smaller (c-c 1.2–1.7 mm, d of calices 0.8–1.0, septa 20–22) than those of the smallest form from the Kössen Beds. The form with small

calices known in Kothalp and Sommeraukogel may represent a species different from *Ch. schafhaeutli* (p. 108).

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos; Kössen Beds of Kothalp and Voralpe near Altenmarkt. Rhaetian of the Southern Alps (Lombardy). Rhaetian of the Carpathians. Norian-Rhaetian of the Pamirs and Afghanistan.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Chondrocoenia waltheri* (FRECH, 1890)

Pl. 33, fig. 6

v. 1890 *Astrocoenia waltheri* — FRECH, p. 34, text-fig. on p. 34

1979 *Astrocoenia waltheri* FRECH — SCHÄFER, p. 48, Pl. 11, fig. 5

Holotypus: BSP AS XII 32; FRECH 1890, text-fig. on p. 34

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: One abraded colony from Fischerwiese, NHMW 1982/57/37; two thin sections

Dimensions (in mm):

Specimen No.	c-c	d	s
NHMW 1982/57/37	2.5–3.0	2.0–2.2	20 (10 + 10)
BSP AS XII 32	1.5–2.0	1.5–2.0	18–20

Description: The colony examined measures 15 mm in diameter and 10 mm in height. The colony is hemispherical, with a well-developed, dense perithecium. The costae are solid. Budding frequent, perithecium. The septa are thick; S1 septa reach the columella, S2 about the sides of S1 septa or have free adaxial margins. Septal faces covered with thick granules. The columella, essentially monotrabeular, is reinforced by trabecular projections from the S1 septa. Endotheca dissepiments thin-walled. The extrathecal, intercostal free space is reduced to rare, narrow, vertical tubes. The remaining space is filled by sclerenchyme. Costal trabeculae strongly thickened, up to 300 µm.

Discussion: The species differs from *Ch. schafhaeutli* only in calicular symmetry. Its pentameral disposition of septal triads can be seen both in adult and in young corallites, and in ontogeny the number of septa increases from 16 (octameral symmetry well marked) to 20.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese; Rhaetian Reefs of Adnet and Rötelswand.

*Chondrocoenia ohmanni* (FRECH, 1890)

Pl. 33, fig. 8

v. 1890 *Astrocoenia Ohmanni* — FRECH, p. 34, text-figs. 1–3 on p. 35

Lectotypus: BSP AS XII 33; FRECH 1890, text-fig. 3 on p. 35; the only specimen preserved from three syntypes figured by FRECH; see also herein p. 146

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

**Material:** Twenty six small colonies and fragments from Fischerwiese, GBA 1982/12/696–716, NHMW 1982/57/79–83, as well as two complete specimens from Kesselwand-Rohrmoos, NHMW 1959/365/42 and 1982/56/36<sub>8</sub>. With the exception of two colonies from Kesselwand-Rohrmoos, the state of preservation of the specimens, the lectotype included is very poor.

**Dimensions (in mm):**

Specimen No.	d	s	c—c
NHMW 1959/365/42	1.2–1.4 (1.8)	16–18 (24)	2–2.8
BSS AS XII 33	1.2	14–16	ca. 2

**Description:** Colony massive, globular or composed of subcolonial, columnar units; surface convex or mamillate. Budding perithecial, but calices dividing symmetrically into two daughter calices also noted. Intercalicular surface granulated (Pl. 33, figs. 8 a, b). Calices deep, octameral: in their centre a styliform, slightly oval columella is surrounded by 8 roundish paliform projections. A deep notch separates the projection from the rest of the septal blade (Pl. 33, fig. 8 b).

Endotheca formed of rare, thick, tabuloid elements. Septa are differentiated into two size orders: S1 septa that reach the columella with their trabecular projections, and S2 septa markedly shorter than S1. The S2 septa abut the faces of S1. The arrangement of septa in the calice follows radio-bilateral symmetry, especially in corallites having 16 septa. At least two S1 septa per calice are involved into *Astrocoenia*-like anastomosis with neighbouring S2 septa. Trabecular projections are regularly distributed along the internal edge. Septal faces are minutely granulated.

Radial elements are differentiated into solid septal portions, and costae which peripherally disintegrate into trabeculae. When the intercalicular space is large, the trabeculae are chaotically spaced and costae can be discriminated only at the calicular margin. The extracalicular trabeculae are vertical, with their crests protruding on the colony surface in the form of granules. Laterally, each trabecula is connected with 3–4 neighbours by connective sclerenchyme (a kind of synapticalae). Connection is dominantly permanent; thus, the intertrabecular free spaces become tubular in character (tubulae are circular in cross section). Depending on rates of skeletonisation, the intertrabecular spaces remain free or are filled by sclerenchyme. In the latter case, the perithecium becomes a solid skeletal mass.

**Remarks:** Variation in size of the exothecal trabeculae is observed in the material examined. In some colonies from Fischerwiese (for example GBA 1982/12/705–708) trabeculae are twice as thick as in others.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos.

*Chondrocoenia* sp. A  
Pl. 5, fig. 4, Pl. 33, fig. 7

**Material:** A considerably recrystallized colony fragment from Kesselwand-Rohrmoos, NHMW 1982/56/22; ten thin sections

**Dimensions (in mm):**

c—c	d	s
2–3	2	24

**Description:** Colony plocoid, with relatively large peritheca. Radial elements exsert. Costae thick, solid at the calice and disintegrated into trabeculae peripherally. Columella monotrabecular, surrounded by trabecular projections of septa.

Septa differentiated into 12 subequal S1 and S2 septa reaching the columella, and S3 septa markedly shorter (Pl. 33, fig. 7 a).

Septal internal edges regularly denticulate. Lateral septal granulation coarse and relatively sparse (in cross section: 2.5 granules per 200  $\mu\text{m}$  along the septum).

Endothecal dissepiments thin-walled, tabuloid, abundant (9–13/3 mm in longitudinal section). Peritheca constructed of costae or subvertical trabeculae and of thin-walled dissepiments (Pl. 33, fig. 7 b).

**Microstructure:** Radial elements are fusiform, differentiated into thin-trabecular septal and thick-trabecular costal portions. The septal trabeculae are isometric, 50  $\mu\text{m}$  in diameter. Those in costae, which are anisometric in the solid costal part, are of  $90 \times 180 \mu\text{m}$  diameter, and those isometric in the peripheral part, are between 60 to 180  $\mu\text{m}$  in diameter. Lateral, strong trabecular offsets are provided with axes (Pl. 5, fig. 4). The trabeculae at the internal edge of S1 septa separate as paliform projections, those on the edge of S2 septa protrude as a regular denticulation. The trabeculae are arranged fan-wise. In septal portion, the trabeculae are strongly inclined adaxially. In the costal portion, they vary from slightly inclined to subvertical (Pl. 33, fig. 7 b). The wall is septothecal.

The skeleton has been deeply recrystallised. Trabeculae and the stereomal component of the skeleton behaved differently during recrystallisation (compare *Thamnasteria concinna* in RONIEWICZ 1983). Trabeculae have kept their shape. Their axial parts are now opaque (Pl. 5, fig. 4). The rest of the trabecular body is a transparent yellowish calcium carbonate, in general completely recrystallised, but in places showing traces of original fibrous structure. In contrast to the trabeculae, the stereome has been almost completely destroyed and even the shapes of stereomal structures have disappeared. This results in a complete change from the original appearance of the endo- and exotheca. In the endothecal vesiculae only a thin, basal layer has been preserved whilst an upper, prismatic layer, which is of stereomal origin, has disappeared. Exothecal vesiculae must have been originally far thicker than those of the endotheca because their prismatic layer is partially preserved. It shows an extensive corrosion of the upper surface: the line of contact with the blocky calcite filling all free space is strongly uneven. Such intracalicular features as the connection between columella and septal projections, as well as septal anastomosis, effected by the deposition of sclerenchymal layers and bars, have also been destroyed due to decomposition of stereome in the course of recrystallisation.

**Discussion:** In diameter and relatively small number of septa the Alpine form resembles *Ch. paradoxa* (MELNIKOVA, 1975) of the Pamirs. Poor preservation makes the comparison difficult.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Kesselwand-Rohrmoos.

### *Chondrocoenia* sp. B

Pl. 33, fig. 4

part., v. 1890 *Stephanocoenia Schaffhäutli* WINKLER – FRECH in coll.

**Material:** A colony fragment from Sommeraukogel, GBA 1982/12/788

## Dimensions (in mm):

d cal	c-c	s	s/1 mm
0.8-1.0	1.4-1.7	20-22	6

Remarks: A form here described displays uneven, mamillate calicular surface of the colony and very small calices. A small colony fragment in FRECH's collection, BSP AS XII 43, shows analogous growth form and only slightly larger corallite diameters. They may represent a new species related to *Ch. schaffhaeuti*.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds from Sommeraukogel and Kössen Beds from Kothalp.

Subordo *Astraeoina* ALLOITEAU, 1952 (as *Astraeoidea* ALLOITEAU, 1952)

Emended diagnosis: Costosepta compact or accidentally perforated ad-axially; distal edge lacerated or regularly dentate, lateral granular ornamentation strong. Endotheca vesicular to subtabuloid. Trabeculae simple and complex, large or very large. Synapticulae may be developed.

Remarks: The emendation concerns the presence of synapticulae (see Discussion below); it identifies the ornamentation as granular and changes the "sclerodermite" to "trabecula" because of the imprecise meaning of the former term.

Familia *Pamiroseriidae* MELNIKOVA, 1984Genus typicus: *Pamiroseris* MELNIKOVA, 1971

Emended diagnosis: Radial elements compact with the exception of the internal edge. Trabeculae thick, arranged vertically or slightly fanwise. Internal edge with regularly projecting trabeculae forming trabecular lobes. Distal edge with rounded denticles. Septal faces granulated; granules rounded or flattened. Endotheca composed of small vesicles. Trabeculae with moderately protruding lateral axes. Synapticulae present.

Genera included: *Pamiroseris* MELNIKOVA, 1971, *Elysastraea* LAUBE, 1865, *Beneckastraea* CUIF, 1976, *Ampakabastraea* ALLOITEAU *sensu* CUIF, 1976, *Crassistella* gen. n.

Discussion: The emendation concerns mainly additional data on septal edge ornamentation and the presence of synapticulae (on the basis of their presence in *Pamiroseris*). It must be stressed, however, that the presence of synapticulae carries no special taxonomic consequences as their taxonomic value is rather low. CHEVALIER (1975) described them in the Recent astraeid coral, *Diploastraea*, whereas GILL (1981) and RONIEWICZ (1983) showed their polystructural nature in different coral groups. The emendation concerns also the scope of the family. MELNIKOVA (1984) included here, beside *Pamiroseris*, the following genera: *Rhopalophyllia* CUIF, 1975, *Myriophyllum* CUIF, 1975, *Morycastraea* MELNIKOVA, 1984, *Elysastraea* LAUBE, 1865, *Rhaetiastraea* RONIEWICZ, 1974, *Beneckastraea* CUIF, 1976 (wrongly in the synonymy of the genus *Rhaetiastraea*), *Ampakabastraea* ALLOITEAU, 1958. Such a proposal turns this family into a very heterogeneous group indeed. If we consider *Pamiroseris* as the norm, we must exclude from the family the group *Rhopalophyllia*-*Morycastraea* (septa very thin and densely-packed, correlated with a styliform columella; *Morycastraea* is a phaceloid form

with a corallite structure like that of *Rhopalophyllia*) as well as the genus *Rhaetiastraea* (endothecal elements tabuloid, trabeculae about 90  $\mu$ m), and *Myriophyllum* (lateral axes lacking in trabeculae).

The Pamiroseriidae may be included in the suborder Astraeoinea because of their corallite structure and microstructural type. A proposal to place them within the order Archaeocoeniina ALLOITEAU, suborder Cuifastraeina MELNIKOVA (MELNIKOVA 1984) seems poorly substantiated.

The new diagnosis has many points in common with that of the Montlivaltiidae DIETRICH, 1926 and especially of the genus *Isastraea* MILNE-EDWARDS et HAIME, 1851. In the latter, trabeculae of the *Montlivaltia*-type, symmetrically setting off lateral axes, are combined with endotheca of the *Pamiroseris*-type (compare GILL and LAFUSTE 1971 and RONIEWICZ 1983). The documented stratigraphical proximity of these groups, i. e. Upper Triassic for the Pamiroseriidae and at least the Dogger for the Montlivaltiidae, suggests that they may be phylogenetically related.

### Genus *Pamiroseris* MELNIKOVA, 1971

Species typica: *Thamnastraea meriani* STOPPANI, 1860

Diagnosis (after MELNIKOVA, slightly shortened): Massive colonies with calices often ordered in short series. Radial elements thamnasterioid, compact. Trabeculae simple, forming divergent systems. Distal edge with pearl-like ornamentation, septal faces granulated. Columella parietal, often rudimentary. Endotheca composed of abundant dissepiments. Synapticulae rare.

Species assigned: *Pamiroseris meriani* (STOPPANI, 1860), *P. rectilamellosa* (WINKLER, 1861), *P. multiseptata* (MELNIKOVA, 1967), ? *P. tibetana* (VINASSA DE REGNY, 1915), *P. silesiaca* (BEYRICH, 1852).

Stratigraphic and geographic ranges: World-wide distribution in the Middle and Upper Triassic.

Discussion: The type species has been described in detail on the basis of the Pamirian material by MELNIKOVA (1971). MELNIKOVA's illustrations show corals similar to the Alpine specimens figured by REUSS (1865, Pl. 3, fig. 2) and FRECH (1890, Pl. 17, fig. 7). FRECH considered *Th. meriani* STOPPANI conspecific of *Thamnastraea rectilamellosa* WINKLER. However, those species differ from each other in their numbers of septa.

The genus *Lupitschia* CUIF, 1976 based on *Thamnastraea rectilamellosa* WINKLER, 1861 falls within the synonymy of the genus *Pamiroseris* MELNIKOVA 1971, the type species of both genera being congeneric.

Originally, the following three species: *Thamnastraea norica* FRECH, *Th. dieneri* HAAS and *Th. tibetana* VINASSA DE REGNY were included in the range of the genus *Pamiroseris*. The detailed microstructural analysis of septa in *Th. rectilamellosa* and *Th. norica* given by CUIF (1976) proved that these species have nothing in common and that they occupy very distant systematic positions (see herein p. 62). As to the species of HAAS, its microstructure shows the features of the genus *Distichomeandra* CUIF, 1976 (see herein, p. 82). The third of the species mentioned, *Th. tibetana*, remains almost unknown and it can be included here only with reservation. As to *P. silesiaca* (BEYRICH), the relics of microstructure and ornamentation observed in the Silesian material allows us to include it in the genus *Pamiroseris* (MORYCOWA 1988).

*Pamiroseris rectilamellosa* (WINKLER, 1861)

Pl. 34, figs. 3–5

- 1861 *Thamnastraea rectilamellosa* – WINKLER, p. 487, Pl. 8, fig. 7  
 1865 *Pterastraea tenuis* – REUSS, p. 163, Pl. 3, fig. 1  
 v. 1890 *Thamnastraea rectilamellosa* WINKLER – FRECH, p. 60, text-fig. on p. 61, Pl. 16, figs. 1–15  
 v. ? 1890 *Stylina norica* – FRECH, p. 33, Pl. 11, figs. 1–1 B  
 1867 *Fungiastraea rectilamellosa pamirensis* – MELNIKOVA, p. 24, Pl. 2, fig. 1  
 1964 *Thamnasteria rectilamellosa rectilamellosa* WINKLER – KRISTAN-TOLLMANN & TOLLMANN, p. 561, Pl. 6, fig. 2  
 1969 *Thamnasteria rectilamellosa* WINKLER – ZANKL, p. 36, fig. 34  
 1969 *Thamnasteria rectilamellosa rectilamellosa* WINKLER – KRISTAN-TOLLMANN, TOLLMANN & GEYSSANT, p. 16, Pl. 3, figs. 1, 2  
 v. 1974 *Pamiroseris rectilamellosa* (WINKLER) – GAŹDZICKI, Pl. 18, figs. 1–4  
 v. 1974 *Pamiroseris rectilamellosa* (WINKLER) – RONIEWICZ, p. 114, Pl. 8, fig. 3, Pl. 10, figs. 1–3  
 1975 *Pamiroseris rectilamellosa pamirensis* – MELNIKOVA, p. 130, Pl. 30, fig. 7, Pl. 33, fig. 1, Pl. 34, fig. 1  
 1976 *Thamnasteria rectilamellosa* WINKLER – CUIF, p. 151, text-fig. 27, Pl. 17, fig. 1  
 1979 *Thamnasteria rectilamellosa* WINKLER – SCHÄFER, p. 46, Pl. 11, fig. 3  
 1980 *Thamnasteria rectilamellosa* (WINKLER) – KRISTAN-TOLLMANN, TOLLMANN & HAMEDANI, p. 169, Pl. 2, figs. 1–3  
 1982 *Thamnastraea rectilamellosa* WINKLER – WURM, p. 218, Pl. 34, fig. 5  
 1984 *Pamiroseris rectilamellosa rectilamellosa* (WINKLER) – FANTINI-SESTINI & MOTTA, p. 353, Pl. 29, fig. 1  
 1984 *Thamnasteria rectilamellosa* WINKLER – SCHÄFER, Pl. 1, fig. 4  
 1986 *Pamiroseris rectilamellosa* (WINKLER) – MATZNER, Pl. 9, figs. 3, 4  
 1986 *Pamiroseris rectilamellosa* (WINKLER) – MELNIKOVA, p. 63, Pl. 25, figs. 1, 2, Pl. 26, fig. 1

Holotypus: BSP AS XV 9; WINKLER 1861, Pl. 8, fig. 7

Locus typicus: Kothalp

Stratum typicum: Kössen Beds

Originals of FRECH: 1890, Pl. 16, figs. 1, 4, 7, 8, 9, 10, 15 and Pl. 17, fig. 8, are stored in BSP (AS XII 113–119) and those of Pl. 16, figs. 5 and 12 – in GBA (Nos. 2800 and 2788)

Material: About twenty fragmentary colonies, GBA 1982/12/248, 368–382, 401, NHMW 1959/365/26<sub>1,2</sub>; nearly thirty thin sections

Dimensions (in mm):

Specimen No.	d (corallite)	s	Remarks
GBA 1982/12/370	7	36	
	6 × 7	31	
	5	25	juvenile
GBA 1982/12/374	6	30	
	5 × 6	21	juvenile

Specimen No.	d	s
	(corallite)	
GBA 1982/12/375	4 × 7	32
	4 × 6	37
GBA 1982/12/380	5 × 7	38
	6	33
GBA 1982/12/381	7	26
	6	26

**Description:** Colonies up to 50 mm thick. Lower surface covered with a thin epitheca (holotheca). Calicular surface plane. In thin colonies or at the margins of colonies, the corallites are ordered in series relatively distant from each other, whilst in the centres of colonies, corallites are densely spaced. Calices slightly elevated. Budding extracalicular, producing regular series of calices at the margins of the colony and single calices inserted between 3–4 adults in central parts (Pl. 34, fig. 3).

Septa fusiform, and straight, sigmoid or geniculated in shape. They are confluent but may be interrupted sporadically in the boundary zone between corallites. Internal edge with regularly distributed trabecular denticles directed upwards. In cross section the space between the main septal blade and the projection appears as a pore. The short septa join with their projections to the septal faces of the larger neighbouring septa, and S1 septa meet in the axial cavity. Septal apparatus differentiated into 2–3 orders. S1 septa long and thickest, S2 septa regularly distributed, varying in size but usually much shorter than S1 septa, S3 septa sporadic and short. Septal faces covered with abundant, circular or flattened granules.

In the middle of the intercorallite area contained between a triad of calices, the external edges of septa meet to form more or less well developed trilobate structures. A tendency to form numerous trilobate elements in an intercorallite area is observed. With the growth of the colony, the calices of the original triad separate and new corallites are inserted in the area, with their septa in contact with prolongations of the original trilobate elements. This process may produce a very complex septal design which can be seen in transverse sections of the colony. Among other features, there are so-called geniculate septa, and a sort of wall which represents the remnants of a lobe of the trilobate element (Pl. 34, fig. 4).

Columella parietal, loose or massive, composed of many trabecular projections.

Endotheca slightly depressed in a periaxial ring but convex peripherally and in the center of the corallite. Vesicles small, often thickened (Pl. 34, fig. 5).

**Microstructure:** Trabeculae are fanwise arranged. They are well defined, 70–80 µm in radial diameter in the thin septa, and 100–140 µm in the thick ones. Transversely, the trabeculae may be thicken up to 200 µm. The main trabecula set off short secondary trabeculae provided with their own axes. The secondary trabeculae form granular septal ornamentation. In the zone of trabecular divergence, single thickened granules may reach the neighbouring septum to form synapticulae. When calices are wide apart, the intercorallite part of the radial element is usually formed of vertical trabeculae which are thinner than those forming divergent systems (CUIF, 1976).

**Discussion:** The species includes a morphotype representing lamellate, abruptly expanding colony which, in all probability, is identical with a form distinguished by FRECH as *Stylina norica* (1890, Pl. 11, fig. 1). A specimen from Kesselwand-Rohrmoos NHMW 1959/365/26 shows the following characteristics analogous to those of the holo-



type of *S. norica* (BSP AS XII 31): low number of septa (18–25 at diameters of calices 3–3.5 mm), low density of costosepta in the intercalicular space (15–16/5 mm), and the same distance between calicular axes (3.5–4 mm, rarely 4.5). The columella in both specimens is very alike, massive in type. The holotype of *Stylina norica* is very poorly preserved and, as it has been admitted by previous students (CUIF 1976), no serious examination can be carried out on this material.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds at Fischerwiese and other localities mentioned by FRECH (1890), i. e. Oedalm, Hallstätter Salzberg, Zlambachgraben. In addition, Dachsteinkalk of the Donnerkogels, Dachsteinkalk of Hochfeln, Rhaetian of the Voralpe near Altenmarkt, Kothalp and others, and (?) Upper Carnian of Goldgubhöhe. Rhaetian of the Tatra Mts. and Norian-Rhaetian of the Caucasus and Central Asia.

### Genus *Crassistella* nov.

**Species typica:** *Stephanocoenia juvavica* FRECH, 1890

**Derivatio nominis:** Latin *crassus* – thick, *stella* – star; *femin.*

**Diagnosis:** Cerioid. Septa thick, confluent. Calices small. Columella trabecular, solid. Internal septal edges regularly denticulate. Endotheca vesicular. Trabeculae with long lateral axes, protruding as granules. Budding intratentacular; linkages indirect.

**Species included:** *C. juvavica* (FRECH, 1890), *C. parvula* (MELNIKOVA, 1982).

**Stratigraphic and geographic ranges:** As for the type species.

**Discussion:** In superficial features of the colony the new genus resembles *Tochastraea* VOLZ, 1896, from which it differs in nondistichophylliid microstructure. Its confluent radial elements and the mode of colony increase differentiate it from all small-calicular genera.

Well defined vertical trabeculae, regular trabecular projections on the internal septal edge, granular lateral ornamentation of the septa and vesicular endotheca enable us to place this genus close to *Pamiroseris* MELNIKOVA.

### *Crassistella juvavica* (FRECH, 1890)

Pl. 34, figs. 1, 2, Pl. 35, figs. 1, 2

- v. 1890 *Astrocoenia* nov. sp. – FRECH, p. 36, text-fig. on p. 36
- 1890 *Stephanocoenia juvavica* – FRECH, p. 38, the left text-fig. on p. 38
- ? 1890 *Stephanocoenia juvavica* – FRECH, the right text-fig. on p. 38
- 1975 *Tropiastraea schindyensis* – MELNIKOVA, p. 67, Pl. 5, figs. 1–2; Pl. 6, figs. 1–2
- 1980 *Actinastraea juvavica* (FRECH) – SENOWBARI-DARYAN, p. 42, Pl. 5, fig. 3
- non 1982 *Actinastraea juvavica* (FRECH) – WURM, p. 218, Pl. 34, fig. 6
- 1982 *Tochastraea plana vesiculosa* – MELNIKOVA in DRONOV *et al.*, p. 118, Pl. 16, figs. 3–5
- 1986 ? *Rhaetiastraea vesiculosa* MELNIKOVA – MELNIKOVA & BYCHKOV, p. 76, Pl. 8, fig. 2, text-figs. 11 and 12

**Holotypus:** Lost; FRECH 1890, text-fig. on p. 38

FRECH's original specimen figured as *Astrocoenia* n. sp. represented in the BSP collection (AS XII 39) is poorly preserved and cannot serve as neotype; the same concerns the specimen figured by FRECH on p. 33, see herein p. 146

**Neotypus** (here chosen): NHMW 1982/56/23<sub>1</sub>; Pl. 34, figs. 2 a–c, Pl. 35, figs. 2 a–c; the specimen shows well preserved microstructure

**Locus typicus**: Kesselwand-Rohrmoos (original label Törleck)

**Stratum typicum**: Zlambach Beds

**Material**: Two fragments of colonies from Schneckengraben, NHMW 1959/364/52 and NHMW 1982/56/23<sub>3</sub>, and three colonies of the same state preservation from Kesselwand-Rohrmoos, NHMW 1982/56/23<sub>1,2</sub>, NHMW 1959/365/23; eight thin sections; the species is represented in NHMW collections by numerous specimens

**Dimensions** (in mm):

Specimen No.	d	s
NHMW 1959/365/52	$2.5 \times 3$	26
	2.5	25
NHMW 1982/56/23 <sub>1</sub>	$2.5 \times 3.2$	27
	$2.5 \times 3$	26
	$2.8 \times 3$	24
	3	22

**Description**: Colonies lamellate with upper surface flat (BSP AS XII 39) or sub-massive having a mamillate surface, each mamilla being the top of a columnar sub-colonial unit (NHMW specimens). Columns fused with each other. Each of them constituted of a bunch of corallites vertical at the centre and diverging outwards peripherally. Corallites of neighbouring columns meet in the contact zone to be overgrown later by corallites of younger generations.

Budding intratentacular with indirect linkages, usually lateral giving 1–2 daughter calices, or symmetrical giving subequal corallites. Dividing wall formed by opposing septa.

Colonies are cerioid in type. The wall is tectiform or slightly rounded, or the surface between calices is flat, the calices deep, septa confluent and subconfluent (Pl. 34, figs. 1 a, b).

The septa are wedge-shaped, thick at the wall and thin adaxially, differentiated into 2–3 size orders. The S1 and S2 septa are subequal, in some systems S2 being markedly shorter. The S3 septa are regularly distributed and usually much shorter than half the radius. As a rule, the septa of neighbouring corallites are perfectly confluent and form regular biseptal blades straight or offset in the wall (Pl. 35, figs. 1 a, 2 a, b). The septal faces are ornamented with protruding round granules. The internal edge has regularly distributed trabecular projections that reach a styliiform or lamellar columella. It may be lacking in the cross sections of some corallites (Pl. 34, figs. 2 a, c, Pl. 35, fig. 2 c).

Endotheca composed of thin-walled abundant vesicles, subhorizontal in a periaxial ring and convex in the center of the corallite (Pl. 34, fig. 2 b).

**Microstructure**: Septa are 50–60 µm thick in their free blades, slightly thickened up to 90 µm adaxially, and reaching 300–450 µm in the wall (Pl. 35, figs. 1 b, 2 a, b). Peripherally they are formed of vertical trabeculae 120–180 µm in radial diameter, inclined and thin adaxially. In the wall, septa become thickened laterally, the overgrown lateral axes constituting a great portion of their body. In the free blade they form lateral septal granulations. Granules protruding and sharp.

The wall is purely septal in origin. Confluent biseptal elements are formed usually of well developed S1 or S2 septa continuing directly into S3 septa of the neighbouring

corallites. When the septa are disposed alternately in the wall, they fuse the sides of their external edges, and appear on the surface as bisepal blades with kinks in mid-length.

**Discussion:** Two growth forms are observed in this species, namely, a simple lamellate form and a composite, compact, multicolumnar form, resembling those of the Jurassic *Thamnasteria concinna* (GOLDFUSS) (see RONIEWICZ 1984). The second of them is typical of numerous fossil corals, viz. *Th. mammosa* (MILNE-EDWARDS et HAIME), *Etallonasteria minima* (ETALLON), *Actinaraeopsis exilis* RONIEWICZ and some Recent *Galaxea* or *Porites*. This compact multicolumnar form cannot be confused with a common Recent growth form in which densely growing vertical columns rest independent and separated from each other by a free space.

The specimen described by FRECH as *Astrocoenia* sp. n. preserved in BSP (AS XII 39) shows thick, confluent septa, styliform columella and irregular arrangement of septa, differentiating that form from the *Astrocoenia*-like group. The budding characteristics of *C. juvavica* are readily observed in that specimen.

The form from the SE Pamirs and NE Asia described under diverse names (synonymy: 1975, 1982, 1986) is conspecific with the Alpine species. Dimensions of corallites (2–3.5 mm, up to 5 mm in elongated corallites) and the number of septa (24–30 in adults, up to 36 in elongated corallites at the initial stages of budding) are identical to those of the Alpine form. MELNIKOVA (1975) characterizes the septal apparatus as differentiated into 3–4 orders: the illustrations, however, show septa of only 3 size orders.

A coral reported from the Dachstein reef limestone by WURM (1982, 218, Pl. 34, fig. 6) as *Actinastraea juvavica* (FRECH) represents *Ch. schafhaeutli* (WINKLER) or some related species.

A coral from Fischerwiese figured by FRECH (1890) in right text-fig. on p. 38 resembles rather *Ch. schafhaeutli* (WINKLER) than FRECH's species in having regular, circular calices and six trabecular paliform projections surrounding the columella.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Schneckengraben and Kesselwand-Rohrmoos, dubious in Fischerwiese; Rhaetian of Gruber Reef. Norian-Rhaetian of the Pamirs and NE Asia.

### Subordo Stylophyllina BEAUVAIS, 1981

**Emended diagnosis:** Skeleton built of steromal tissue organized in bundles of fibres forming wall, radial elements and dissepiments; bundles of fibres are subcylindric or scale-like in shape. Septal apparatus built of septa of variable shape: septal blades, rows of septal spines or rudimentary ridges on the wall. Colony increase by variable intracalicular or extracalicular budding.

In the suborder Stylophyllina I include two families: Stylophyllidae FRECH, 1890, which comprises numerous genera, and the monotypic family Gigantostyliidae FRECH, 1890. I follow FRECH in distinguishing the family Gigantostyliidae from the Stylophyllidae, because, in contrast to the Stylophyllidae, gigantostyliids lack septal spines and endotheca and have lamellate septa and a solid columella. The microstructural features of wall stereome are similar in both families.

**Discussion:** Genera assigned to this group were contrasted with trabecular corals on a microstructural basis by CUIF (1977 b). He stated that here septa are built of trabecula-like elements, known as septal spines, which are not homologues of trabecu-

lae. These elements are built of stereomal tissue which continues throughout all parts of the skeleton: septa, dissepiments and wall, whereas in trabecular corals the septal tissue is independent of the remaining skeleton and is the earliest tissue to appear in the development of the skeleton.

On the basis of these observations, L. BEAUVAIS (1981) erected the suborder Stylophyllina, providing it with a brief diagnosis (Structure non-trabéculaire. Pas de plan médio-septal), and ascribed to it two families: Stylophyllidae and Zardinophyllidae. The latter, however, must be excluded from that suborder as it represents suborder Pachythecaliina.

#### Familia Stylophyllidae FRECH, 1890

Genus typicus: *Stylophyllum* REUSS, 1854

Emended diagnosis: Radial elements composed of septal spines, more or less fused with each other; on the inner margin of the septal blade the spines are free. Endotheca composed of vesicular or tabuloid elements. Septal spines contain a core composed of bundles of fibres which bend sideways. The bundles protrude over the skeletal surface in the form of irregular micro-granulation.

Genera included: *Stylophyllum* REUSS, 1854, *Stylophyllopsis* FRECH, 1890, *Coccophyllum* REUSS, 1864, *Meandrostylis* FRECH, 1890, *Anthostylis* gen. n., *Heterastraea* TOMES, 1888, *Pinacophyllum* FRECH, 1890, ? *Oppelismilia* DUNCAN, 1867, ? *Lepidophyllia* DUNCAN, 1868.

Discussion: The subfamily Stylophyllinae (family Astraeidae) has been established by FRECH (1890, 42)<sup>11</sup> on a morphological basis: the presence of radial elements in the form of septal spines, tabuloid or large-dissepimental endotheca, structural continuation between the wall and radial elements, as well as intracalicular marginal budding. Originally, the subfamily comprised only three genera: *Stylophyllum* REUSS, *Stylophyllopsis* FRECH, and *Stylophyllum* (*Meandrostylis*) FRECH. In 1896 VOLZ elevated the taxon to the family rank with the following constituent genera: *Stylophyllum* REUSS, *Stylophyllopsis* FRECH, *Meandrostylis* FRECH, *Hexastraea* VOLZ, and *Cyathocoenia* DUNCAN emend. VOLZ. Later, systematic revisions proposed by VAUGHAN and WELLS (1943), ALLOITEAU (1952) and WELLS (1956) added two Liassic genera to the list: *Lepidophyllia* DUNCAN and *Heterastraea* TOMES; the name *Hexastraea* VOLZ was replaced by *Protoheterastraea* WELLS, 1942, and *Stylophyllopsis* FRECH, 1890 together with *Molukia* JAWORSKI 1915 were included in the synonymy of *Oppelismilia* DUNCAN 1867. FLÜGEL (1964), on the basis of a morphological examination of the septa rejected the latter proposition and considered the three genera as separate taxa of diverse systematic affiliations.

Microstructural rather than morphological criteria have proved to be a more reliable systematic guide. On the basis of microstructural data CUIF (1973) revised the family Stylophyllidae and his studies on *Stylophyllum*, *Stylophyllopsis*, *Coccophyllum* and *Protoheterastraea*, resulted in the elimination of the last genus from the family. As a result of a similar examination (CUIF 1965, 1977) he added the genus *Gigantostylis* to the family. The latter genus, however, is considered in the present paper as the type of the distinct family Gigantostyliidae FRECH, within the suborder Stylophyllina.

New observations suggest the inclusion of the genus *Pinacophyllum* in the family Stylophyllidae. The systematic status of the genera *Oppelismilia* and *Lepidophyllia* is still to be determined by future microstructural examination.

<sup>11</sup> The authorship of the taxon has been erroneously ascribed to VOLZ (1896) in the literature.

Stratigraphically, the family Stylophyllidae ranges from the Carnian to the Lias. The genera with the most "primitive" architectural pattern: *Stylophyllum* and *Coccophyllum* are known only in the Norian-Rhaetian interval. As for the Carnian *Stylophyllum praenuntians* VOLZ, it must be re-classified with *Stylophyllopsis* due to its microscopic features (CUIF 1973). The youngest stratigraphically seem to be stylophyllopsid-like forms (*Stylophyllopsis*, *Oppelismilia* and *Lepidophyllia*) from the diverse stages of the English Lias.

Microstructural characteristics of the family: The material presented here enables a precise description of aspects of stylophyllid microstructure, completing the observations of CUIF (1973). In all genera examined the following characteristics are present: (1) The stereome is organized in rather large bundles of fibres that emerge on the surface of skeleton as minute granules 30–60  $\mu\text{m}$  in diameter, making the skeletal surface rough, sometimes even sponge-like; the bundles are clearly discriminated from each other, and in septal spines they are long, becoming mini-trabecular in character; (2) in the wall, the fibre bundles may enlarge and form flat scales with dimensions varying between genera; (3) septal spines have an axial rod or plate formed from a small number of laterally diverging long bundles, and differs in this way from trabeculae.

All these features are easily seen, especially in slightly diagenetically altered skeleton, where the limits and growth lines of the skeletal elements are emphasised.

This structure of septal spines just described displays an essential unity with that of distichophylliid septa: internal rods or lamellae in stylophyllid septal spines and the median portion of distichophylliid septa are built of elements of the same type, i. e. thin (20–30  $\mu\text{m}$  in diameter), long, continuously growing, and formed of extremely thin fibres. The similarity seems too close to be an effect of convergent evolution; it implies that both groups may be phylogenetically related. It should be considered that the groups were contemporary and lived in the early stage of the development of the Scleractinia. It seems highly probable that distichophylliids and stylophyllids are two divergent lines originating from a common stock which had minute "growth centres" packed densely lengthwise along the distal edges of the radial elements.

A resemblance exists as well between stylophyllids and Upper Jurassic rhipidogyrids, the long fibre bundles of the former being of the same range of magnitude as the long, crowded, ca. 50  $\mu\text{m}$  diameter trabeculae of the latter. Because of a lack of any arrangement of these elements on the sides of septa in both groups, their resemblance seems to be even more striking than in the case of distichophylliids. From the other side, a resemblance between stylophyllid peculiar septal structure and multitrabecular mussid one cannot be neglected. Thus, a phylogenic relationship between stylophyllids and rhipidogyrids or even mussids cannot be ruled out.

### Genus *Stylophyllum* REUSS, 1854

Species typica: *Stylophyllum polyacanthum* REUSS, 1854

Diagnosis (after CUIF 1973, extended): Simple and colonial: phaceloid to cerioid. Budding intracalicular of variable pattern. Wall stereomal. Radial elements in the form of septal spines, free or incompletely joined by stereomal deposits to form rudimentary septal blades. Septal spines originate in the wall or on the dissepimental upper surface. Septal spines vertically continuous or discontinuous (lonsdaleoid pattern). Endotheca of vesicular or tabuloid dissepiments. Microstructure homogeneous: wall, septal spines and upper dissepimental layer composed of clearly discriminated bundles of fibres. Tissue

layers of all skeletal elements continuous with each other. In septal spines a core is present composed of a few fibre bundles.

Species assigned: *Stylophyllum cocchii* (STOPPANI) in FANTINI-SESTINI & MOTTA, 1984, *S. gastaldii* (STOPPANI) in FANTINI-SESTINI & MOTTA, 1984, *S. lejowae* (RONIEWICZ, 1974), *S. robustum* (RONIEWICZ, 1974), *S. paradoxum* FRECH, 1890, *S. polyacanthum* REUSS, 1854, *S. pygmaeum* FRECH, 1890, *S. tenuispinum* FRECH, 1890, *S. vesiculatum* sp. n.

Stratigraphic and geographic ranges: Rhaetian of the Alps and Carpathians, Norian of North America.

Discussion: Morphologically, the genus was described by REUSS (1854), FRECH (1890), CUIF (1973) and MELNIKOVA (1975). A microscopic examination of the skeleton was made by CUIF (1973) on Alpine material (*S. polyacanthum*, *S. paradoxum*, and also *Stylophyllopsis polyactis*), and this author emended the generic diagnosis given by FRECH. MELNIKOVA (1972, 1975), independent of CUIF's discussion, gave her own diagnosis of the genus. The latter author limited the generic range to corals of cerioid form<sup>12</sup> following the original diagnosis of REUSS, whilst CUIF shared the opinion of FRECH in this respect and included in the genus solitary as well as cerioid corals with corallites more or less perfectly joined with each other.

I include in this genus the species I have described earlier as *Pinacophyllum* (RONIEWICZ 1974: *P. lejowae*), some *Phacelostylophyllum* from the Tatic Rhaetian (*op. cit.*: *P. robustum*), whose septal spines are discontinuous and *Phacelostylophyllum* described by MELNIKOVA (1972, 1975) from the Pamirs. Other *Phacelostylophyllum* I have described from the Tatic Rhaetian (*op. cit.*: *Phacelostylophyllum* sp., *P. medium*) seem to belong to the genus *Stylophyllopsis*.

CUIF proved (1973, 1977) that in *Stylophyllum* the tissue of septal spines, dissepiments and wall is in continuity, and that the septal spines are built of layers arranged just like glove fingers superimposed on each other. He stated that in the related genus *Stylophyllopsis*, continuation between the tissue of septal spines and nearby dissepiments occurs at the beginning of spine development, whilst in later stages it is observed only between dissepiments and stereome which fills the interspine space in the septa and covers the septal sides.

Thanks to suitably preserved corals from the Zlambach Beds, the knowledge of the nature of stereome in *Stylophyllum* (and other stylophyllids) could be augmented. The results of these observations are presented when describing the microstructure of individual species.

### *Stylophyllum polyacanthum* REUSS, 1854

Pl. 36, figs. 2, 5, 10, Pl. 38, figs. 1–4, Pl. 42, fig. 8

1854 *Stylophyllum polyacanthum* — REUSS, p. 133, Pl. 21, figs. 1–3

v. 1890 *Stylophyllum polyacanthum* REUSS — FRECH, p. 57, Pl. 15, figs. 1–11

part. 1973 *Stylophyllum polyacanthum* REUSS — CUIF, p. 221, text-figs. 1–7 (*non* figs. 9 and 10, presenting *S. paradoxum*)

1977 *Stylophyllum polyacanthum* REUSS — CUIF, p. 14, Pl. 1, figs. 4, 6

1979 *Stylophyllum polyacanthum* REUSS — SCHÄFER, p. 45, Pl. 9, figs. 3, 4

<sup>12</sup> Corals described by MELNIKOVA as *Stylophyllum* represent a new genus, with perfectly cerioid colonies and *Stylophyllopsis*-like corallite architecture; the wall is septothecal, simple.

1980 *Stylophyllum polyacanthum* REUSS – SENOWBARI-DARYAN, p. 39, Pl. 3, figs. 1, 2

1984 *Stylophyllum polyacanthum* REUSS – SCHÄFER, Pl. 1, fig. 7

Holotypus: Lost; specimen figured by REUSS 1854, Pl. 21, figs. 1–3

Locus typicus: "Gosau" (without detailed location)

Types of FRECH (1890): these figured in Pl. 15, figs. 1, 2, 6, 7, 8, 9, are housed in GBA FRECH's collection Nos. 2793 (first four specimens enumerated), 2809 and 2796, and that of Pl. 15, fig. 3 in BSP (AS XII 111); from among them the neotype has been chosen

Neotypus: Specimen of FRECH's collection GBA No. 2809, a fragment of which was figured by FRECH 1890, Pl. 15, fig. 8

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: About fifty specimens from Fischerwiese, GBA 1982/12/440–472, and NHMW 1982/57/177–192 and one specimen from Kesselwand-Rohrmoos, NHMW 1959/365/54; twelve thin sections

#### Dimensions (in mm):

Specimen No.	d	Remarks
GBA 1982/12/465	18	} branches of phaceloid colonies
GBA 1982/12/470	8	
GBA 1982/12/464	6–10	subcerioid
GBA 1982/12/440	12–14 × 20	cerioid
GBA 1982/12/445	10–12	cerioid

The collection examined comprises colonies of large as well as small diameter corallites and, in this respect, it resembles the collection described by FRECH (compare herein Pl. 36, figs. 2 and 5).

Description: Phaceloid as well as cerioid colonies (compare Pl. 38, figs. 1–2 and 3–4). Wall tectiform, bilaminar. Septal spines usually long, piercing the dissepiments of the next floor; some of them may join in twos or threes to form plates of irregular extent. Endotheca markedly depressed at the corallite center, built of rather large vesiculous dissepiments. Dissepiments rather thin, their upper, stereomal layer being moderately developed (Pl. 38, figs. 2 b, 4 b).

Microstructure: Wall composed of an outer thin layer, the structure of which is difficult to discern, and an inner layer growing inwards, varying in thickness. This layer is composed either of fibre bundles arranged in regular, vertical, thin rows, or of fibres that form small scale-like lamellae. The course of the rows is marked on the wall surface (Pl. 36, fig. 10 b). Intermediate forms also exist, but bundles dominate. The innermost wall stereome forms septal spines which are arranged in vertical rows. Septal spine rows seem to be independent from the above mentioned thin, stereomal rows (Pl. 36, fig. 10 a). In the spines, stereome is arranged in elongated fibre bundles, about 20 µm in diameter. In the spine axis there are always a few bundles which undergo diagenesis in a different way than the remaining part of the spine frequently becoming optically contrasted to the remaining skeleton. They form an axial rod which is thin and quite smooth (Pl. 42, fig. 8). The dissepimental basal layer, due to its complete recrystallization, has the form of a thin transparent layer. The upper layer of variable thickness is composed of bundles of stereomal fibres. Spines, wall and dissepiments are covered by granula-

tions (50–90  $\mu\text{m}$  in diameter) formed of the distal extremities of bundles protruding over the surface of the skeleton. Occasionally, spines are secondarily linked by stereomal layers that cover their sides and pass into the upper dissepimental layer.

**Distribution:** Rhaetian of the Northern Calcareous Alps: common in the Zlambach Beds of Fischerwiese, and in Rhaetian Reefs of Rötelswand, Feichtenstein and Gruber near Salzburg, rare in the Zlambach Beds of Kesselwand-Rohrmoos.

*Stylophyllum vesiculatum* sp. n.

Pl. 36, fig. 11, Pl. 38, fig. 7, Pl. 42, fig. 4, Pl. 43, fig. 2

**Holotypus:** NHMW 1982/56/34; Pl. 38, figs. 7 a, b, Pl. 42, figs. 4 a–c, Pl. 43, figs. 2 a–c

**Locus typicus:** Kesselwand-Rohrmoos (original label "Törleck")

**Stratum typicum:** Zlambach Beds

**Derivatio nominis:** Latin *vesicula* – from endotheca strongly vesicular in character.

**Diagnosis:** Colony of cerioid type. Adult individuals from about 15 mm up to 25 mm in diameter. Endotheca of small, very convex dissepiments. Septal spines short, isolated from each other.

**Material:** One colony from the Gosaukamm vicinity, NHMW 1982/56/34 and three fragmentary colonies from Fischerwiese, NHMW 1982/57/115, 116, 117; four thin sections

**Dimensions (in mm):**

Specimen No.	d	Remarks
NHMW 1982/56/34	15	adults
NHMW 1982/57/115	12 $\times$ 14, 15	adults
NHMW 1982/57/116	24 $\times$ 26, 25	adults

**Description:** Colonies cerioid; wall bilaminar. Budding intracalicular; a division of the parental corallite into two unequal daughters has been observed (Pl. 38, fig. 7 a). Corallites polygonal of variable dimensions: two colonies examined are composed of small corallites (NHMW 1982/56/34 and 1982/57/115) and two of large ones (NHMW 1982/57/116, 117). Endotheca declined axially, formed by abundant, small, subequal vesicles (Pl. 38, fig. 7 b). Septal spines numerous, short, developed on the wall and on the dissepimental surface (Pl. 38, figs. 7 a, b, Pl. 42, fig. 4 a, Pl. 43, fig. 2 a). In the wall, the septal spines are disposed in vertical rows.

**Microstructure:** The microstructure shows the same pattern as in *S. polyacanthum*. Stereomal microstructure is well preserved in the holotype: bundles of fibres are well delineated (Pl. 43, figs. 2 a, b) and emerge on the skeleton surface as a coarse micro-ornamentation (Pl. 42, figs. 4 a–c); wall scales frequently observed (Pl. 43, figs. 2 b, c); vertical rows of wall bundles of fibres clearly distinguished (Pl. 43, fig. 2 c), initiating development of radial elements. Dissepimental upper layer and septal spines display the same structure as the wall (Pl. 43, fig. 2 a).

**Discussion:** In the appearance of the calicular surface the species resembles very much *S. polyacanthum* (compare REUSS 1854, Pl. 21, fig. 1). The new species differs from the type species in possessing larger corallites, smaller and more abundant dissepiments, and in shorter septal spines. The latter are so short that they do not reach the dissepiments of the next floor.



The new species seems to have much greater variability of the calicular diameter than the type species. No specimen of the latter, mentioned in literature, has diameters greater than 20 mm. In *S. vesiculatum*, however, such dimensions are seen in as much as two out of four specimens examined. In contrast with the type species, the colonies examined do not show any tendency towards the phaceloid growth form.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos.

*Stylophyllum paradoxum* FRECH, 1890

Pl. 36, figs. 3, 4, 8, Pl. 38, fig. 5, Pl. 42, fig. 9

v. 1890 *Stylophyllum paradoxum* — FRECH, p. 54, text-figs. on pp. 54 and 55; Pl. 14, figs. 1–24; Pl. 15, fig. 12

1973 *Stylophyllum paradoxum* FRECH — CUIF, p. 227, text-figs. 9–11 (in explanation to figs. 9 and 10 erroneously as *polyacanthum*)

1973 *Stylophyllum pygmaeum* FRECH — CUIF, p. 232, text-figs. 12, 13

Syntypi: BSP and GBA collections:

From the vicinity of Gosaukamm (Kesselwand-Rohrmoos): BSP (AS XII 75–78, 87, 88, 93) figured by FRECH 1890, text-fig. on p. 54 (left) and Pl. 14, figs. 1–3, 18, 19, 22, 27;

From Fischerwiese: BSP (AS XII 90) figured by FRECH 1890, Pl. 14, fig. 21, re-figured by CUIF 1973, text-fig. 9 a;

From Hallstätter Salzberg: BSP (AS XII 75 and 89) figured by FRECH 1890, Pl. 14, figs. 5 and 20; GBA (FRECH's type collection, No. 2810, four specimens) figured by FRECH 1890, Pl. 14, figs. 6, 7, 9, 17;

From Kothalp: BSP (AS XII 80–83, 85, 86, 91, 92) figured by FRECH 1890, Pl. 14, figs. 10 A B–12, 15, 16, 25 and 26

Material: Nearly one hundred specimens from Fischerwiese, GBA 1982/12/478–519, NHMW 1982/57/100–114, 119–157 and three specimens from Kesselwand-Rohrmoos, NHMW 1982/56/33<sub>5</sub>, 33<sub>6</sub>, NHMW 1959/345/48<sub>1</sub>; seventeen thin sections

Dimensions (in mm):

Specimen No.	d	h
GBA 1982/12/486	15	45
GBA 1982/12/504	20 × 30	10
NHMW 1982/56/33 <sub>5</sub>	35	70

Description: Corallites from cylindrical (Pl. 36, figs. 3 a, b, 4 a, b, 8) to bowl-shaped. Calices flat or convex. Septal spines long (Pl. 38, fig. 5), crossing many levels of dissepiments, the thickness and number of spines very variable (Pl. 36, figs. 3 a, 4 a). Endotheca built of large flat dissepiments, arranged almost horizontally. Wall thick, transversely folded, partly covering the corallite (Pl. 36, figs. 3 b, 4 b).

Microstructure: Skeleton built of very thin fibres. Bundles of fibres distinct in spine cores where they form an axis circular in cross-section, or a straight or zigzag plate. The core surface is usually strongly ornamented by the protruding tips of the bundles (Pl. 42, fig. 9). This is enhanced by the successive growth layers of stereome which form the external part of the septal spine. In the upper dissepimental layer bundles of fibres are thin. Basal dissepimental plate strongly altered diagenetically. The surface of the skeletal elements is slightly rough or smooth.

**Discussion:** CUIF has examined the ontogenic changes in corallite structure. In his work on stylophyllid skeletal structure, he chose this particular species to illustrate the structure of septal spines (1973, text-fig. 11).

This species, abundant in Fischerwiese, the region of Gosaukamm and other areas (FRECH 1890), is highly variable in structure and corallite size. FRECH and later CUIF (1973) described the range of variability in this species. The latter author included in *S. pygmaeum* FRECH (CUIF 1973, 232–236, text-figs. 12, 13) a morphotype from the type series from Kothalp which does not resemble any of the *S. pygmaeum* morphotypes described by FRECH. This morphotype may be better considered as an extreme form of the morphotype series of *S. paradoxum* and I therefore leave it in the latter species.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos; Kössen Beds of Kothalp; Gruber and Feichtenstein Rhaetian Reefs at Salzburg (SENOWBARI-DARYAN 1982). Dachstein limestone (WURM 1982).

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Stylophyllum pygmaeum* FRECH, 1890

Pl. 36, fig. 9, Pl. 38, fig. 6

1890 *Stylophyllum pygmaeum* – FRECH, p. 56, text-fig. on p. 56

non 1973 *Stylophyllum pygmaeum* FRECH – CUIF, p. 232, text-figs. 12, 13

**Syntypi:** Three specimens from Hallstätter Salzberg, BSP AS XII 108–110; FRECH 1890, text-fig. on p. 56

**Material:** About fifty fragments of phaceloid colonies from Hallstätter Salzberg and Sommeraukogel, GBA 1982/12/807–854

**Dimensions (in mm):**

d	septal spines at the calicular rim
5–7	16–20 per calice

**Description:** In the collection examined, as in that of FRECH, there are two morphotypes: phaceloid colonies (isolated branches), as well as single ceratoid corallites, strongly tapered proximally. I take into consideration the first of them only, the second being of nonstylophyllid affinity. The branches are cylindrical, bifurcating or budding marginally (Pl. 36, fig. 9). The calices are deepened with an irregularly developed septal apparatus. Septal spines thick, differing in numbers from calice to calice. Septa protrude from the wall. Dissepiments tabuloid, sparse. Corallite surface covered by a thick folded wall. Skeleton completely recrystallized (Pl. 38, figs. 6 a, b).

**Discussion:** The morphotype from Fischerwiese identified by CUIF (1973) as *S. pygmaeum* FRECH in no way resembles *S. pygmaeum* of the type series, but falls within the variability range of *S. paradoxum* FRECH. *S. pygmaeum* has not so far been recognized in Fischerwiese. *S. lejowae* (RONIEWICZ, 1974) and WURM's form figured as *Pinacophyllum* sp. (1982, Pl. 39, fig. 1) belong to a related species.

**Distribution:** Rhaetian of the Northern Calcareous Alps; known in Hallstätter Salzberg and Sommeraukogel.

Genus *Stylophyllopsis* FRECH, 1890

Species typica: *Stylophyllopsis polyactis* FRECH, 1890 (designated by DIENER, 1921)

Completed diagnosis: Solitary and colonial, phaceloid. Budding intracalicular of variable pattern. Septal spines long and linked by stereome to form subcompact septal blades with isolated pores. The internal septal edge dissociated into the septal spines. Distal edge denticulate with large spines. Wall fibrous. Columella papillar, composed of septal spines. Endotheca formed by large, densely packed dissepiments. Microstructure homogeneous: skeleton composed of bundles of fibres. Septal spines with an axial rod or lamella. Stereome links the septal spines with each other and passes into the upper dissepimental layer.

Species included: Triassic — *S. polyactis* FRECH, 1890, *S. zitteli* FRECH, 1890, *S. rudis* (EMMRICH, 1854), *S. lindstroemi* FRECH, 1890, *S. caespitosa* FRECH, 1890, *S. borstepensis* MELNIKOVA, 1972, *S. karauldyndalensis* (MELNIKOVA, 1972), *S. media* (RONIEWICZ, 1974), *S. ramosa* sp. n.

MORYCOWA (1988) described an Anisian coral having well expressed features of *Stylophyllopsis*.

In the Rhaetian of the Tatra Mts., a morphotype described as ? *Phacelostylophyllum* sp. (RONIEWICZ 1974) may represent a new species of *Stylophyllopsis*.

Liassic — *S. brevis* (DUNCAN, 1867), *S. mucronata* (DUNCAN, 1867), *S. murchisoniae* (DUNCAN, 1867), *S. patula* (DUNCAN, 1867), *S. rugosa* (DUNCAN et WRIGHT, 1867), *S. victoriae* (DUNCAN, 1867), *S. walliae* (DUNCAN, 1867), *S. elchabirensis* BEAUVAIS, 1886; corals described as *Stylophyllopsis* by TURNŠEK *et al.* (1975).

Stratigraphic and geographic ranges: Anisian of the European epicontinent. Carnian-Rhaetian of the Tethyan realm and North America. Lias of the European epicontinent as well as of South European and North African Tethyan regions.

Discussion: FRECH (1890) distinguished genera *Stylophyllum* and *Stylophyllopsis* on the basis of the shape of their radial elements which are developed either as isolated septal spines — in *Stylophyllum*, or in the form of subcompact septa — in *Stylophyllopsis*.

CUIF (1973) separated these genera from each other on the basis of their septal spine microstructures: he stated that in *Stylophyllum* the dissepimental stereome continues to the structure of the septal spines whilst in *Stylophyllopsis* the dissepimental stereome takes part in the septal spine structure only in the early stages of septum development.

I follow FRECH's taxonomic proposals and I consider a presence or a lack of vertically continuous septal blades as distinctive features of these two genera. As to the continuity of stereome between septal and dissepimental skeleton, I consider it to be a character typical of all stylophyllid corals and manifested variably in diverse genera or even species.

Genus *Stylophyllopsis* has been included by VAUGHAN and WELLS (1943, and also ALLOITEAU, 1952 and WELLS, 1956) to the synonymy of *Oppelismilia* DUNCAN. In fact, in certain morphological features (folded wall, large diameter of septal elements and resulting strong dentation of the distal septal margin) the genera are similar. However, as FLÜGEL (1964) points out, in *Oppelismilia*, contrary to *Stylophyllopsis*, the septa contain equal "centres of calcification" which are arranged regularly along the septum and the septa are not perforated. It will be possible to determine the relationship between the two genera only after detailed examination of the skeletal microstructure.

Recently, FANTINI-SESTINI & MOTTA (1984) proposed to reevaluate the older subjective synonym of *Stylophylloopsis*, *Lepiconus* STOPPANI, 1862. The authors illustrated the topotype material of the type species of *Lepiconus*, preserved as the mould of the calicular corallite surface. Casts made from the mould satisfactorily display external features fitting the diagnosis of *Stylophylloopsis*. However, the type material being of a low taxonomical value (specimens are devoid of endotheca), the type species cannot be identified. Moreover, the name *Lepiconus*, having not been used in the literature since its first publication, falls into the category of names rejected, whilst the name *Stylophylloopsis* was from the beginning in current usage in the geological and palaeontological literature.

After morphological descriptions by FRECH (1890) and later STRAW (1925) and FLÜGEL (1964), recent studies have followed microstructural work on some species of *Stylophylloopsis* by CUIF (1973). He gave microstructural analyses for the following species: *S. polyactis* FRECH, *S. zitteli* FRECH, *S. mojsvari* FRECH, *S. rudis* (EMMRICH) and *S. praenuntians* (VOLZ). An analysis of increase in the skeleton during ontogeny in *S. zitteli* led him to the conclusion that in *Stylophylloopsis* the skeletal tissue of the septa is continuous with that of other skeletal elements only at early ontogenetic stages, becoming (in contrast to *Stylophyllum*) independent during later growth. For the elements constituting septa he used the term trabecula.

The stereomal continuity between dissepiments and septa, observed in *S. polyactis*, he found to be typical of *Stylophyllum* and removed this species from the genus *Stylophylloopsis*.

In the septa of *S. zitteli* and *S. praenuntians* figured by CUIF (1973, text-figs. 17 c and 22 c), a complex pattern of axial rods in the septal spines is apparent. He was intrigued by the fascicular structure of the trabecular stereome and its granular expression on the surface of skeletal elements (1973, 252). In discerning these features only in *S. praenuntians* VOLZ, CUIF supposed them to be the characters differentiating this species from other *Stylophylloopsis*. However, in the material examined here it is possible to observe analogous structures variably developed in all species of this genus.

*Stylophylloopsis polyactis* FRECH, 1890

Pl. 36, figs. 6, 7, Pl. 37, fig. 1, Pl. 38, figs. 8, 9

v. 1890 *Stylophylloopsis polyactis* — FRECH, p. 48, text-fig. on p. 49, Pl. 12, fig. 3, Pl. 15, figs. 17–23

non 1909 *Stylophylloopsis polyactis variisepta* — HAAS, p. 149, Pl. 5, fig. 8

non 1972 *Stylophylloopsis polyactis* FRECH — MELNIKOVA, p. 56, Pl. 9, figs. 1–2

1973 *Stylophylloopsis polyactis* FRECH — CUIF, p. 239, text-figs. 14 a–c

non 1975 *Stylophylloopsis polyactis* FRECH — MELNIKOVA, p. 71, Pl. 7, figs. 1–3

Lectotypus (here chosen): BSP AS XII 53; FRECH 1890, Pl. 15, fig. 19; refigured herein Pl. 37, figs. 1 a, b

Locus typicus: Kesselwand-Rohrmoos

Stratum typicum: Zlambach Beds

Other FRECH's originals: specimen from the vicinity of Gosaukamm (BSP AS XII 52) figured by FRECH 1890, Pl. 15, fig. 17, specimens from Fischerwiese (GBA FRECH's type collection, No. 2770) and Hallstätter Salzberg (No. 2807) figured *ibidem*, Pl. 15, figs. 18 and 22, respectively

**Material:** Twelve specimens from Fischerwiese, GBA 1982/12/650–654, NHMW 1982/57/174–176, NHMW 1959/364/15<sub>2,5,6,9</sub>; four specimens from the vicinity of Gosaukamm, NHMW 1982/56/23<sub>3</sub>, 33<sub>1-3</sub>; ten thin sections

**Dimensions (in mm):**

Specimen No.	d	h	s
GBA 1982/12/651	30 × 35	30	166
GBA 1982/12/654	35	55	100

**Description:** Solitary corals attaining great size (Pl. 36, figs. 6, 7, Pl. 37, fig. 1). Calices shallow. Radial elements developed as thin and more or less porous septal blades (Pl. 36, fig. 6, Pl. 37, figs. 1 a, b, Pl. 38, fig. 9). Pores appearing irregularly in the inter-spine spaces (Pl. 37, fig. 1 b). In general, spines thin but slightly varying in thickness from corallum to corallum.

Endotheca composed of large dissepiments arranged in densely packed horizons which are concave in the central part of the corallite (Pl. 37, fig. 1 b, Pl. 38, fig. 8).

Wall very thin, usually preserved in fragments.

**Microstructure:** Skeleton of delicate construction. Both radial elements and dissepiments unthickened or very slightly thickened. Stereome with strong micro-granular ornamentation, especially on the septal spines, less often on dissepiments. Fibre bundles clearly discernible in cross-sections of dissepiments. Skeleton usually strongly recrystallized.

**Discussion:** CUIF (1973) considered *S. polyactis* to be of rather *Stylophyllum* than *Stylophylloopsis* affinity due to the structural continuity which he has observed in this species between septal spines and an extra-septal stereome. However, such a continuous structure is to be found not only in *Stylophyllum*. In fact, some species of *Stylophylloopsis*, not only *S. polyactis* but also *S. rudis*, display this feature.

HAAS' specimen (PIUW, HAAS collection, No. 33) represents *S. rudis* (EMMRICH) and it resembles the specimen described by FRECH as *S. mojsvari* from Fischerwiese (1890, Pl. 10, fig. 10, refigured herein Pl. 39, fig. 3).

MELNIKOVA's form described as *S. polyactis* from the Pamirs differs from the Alpine species in having thicker and less numerous septa (ca. 90), as well as less densely spaced dissepiments (1972, 1975).

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds of Fischerwiese, Kesselwand-Rohrmoos, Schneckengraben and Hallstätter Salzberg.

*Stylophylloopsis zitteli* FRECH, 1890

Pl. 39, fig. 8, Pl. 40, figs. 5–7

- 1890 *Stylophylloopsis zitteli* – FRECH, p. 49, Pl. 13, figs. 9–15, 17–24  
 v. 1909 *Stylophylloopsis Zitteli* var. *crassisepta* – HAAS, p. 149, Pl. 5, fig. 9  
 non 1964 *Oppelismilia zitteli* (FRECH) – KRISTAN-TOLLMANN & TOLLMANN, p. 562, Pl. 7, fig. 1, Pl. 8, figs. 2–5  
 non 1972 *Phacelostylophyllum zitteli* (FRECH) – MELNIKOVA, p. 70, text-fig. 5, Pl. 9, figs. 6–7  
 1973 *Stylophylloopsis zitteli* FRECH – CUIF, p. 243, text-figs. 15–18  
 non 1975 *Phacelostylophyllum zitteli* (FRECH) – MELNIKOVA, p. 79, text-fig. 6, Pl. 11, figs. 2–7

Lectotypus (here chosen): BSP AS XII 56; FRECH 1890, Pl. 13, fig. 13

Paralectotypi: BSP AS XII 54, 55, 57, *ibidem*, text-fig. on p. 50, Pl. 13, figs. 9 and 22, respectively; GBA FRECH's type collection, No. 2768, *ibidem*, Pl. 13, figs. 11, 12, 19, 21

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: About one hundred specimens from Fischerwiese, GBA 1982/12/584–645 and NHMW 1982/57/158–173; twenty thin sections

Dimensions (in mm):

Specimen No.	h	d	s
NHMW 1959/364/11 <sub>17</sub>	e. 50	20 × 25	42 (28 S1–S3)
NHMW 1959/364/11 <sub>15</sub>	40	10 × 16	34 (24 S1–S3)

Description: Solitary and colonial, phaceloid to subcerioid. Budding lateral. Corallites incompletely covered by thick, wrinkled wall. Septa rather thin, hexameral symmetry visible in specimens of small diameter. Septal plates compact with the exception of the internal edges (Pl. 39, fig. 8, Pl. 40, figs. 5, 7). Columella limited to the narrow axial portion of the calice and built of a few septal spines. Septa S1 and S2 approach the axis. Septa S4 inserted very irregularly. Ornamentation of septal faces in the form of irregular sharp granulation, or lacking.

Dissepiments large. Endotheca strongly concave at the centre (Pl. 40, fig. 6).

Microstructure: Internal rod of septal spines thin and simple. Stereome usually moderately developed, so that structure of the skeleton is rather delicate. Wall usually thin, of simple fibrous structure.

Discussion: The morphological variability and skeletal development during ontogeny have been discussed by CUIF (1973). This author also characterised the microstructure of the skeleton in detail.

The form figured by KRISTAN-TOLLMANN & TOLLMANN (1964, Pl. 7, fig. 1 and Pl. 8, figs. 2, 3 and 5) represents the genus *Stylophyllum* rather than *Stylophylloopsis* and resembles in structure (but not in corallite diameter which is much greater) a Tatic species, *Stylophyllum lejowae* (RONIEWICZ, 1974); the form figured in Pl. 8, fig. 4 shows septa of a very regular trabecular structure which does not resemble that of *Stylophylloopsis*.

The form described by MELNIKOVA (1972, 1975), although resembling *S. zitteli* in cross-section, differs from it in having endotheca built of small, vesicular dissepiments.

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds at Fischerwiese; FRECH (1890) mentioned it also from the Gosaukamm region and from the vicinity of Hallstatt.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

*Stylophylloopsis rudis* (EMMRICH, 1853)

Pl. 39, figs. 2–6, Pl. 40, figs. 1, 2, Pl. 42, fig. 7

1853 *Fungia rudis* – EMMRICH, p. 378

1863 *Thecophyllia helianthoides* – SCHAFFHÄUTL, Pl. 66, fig. 4

v. 1890 *Stylophylloopsis rudis* EMMRICH – FRECH, p. 50, Pl. 12, figs. 1, 4–14

- v. 1890 *Stylophyllopsis Mojsvari* — FRECH, p. 52, Pl. 10, figs. 7–14, Pl. 12, fig. 15, Pl. 13, fig. 16  
 1973 *Stylophyllopsis mojsvari* FRECH — CUIF, p. 249, text-figs. 19, 20  
 1973 *Stylophyllopsis rudis* (EMMRICH) — CUIF, p. 252, text-fig. 21  
 1975 *Stylophyllopsis rudis* (EMMRICH) — MELNIKOVA, p. 74, Pl. 11, fig. 1  
 1980 *Stylophyllopsis mojsvari* FRECH — KRISTAN-TOLLMANN *et al.*, p. 173, Pl. 5, fig. 3  
 non 1984 *Lepiconus rudis* (EMMRICH) — FANTINI-SESTINI & MOTTA, p. 356, Pl. 28, figs. 1, 2

Holotypus: Museum Halle: specimen figured by FRECH 1890, Pl. 12, fig. 14

Locus typicus: Wundergraben at Ruhdolping

Stratum typicum: Rhaetian

FRECH's originals: *S. rudis* (FRECH 1890, Pl. 12, figs. 1, 5, 6, 8, 9, 10, 11, 12,) and *S. mojsvari* (*ibid.*, Pl. 10, figs. 7, 8, 10) are housed in BSP with No. AS XII 59–65, 67–68 and 70–72; SCHAFFHÄUTL's original of *Thecophyllia helianthoides* refigured by FRECH (1890, Pl. 12, fig. 14) and recently by CUIF (1973, text-fig. 21 a) is housed in BSP with No. AS XII 10

Material: Fourteen specimens from Fischerwiese, GBA 1982/12/655–665, NHMW 1982/57/94–96; five specimens from Kesselwand-Rohrmoos, NHMW 1982/56/32<sub>1-3</sub>, 41, 1959/365/48<sub>2</sub>; sixteen thin sections

#### Dimensions (in mm):

Specimens No.	h	d	s	s/10 mm
GBA 1982/12/662	e. 20	20	68	11
GBA 1982/12/655	—	28	69 (12 + 12 + 24 + 21)	10
NHMW 1982/56/41 <sub>1</sub>	e. 17	24	68 (12 + 12 + 16 + 22)	9
NHMW 1982/56/32 <sub>2</sub>	35	40	54 (8 + 8 + 16 + 22)	7–8
NHMW 1982/56/32 <sub>1</sub>	45	40 × 35	88 (13 + 13 + 25 + 37)	6–10

Description: The morphology was described by FRECH (1890) and microstructure by CUIF (1972). The following remarks are based on the material studied here:

Corals conical in small morphotypes and subcylindrical or turbinate in large morphotypes. Calices irregular or regularly circular, or oval in shape.

Septa plate-like with 1–2 or 3 free spines at the internal edge (Pl. 40, figs. 1, 2). Axial cavity narrow, occupied by a few spines of S1–S2 septa. Distribution of S1–S3 septa in systems is regular (Pl. 39, figs. 2–6 a, Pl. 40, fig. 1). The S1 septa are the thickest and their solid blades approach the axial cavity. Solid blades of S2 septa are distinctly shorter than those of S1 septa. The blades of S3 septa are thinner than S1 and S2, and are more than half the length of S1. S4 septa short, 200–400 µm thick, numerous.

Dissepiments vesicular, abundant, thick-walled, arranged subhorizontally (Pl. 39, fig. 6 b).

Microstructure: The septal spines are closely apposed, analogous to trabeculae, to form a solid septal blade. The spines are isometric or elongated in a radial direction when observed in cross-section. The elongation varies depending on the morphotype: little in small corallites but considerable in large forms. The diameter of free spines ranges from 200 µm (S4 septa) to 1500 µm (S1). The elongated spines are provided with median core plates composed of numerous vertical bundles of fibres arranged in

single rows. The organization of skeletal tissue in radially elongated spines, at least when affected by diagenesis, much resembles that observed in the median septal portion of distichophylliids. In thick spines subcircular in section, the median plate may be abruptly bent at one end or forked (Pl. 42, fig. 7). Septal spines may be covered with thorny ornamentation. Accretionary layers of stereome are seen in the spines. The sides of septa are slightly thickened by stereomal layers which constitute the prolongation of the stereome of the dissepimental upper layers. The surface of the stereome is micro-ornamented, rough.

**Discussion:** The morphotype distinguished by FRECH as *S. mojsvari* have been here included in the range of *S. rudis*. The original specimens of FRECH, SCHAFHÄUTL and CUIF (see synonymy) as well as those of the collections examined, constitute a continuous morphological series from small, relatively thin-septal to large, thick-septal corallites (compare Pl. 39, figs. 2–6). This series reflects not only a simple age differentiation in size but also variability in size, number of septa and shape, caused by other factors. Shapes are from broadly conical to tall subcylindrical, calices from regularly circular to irregular, septa from numerous and nearly uniformly thickened (S1–S3) to few and strongly differentiated in thickness. Analogous extensive variability is observed in *Stylophyllum paradoxum*. The characters common to the majority of the morphotypes under examination are: relatively high density of septa and abundant, subhorizontally arranged, vesicular endotheca; corals with extremely thick and scarce septa are rare (Pl. 39, fig. 5, Pl. 40, fig. 2).

A possible ecological differentiation in shape and dimensions is suggested by the fact that the species at Kothalp and Fischerwiese is represented by small and moderately large corals, some of them forming incipient colonies (compare FRECH's and CUIF's illustrations of *S. rudis* and *S. mojsvari*) whilst in Kesselwand-Rohrmoos, the largest, simple corals are found (compare FRECH's figures of *S. mojsvari* and figures herein, Pl. 39, figs. 5, 6 a).

The morphotype described from Lombardy as *Lepiconus rudis* (EMMRICH) by FANTINI-SESTINI & MOTTA (1984) has not been placed in *S. rudis* here due to its numerous, thin septa and small calicular diameters (compare p. 129).

**Distribution:** Rhaetian of the Northern Calcareous Alps, Iran and Pamirs; in the Alps the species is known in the Zlambach Beds from Fischerwiese and Kesselwand-Rohrmoos, and in the Kössen Beds from Kothalp.

*Stylophyllopsis lindstroemi* FRECH, 1890

Pl. 39, fig. 7, Pl. 40, figs. 3, 4

- v. 1890 *Stylophyllopsis Lindströmi* – FRECH, p. 53, Pl. 10, figs. 15–20, Pl. 12, fig. 2
- 1896 *Stylophyllum praenuntians* – VOLZ, p. 87, Pl. 11, figs. 1–4
- 1973 *Stylophyllopsis praenuntians* (VOLZ, 1896) – CUIF, p. 254, text-fig. 22
- ? 1984 *Lepiconus rudis* (EMMRICH) – FANTINI-SESTINI & MOTTA, p. 356, Pl. 28, figs. 1, 2

Lectotypus and paralectotypus (here chosen): BSP AS XII 73, 74; FRECH 1890, Pl. 10, figs. 16 and 19, respectively

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds



**Material:** More than thirty specimens from Fischerwiese, GBA 1982/12/666–687, NHMW 1982/57/87–93, NHMW 1959/364/13; seventeen thin sections

**Dimensions (in mm):**

Specimen No.	h	d	s	s/5
NHMW 1959/364/13 <sub>1</sub>	12	15 × 17	92 (12 + 12 + 24 + 44)	12
NHMW 1982/57/92	–	10	70 (12 + 12 + 24 + 22)	11–12

**Description:** Conical, subcylindrical or irregular in shape. In the specimens examined the proximal end is irregular, overlapping isolated, solid clasts of the bottom sediment. Wall thick. Calices circular, or irregular, deep, edges sharp (Pl. 39, fig. 7). Axial cavity rather large, filled with numerous septal spines. Septa very thin, differentiated into 4 size orders, regularly arranged in systems. Each septum is provided with 1–3 free septal spines at the internal edge. Septal blades of S1 septa approach the axial cavity; S2 septa are slightly thinner and shorter; S3 septa are more than half the length of S1; S4 septa numerous, developed in nearly all systems, frequently lonsdaleoid (Pl. 40, figs. 3, 4).

Endotheca concave, built of large, thin, subtabuloid elements.

**Microstructure:** In general, the septal tissue does not continue directly into that of dissepiments. Only exceptionally is stereome of the upper dissepimental layer discernable on the septal flanks. Septal spines are built of typical, clearly individualized, long, thin bundles of fibres. They emerge on the septal surface as sharp micro-granulation. Bundles opaque due to diagenesis are easily traceable in sections of the septal spines. In the middle of the spines an irregular core plate may be discerned (Pl. 42, fig. 7, compare CUIF 1973, text-fig. 22 c).

The thinnest, free septal spines (S4) are 90 µm in diameter; thick septal spines (in S1 septal blades) are usually around 300 µm. The wall is septothecal, displaying on its slightly worn external surface traces of septa in the form of delicate vertical striation.

**Discussion:** The peculiarity of this species lies, primarily, in its large stratigraphical range. As CUIF admitted (1973), two morphotypes, i. e., that described here from the Fischerwiese Zlambach Beds and that of the Saint-Cassian, Carnian, are practically identical in morphology, dimensions and microstructure. The present observations on quite extensive material agree with CUIF's statements. The parameters of VOLZ's specimen (16 mm in diameter, 80 septa in four size orders: *fide* CUIF 1973, text-fig. 22 b) are comparable in details to those of specimens from Fischerwiese (*op. cit.* text-fig. 22 a and herein Pl. 40, fig. 3). Such a large stratigraphical range is unique among the Triassic corals. Further studies of large collections may show relations between Carnian and Rhaetian morphotypes.

As concerns septal microstructure, this species differs slightly from other species of *Stylophyllopsis* discussed by CUIF (1973, 254). In comparison with other species, the development of stereome is here insignificant with the exception of the wall region, the septa as a rule being thin and strongly micro-granulated. On the other hand, the character of the septal spines, provided with an internal core plate and covered with granulation, places the species close to *S. zitteli* and, especially, *S. rudis*.

Based on the delicate septal structure, I include in the scope of the species a Lombardy form described as *Lepiconus rudis* (EMMRICH) by FANTINI-SESTINI & MOTTA (1984). The latter, in its dimensions and number of septa, fits well within the range of *S. lindstroemi*: it is 12 × 14–14 × 19 mm in diameter with around 70 septa per calice (*fide*

*op. cit.* Pl. 28, figs. 1, 2). However, arrangement and dimensions of dissepiments being unknown, specific assignment of this form rests doubtful.

**Distribution:** The Carnian and Rhaetian of the Alps; known from the Carnian Beds in Saint-Cassian and from the Zlambach Beds in Fischerwiese and Gosaukamm region.

*Stylophylloids ramosa* sp. n.

Pl. 39, fig. 1

**Holotypus:** GBA 1982/12/693; Pl. 39, fig. 1

**Paratypi:** GBA 1982/12/694, 695; NHMW 1959/364/11<sub>1</sub>

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Derivatio nominis:** Latin *ramosus* – branching.

**Diagnosis:** Branching or solitary. Septal apparatus irregular, consisting of 30–40 septa of three orders. Calicular mean diameter 8–12 mm.

**Material:** Nine specimens from Fischerwiese, GBA 1982/12/688–695 and NHMW 1982/364/11<sub>1</sub>; two thin sections

**Dimensions (in mm):**

Specimen No.	d	s
GBA 1982/12/693	10	41 (13 + 13 + 15)
GBA 1982/12/695	10 × 12	35 (8 + 9 + 17 + 1)

**Description:** Branching colonies composed of a small number (up to 5–6) of short, densely packed corallites. Budding marginal, extratentacular, resembling “Taschenknospung” Septa S1–S2 varying in number, subequal, S3 short, S4 small and sporadic. Axial cavity large, with few internal septal spines.

**Endotheca** subtabuloid, axially concave. Wall thick, composed of septa and an additional stereomal deposit filling up the interseptal spaces.

**Microstructure** typical of stylophyllids, poorly preserved.

**Discussion:** The species, in its ability to form branching colonies, resembles phaceloid *S. caespitosa* FRECH, 1890. They differ through the short-corallite, irregular colonies and markedly more numerous septa of *S. ramosa*. In the shape of individual corallites and in its thick wall it is close to *S. lindstroemi* FRECH, from which it differs by a septal apparatus practically devoid of S4 septa.

**Distribution:** As for the holotype.

Genus *Meandrostylis* FRECH 1890

**Species typica:** *Stylophyllum (Meandrostylis) irregulare* FRECH, 1890

**Emended diagnosis:** Colonies meandroid-ceriod. Budding intracalicular with lamellar linkages. Wall simple, septothecal. Radial elements plate-like, often vertically discontinuous; free septal spines at the inner margin. In the wall, septa are nonconfluent or subconfluent. In the series, the corallite centres are connected by a number of septes-de-vallée. Endotheca of large, tabuloid and vesicular dissepiments. Microstructure typical stylophyllid.

**Species included:** *Meandrostylis irregularis* FRECH, 1890, *Meandrostylis frechi* HAAS, 1909, *Meandrostylis kochi* (BEAUVAIS et POULTON, 1980).

Stratigraphical and geographical ranges: Rhaetian of the Northern Calcareous Alps. Upper Triassic of British Columbia, Canada.

Discussion: *Meandrostylis* is a clearly delimited genus of stylophyllid microstructure and a unique morphology. It differs from *Stylophyllum* in being an exclusively colonial form of highly integrated type, its individuals multiplying by intracalicular budding with lamellar linkages. Its septal apparatus and endotheca much resemble those of *Heterastraea* TOMES (1888; compare DUNCAN 1867, WEYER 1963, BEAUVAIS 1976). The main difference between these genera lies in their wall structure, which is simple septotheca in *Meandrostylis* but bilaminar provided with a fissure in *Heterastraea* (compare WEYER 1963, text-fig. 1 a).

Genus *Coelomeandra* BEAUVAIS et POULTON, 1980 described from the Upper Triassic of Canada falls into the synonymy of *Meandrostylis* FRECH, the two taxa being characterized by ceriomeandroid colony, septes-de-vallée, tabuloid endotheca, radial elements dissociated into septal spines, and septothecal wall.

*Meandrostylis irregularis* FRECH, 1890

Pl. 39, figs. 9, 10, Pl. 40, figs. 9–11

v. 1890 *Stylophyllum (Meandrostylis) irregulare* – FRECH, p. 58, text-fig. on p. 58, Pl. 15, figs. 13–17

part., v. 1890 *Isastraea eucystis* – FRECH, p. 26, Pl. 7, figs. 11 and 12 (non Pl. 6, fig. 10)

Lectotypus: GBA FRECH's type collection No. 2802; FRECH 1890, Pl. 15, fig. 14

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: Nineteen specimens from Fischerwiese, GBA 1982/12/524–538, NHMW 1982/57/33–36; fourteen thin sections including that of FRECH – see p. 146

Dimensions (in mm):

Specimen No.	d	s	width of series	c-c	s/5 mm	t/5 mm
GBA 1982/12/536	4	24	4–4.5	4–5	14	7
GBA 1982/12/528	5	ca. 20	5–6	5	11	8

Description: Colonies meandroid-cerioid. Budding frequent, terminal. Proto-corallite budding circumorally (Pl. 40, fig. 11): Series polycentric, monolinear, relatively permanent (Pl. 39, figs. 9, 10, Pl. 40, fig. 10). Wall tectiform. Series bifurcating, corallites linked by 2–3 septes-de-vallée. In the wall, septa nonconfluent, interdigitating or subconfluent. Septa differentiated into 2–3 size orders. Half of them reach the axial fossa, which is empty. Septal blades vertically discontinuous or continuous. Inner margin of shortest septa with regular free spines.

Endotheca slightly concave at the corallite centre, subhorizontal between corallites, formed of vesicular and tabuloid dissepiments (Pl. 40, fig. 9).

Microstructure: Septal spines very thin, submerged in stereome which covers the septal flanks. Spine surface rough, occasionally with distinct granules. There is a marked tendency to thicken dissepiments and wall. Fibre bundles poorly defined due to advanced recrystallization.

Discussion: In this species I include the well-preserved specimens described by FRECH as *I. eucystis* (1890, Pl. 7, figs. 11 and 12). They have well defined generic features: septes-de-vallée visible in the specimen figured on fig. 11, and tabuloid

endotheca composed of large dissepiments, observable in both specimens. Both those features are lacking in the holotype of *Isastraea eucystis* FRECH, 1890 (= *Distichomeandra austriaca* see p. 80). The assignment by FRECH of these specimens to *I. eucystis* influenced the diagnosis of the latter species: the diagnosis erroneously included reference to endotheca built of large elements (FRECH 1890, 26).

Distribution: Rhaetian of the Northern Calcareous Alps: Zlambach Beds from Fischerwiese and Gosaukamm region.

*Meandrostylis frechi* HAAS, 1909

Pl. 39, fig. 11, Pl. 40, fig. 8

v. 1909 *Stylophyllum (Meandrostylis) Frechi* — HAAS, p. 150, Pl. 5, fig. 10

Holotypus: IPPU HAAS' type collection No. 48; figured as above

Locus typicus: Fischerwiese

Stratum typicum: Zlambach Beds

Material: Five specimens from Fischerwiese, GBA 1982/12/520–523, NHMW 1982/57/13, one specimen from Kesselwand-Rohrmoos, NHMW 1982/56/40, six thin sections

Dimensions (in mm):

Specimen No.	d	width of series	c-c	s	s/5 mm	t/5 mm
GBA 1982/12/520	8–10	—	—	24–26	8	4–5
GBA 1982/12/522	—	8–10	4–10	20–26	8–9	5–6
NHMW 1982/56/40	8 × 12 10 × 12	—	—	—	7	—

Description: Colonies cerio-meandroid; cerioid condition permanent. Series monolinear; 2–3 septes-de-vallée; wall weakly defined. Distal septal margin with protruding spines. Septa meet in the wall where they fuse or stay free (Pl. 40, fig. 8 a). Long septa, which approach the corallite centre, alternate with short ones. The short septa are usually vertically discontinuous, developed on the surface of the dissepiments in the central part of the corallite. At the inner septal edge free septal spines may appear.

Endotheca composed of large tabuloid dissepiments (Pl. 40, fig. 8 b).

Microstructure: Fibre bundles appear on the surface of skeletal elements as fine granulation (Pl. 40, fig. 8 c). The granulation may be strongly developed. Septal spines contain a distinct polycentric core.

Discussion: Canadian *Coelomendra kochi* BEAUVAIS et POULTON (1980, 96, Pl. 9, figs. 1 a–f) is very close to *M. frechi* in colony structure, and differs from it in slightly larger diameters (width of series 6–12 mm, c-c 10–15 mm) and more numerous septa (30–35).

Distribution: Rhaetian of the Northern Calcareous Alps; known in Zlambach Beds of Fischerwiese and Kesselwand-Rohrmoos.

Genus *Anthostylis* nov.

Species typica: *Coccophyllum acanthophorum* FRECH, 1890

Derivatio nominis: Greek *anthos* — flower and *stylis* — yard (femin.), a name referring to the structure of the septa, formed of spar-like septal spines.

**Diagnosis:** Colony cerioid. Septa subconfluent or nonconfluent, reaching with their external edges the septa of neighbouring corallites to form a simple wall. Septa plate-like, built of thin setal spines which are vertical at periphery and inclined ad-axially. Septal faces smooth. Distal septal granulation and denticulation of the internal edges is regular. Endotheca subtabular. Budding intercorallite. Microstructure fibrous, organized in bundles. Columella lacking.

The genus is monotypic.

**Stratigraphic and geographic ranges:** Rhaetian of the Alpine region.

**Discussion:** The genus resembles very much corals of the trabecular group in its plate-like septa regularly ornamented at their edges, small and clearly delimited corallites and in extrathecal budding (similar to perithecal budding). Its purely fibrous microstructure, however, indicates that the genus is related to the Stylophyllina.

The genus *Anthostylis* resembles *Coccophyllum* REUSS in the structure of radial elements built of adaxially inclined septal spines. It differs from the latter genus in having well defined septal blades and a simple, septothecal wall.

CUIF demonstrated the microstructural peculiarities of the type species (1973, text-figs. 32 c and d). Size differentiation of the peripheral and intracalicular septal spines is presented in his text-fig. 32 d; peripheral septal spines were considered by him as a peripheral axis of divergence of the septal fibres. He interpreted the septal fibrous tissue as devoid of any organization into spines. However, the material examined here, although poorly preserved microstructurally is very instructive in morphological aspects and it shows the septal edges to be covered with granular ornamentation. The regular ornamentation of the septal internal edges, analogous to that of the genus *Coccophyllum*, proves that the septa in *Anthostylis* are similarly built of septal spines.

*Anthostylis acanthophora* (FRECH, 1890)

Pl. 41, figs. 5–7

- v. 1890 *Coccophyllum acanthophorum* — FRECH, p. 89, Pl. 20, figs. 4–11
- 1973 *Coccophyllum acanthophorum* FRECH — CUIF, p. 280, figs. 31, 32
- 1977 *Coccophyllum acanthophorum* FRECH — CUIF, p. 17, Pl. 1, figs. 12, 13, Pl. 2, fig. 5
- 1980 *Coccophyllum acanthophorum* FRECH — SENOWBARI-DARYAN, p. 40, Pl. 4, fig. 6

**Syntypi:** GBA FRECH's type collection, No. 2272 — FRECH 1890, Pl. 20, figs. 6 and 8; No. 2804 — *ibidem*, fig. 4; see also herein p. 146

**Locus typicus:** Fischerwiese

**Stratum typicum:** Zlambach Beds

**Material:** About thirty specimens from Fischerwiese, GBA 1982/12/403–405, 725–745, NHMW 1982/57/29–32; seven thin sections; the majority of specimens are recrystallised

**Dimensions (in mm):**

Specimens No.	d of calice	c–c	s
GBA 1982/12/738	usually 2.5	2.5–3.0	23–26
GBA 1982/12/737	2.5–3.0	3.0	24–26
NHMW 1982/57/30	2.8–3.0	2.8–3.0	24–29

**Description:** Colonies cerioid, variable in shape: nodular, lamellate unifacial or bifacial, or digitiform with an irregular surface. The intense budding produces corallites with large, densely spaced polygonal calices, delimited by tectiform walls; elsewhere calicular pits are small and circular, separated by a flattened surface with the zigzag wall line at its middle (Pl. 41, figs. 6, 7).

Twelve short and 12 long plate-like septa. Distal edge with regular granulation. Internal edge regularly denticulate, lateral sides smooth. Axial cavity large (Pl. 41, fig. 5 a).

Endotheca abundant, built of large, densely spaced, tabuloid dissepiments convex at the axis (Pl. 41, fig. 5 b).

Wall simple, septothecal, built of laterally enlarged peripheral edges of septa.

Microstructure fibrous. Septal spines smooth, differentiated in thickness: these from the adaxial septal portion are thinner than those disposed peripherally. Septal spine tips are seen on distal edges as relatively thick granules, and on inner edges as thin denticulation. Stereomal thickening of the upper dissepimental layer is common.

**Remarks:** The specimen of SENOWBARI-DARYAN (1980, Pl. 4, fig. 6) is figured upside down, with the thickening and convexity of the dissepiments directed downwards when in reality they are directed upwards.

**Distribution:** Rhaetian of the Northern Calcareous Alps; known in the Zlam-bach Beds of Fischerwiese and in limestones of the Feichtenstein Reef near Hintersee.

According to STANLEY (1986, 27: a list of verified taxa) present in the Norian of North America.

#### Genus *Coccophyllum* REUSS, 1865

**Species typica:** *Coccophyllum sturi* REUSS, 1865

**Emended diagnosis** (morphology after REUSS 1865, completed with micro-structural features after CUIF, 1972 and new data): Cerioid. Corallites prismatic. Budding intercorallite. Bilaminar wall permanent; median fissure present. Radial elements developed as longitudinal thick ridges, the internal edges of which are covered with a thick denticulation. Endotheca of slightly concave tabuloid elements. Wall, septal ridges and endotheca are in structural continuation. Microstructure fibrous; fibres organized in bundles.

**Species assigned:** The genus is monotypic.

**Stratigraphic and geographic ranges:** Rhaetian of the Alpine region.

**Discussion:** CUIF (1973) proposed inclusion of the genus in the synonymy of *Stylophyllum* REUSS due to such common features as fibrous microstructure, homogeneity of all skeletal tissue and architectural continuity of wall, septa and endothecal elements. However, such characters as radial elements in the form of solid septal ridges combined with tabular endotheca differentiate *Coccophyllum* from *Stylophyllum*.

#### *Coccophyllum sturi* REUSS, 1865

Pl. 41, figs. 1, 2, Pl. 42, fig. 3

v. 1865 *Coccophyllum Sturi* — REUSS, p. 165, Pl. 1, fig. 1

1890 *Coccophyllum Sturi* REUSS — FRECH, p. 88, text-fig. on p. 88, Pl. 20, figs. 1–3 A

1969 *Coccophyllum sturi* REUSS — ZANKL, p. 35, text-fig. 30, Pl. 3, fig. 6

1973 *Coccophyllum sturi* REUSS — CUIF, p. 278, text-fig. 30

1980 *Coccophyllum sturi* REUSS — SENOWBARI-DARYAN, p. 40, Pl. 4, fig. 3

**Holotypus:** GBA type collections No. 2806; REUSS 1865, Pl. 1, fig. 1; FRECH 1890, Pl. 20, figs. 1–1 c

**Locus typicus:** Waldgraben near Altaussee

**Stratum typicum:** Zlambach Beds

**Material:** Two fragmentary colonies from Kesselwand-Rohrmoos, NHMW 1982/56/35<sub>1</sub>, 35<sub>2</sub>; five thin sections; the species is well represented in the NHMW collections

**Dimensions (in mm):**

Specimen No.	d	denticles
NHMW 1982/56/35 <sub>1</sub>	5 × 7, 5 × 8	4/3 mm
NHMW 1982/56/35 <sub>2</sub>	7 × 9, 8 × 11	

**Description:** Colonies cerioid, with a common, bilaminar wall (Pl. 41, fig. 2 b). Calicular edges tectiform. Septal ridges uneven, with internal edges denticulate. Denticles thick, short, regular.

Endotheca of thick, rare, tabuloid dissepiments (Pl. 41, fig. 2 c).

Microstructure homogeneous, the skeleton fibrous (Pl. 42, fig. 3). Fibres organized in bundles of various size, mostly 40 µm in diameter and of variable length. Internal skeletal surface covered with thick, rather irregular micro-granulation produced by the tips of fibre bundles. Radial elements originate at the corallite circumference as short septal spines that form continuous septal ridges on the internal wall surface. The tips of septal spines protrude into the lumen as regular denticulation. The wall is built of the septal ridges and fibre bundles lying between them. The upper dissepimental layer continues into the wall, but septal spines do not appear on the dissepimental surface. A thin fissure is present at the boundary between calices.

**Remarks:** Each of the colonies examined is characterized by different maximum dimensions of corallites prevailing in the colony (Pl. 41, figs. 1, 2 a).

**Distribution:** Rhaetian of the Northern Calcareous Alps; known in the Zlambach Beds of Fischerwiese and Waldgraben near Altaussee, the Gosaukamm region (Kesselwand-Rohrmoos) and Hallstätter Salzberg as well as in Rhaetian limestones at Hohe Göll, and in the Gruber and Feichtenstein Reefs near Hintersee.

### Genus *Pinacophyllum* FRECH, 1890

**Species typica:** *Pinacophyllum parallelum* FRECH, 1890

**Emended diagnosis:** Phaceloid to cerioid. Budding lateral. Wall formed of lamellae and squamae of fibrous structure with a centripetal arrangement of fibres. Radial elements spiniform or partly plate-like; septal spines arranged in simple longitudinal rows. Septal spines are formed of single bunches of subparallel fibers that originate in the wall and, additionally, of prolongations of the surrounding wall squamae. Endotheca tabuloid.

**Species assigned:** *P. parallelum* FRECH, 1890, *P. annulatum* (REUSS, 1855), *P. gracile* VOLZ, 1896.

**Stratigraphic and geographic ranges:** Carnian-Rhaetian of the Alpine region.

**Discussion:** In the literature, there are other species mentioned as belonging to the genus *Pinacophyllum*. The majority of them, however, shows characters that differentiate them from this genus: *P. parvisseptatum* SQUIRES (1956) resembles *Stylophyllum* (*S. pygmaeum* FRECH) in producing equivalent individuals by bifurcation; *P. thurin-*

*giacum* WEISSERMEL (1928) has a costulate wall: *P. lejowae* RONIEWICZ (1974) and *P. sp.* of WURM (1982, Pl. 39, fig. 1) show septal apparatus typical of *Stylophyllum*; *Pinacophyllum* ? sp. of BHAGRAVA and BASSI (1985) has zigzag septa. However, the forms distinguished by ZANKL (1969) but not diagnosed formally, *Pinacophyllum* sp. 1 and sp. 2, may be included in the scope of the genus.

Microstructural characters of the type species are discussed below. *P. gracile* is the only *Pinacophyllum* microstructural features of which have been mentioned in the modern coral literature (MONTANARO-GALLITELLI 1974 b).

In its general corallite architecture and some general features of septa and wall, the genus resembles the trabecular coral, *Kompsasteria* gen. n., and in septal and wall microstructure, the genus *Gigantostylis* FRECH.

*Pinacophyllum parallelum* FRECH, 1890

Pl. 41, figs. 3, 4, Pl. 42, figs. 5, 6, Pl. 43, fig. 3

- v. 1890 *Pinacophyllum parallelum* — FRECH, p. 86, text-fig. on p. 86, Pl. 21, figs. 1, 5, 6  
 v. ? 1909 *Michelinia* ? sp. — HAAS, p. 159, Pl. 6, figs. 4 a, b  
 1969 *Pinacophyllum* sp. 1 — ZANKL, p. 33, text-fig. 28, Pl. 3, fig. 1  
 1979 *Pinacophyllum* sp. 1 — SCHÄFER, p. 47, Pl. 11, fig. 1  
 1984 *Pinacophyllum* sp. — SCHÄFER, Pl. 1, fig. 5

Lectotypus (here chosen): BSP AS XII 142; FRECH 1890, Pl. 21, fig. 6

Stratum typicum: Zlambach Beds

Locus typicus: Hammerkogel (= Kesselwand-Rohrmoos)

Material: Morphotype A — two specimens, NHMW 1903 XII 82, NHMW 1982/56/19<sub>1</sub>, and five thin sections; morphotype B — one specimen, NHMW 1982/56/19<sub>2</sub>, and two thin sections

Dimensions (in mm):

Specimen No.	d	s	s/1 mm	t/5 mm
BSP AS XII 142	4–4.8		3	
NHMW 1903 XII 82	4–4.5			
NHMW 1982/56/19 <sub>1</sub>	4–5	16–22	2–3	3–4
NHMW 1982/56/19 <sub>2</sub>	5	23	2–3	4
	5 × 6	28	2–3	

Description: Two morphotypes differing in colony growth form have been observed in the collection: phaceloid morphotype A and cerioid morphotype B.

Morphotype A (Pl. 41, figs. 3 a, b): Colony phaceloid, dense. Diameters of the smallest free individuals in the colony equal half the adult diameters; budding corallites have not been observed. The wall is thick (Pl. 42, figs. 5 a, b). The septal spines are thin, short and rather poorly differentiated into size orders.

Endothecal elements tabuloid, horizontal.

Morphotype B (Pl. 41, figs. 4 a, b): Colony massive, cerioid. Calices polygonal, edges tectiform. Dividing fissure narrow. Budding marginal, at the wall. One case of the division of a calice into three daughter corallites has been observed. Septa partly plate-like, differentiated into long septa, subequal to the radius and rare, short septa developed as rows of septal spines (7 per 2 mm in longitudinal section).

Endothecal of tabuloid elements, subhorizontal or convex upwards.



**Microstructure:** The wall is divided into two zones. An outer zone, made of radially arranged fibres (Pl. 42, fig. 5 b), passes directly into an inner zone built of clearly individualized squamae (Pl. 42, fig. 6, Pl. 43, fig. 3). Squamae are built of thin, short fibres. The fibres tend to centripetal in the middle of the squamae, changing their orientation toward lateral at the edges of the squamae. Septal spines are initiated right at the limits of the outer and the inner zones. They originate as singular bundles of long subparallel fibres to which the neighbouring squamae adjoin. The spine surface is smooth.

**Remarks and discussion:** For the lectotype a specimen has been chosen with a well preserved aragonitic skeleton and details of the internal corallites structure visible on its weathered surface. The second of FRECH's originals preserved (1890, Pl. 21, fig. 1) has much longer septa and larger calices, and it is ZANKL's *Pinacophyllum* sp. 2 (ZANKL 1969) which fits well with the characteristics of the latter form. It may represent another species rather than *P. parallelum*.

I have included in this species two morphotypes differing from each other in colony form, but similar in corallite structure and microstructure of the wall and septal spines. In its general aspect, the cerioid morphotype resembles species of the genus *Kompsasteria* gen. n. of the family Cyclophylliidae or *Heterastraea* TOMES, but differs from them, above all, in microstructure.

Among the species described by ZANKL (1969), SCHÄFER (1979), SENOWBARI-DARYAN (1980) and WURM (1982, Pl. 34, fig. 9) there is a form identified as *Pinacophyllum* sp. 1 which might be conspecific with *P. parallelum* FRECH.

HAAS (1909) assumed that the genus *Pinacophyllum* is represented in Fischerwiese by a typically expressed *P. parallelum* as well as two other morphotypes. Unfortunately, neither did he figure them, nor are they preserved in his collection.

HAAS' specimen from Fischerwiese (HAAS 1909: specimen PIUW No. 82, HAAS collection) determined as *Michelinia*? sp. may represent morphotype B as described here. It is very poorly preserved, but nevertheless, shows a fissure in the middle of the wall on its upper colony surface, and on the internal corallite surface – rows of weakly expressed spines.

**Distribution:** Rhaetian of the Northern Calcareous Alps: Zlambach Beds at Fischerwiese and Kesselwand-Rohrmoos; reef limestones of Hohe Göll, Adnet, Röteland, Feichtenstein and Gruber Reefs. Dachstein limestone of Gosaukamm region.

### Familia Gigantostyliidae FRECH, 1890

Genus typicus: *Gigantostylis* FRECH, 1890

**Emended diagnosis** (after FRECH, 1890, completed with microstructural characteristics): Septa plate-like; septal spines lacking. Columella solid, independent of septa, thick. Wall well developed, built of squamae. Endotheca lacking. Microstructure non-trabecular; skeleton built of fibres organized into scale-like units in the wall and parallel fibres in the columella; septa in structural continuation with the wall.

The family contains the only genus, *Gigantostylis* FRECH, 1890.

**Discussion:** Skeletal architecture differentiates the genus *Gigantostylis* from other Triassic corals. Its thick wall, although similar in importance to that in the *Pachythecalina*, is quite different microstructurally from the wall of the latter (compare CUIF 1965, 1975 b, and Pl. 42, fig. 1 a and Pl. 43, figs. 1 a, b herein).

FRECH considered *Gigantostylis* as a representative of the rugosans and erected for it a subfamily unit within the family Cyathaxoniidae. The genus, however, does not show

rugosan characters. CUIF, on microstructural data, decided to place it in the family Stylophyllidae. The microstructure of the genus: micro-scales ordered radially or in concentric wall layers and giving a peculiar sculpture to the corallite surface, and such architectural features as plate-like septa and a solid columella, allows it to be distinguished within the stylophyllid group as a separate family.

Genus *Gigantostylis* FRECH, 1890

Species typica: *G. epigonus* FRECH, 1890

Diagnosis (emended): Simple. Calice tube-like distally. Septa plate-like, continuous, failing distally in the calice. Columella solid, fibrous. Wall built of fibres organized into scaly units that may be ordered more or less radially or concentrically. Wall in continuation with the septal tissue.

Species composition: The genus is monotypic.

Stratigraphic and geographic ranges: Rhaetian of the Alpine region.

*Gigantostylis epigonus* FRECH, 1890

Pl. 36, fig. 1, Pl. 42, figs. 1, 2, Pl. 43, fig. 1

1890 *Gigantostylis epigonus* — FRECH, p. 82, text-fig. on p. 83, Pl. 21, figs. 9–15 b

1909 *Gigantostylis epigonus* FRECH — HAAS, p. 156, Pl. 5, fig. 18

1965 *Gigantostylis epigonus* FRECH — CUIF, p. 1046, text-figs. 1–3

1977 b *Gigantostylis* — CUIF, p. 27, text-fig. 5

Lectotypus (here chosen): Of the nine specimens of FRECH, only one figured by this author, 1890, Pl. 21, fig. 16 is known to be preserved in the BSP collection, with number AS XII 139

Locus typicus: Kesselwand-Rohrmoos (originally Oedalm)

Stratum typicum: Zlambach Beds

Material: About fifty incomplete specimens from Fischerwiese GBA 1982/12/539–583 and NHMW 1982/57/84–86; twenty thin sections

Dimensions (in mm):

d:	up to 8–10
maximum h:	more than 25
density of external furrows:	6–8/3 mm
s:	46 (23 + 23) at d 6.5

Description: Solitary, slender, conical (Pl. 36, fig. 1) or subcylindrical corals, frequently vermicular in shape, isolated, rarely gregarious. Surface delicately furrowed vertically and covered with minute granulation or scale-like sculpture. The wall represents an essential morphological element of the coral (Pl. 42, fig. 1 a). The wall is distally thin and proximally thick. At the circumference, the rudiments of radial elements are present, externally marked as the vertical flattened ridges separated by shallow furrows mentioned above.

Septa thin, lamellar, numerous, differentiated into two sizes. They originate as delicate ridges on the internal surface of the wall and slowly grow in length down the calice. Some of them reach the columella. Columella solid, usually smooth, oval in cross section, thick proximally and narrow distally.

**Microstructure:** The skeleton is fibrous, non-trabecular. The wall and septa differ from the columella in microstructure. The fibres in the two former elements tend to be organized in squamae – scale-like skeletal “portions”, the dimensions of which vary from ca. 70  $\mu\text{m}$  in length and 30  $\mu\text{m}$  in thickness up to two or three times these values (Pl. 43, figs. 1 a, b). The fibres grow centripetally. The wall structure is complex. Essentially it consists of radial elements built of the vertically continuous rows of squamae mentioned above. Radial elements continuously grow centripetally, or their growth may be interrupted at any stage, once or many times, by accretion of rather disorderly structured skeleton (Pl. 42, fig. 1 b). The innermost wall layer consists of long-fibrous stereome covering septa and filling the interseptal spaces, quickly growing and resembling the columellar skeleton in nature (Pl. 43, fig. 2). The stereome may completely fill the free space in the bottom of the calice. The columella has no traces of scaly structure and is made of long, densely packed fibres parallel to each other. They grow radially from the axis outwards. The interior of the columella may be empty due to secondary dissolution. A columella spongy in structure seems to express some abnormal development.

**Discussion:** In the material examined some specimens are found that seem to be appressed rather than connected to form a colony. They seem to represent fragments of aggregations of vermicular individuals. However, the possibility of the formation of incipient colonies is not excluded in this species, as HAAS figured a budding specimen (1909, Pl. 5, fig. 18).

**Distribution:** Rhaetian of the Northern Calcareous Alps; abundant only at Fischerwiese, rare at Gosaukamm region.

#### Incertae familiae

Genus *Molukikia* JAWORSKI, 1915

? *Molukikia* sp.

Pl. 15, figs. 5 a–c

A form, coming from Fischerwiese, is represented by a fragmentary discoid corallum (GBA 1982/12/429). It is 45 mm in diameter and 15 mm in height. The septa, about 100 in number, are differentiated into four distinct orders. The S1 septa approach the axis and are thicker and more prominent distally than others. Septal blades are compact and thick. The distal edges show vestiges of large denticulation, the internal edges are provided with large and sharp denticles. Septal surface smooth. The endotheca is formed of vesicular dissepiments. The lower surface of the corallum is smooth. The skeleton is badly recrystallized.

Externally, this form resembles *Molukikia* JAWORSKI, 1915, the systematic position of which – stylophyllid or faviid – is still controversial (compare JAWORSKI 1915 and FLÜGEL 1964).

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Note added in the proof:

Recently, I was able to state that the following FRECH's originals (specimens and thin sections), figured in FRECH 1890, are stored at the Museum of the Institute of Geological Sciences, University of Wrocław (Breslau):

*Montilivaltia norica* FRECH: Pl. 3, figs. 8, 9A–B, Pl. 10, figs. 3, 5

*Thecosmilia fenestrata* REUSS: Pl. 2, figs. 1, 3–6, 8, 9

*Phyllocoenia decussata* REUSS: Pl. 7, figs. 1–1A, 3–5

*Astrocoenia Ohmanni* FRECH and *Gigantostylis epigonus* FRECH: text-fig. 2 on p. 35

*Stephanocoenia Schafhäutli* WINKLER: text-fig. on p. 37, lower

*Stephanocoenia juvavica* FRECH: text-fig. B on p. 33

*Stylophyllum (Meandrostylis) irregulare* FRECH: Pl. 15, fig. 15

*Coccophyllum acanthophorum* FRECH: Pl. 20, figs. 9–9A, 10

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# PLATES

PLATE 1

Figs. 1, 4–6: *Cyclophyllia cyclica* SCHÄFER et SENOWABRI-DARYAN, 1978), p. 27

1. NHMW 1982/57/14, 1 a – transverse thin section,  $\times 2$ , 1 b – polished surface, skeleton recrystallized,  $\times 1$
  4. GBA 1982/12/146, thin, slightly oblique transverse section showing trabecular projections of the internal septal edge,  $\times 4$
  5. NHMW 1982/57/54, tangential section cutting lateral septal granules,  $\times 76$
  6. GBA 1982/12/797, longitudinal section, polished surface showing large dissepiments and horizontally arranged trabeculae in the S 3 septa (encircled).  $\times 8$
- Microstructure in Pl. 2, fig. 1

Figs. 2, 3: *Cyclophyllia major* gen. et sp. n., p. 29

2. NHMW 1982/56/26<sub>1</sub>, 2 a – transverse section, polished surface, skeleton recrystallized,  $\times 1$ , 2 b – a detail of thin section showing trabecular projections of the internal septal edge,  $\times 76$
3. NHMW 1982/56/26<sub>2</sub>, holotype, 3 a – transverse section of a dense, phaceloid colony, polished surface,  $\times 1$ , 3 b – thin section,  $\times 5$ , 3 c – longitudinal, oblique section,  $\times 4$ . Note (fig. 3 a) the position and small size of a daughter corallite (arrow).

Figs. 1, 4–6: Fischerwiese. Fig. 2: Kesselwand-Rohrmoos. Fig. 3: Schneckengraben

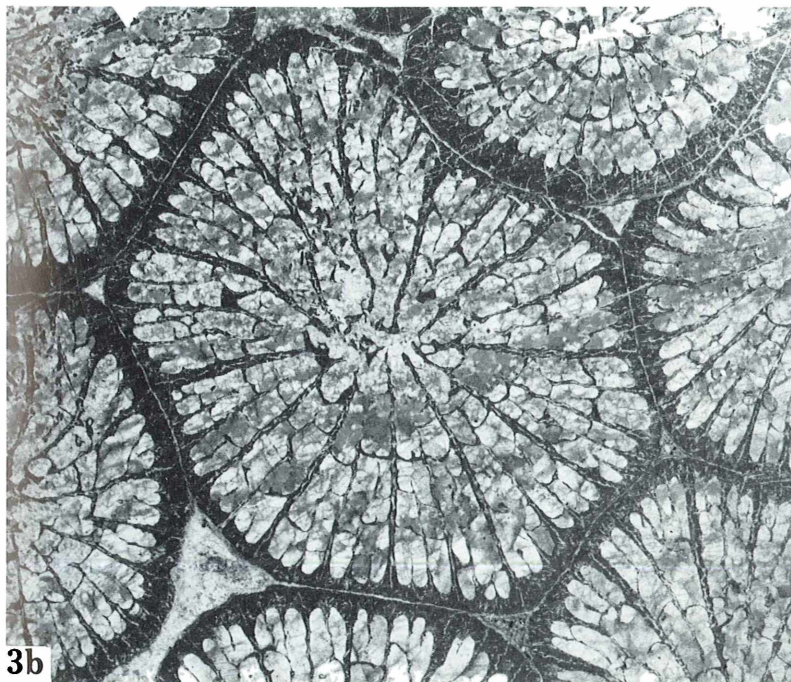
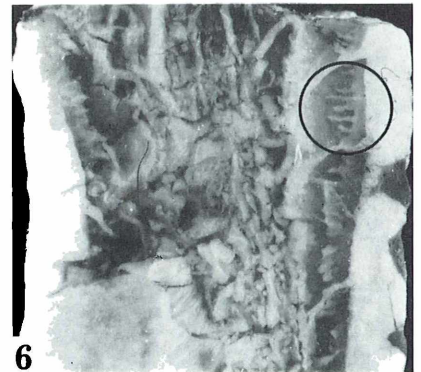
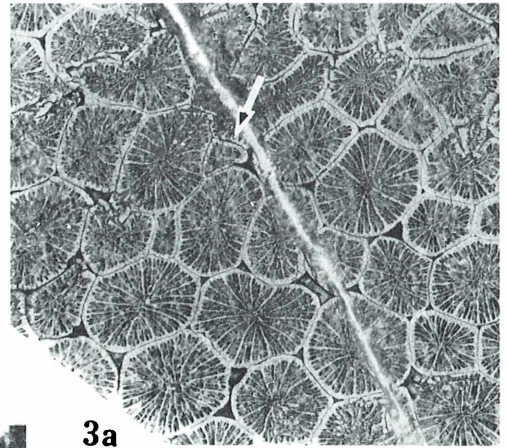
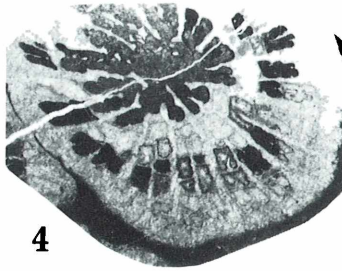
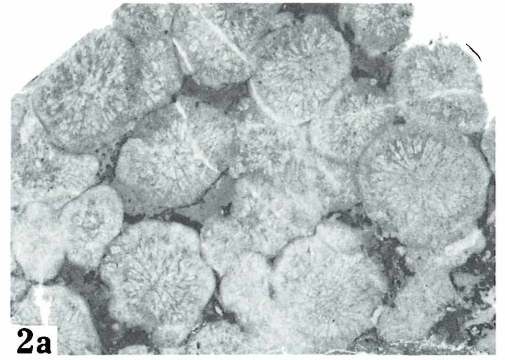
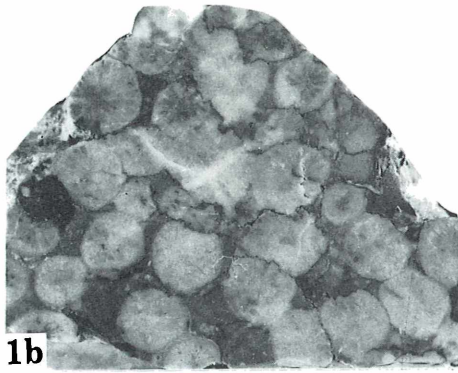


PLATE 2

Figs. 1–3: Cyclophylliid microstructure

1. *Cyclophyllia cyclica* (SCHÄFER et SENOWBARI-DARYAN, 1978), p. 28. NHMW 1982/57/54, 1 a – transverse section displaying thickened S1 septum (note zigzagged mid-septal line), thin S3 septum and – in the interseptal space – the internal layer (L) of the wall built of radially arranged, long, stereomal fibres (also in fig. 1 c),  $\times 76$ , 1 b – longitudinal radial section of the S1 septum displaying trabeculae (an arrow shows the direction of the corallite growth); note the changes in the direction of trabecular growth from subvertical in the periphery of the corallite to subhorizontal adaxially,  $\times 76$ , 1 c – wall region of two closely apposed corallites in transverse section, with the external pellicular wall (W) and the internal wall layer (L) built of radially arranged, stereomal long fibres filling the interseptal space (also fig. 1 a),  $\times 76$ , 1 d – a detail showing the wall (W) to septum relation,  $\times 195$   
See also Pl. 1, figs. 1, 4–6
2. *Kompsasteria oligocystis* (FRECH, 1890), p. 31. NHMW 1982/56/4<sub>3</sub>, transverse section of the wall showing a median wall line; note that the line (arrow) is not sharply delimited,  $\times 84$
3. The same species. NHMW 1959/365/45, walls of two corallites in transverse section showing radial arrangement of fibres and a wall fissure (= wall median line) of variable appearance (arrow),  $\times 195$   
See also Pl. 3, figs. 1–5

Fig. 1: Fischerwiese. Fig. 2: Kesselwand-Rohrmoos. Fig. 3: Schneckengraben



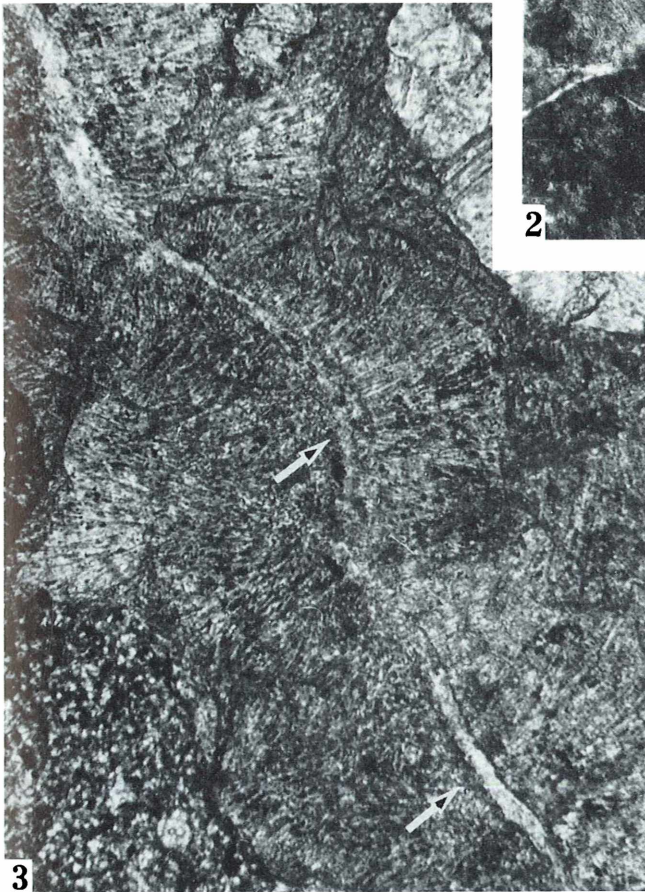
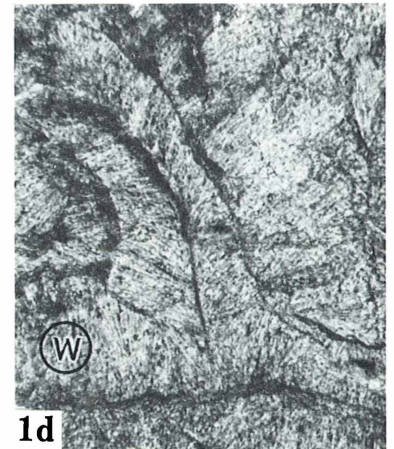
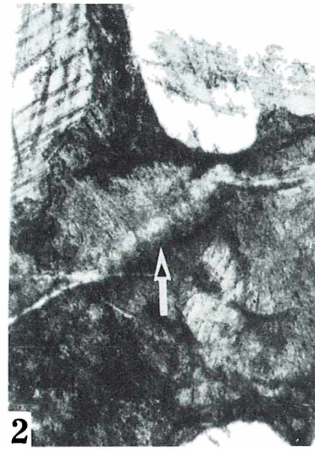
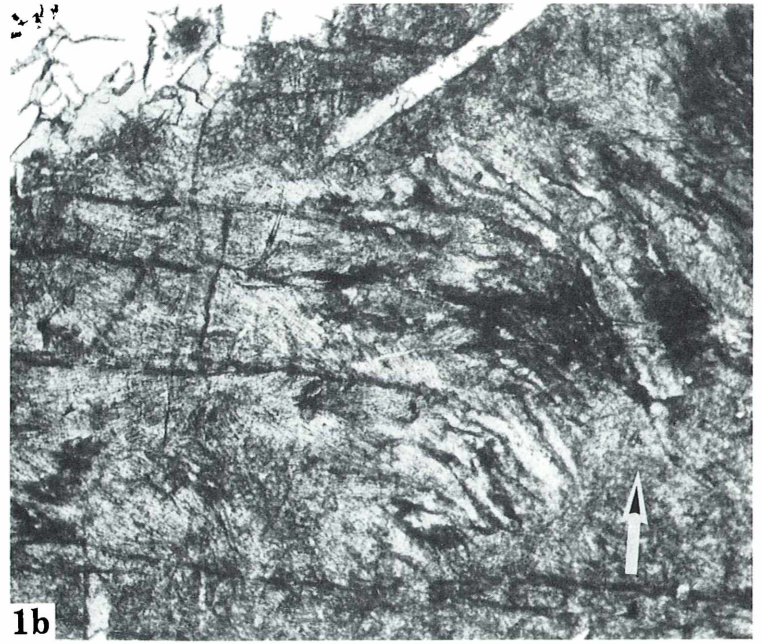
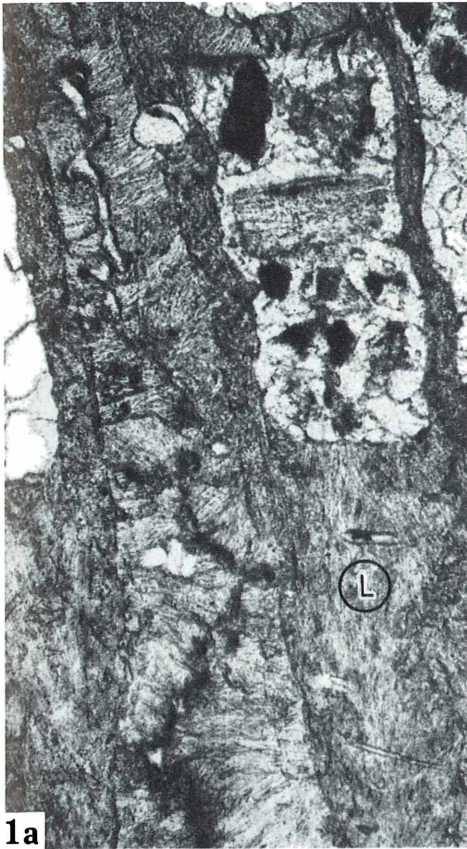


PLATE 3

Figs. 1–5: *Kompsasteria oligocystis* FRECH, 1890, p. 30

1. NHMW 1959/365/45, 1 a – wall in longitudinal radial section displaying fanwise arrangement of fibres (upper right corner),  $\times 195$ , 1 b – endotheca in longitudinal section,  $\times 4$ , 1 c – longitudinal section perpendicular to the septal blade, showing septal trabeculae,  $\times 195$ , 1 d – transverse section of septum obliquely cutting trabecular axes,  $\times 134$ , 1 e – transverse section of thin-septal colony,  $\times 4$
  2. NHMW 1909 XII 86, transverse section of thick-septal colony, polished surface,  $\times 1$
  3. NHMW 1982/56/4<sub>2</sub>, at the upper half of the picture – a fragment of calice showing trabecular projections of the internal edges of septa of diverse orders; at the lower right corner – transversely striated surface exposed by exfoliation of the wall along the median wall fissure,  $\times 10$
  4. NHMW 1982/56/4<sub>1</sub>, abraded calicular surface of the colony showing numerous juveniles at diverse stages of development; note the median wall fissure well exposed,  $\times 6$
  5. NHMW 1982/56/4<sub>4</sub>, calicular colony surface displaying sharp distal edges of calices,  $\times 4$
- See also Pl. 2, figs. 2, 3

Figs. 1, 5: Schnecken graben. Figs. 2–4: Kesselwand-Rohrmoos



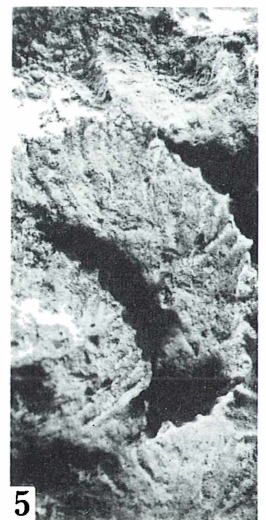
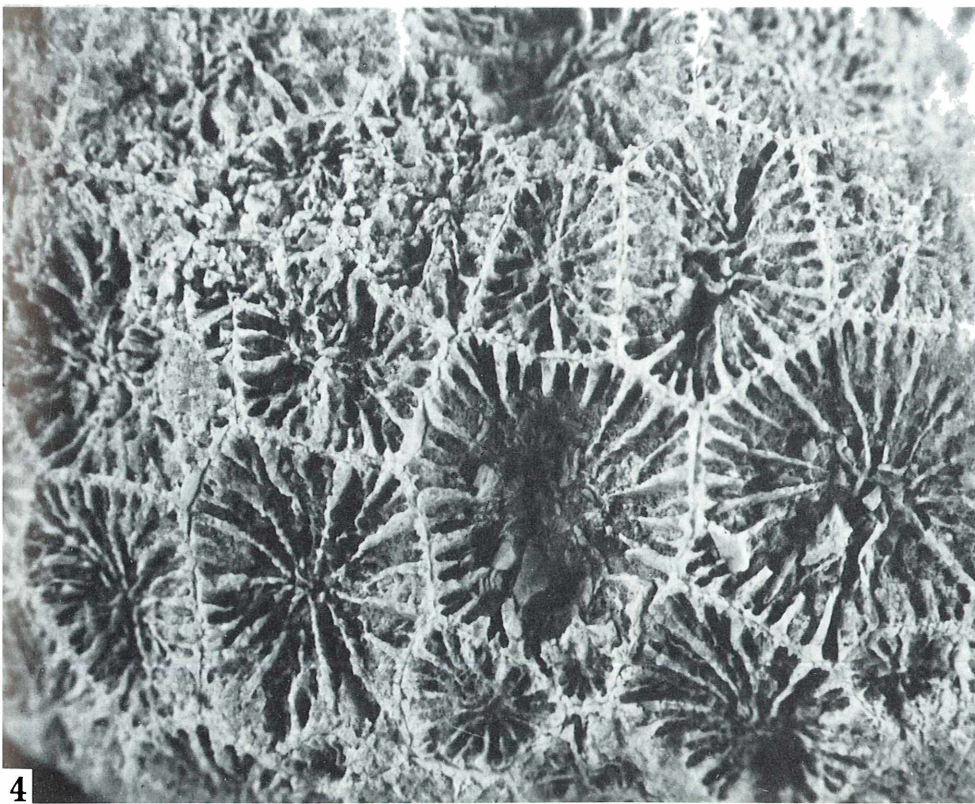
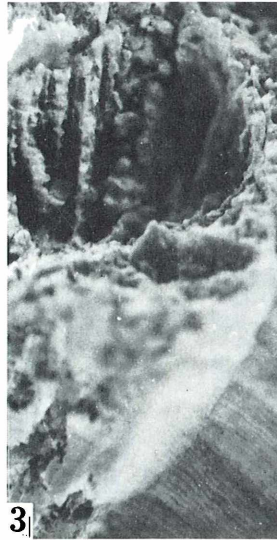
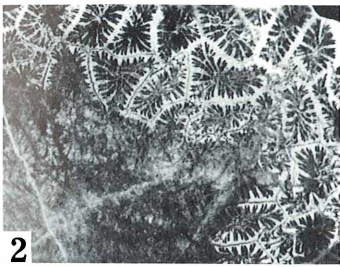
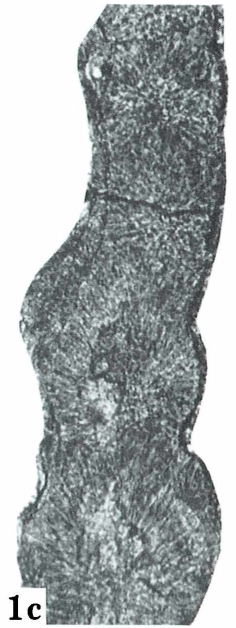


PLATE 4

Fig. 1: *Gablonzeria profunda* (REUSS, 1854), p. 33

NHMW 1851 XXI 1898, 1 a – transverse section,  $\times 4$ , 1 b – longitudinal section,  $\times 4$ , 1 c – septum in longitudinal section perpendicular to the septal blade, showing lateral septal ornamentation,  $\times 185$ , 1 d – transverse septal section  $\times 185$ , 1 e – transverse septal section of the S1 (right) and S3 septum (left), differing markedly in thickness,  $\times 185$ . Note the dentition on the granule distal edges (1 c). See also Pl. 5, figs. 3 a–c

Figs. 2–4: *Gablonzeria major* (FRECH, 1890), p. 32

2. NHMW 1837 XII 1106, 2 a – colony in transverse section, polished surface,  $\times 1$ , 2 b –  $\times 4$
3. NHMW 1959/365/21, longitudinal thin section showing corallite walls and lateral septal granulation,  $\times 4$
4. NHMW 1982/56/31, septal ornamentation in longitudinal tangential section: granules flat and distally denticulated,  $\times 84$

See also Pl. 5, figs. 1, 2

Figs. 1–3: Kesselwand-Rohrmoos. Fig. 4: Schneckengraben



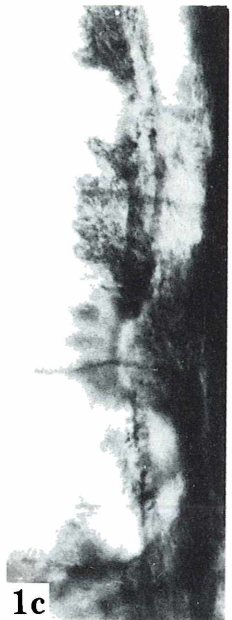
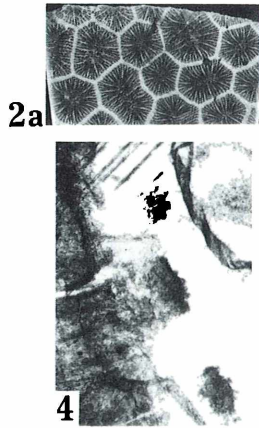
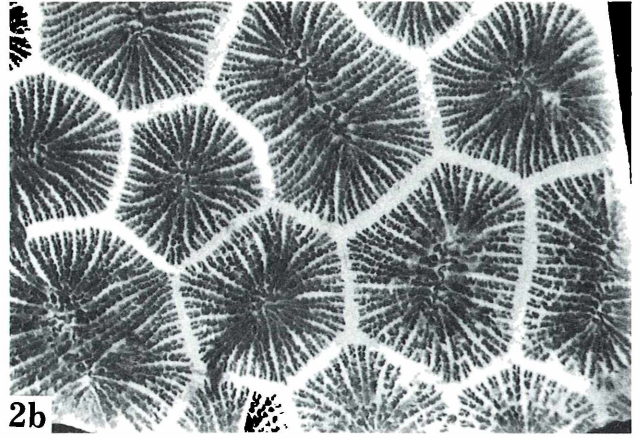
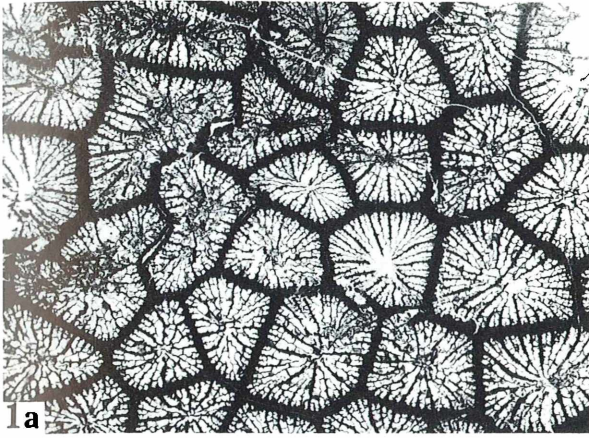


PLATE 5

Figs. 1–3: Microstructure in the genus *Gablonzeria*

1. *Gablonzeria major* (FRECH, 1890), p. 33. NHMW 1982/56/31, 1 a – wall region in transverse thin section,  $\times 20$ , 1 b – a detail displaying a row of vertical wall trabeculae,  $\times 134$
2. The same species. GBA 1982/12/803, septum in longitudinal radial section showing the arrangement of trabeculae,  $\times 134$ ; note that the trabeculae change their growth direction from subvertical or oblique at the periphery to horizontal adaxially.  
See also Pl. 4, figs. 2–4
3. *Gablonzeria profunda* (REUSS, 1854), p. 34. NHMW 1851 XII 1898, 3 a – corallite at the initial stage of division,  $\times 30$ ; note the dividing wall (which develops from opposing septa) and the newly arising septa (arrow), 3 b – transverse section showing vertically arranged septal trabeculae,  $\times 185$ , 3 c – large granule provided with an axis (arrow), transverse section,  $\times 185$   
See also Pl. 4, figs. 1 a–e

Fig. 4: Microstructure in the genus *Chondrocoenia*

*Chondrocoenia* sp. A, p. 108. NHMW 1982/56/22, trabeculae of the peripheral part of costo-septa with lateral axes (arrow), transverse section,  $\times 76$   
See also Pl. 33, figs. 7 a, b

Figs. 1, 2: Schneckengraben. Figs. 3, 4: Kesselwand-Rohrmoos



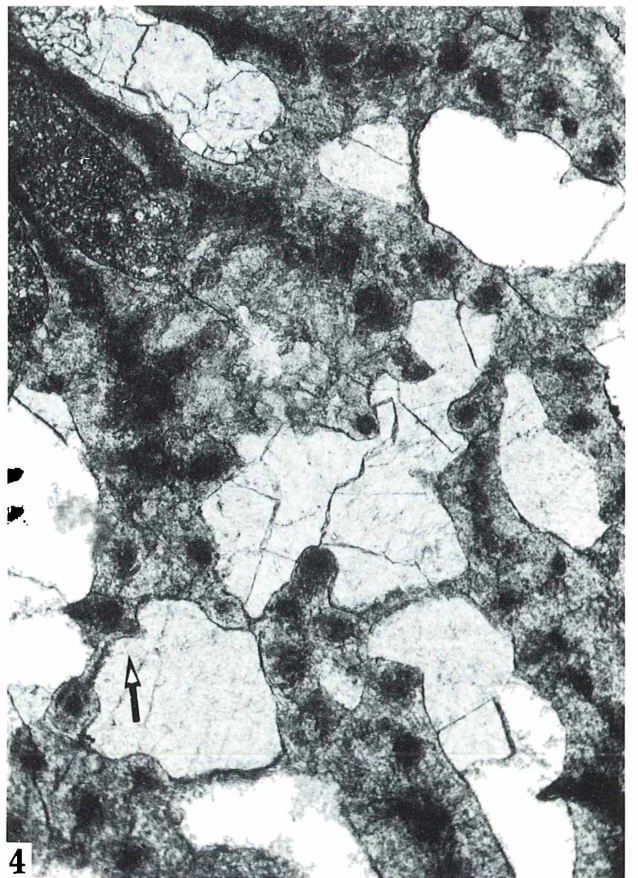
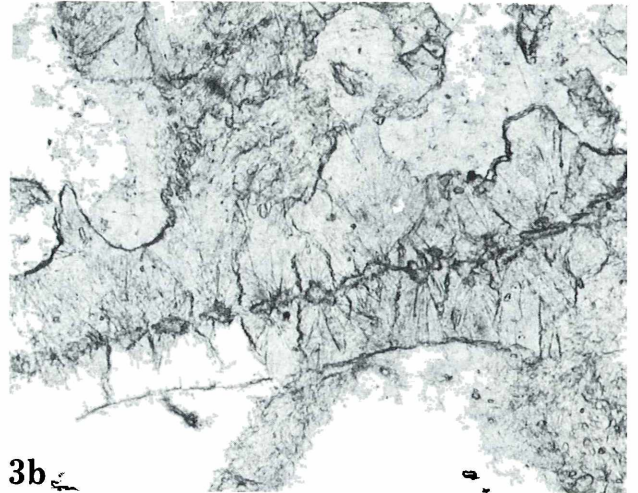
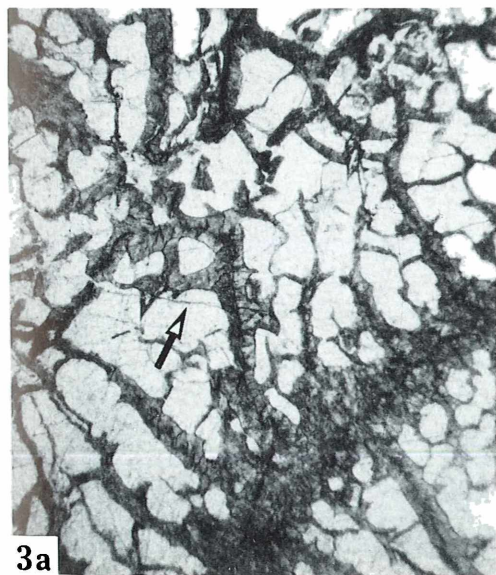
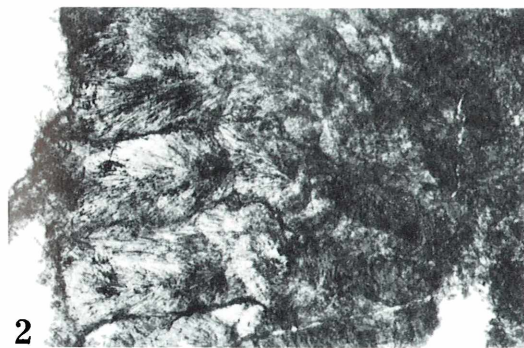
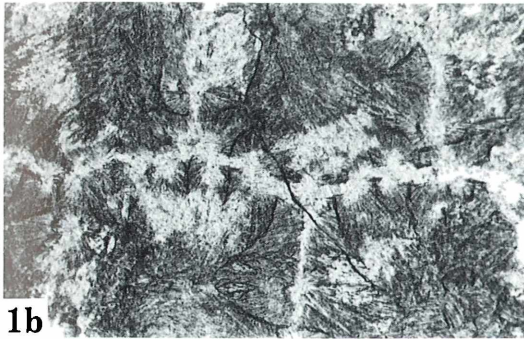
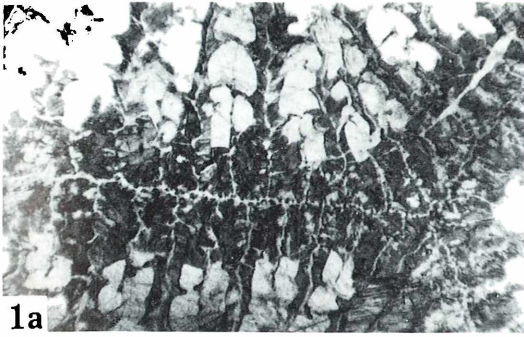


PLATE 6

Fig. 1: *Distichophyllia fritschi* (FRECH, 1890), p. 41

GBA 1982/12/801, transverse section, polished surface,  $\times 4$

Figs. 2–4: *Distichophyllia norica* (FRECH, 1890), p. 39

2. GBA 1982/12/293, fully developed individual with septal apparatus composed of septa of four orders regularly distributed and sporadic S5,  $\times 4$
3. GBA 1982/12/293, longitudinal section showing small-dissepimental endotheca and tangential sections of septa with regularly distributed granulation,  $\times 4$
4. NHMW 1982/56/29<sub>1</sub>, transverse section of S1–S3 septa differing in structure; S1 septum with thick lateral axes developed asymmetrically, on one septal side (arrow), S2 and S3 septa with no lateral axes distinguishable,  $\times 30$

Fig. 5: *Distichoflabellum zapfei* gen. et sp. n., p. 74

Prof. H. ZAPFE's collection, 5 a – transverse thin section showing a fragment of colony with its long calicular fossa,  $\times 4$ , 5 b – longitudinal section with large, subtabuloid dissepiments sloping axialwards from the wall region,  $\times 2$ , 5 c – calicular view,  $\times 1$ , 5 d – side view,  $\times 1$

Figs. 1–3: Fischerwiese. Fig. 4: Schneckengraben. Fig. 5: Kesselwand-Rohrmoos



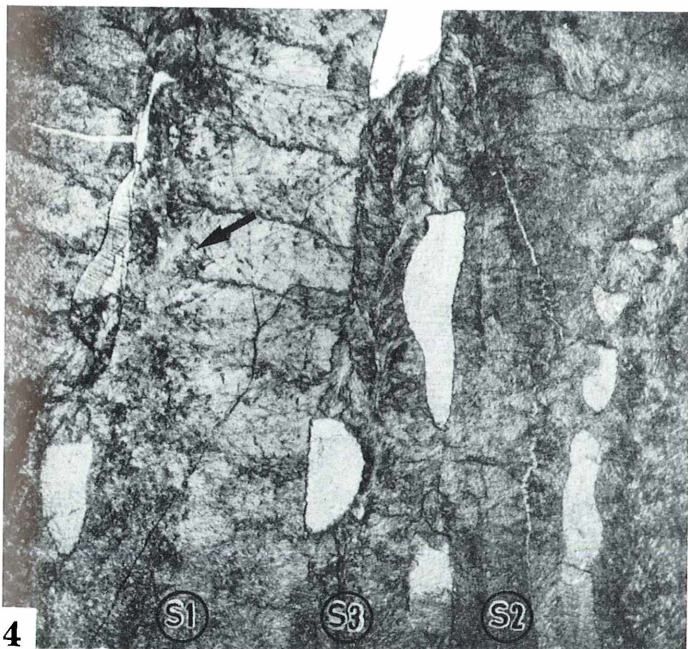
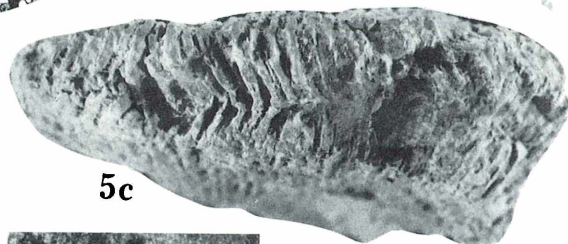
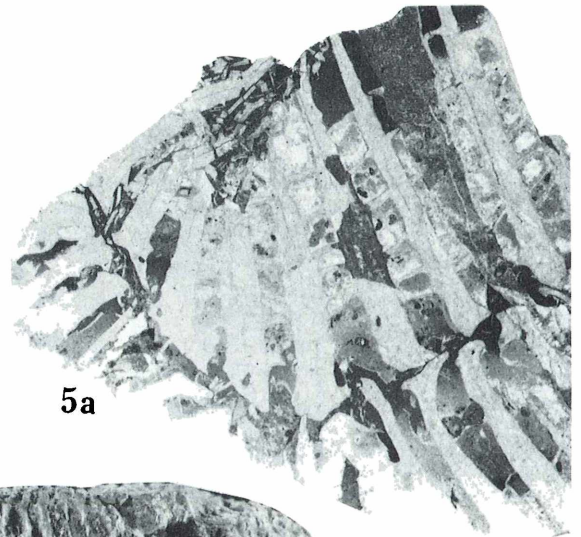
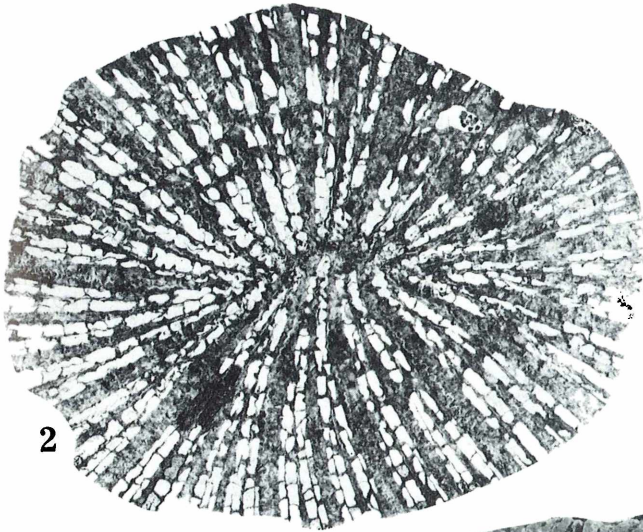
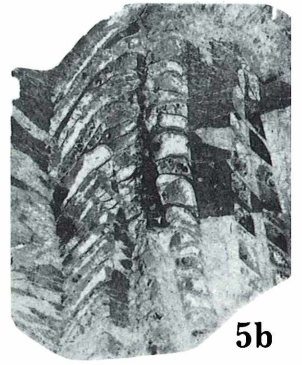
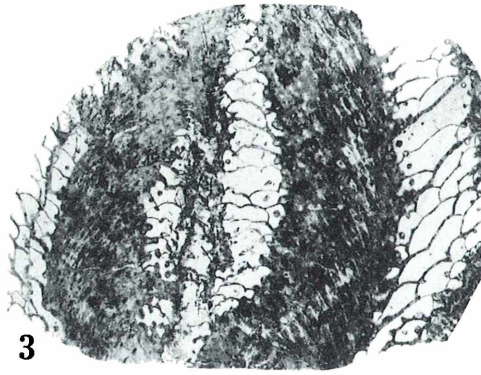
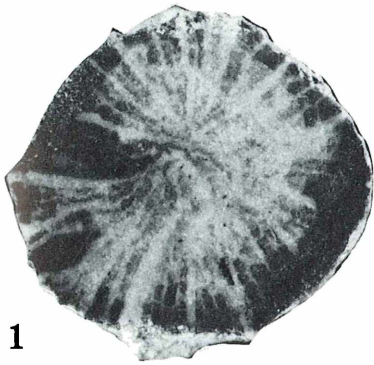


PLATE 7

Figs. 1–8: *Retiophyllia frechi* sp. n., p. 48

1. GBA 1982/12/647, side view of dividing calice with strongly uneven costae,  $\times 2$
2. GBA 1982/12/59, side view of corallite with alternating zones of variably developed skeleton,  $\times 2$
- 3, 4, 5. GBA 1982/12/753, ZPAL HVIII/1, GBA 1982/12/26, thin sections of specimens representing diverse patterns of septal and dissepimental development, fig. 3 –  $\times 5$ , figs. 4 and 5 –  $\times 8$
6. GBA 1982/12/55, 6 a and 6 b – details of corallite surface with preserved fragments of primary pellicular covering, small dissepiments and S4 septa appearing and disappearing in succeeding stages of corallite growth,  $\times 8$  (the specimen is presented upside down)
7. GBA 1982/12/56, specimen with well developed connecting processes,  $\times 2$
8. GBA 1982/12/61, specimen with thin pellicular wall lying on the costae,  $\times 2$   
Longitudinal section in Pl. 9, fig. 5, microstructure in Pl. 13, fig. 2

Fig. 9: *Retiophyllia* sp. A, p. 58

GBA 1982/12/792, 794–796, colony fragments showing a characteristic mode of corallite division,  $\times 2$   
(compare with FRECH's specimens of *Thecosmilia oppeli* figured in 1890, Pl. 2, figs. 21–23)

Figs. 1–8: Fischerwiese. Fig. 9: Hallstätter Salzberg



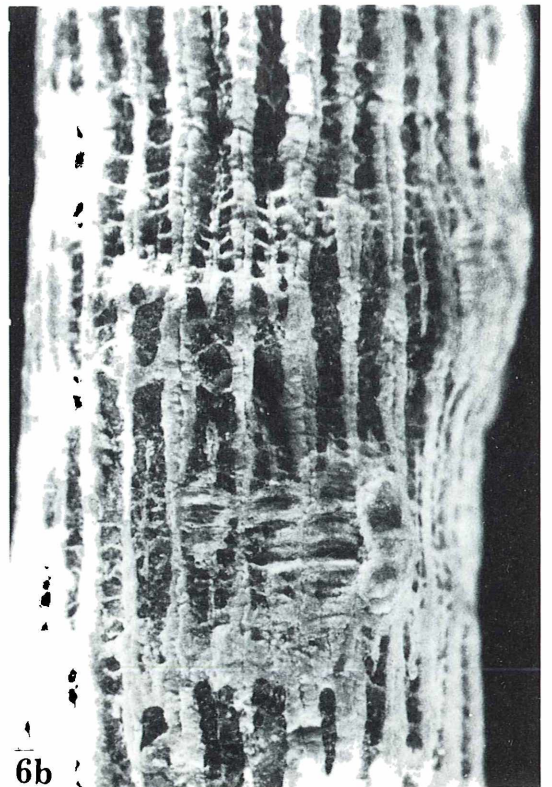
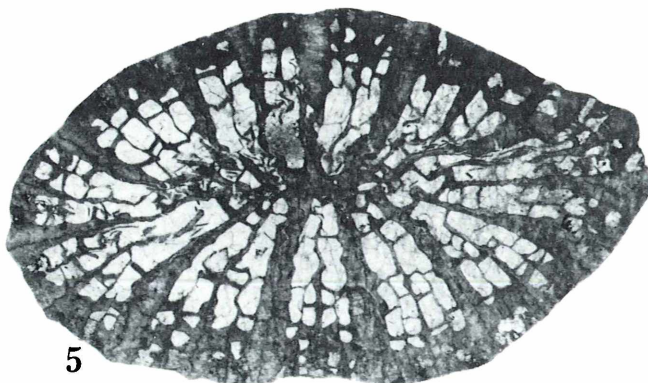
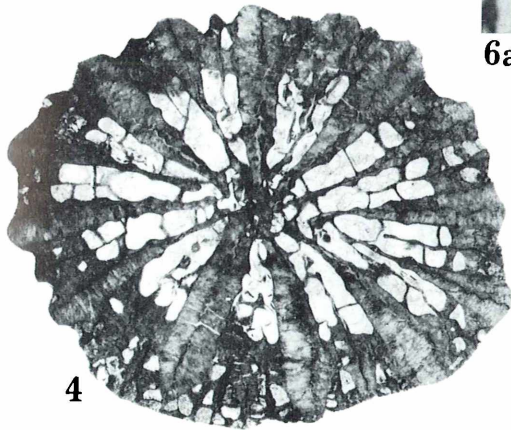
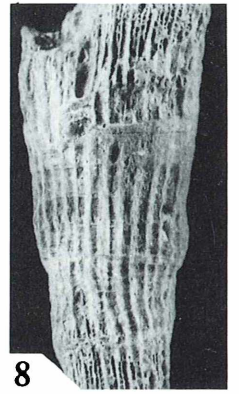
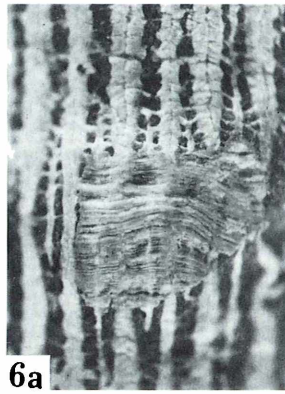
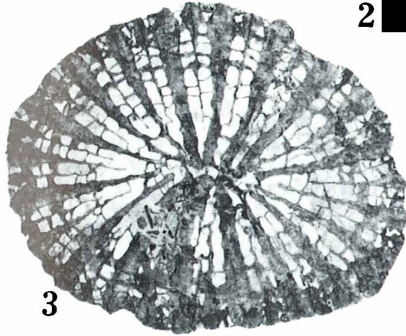
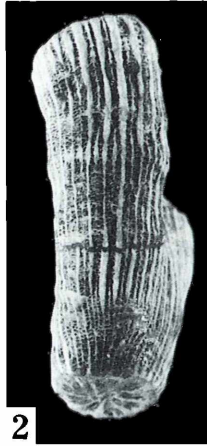
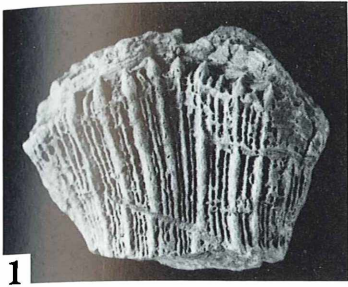


PLATE 8

Figs. 1, 3, 10: *Retiophyllia robusta* sp. n., p. 54

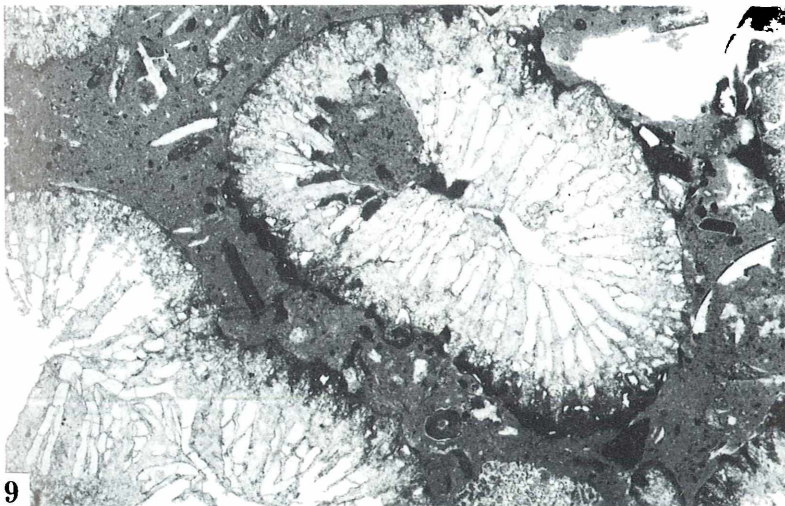
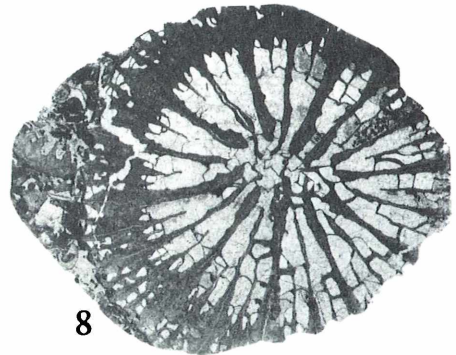
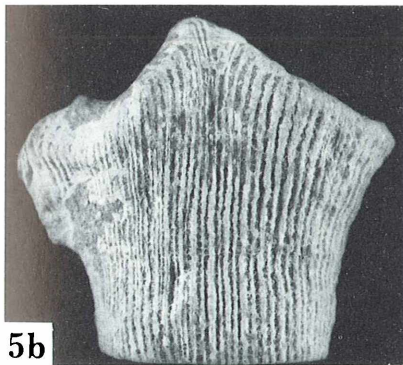
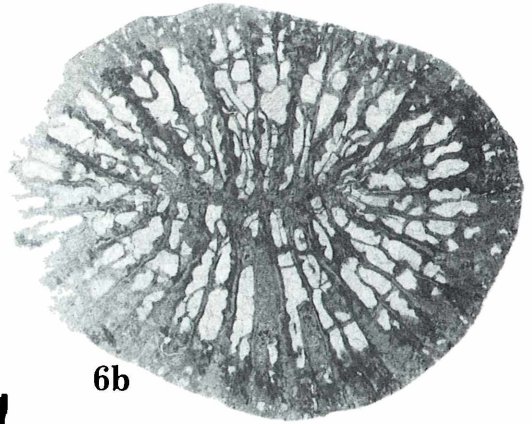
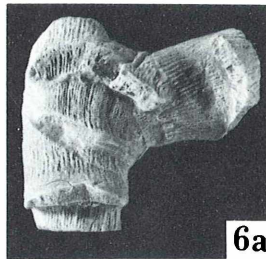
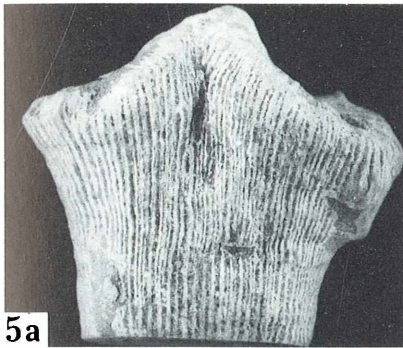
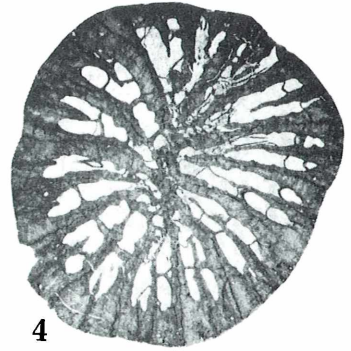
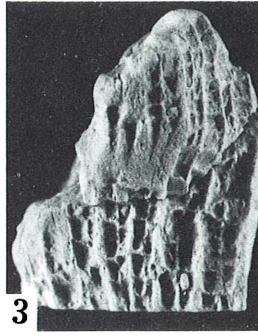
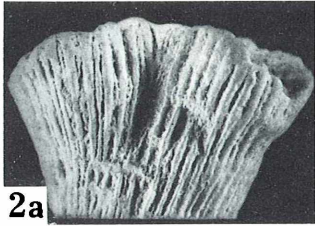
1. NHMW 1982/56/15<sub>1</sub>, a colony in side view, surface abraded, calices broken,  $\times 1$
3. GBA 1982/12/767, syntype, a distal portion of dividing corallite devoid of external wall and exposing thick septa and rare dissepiments,  $\times 2$
10. GBA 1982/12/766, syntype, transverse section, polished surface showing thick and rare septa,  $\times 4$   
Figs. 2, 4, 9: *Retiophyllia caespitosa* (REUSS, 1865), p. 50
2. GBA 1982/12/58, 2 a and 2 b – side views of a corallite at an early stage of division, exposing thick external edges of radial elements,  $\times 2$
4. GBA 1982/12/89, transverse thin section of an isolated corallite with abraded surface,  $\times 4.8$
9. GBA 1982/12/764, thin section of a colony fragment with corallites well preserved externally and partially covered with pellicular wall,  $\times 5$   
Longitudinal section in Pl. 9, fig. 3

Figs. 5–8: *Retiophyllia norica* (FRECH, 1890), p. 52

5. GBA 1982/12/115, 5 a and 5 b – side views of a dividing corallite exposing thin and numerous radial elements on its abraded surface,  $\times 2$
6. NHMW 1982/57/41, 6 a – side view of corallite with lateral folds,  $\times 1$ , 6 b – transverse thin section showing numerous small dissepiments leaning against the septal blades,  $\times 4.8$
7. GBA 1982/12/109, a detail of a corallite surface, devoid of wall, showing newly inserted septa (arrow) and numerous lateral septal projections developed on the sides of remaining septa (encircled),  $\times 8$
8. GBA 1982/12/113, thin section showing a corallite with regularly developed septal apparatus and with external wall preserved,  $\times 4.2$   
Longitudinal section in Pl. 9, fig. 2, microstructure in Pl. 14, figs. 1, 2

Fig. 1: Kesselwand-Rohrmoos. Figs. 2–8: Fischerwiese





# PLATE 9

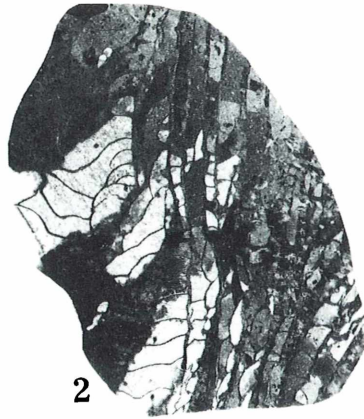
Figs. 1–10: Endotheca in diverse species of *Retiophyllia* (longitudinal sections), p. 46

1. *Retiophyllia gosaviensis* sp. n.: NHMW 1903 XII 17, endotheca at the centre concave, peripherally built of small dissepiments,  $\times 5$ . Transverse section in Pl. 11, figs. 4 a–c
2. *Retiophyllia norica* (FRECH, 1890): GBA 1982/12/111, corallite fragment at the early stage of division, with small dissepiments leaning against the septal blades at the wall formation zone (right); normally developed endotheca (left) built of large, rare and rather flat dissepiments,  $\times 4.2$ . Transverse sections in Pl. 8, figs. 6 b, 8
3. *Retiophyllia caespitosa* (REUSS, 1865): GBA 1982/12/85, endotheca slightly concave, built of large, rare dissepiments,  $\times 8$ . Transverse sections in Pl. 8, figs. 4, 9
4. *Retiophyllia multiramis* sp. n.: NHMW 1982/57/97, endotheca concave at the centre, adaxial dissepiments small (arrow),  $\times 8$ . Transverse sections in Pl. 11, figs. 1–3 and Pl. 12, figs. 1 a, c
5. *Retiophyllia frechi* sp. n.: GBA 1982/12/14, endotheca concave with well marked zonation; at the centre – relatively large vesicles, and at the periphery – small, steep dissepiments, forming a rim of variable thickness,  $\times 4.2$ . Transverse sections in Pl. 7, figs. 3–5
6. *Retiophyllia fenestrata* (REUSS, 1854): NHMW collection of types No. 148, dissepiments large, rare, tabuloid and slightly convex,  $\times 4.5$ . Transverse sections in Pl. 10, figs. 1 a, b
7. *Retiophyllia oppeli* (REUSS, 1865): GBA 1982/12/139, endotheca concave, dissepiments large,  $\times 12$
8. The same species: NHMW 1982/56/3<sub>3</sub>, dissepiments uneven, zonation lacking,  $\times 8$ . Transverse sections in Pl. 10, figs. 3, 4
9. *Retiophyllia gracilis* sp. n.: GBA 1982/12/145, endotheca convex, dissepiments large, zonation lacking,  $\times 8$ . Transverse section in Pl. 10, fig. 2
10. *Retiophyllia gephyrophora* sp. n.: NHMW 1982/56/14, 10 a and 10 b – two corallites showing well zonated convex endotheca built of very uneven dissepiments crossing the axial cavity and minute, crowded vesicles forming the peripheral rim,  $\times 4.7$ . Transverse sections in Pl. 10, figs. 5 a, b  
Figs. 1, 6: Kesselwand-Rohrmoos. Figs. 8, 10: Schneckengraben. Figs. 2–5, 7, 9: Fischerwiese

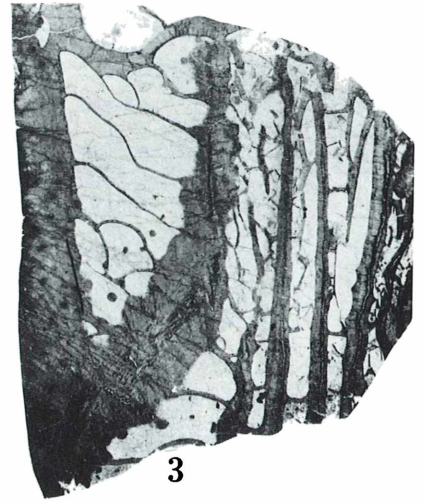




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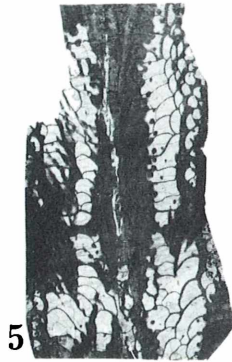
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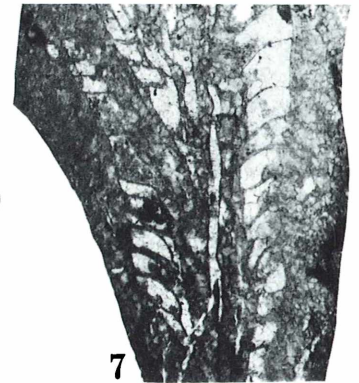
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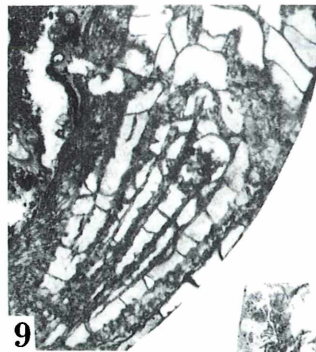
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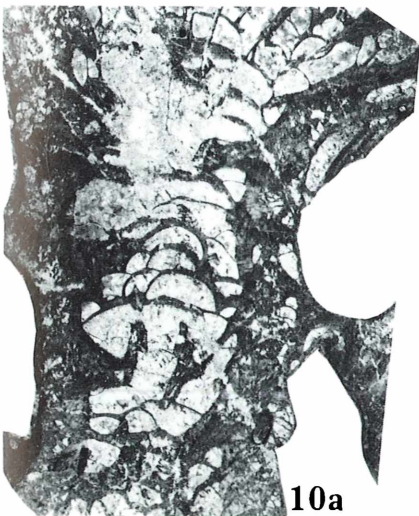
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9



10b



10a



8

PLATE 10

Fig. 1: *Retiophyllia fenestrata* (REUSS, 1854), p. 59

NHMW collection of types No. 148, REUSS' holotype of *Calamophyllia fenestrata*, 1 a – transverse section, polished surface,  $\times 1$ , 1 b – thin section,  $\times 6.5$

Longitudinal section in Pl. 9, fig. 6, microstructure in Pl. 13, figs. 1 a–c

Fig. 2: *Retiophyllia gracilis* sp. n., p. 58

NHMW 1982/56/9, holotype, transverse thin section,  $\times 6$

Longitudinal section in Pl. 9, fig. 9, microstructure in Pl. 13, fig. 3

Figs. 3, 4: *Retiophyllia oppeli* (REUSS, 1865), p. 47

3. GBA 1982/12/137, typically developed form, transverse thin section,  $\times 4$

4. NHMW 1982/56/3<sub>2</sub>, polished surface of a colony partially built of phaceloid corallites and partially of coalesced ones,  $\times 4$

Longitudinal sections in Pl. 9, figs. 7, 8

Fig. 5: *Retiophyllia gephyrophora* sp. n., p. 61

NHMW 1982/56/14, holotype, transverse sections, 5 a – polished surface,  $\times 1$ , 5 b – thin section,  $\times 8$ .

Longitudinal sections in Pl. 9, figs. 10 a, b

Figs. 1, 2, 4: Kesselwand-Rohrmoos. Fig. 3: Fischerwiese. Fig. 5: Schneckengraben



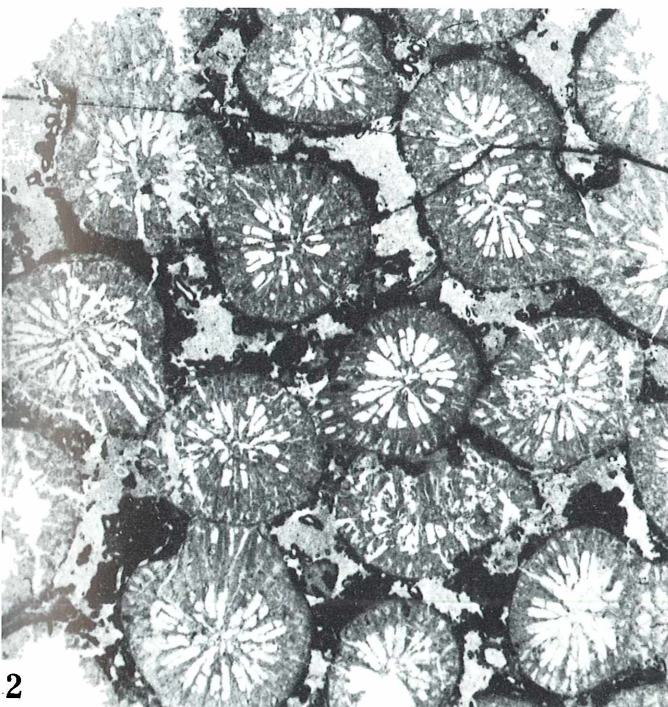
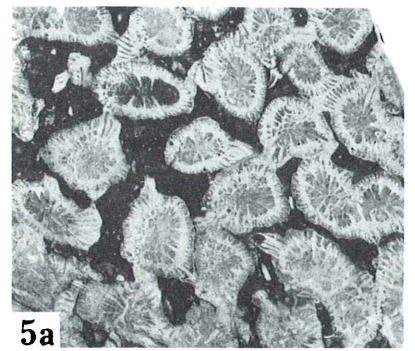
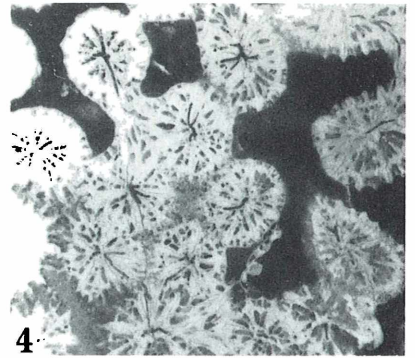
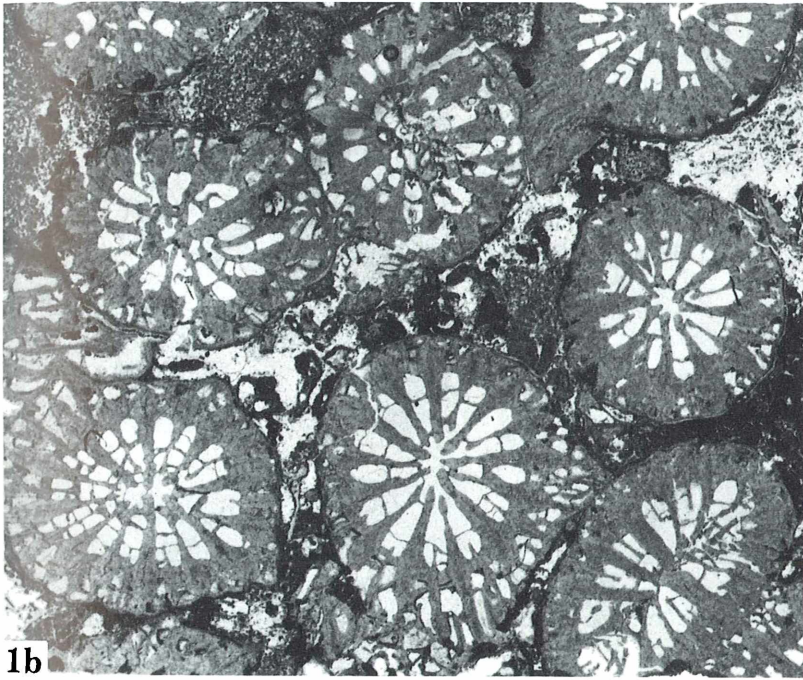
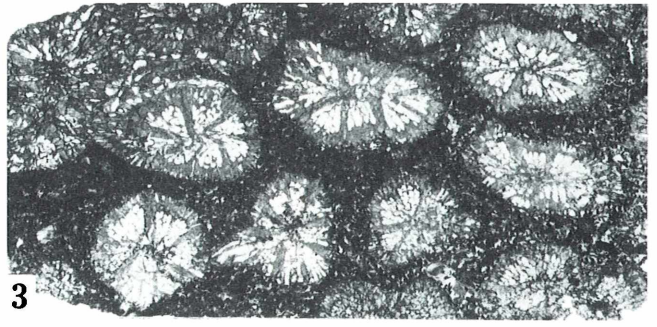
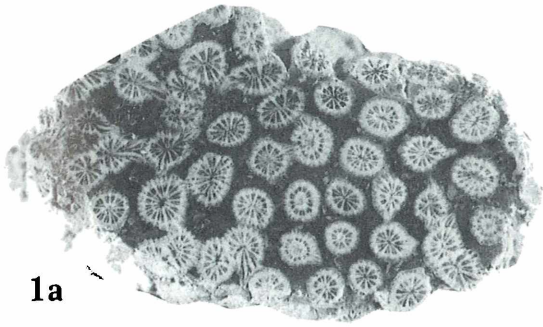


PLATE 11

Figs. 1–3: *Retiophyllia multiramis* sp. n., p. 56

1. NHMW 1959/361/9, colony in transverse section, polished surface, 1 a –  $\times 1$ , 1 b –  $\times 4$
2. NHMW 1982/56/7<sub>1</sub>, transverse thin section showing axial corallite region,  $\times 18$
3. NHMW 1982/56/8, transverse thin section showing thick and long S1 septa,  $\times 8$   
See also Pl. 9, figs. 4, Pl. 12, fig. 1 a–h

Figs. 4, 5: *Retiophyllia gosaviensis* sp. n., p. 55

4. NHMW 1909 XII 17, colony in transverse section, polished surface, 4 a –  $\times 1$ , 4 b –  $\times 4$ , and 4 c – thin section,  $\times 5$ .  
Note abundant, underdeveloped S4 septa.
5. NHMW 1903 XII 95, side view of corallites devoid of wall and showing thin and even costae, 5 a –  $\times 2$ , 5 b –  $\times 8$   
Longitudinal section in Pl. 9, fig. 1

Figs. 1–5: Kesselwand-Rohrmoos



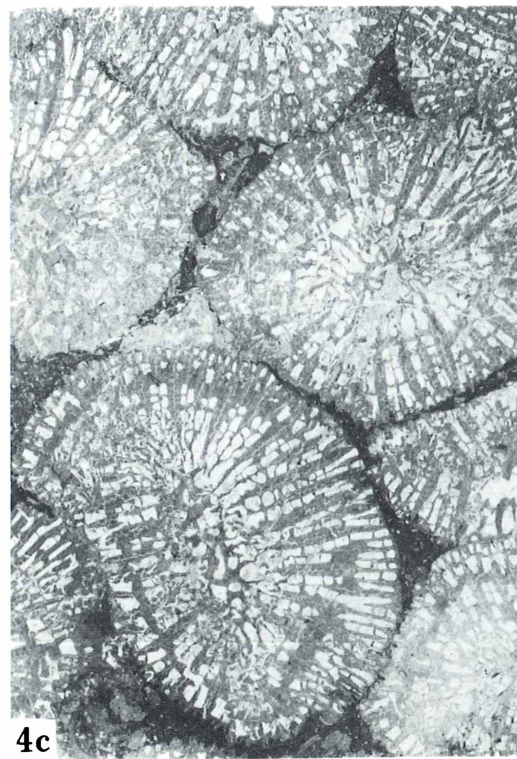
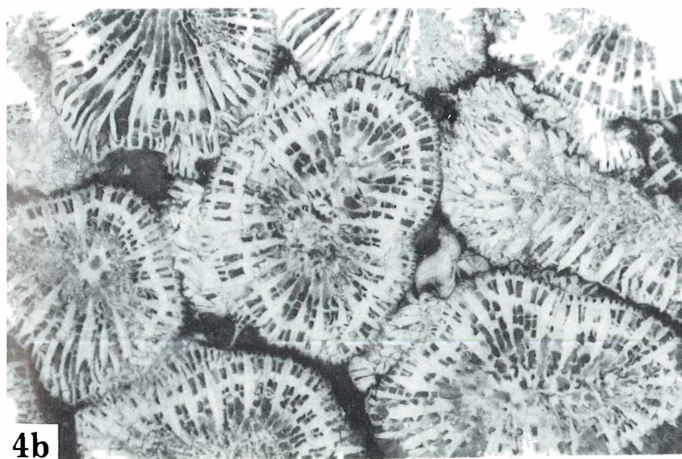
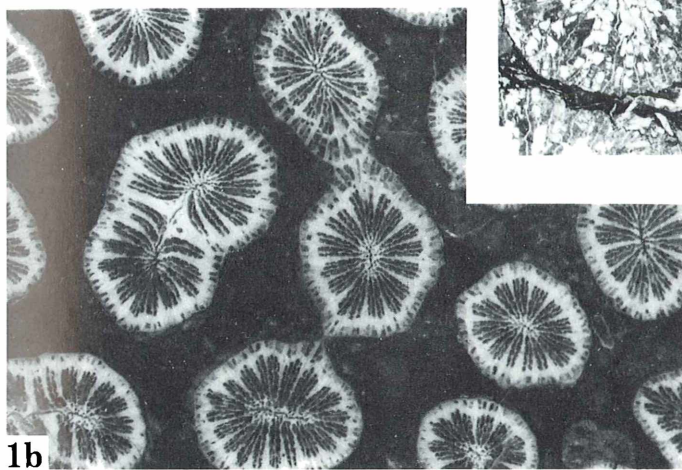
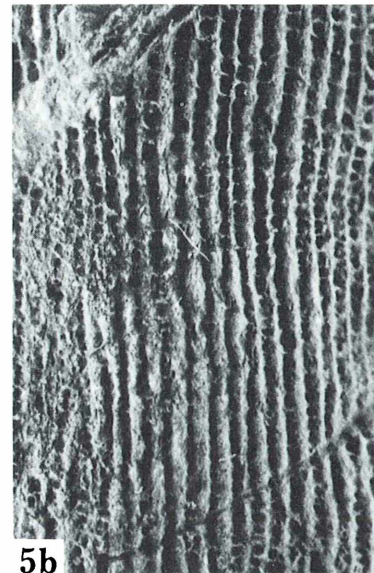
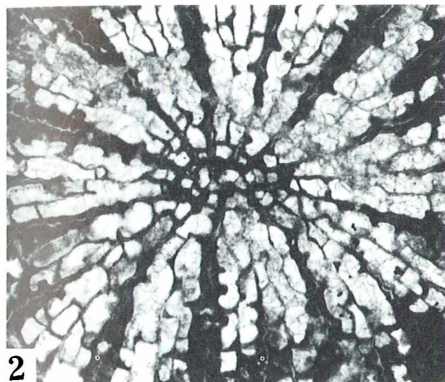
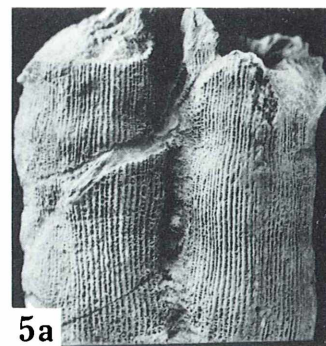
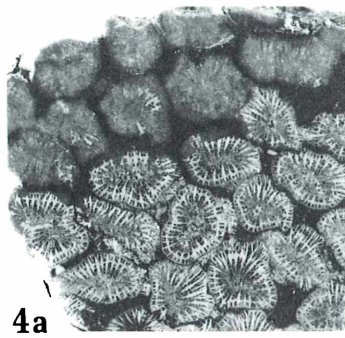
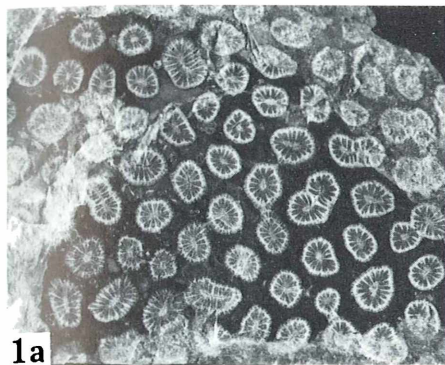


PLATE 12

Fig. 1: *Retiophyllia multiramis* sp. n., Kesselwand-Rohrmoos, p. 56

NHMW 1982/56/10<sub>1</sub>, 1 a – transverse thin section of a juvenile corallite,  $\times 15$ , 1 b – longitudinal section showing menianes and granules (lower left corner) and vesicular endotheca,  $\times 15$ , 1 c – transverse section of a colony fragment,  $\times 8$ , 1 d – transverse section of the septal blade with well individualized trabeculae which are expanding laterally into a meniane (lower left corner),  $\times 123$ , 1 e – a detail of fig. 1 a showing menianes directed at an acute angle to the septal blade,  $\times 123$ , 1 f – transverse section of septum built of poorly individualized small trabeculae arranged in zigzag row,  $\times 123$ , 1 g – transverse section of the peripheral corallite region showing a pellicular wall with radially arranged fibres (W) and synapticular septal projections (SY),  $\times 123$ , 1 h – longitudinal radial section tangential to the septal blade, showing short menianes and dissepiments,  $\times 123$ .

See also Pl. 9, fig. 4 and Pl. 11, figs. 1–3



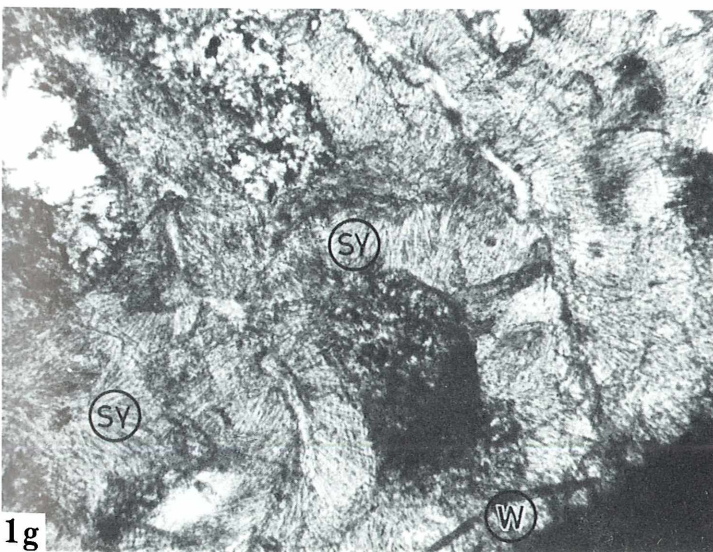
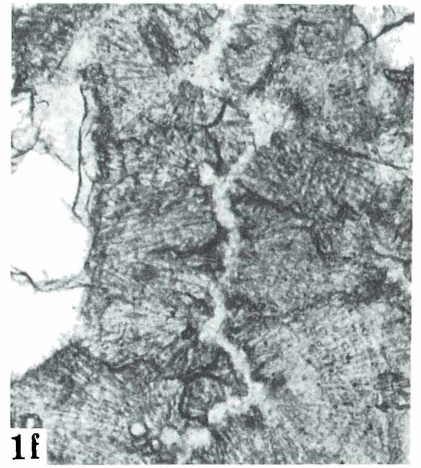
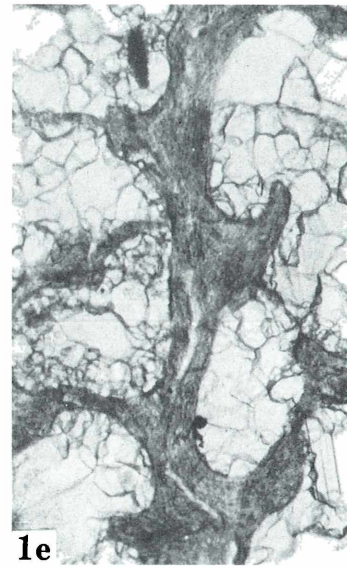
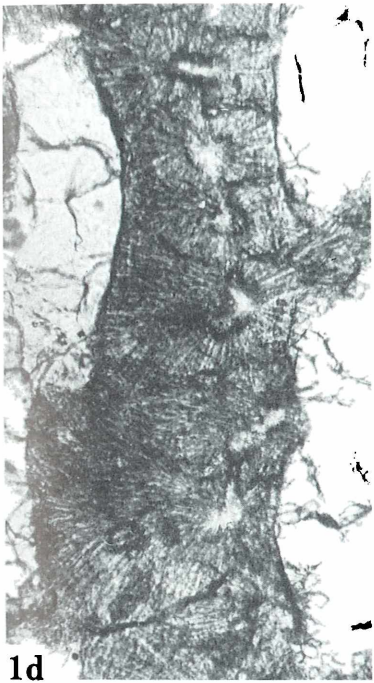
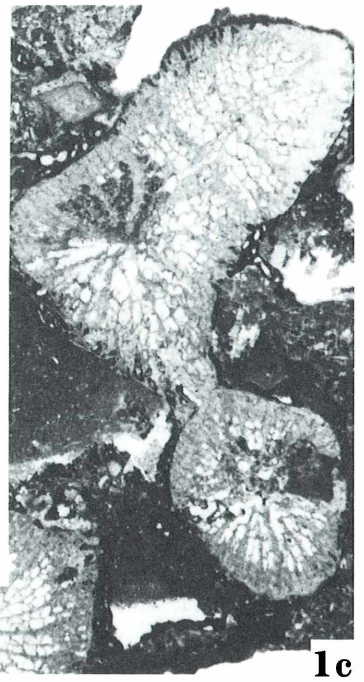
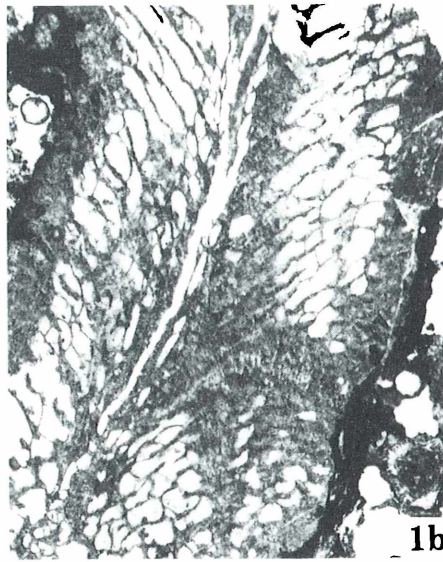
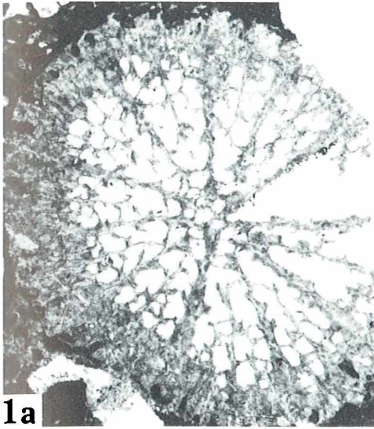


PLATE 13

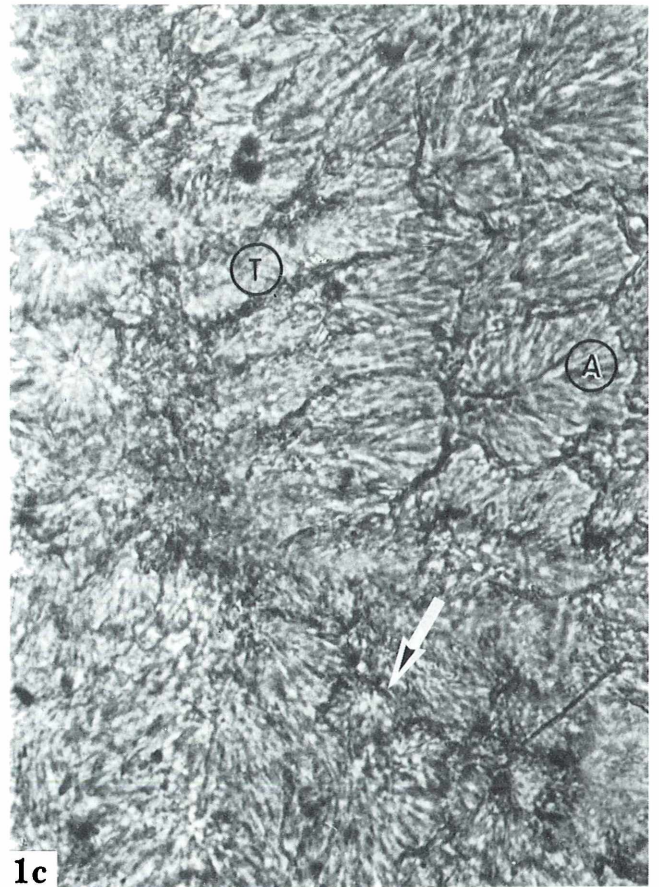
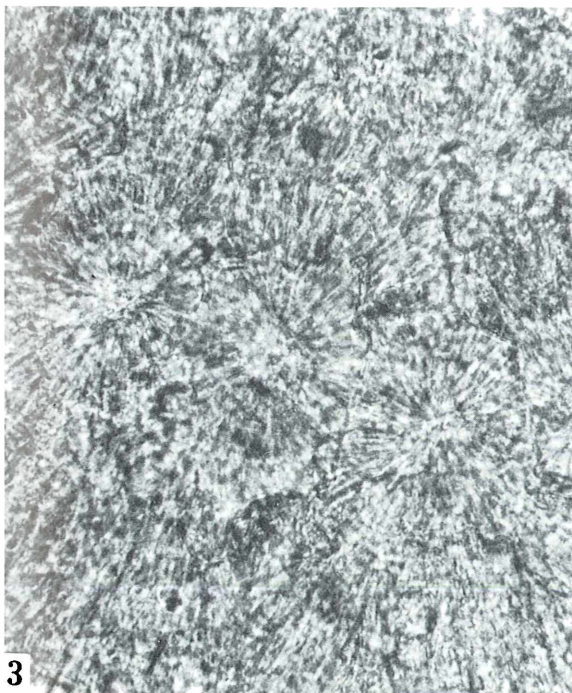
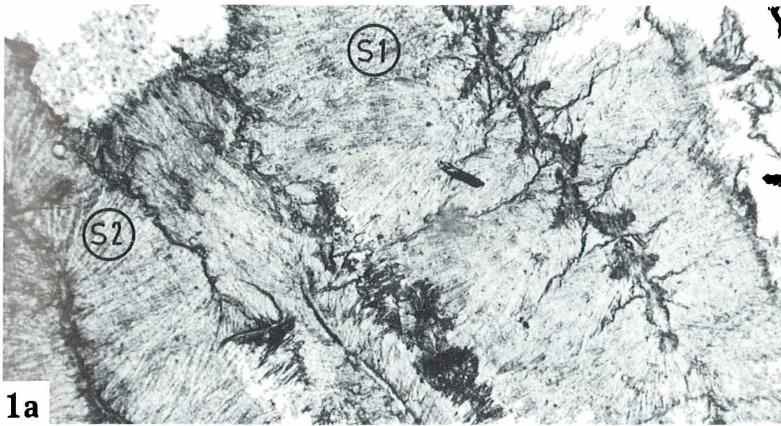
Figs. 1–3: Distichophylliid original microstructure and its diagenetic transformations (continued in Pl. 14), pp. 36–38, 43 and pages mentioned below

1. *Retiophyllia fenestrata* (REUSS, 1854), p. 59. NHMW collection of types, No. 148, holotype, 1 a – transverse section showing S1 septum with zigzagged and S2 septum with straight mid-septal zones,  $\times 50$ , 1 b – transverse, slightly oblique section of a thick costo-septum with wavy mid-septal zone,  $\times 50$ , 1 c – a detail showing obliquely sectioned trabeculae of the mid-septal zone (T), transversely sectioned trabeculae (arrow), as well as large, lateral axes in tangential septal section (A),  $\times 308$
2. *Retiophyllia frechi* sp. n., p. 49. GBA 1982/12/26, mid-septal zone built of well delimited, thin trabeculae with axes dissolved (arrow) and replaced by calcite; lateral axes regularly distributed (A),  $\times 195$
3. *Retiophyllia gracilis* sp. n., p. 45. NHMW 1982/56/9, costal part with the mid-septal zone built of a row of well delimited trabeculae,  $\times 252$

See also microstructure of *Distichophyllia norica* in Pl. 6, fig. 4, *Retiophyllia multiramis* in Pl. 12, figs. 1 d–h, *Palaeastraea grandissima*, Pl. 17, figs. 2 c, d, *Kuhnastraea decussata*, Pl. 14, fig. 3 and Pl. 17, fig. 1

Figs. 1, 3: Kesselwand-Rohrmoos. Fig. 2: Fischerwiese





# PLATE 14

Figs. 1–3: Distichophylliid original microstructure and its diagenetic transformations (continued from Pl. 13)

1. *Retiophyllia norica* (FRECH, 1890), p. 53. GBA 1982/12/113, 1 a – transverse section, peripheral edge of costo-septum embedded in the external pellicular wall built of radially arranged fibres; note the axes of two thick trabeculae obliquely cut at the costal margin (arrows),  $\times 108$ , 1 b – transverse section showing septa and their lateral synapticular projections (SY); note that the median septal zones may be sharply delimited or may have undistinct borders (right) and that the trabeculae may be practically unrecognizable;  $\times 76$ , 1 c – mid-septal zone reduced to a dark line interrupted by rare trabecular axes (arrow),  $\times 108$ , 1 d – a mid-zone with traces of relatively thick trabeculae,  $\times 108$ , 1 e – mid-septal zone developed partially as a uniform dark line and partially as a row of trabeculae with lateral axes rather irregularly distributed,  $\times 195$
2. The same species. GBA 1981/12/116, mid-septal zone in form of a dark, zigzag line with regularly distributed lateral axes,  $\times 195$
3. *Kuhnastraea decussata* (REUSS, 1854), p. 72. NHMW 1959/361/2, intercorallite wall region displaying a trabecular wall (W) and costo-septa of variable structure; note that the septal blade of S2 septum is thin and simple in structure whilst S1 septum – thick and complex and that its costal part (C) is built of a row of simple, thick trabeculae resembling wall trabeculae,  $\times 123$ . Another detail of the same specimen is figured in Pl. 17, fig. 1

Figs. 1, 2: Fischerwiese. Fig. 3: Kesselwand-Rohrmoos



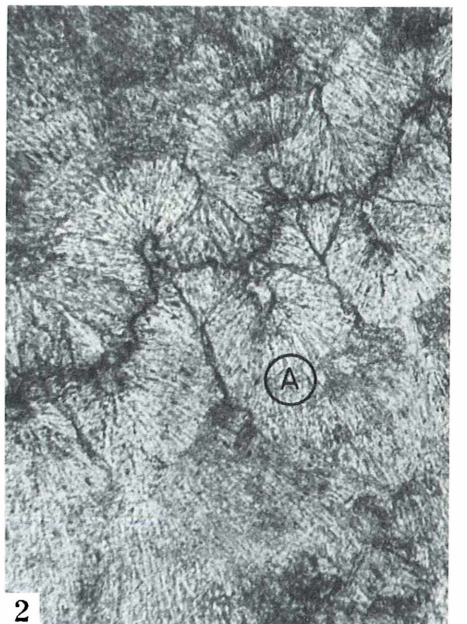
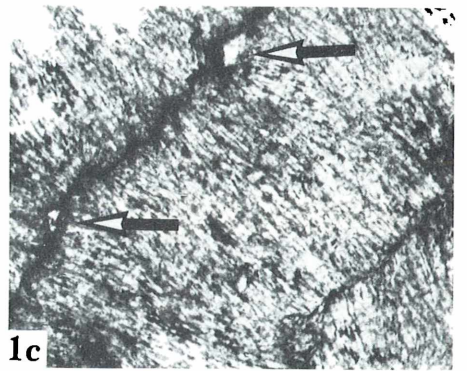
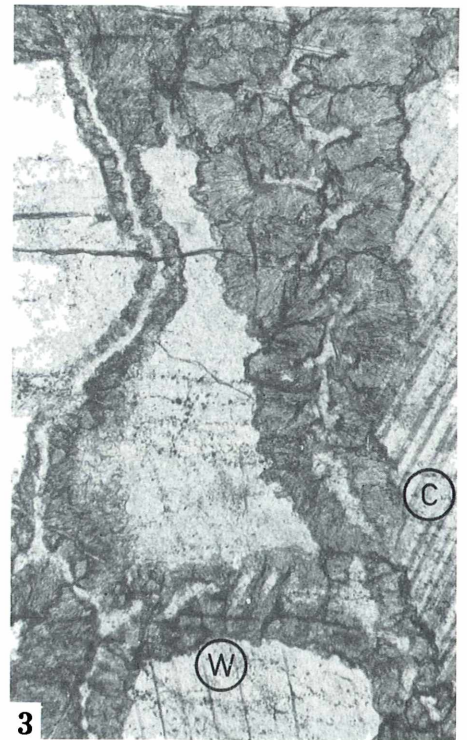
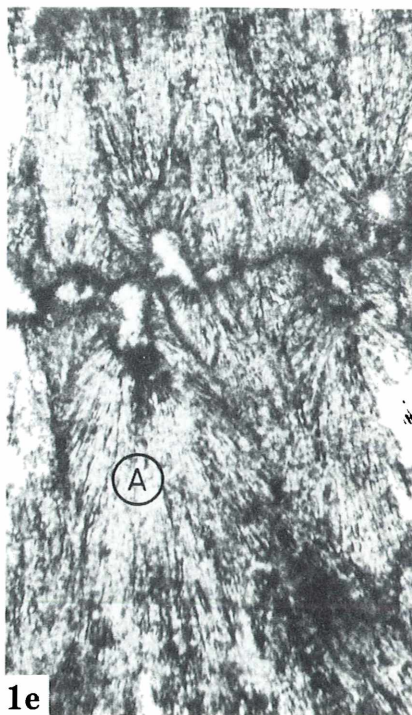
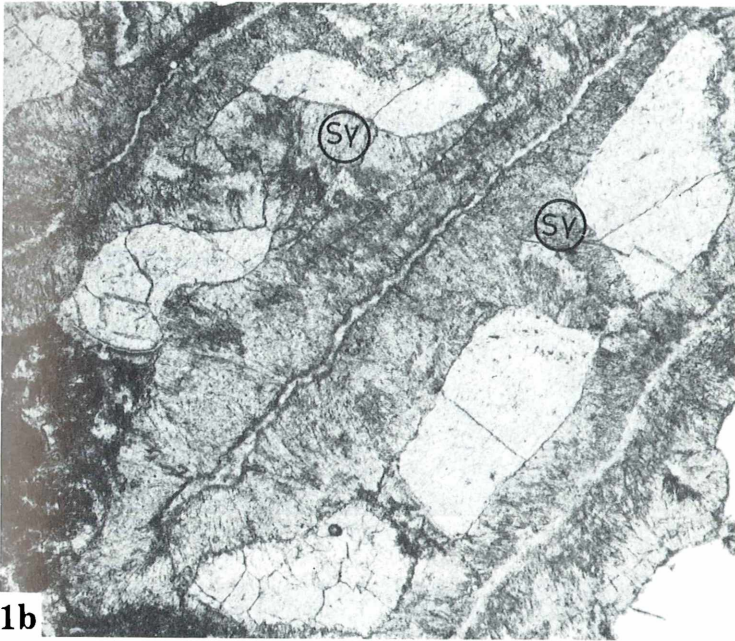
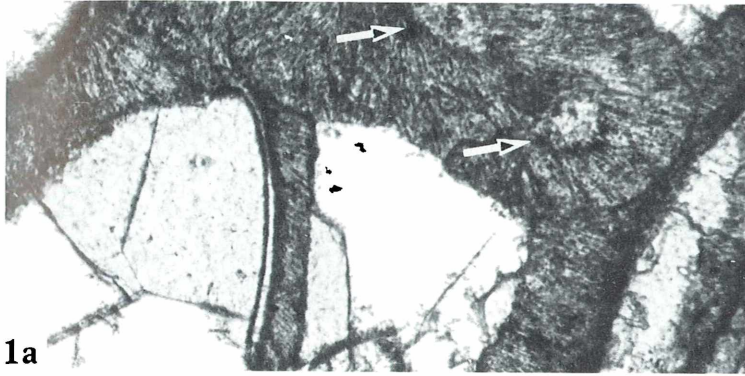


PLATE 15

Figs. 1, 2, 7: *Coryphyllia elliptica* (MELNIKOVA, 1975), p. 65

1. NHMW 1982/56/39<sub>1</sub>, 1 a – longitudinal section showing relatively large vesicular dissepiments and regularly distributed minute septal granulation, × 4, 1 b – a detail of transverse section showing lonsdaleoid S4 septum, × 20
2. NHMW 1982/56/39<sub>3</sub>, 2 a – transverse section showing skeleton in different states of preservation (opaque or transparent septa), × 2, 2 b – corallum in upper view with calicular end abraded, × 1. Note strong mechanical destruction of septa visible in figures 2 a and 2 b
7. NHMW 1982/56/39<sub>2</sub>, side view of a corallum devoid of wall, × 1

Figs. 3, 4, 6: *Oedalmia norica* (FRECH, 1890), p. 62

3. NHMW 1959/365/43, transverse section, × 4
4. GBA 1982/12/799, longitudinal section showing abundant endotheca, × 4
6. NHMW 1982/56/28, colony in calicular view, × 2

Fig. 5: ?*Molukia* sp., p. 139

GBA 1982/12/429, fragmentary corallum in side (5 a), calicular (5 b) and proximal (5 c) views, × 1

Figs. 1, 2, 6, 7: Kesselwand-Rohrmoos. Fig. 3: Schneckengraben. Figs. 4, 5: Fischerwiese



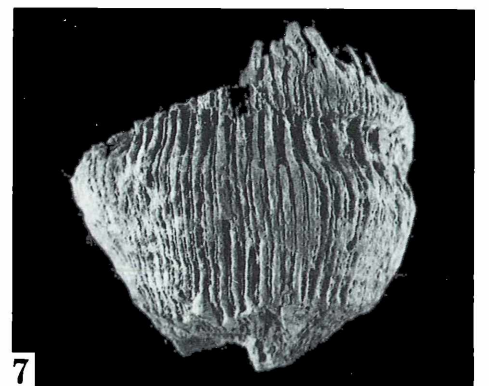
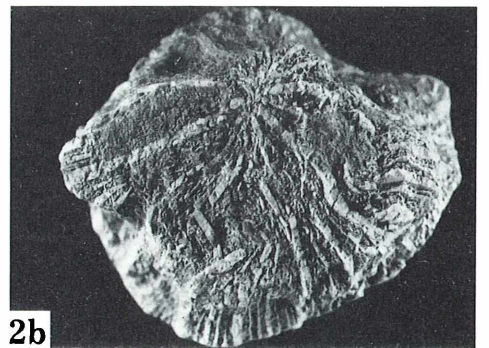
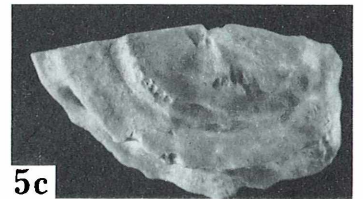
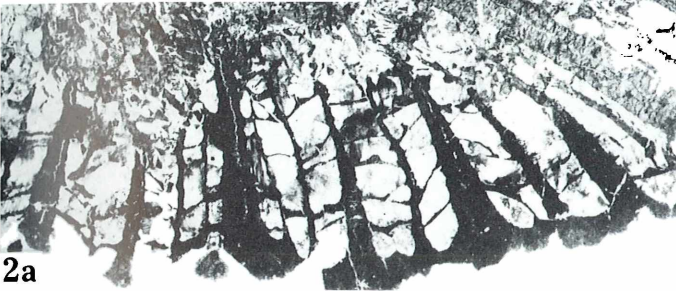
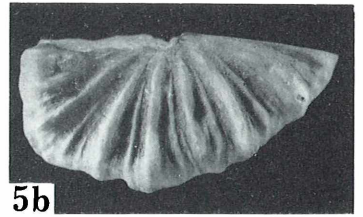
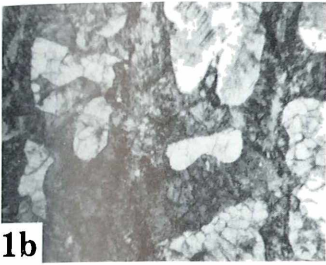
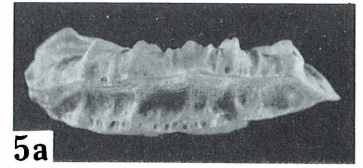
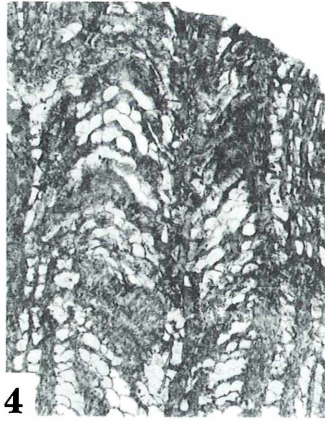
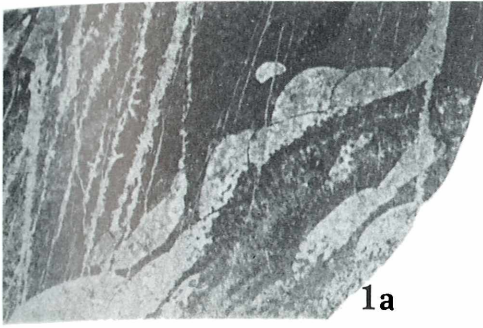


PLATE 16

Fig. 1: *Palaeastraea grandissima* (FRECH, 1890), p. 68

GPS Graz, KÜHN's collection, holotype of *P. grandistellata* KÜHN, 1936, 1 a –  $\times 1$ , 1 b –  $\times 2$ .

See also Pl. 17, figs. 2 a–d

Figs. 2–4: *Palaeastraea cyathophylloides* (FRECH, 1890), p. 67

2. GPS Graz, KÜHN's collection, original of *P. grandissima* (FRECH) in KÜHN 1936, 2 a –  $\times 1$ , 2 b –  $\times 2$
3. BSP AS XII 6, polished surface figured by FRECH 1890, Pl. 3, fig. 6 A
4. BSP AS XII 7, lectotype colony in transverse (4 a, b) and longitudinal (4 c) sections, polished surfaces figured by FRECH 1890, Pl. 3, figs. 6 B, C, 4 a and 4 c –  $\times 1$ , 4 b –  $\times 4.5$ . Note the spaces filled with sediment and only partly separating the corallites (fig. 4 b), as well as an apparent trace of a boring organism vertically penetrating the colony (fig. 4 c and Pl. 18, fig. 7).

Figs. 1, 2: Plabutsch. Figs. 3, 4: Fischerwiese



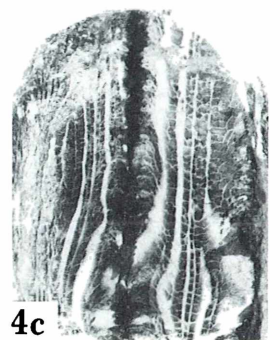
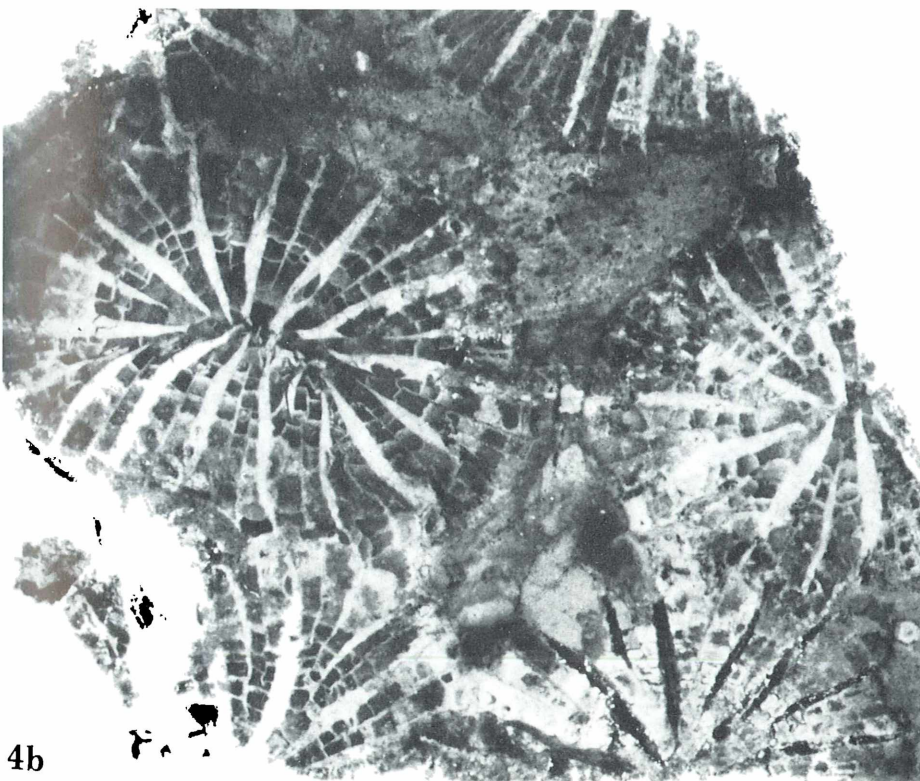
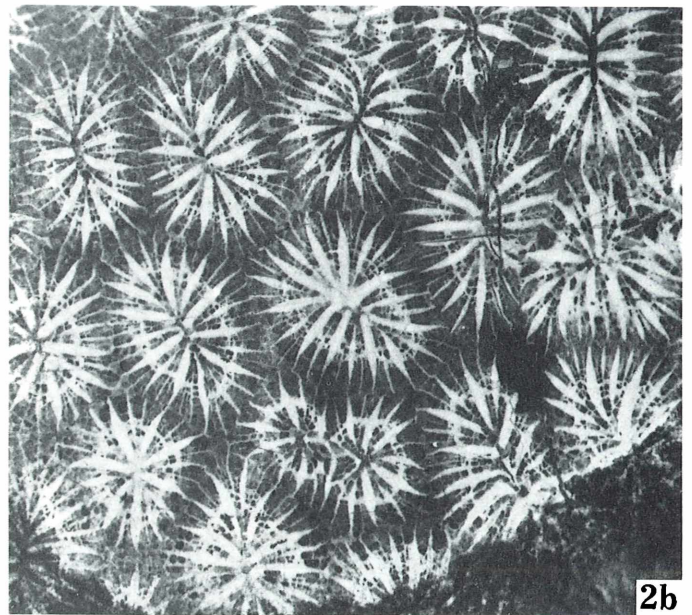
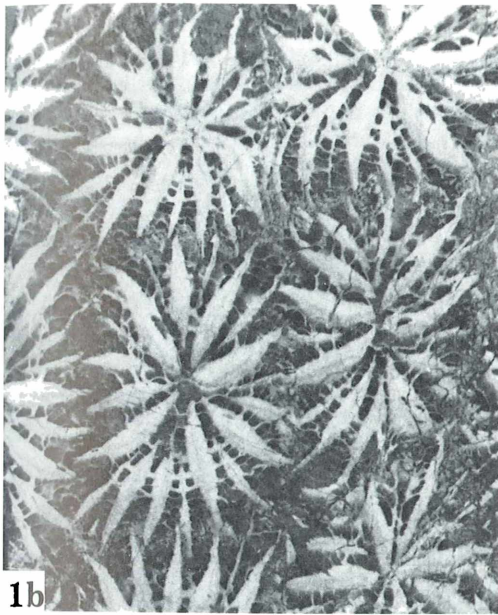
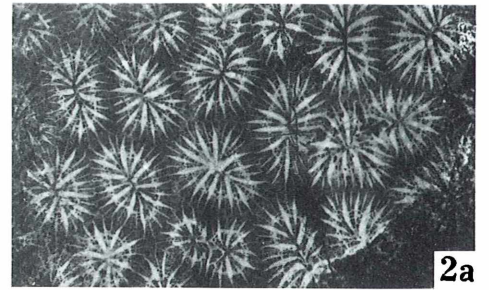


PLATE 17

Figs. 1, 2: Microstructure in the genera *Palaeastraea* and *Kuhnastraea*

1. *Kuhnastraea decussata* (REUSS, 1854), p. 72. NHMW 1959/361/2, a detail of transverse section showing peripheral portion of the costo-septum (C) differing in thickness from the rest of the blade and resembling the wall (W) in structure,  $\times 123$ .  
Another detail of the same specimen is figured in Pl. 14, fig. 3
2. *Palaeastraea grandissima* (FRECH, 1890), p. 69. GBA 1982/12/283, 2 a – transverse section showing a complex structure of the S1 and S2 septa (arrow),  $\times 3.6$ , 2 b – longitudinal section with lonsdaleoid S3 septa, as well as S1–S2 septa incorporating dissepiments (arrow),  $\times 8$ , 2 c – septum in transverse section showing a thin mid-septal zone composed of small trabeculae and a thick deposit of stereome constituting septal sides,  $\times 76$ , 2 d – a detail of fig. 2 c (encircled) showing a mid-septal row of thin trabeculae,  $\times 250$

Microstructure of other distichophylliid corals – see Pls. 6, 12–14

Fig. 1: Kesselwand-Rohrmoos. Fig. 2: Fischerwiese



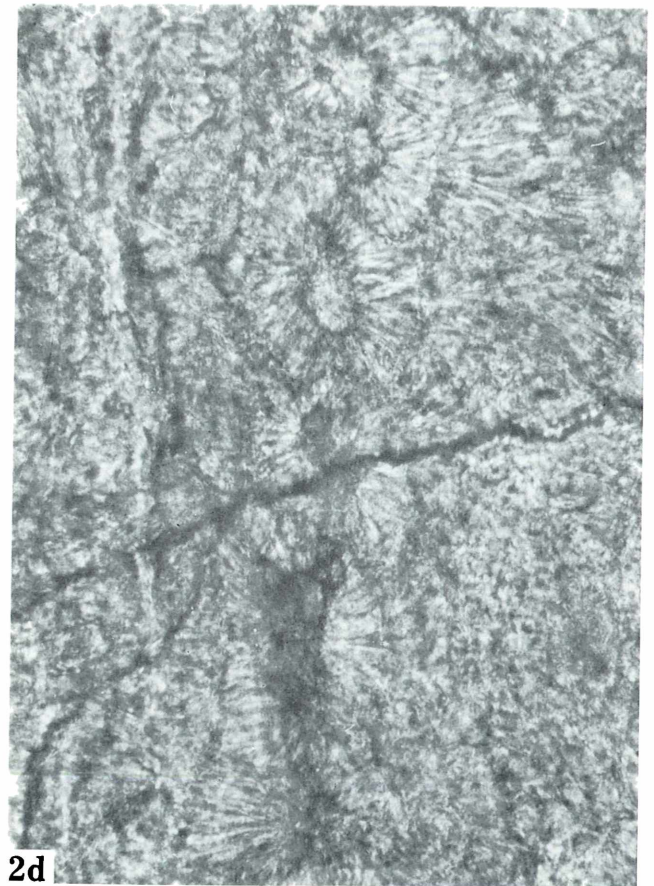
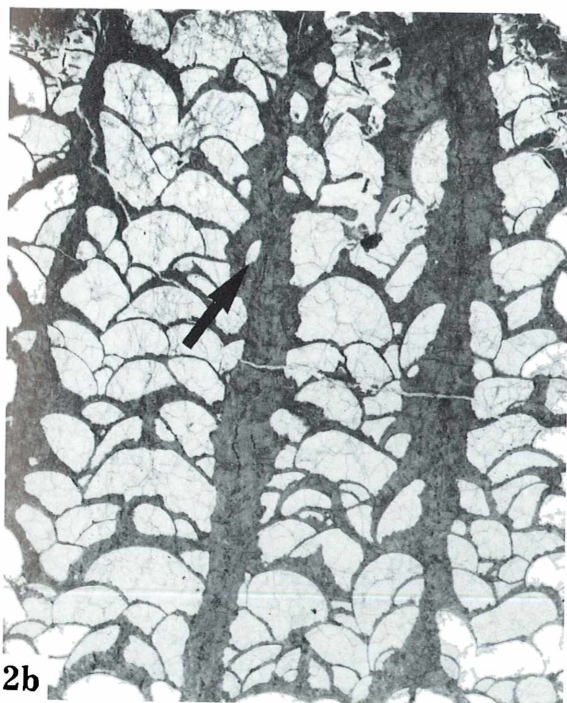
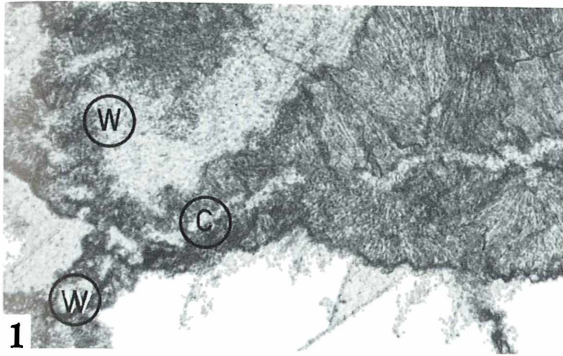


PLATE 18

Figs. 1, 2: *Kuhnastraea decussata* (REUSS, 1854), p. 71

1. GBA 1982/12/282, calicular surface with corallites developed in subphaceloid form,  $\times 2$
2. GBA 1982/12/787, neotype, 2 a – transverse section,  $\times 4$ , 2 b – longitudinal section,  $\times 4$ . Note large pericalicular dissepiments. Microstructure see Pl. 14, fig. 3 and Pl. 17, fig. 1

Figs. 3–6: *Kuhnastraea incrassata* (FRECH, 1890), p. 72

3. NHMW 1982/56/7<sub>3</sub>, colony in upper view showing elevated calices,  $\times 2$
4. GBA 1982/12/285, colony with unthickened skeleton in transverse (4 a) and longitudinal (4 b) sections, both  $\times 2$
5. GBA 1982/12/257, colony with thickened skeleton, transverse section,  $\times 4$
6. GBA 1982/12/256, colony with the alternating zones of thickened and unthickened skeleton, 6 a – transverse section,  $\times 8$ , 6 b – longitudinal section,  $\times 4$ . Note small dimensions of pericalicular and intracalicular dissepiments.

Fig. 7: *Palaeastraea cyathophylloides* (FRECH, 1890), p. 67

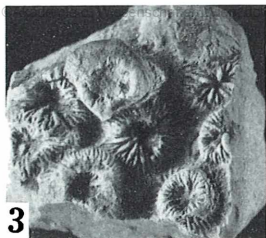
BSP AS XII 7, lectotype colony in longitudinal section, polished surface with vertical boring (arrow).

The same in Pl. 16, fig. 4 c

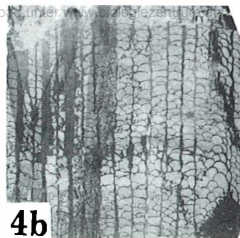
See also Pl. 16, figs. 2–4

Figs. 1, 2, 4–7: Fischerwiese. Fig. 3: Kesselwand

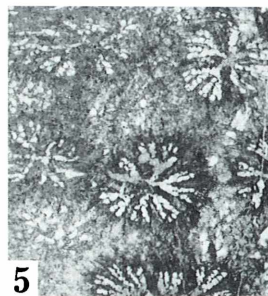




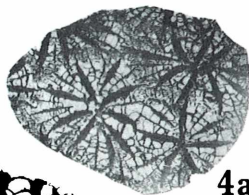
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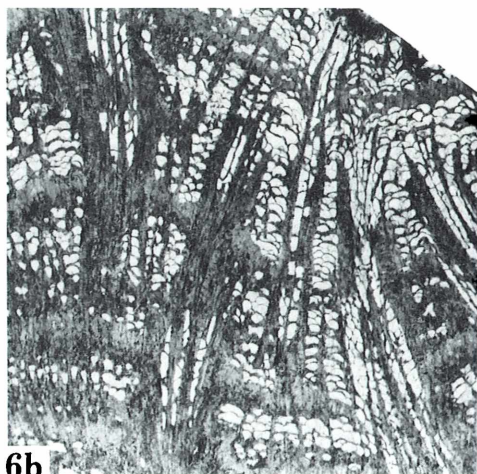
4b



5



4a



6b

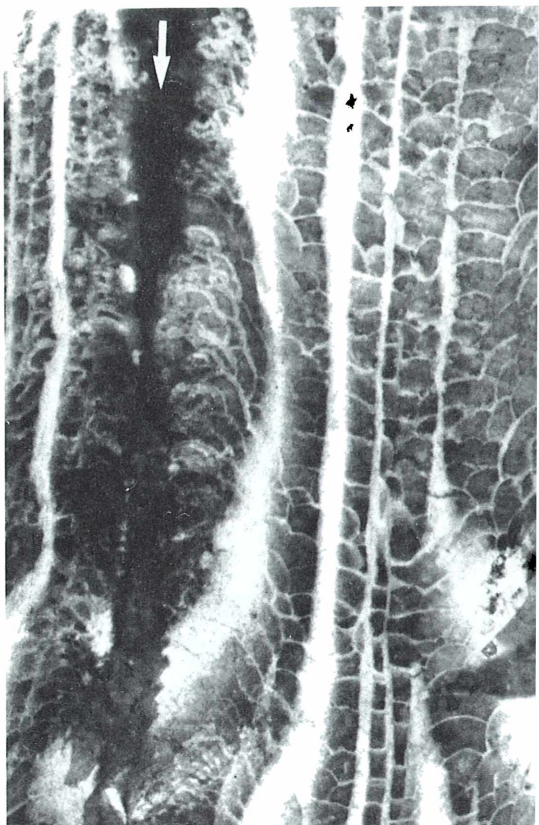
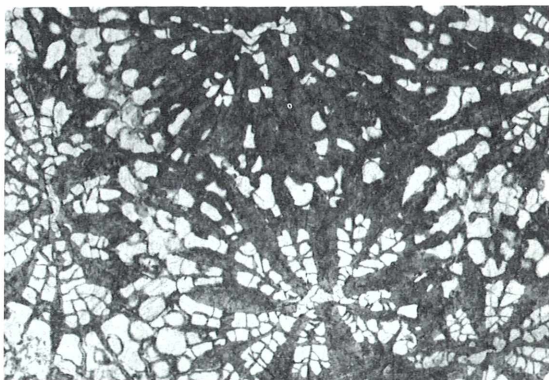
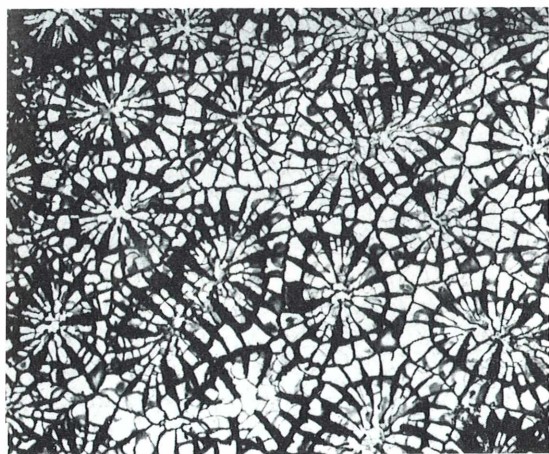


PLATE 19

Figs. 1–4: *Margarosmilia charlyana* (FRECH, 1890), p. 77

1. NHMW 1982/57/6, transverse section of corallites at the late stage of division,  $\times 8$
2. NHMW 1982/56/5, 2 a – transverse section of corallite with vestiges of microstructure visible,  $\times 20$ , 2 b – corallites at the early stage of division with characteristic pattern of septal arrangement in the region of the new wall,  $\times 8$
3. NHMW 1982/57/2, transverse section of colony with frequently dividing branches,  $\times 4$
4. NHMW 1982/57/3, 4 a – transverse section,  $\times 4$ , 4 b – longitudinal section,  $\times 8$ . Note small-dissepimental endotheca. Microstructure in Pl. 22, figs. 3, 4

Figs. 1, 3, 4: Fischerwiese. Fig. 2: Kesselwand-Rohrmoos



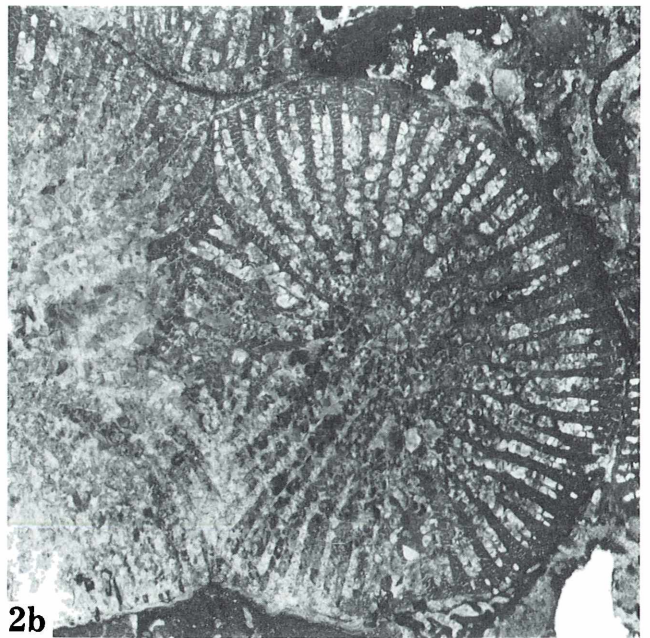
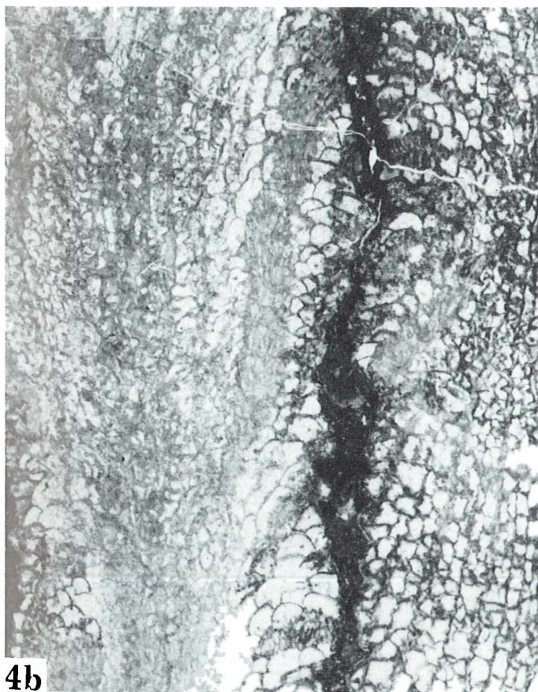
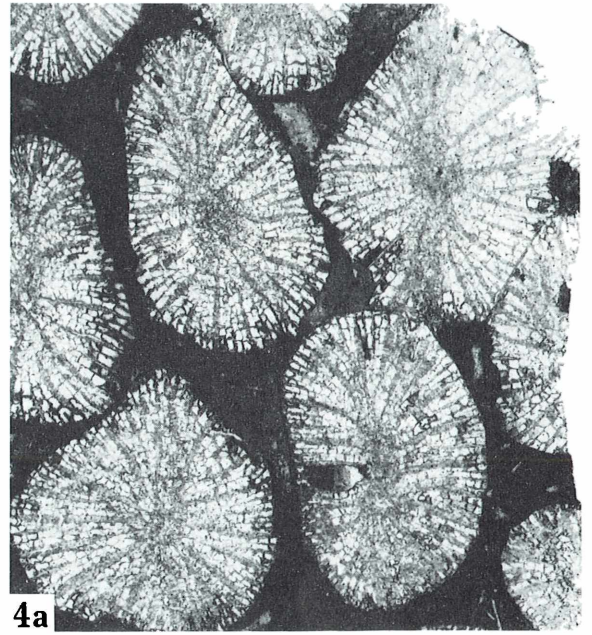
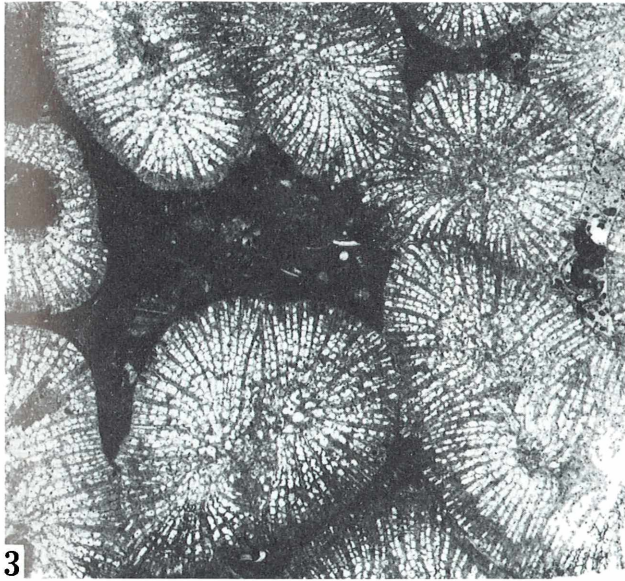
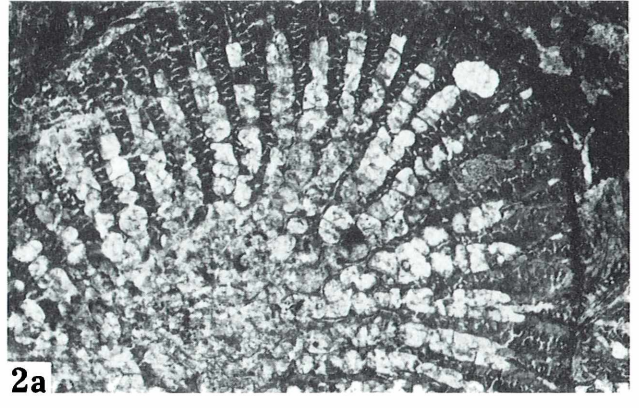
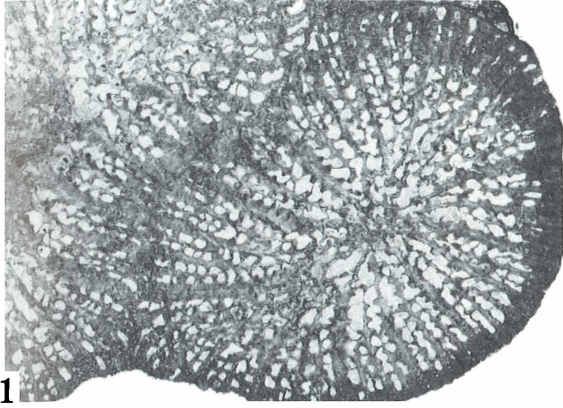




PLATE 20

Figs. 1, 6: *Distichomeandra austriaca* (FRECH, 1890), p. 79

1. GBA FRECH's type collection No. 2762, upper view of a colony of *Isastraea eucystis* FRECH (1890, Pl. 6, fig. 10), 1 a –  $\times 1$ , 1 b –  $\times 3$
6. NHMW 1982/56/24<sub>1</sub>, colony in upper view, 6 a –  $\times 1$ , 6 b –  $\times 4$   
See also Pl. 21, figs. 5, 6 and Pl. 22, figs. 1 a, b

Figs. 2–5: *Distichomeandra minor* (FRECH, 1890), p. 81

2. NHMW 1982/56/25<sub>1</sub> – colony in upper view, 2 a –  $\times 1$ , 2 b –  $\times 4$ . Note thin and numerous septa.
3. GBA FRECH's type collection, No. 2786, upper view of holotype of *Isastraea norica* var. *minor* FRECH (1890, Pl. 6, fig. 9), 3 a –  $\times 1$ , 3 b –  $\times 3$
4. NHMW 1959/365/36, transverse section, polished surface,  $\times 1$
5. NHMW 1982/56/25<sub>4</sub>, transverse section, polished surface of a colony with cerioid and phaceloid corallites,  $\times 2$   
See also Pl. 21, figs. 1, 2

Figs. 1, 2, 4–6: Kesselwand-Rohrmoos. Fig. 3: Fischerwiese

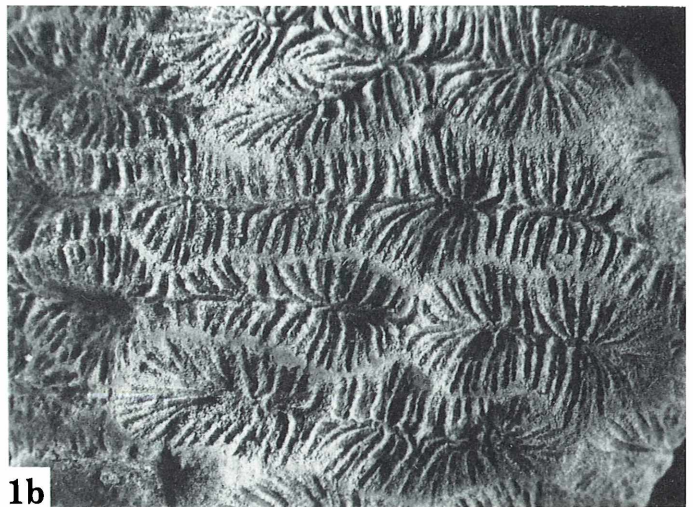
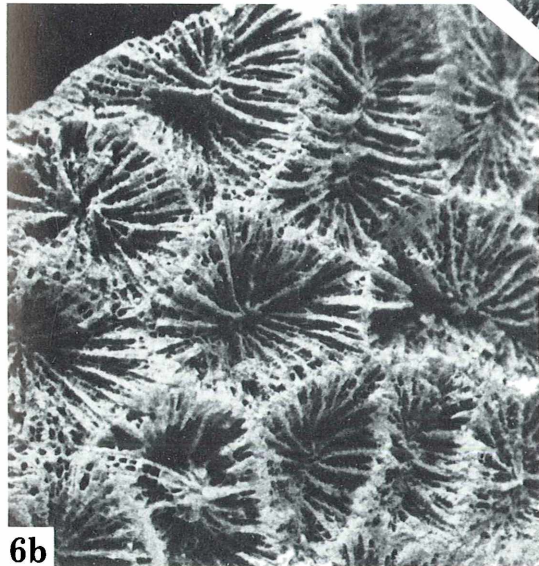
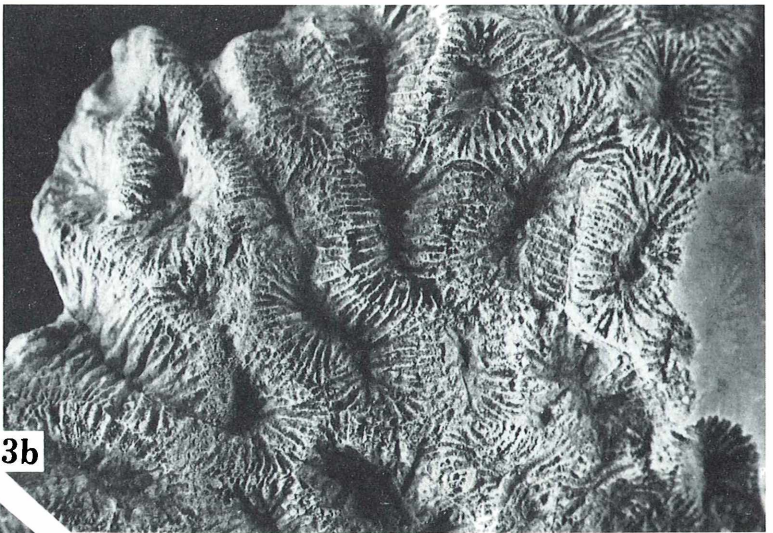
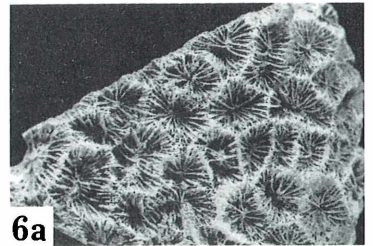
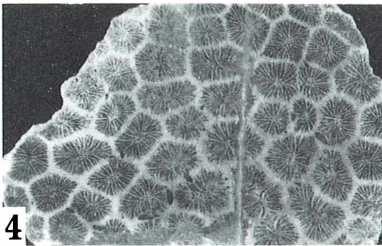
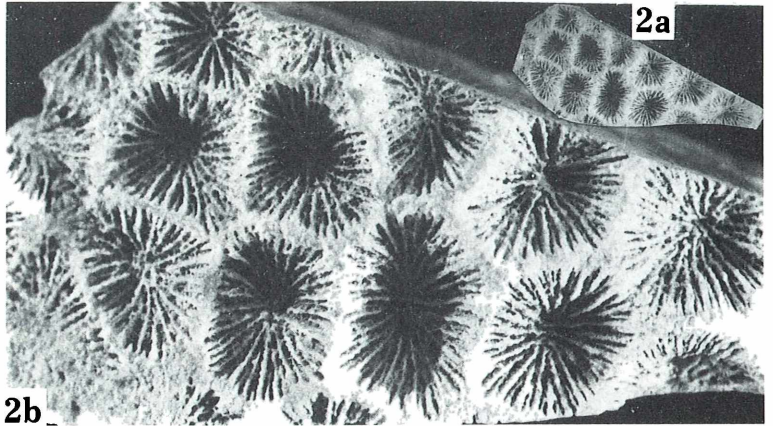
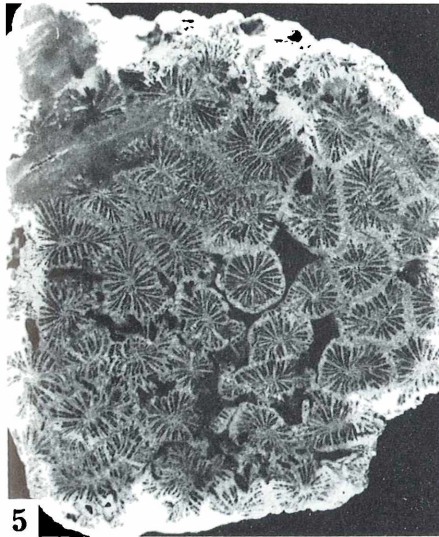
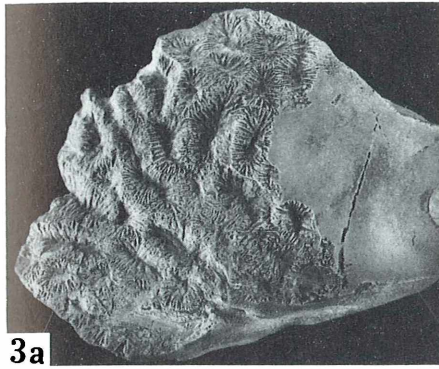
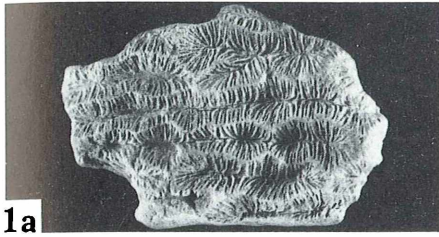


PLATE 21

Figs. 1, 2: *Distichomeandra minor* (FRECH, 1890), p. 81

1. NHMW 1982/56/25<sub>1</sub>, 1 a – transverse section,  $\times 4$ , 1 b – longitudinal section,  $\times 6$
2. NHMW 1909 XII 130, transverse section showing corallite axis filled with stereome,  $\times 2$   
See also Pl. 20, figs. 2–5

Figs. 3, 4: *Distichomeandra dieneri* (HAAS, 1909), p. 82

3. NHMW 1959/365/18<sub>1</sub>, 3 a – colony surface in upper view,  $\times 1$ , 3 b – wall region in transverse section showing septotheca built of peripheral septal edges and synapticular projections,  $\times 30$ , 3 c – longitudinal section,  $\times 4$
4. NHMW 1959/365/15, transverse section,  $\times 4.5$   
See also microstructure in Pl. 22, fig. 2

Figs. 5, 6: *Distichomeandra austriaca* (FRECH, 1890), p. 79

5. NHMW 1982/56/24<sub>1</sub>, 5 a – transverse section,  $\times 4$ , 5 b – longitudinal section,  $\times 4.5$
6. NHMW 1959/365/41, wall region in transverse section showing zigzag course of septotheca built of peripheral septal edges and synapticular projections,  $\times 52$   
See also Pl. 20, figs. 1, 6 and Pl. 22, figs. 1 a, b

Figs. 1–6: Kesselwand-Rohrmoos



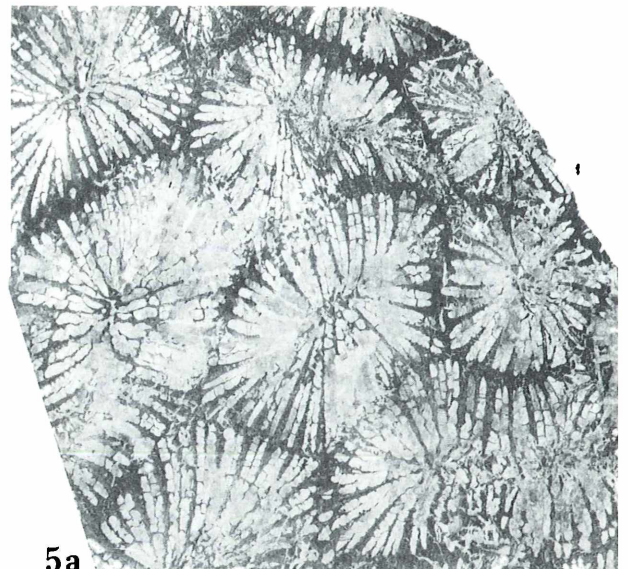
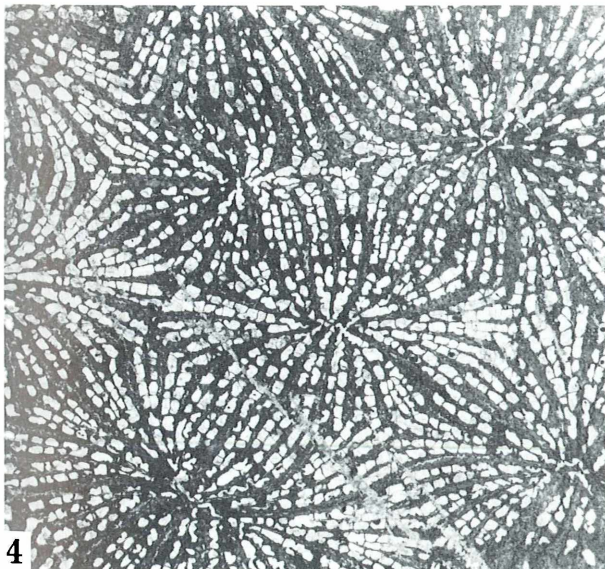
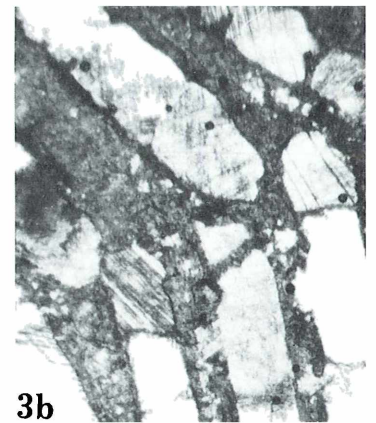
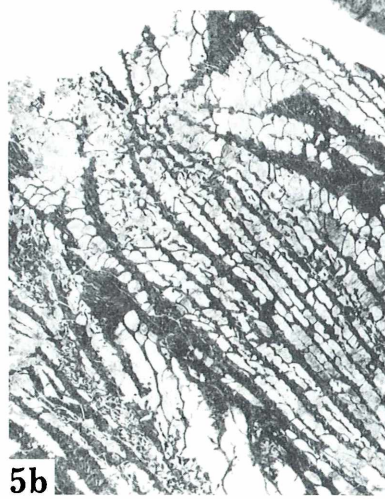
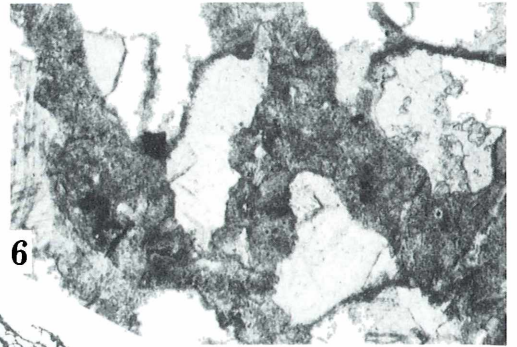
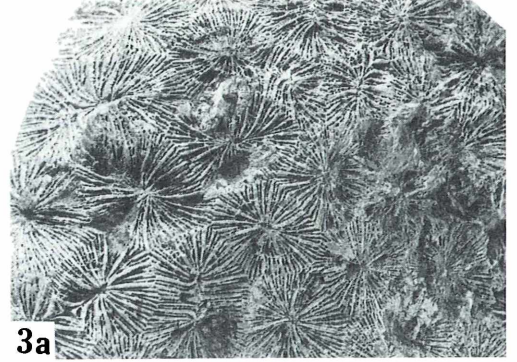
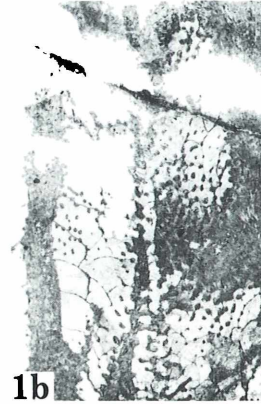
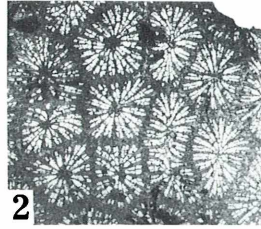
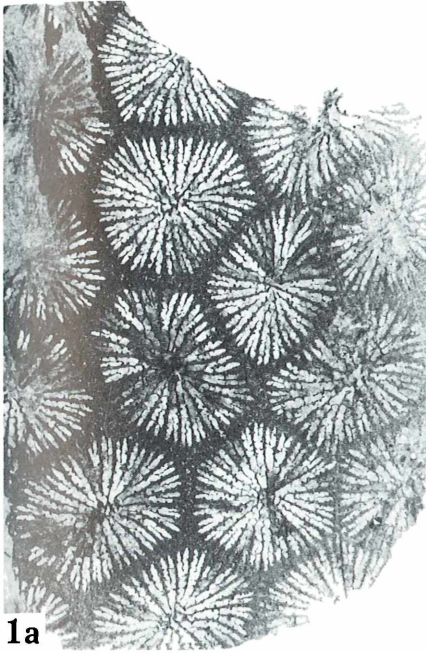


PLATE 22

Figs. 1–4: Margarophylliid microstructures, p. 76 and pages enumerated below

1. *Distichomeandra austriaca* (FRECH, 1890), p. 80. NHMW 1982/56/24<sub>1</sub>, 1 a – longitudinal broken section showing granular ornamentation of septa,  $\times 10$ , 1 b – transverse section showing trabeculae (arrows) giving symmetrical lateral axes (A),  $\times 195$
2. *Distichomeandra dieneri* (HAAS, 1909), p. 83. NHMW 1959/365/15, tangential section of septum showing alternately arranged lateral septal trabecular axes (arrow),  $\times 76$
- 3, 4. *Margarosmia charlyana* (FRECH, 1890), p. 78. NHMW 1982/57/3 and NHMW 1982/56/5, transverse section showing lateral axes (A) arranged asymmetrically in relation to the main trabeculae of the mid-septal zone, fig. 3 –  $\times 120$ , fig. 4 a, b –  $\times 185$ . Note recrystallization of trabecular axes. Main trabeculae indicated by arrows.

Figs. 1, 2, 4: Kesselwand-Rohrmoos. Fig. 3: Fischerwiese



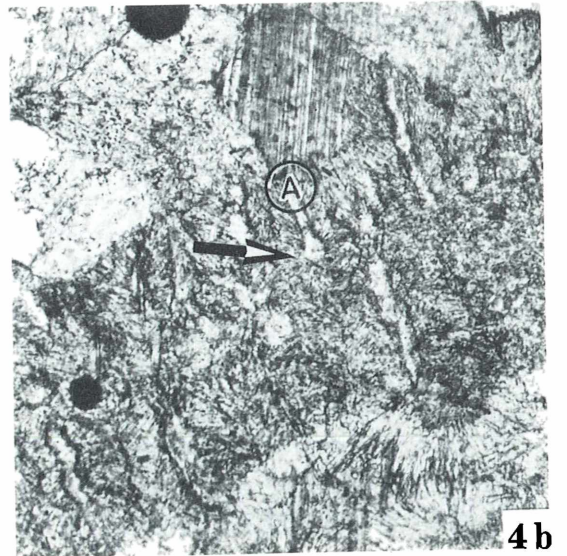
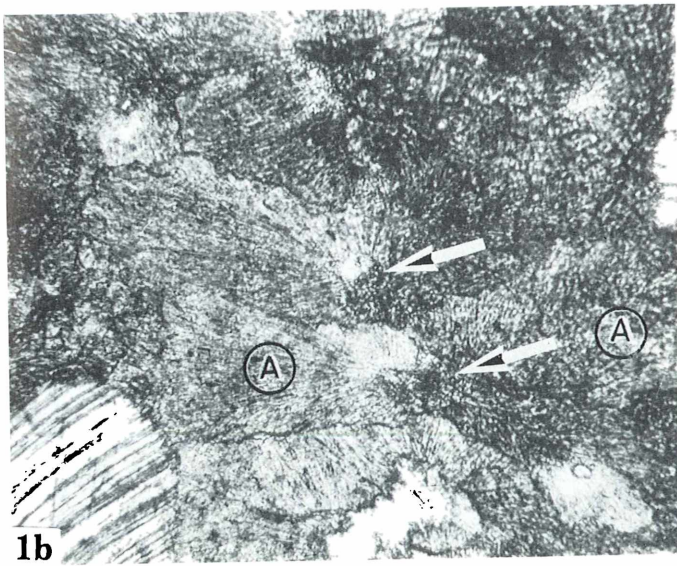
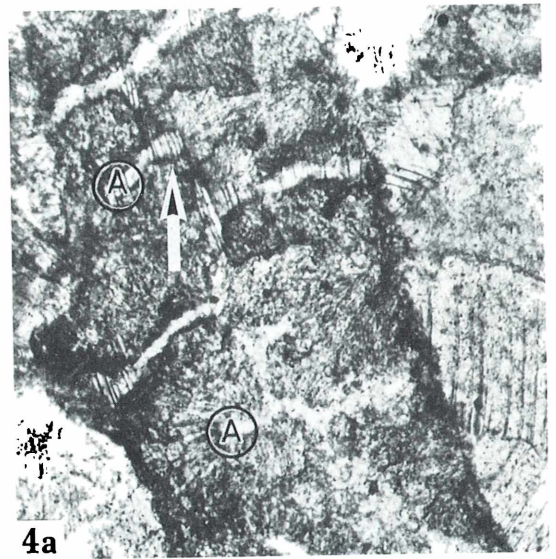
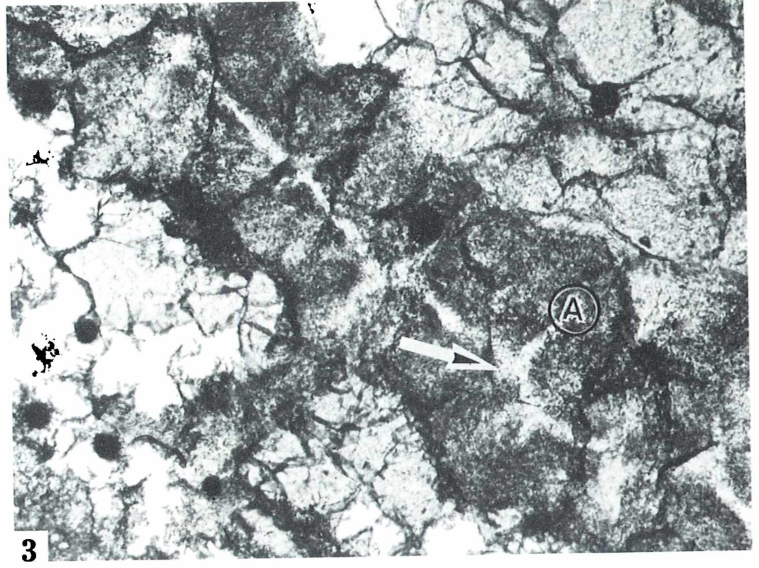
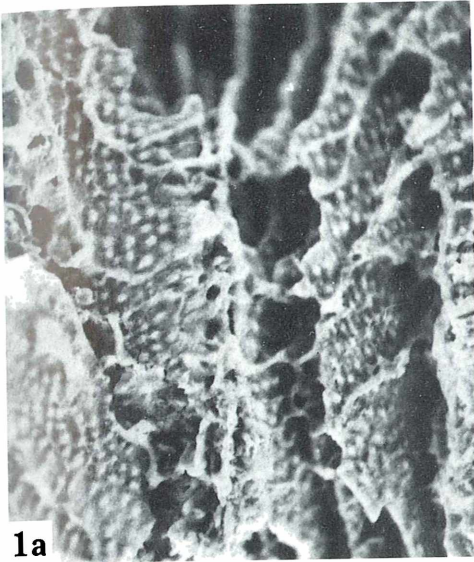




PLATE 23

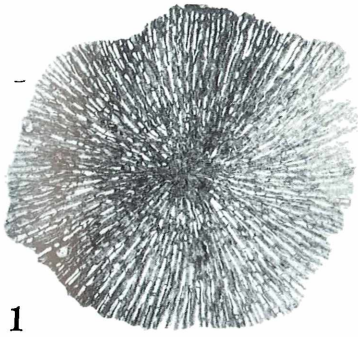
Figs. 1–3: *Procyclolites triadicus* FRECH, 1890, p. 85

1. GBA 1982/12/168, transverse section of abraded specimen,  $\times 2$
2. GBA 1982/12/223, longitudinal radial section showing long menianes and vesicular dissepiments,  $\times 8$
3. GBA 1982/12/224, longitudinal section perpendicular to the septal blades,  $\times 8$   
Microstructure in Pl. 24, figs. 1 and 2

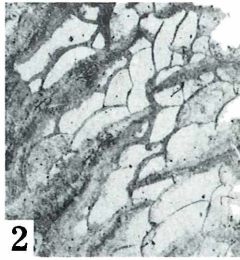
Fig. 4: *Cuifastraea arthaberi* (HAAS, 1909), p. 92

GBA 1982/12/230, 4 a – transverse section,  $\times 4$ , 4 b – a detail with the meniane distally ornamented with small granules,  $\times 76$ , 4 c – the same meniane,  $\times 195$ , 4 d – transverse section cutting the septum at the meniane level and showing densely spaced trabeculae expanding laterally to form a meniane,  $\times 195$ , 4 e – longitudinal section,  $\times 4$ , 4 f – longitudinal section cutting the septum along the mid-line and showing trabecular axes,  $\times 195$

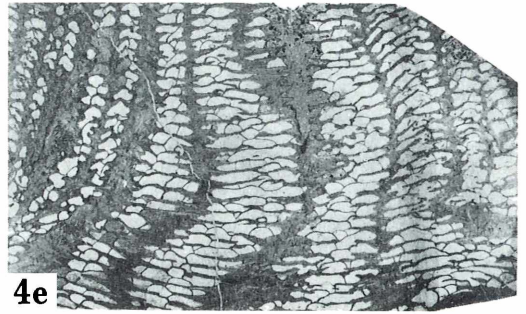
Figs. 1–4: Fischerwiese



1



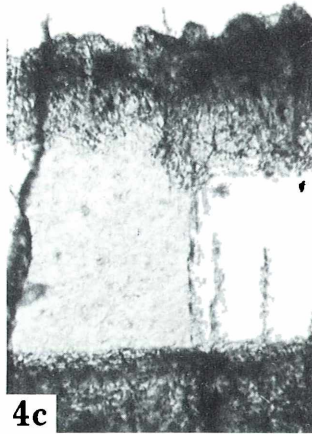
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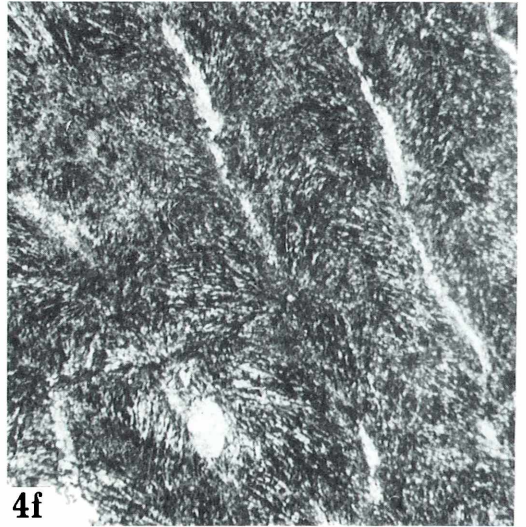
4e



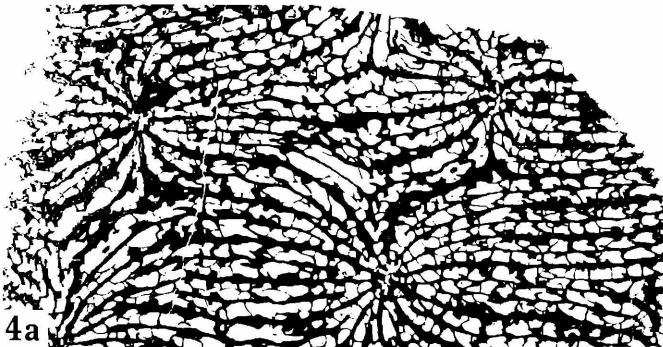
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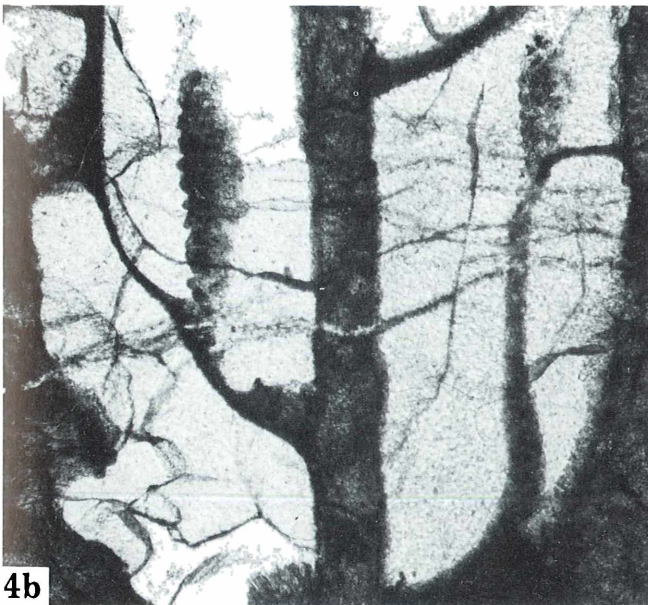
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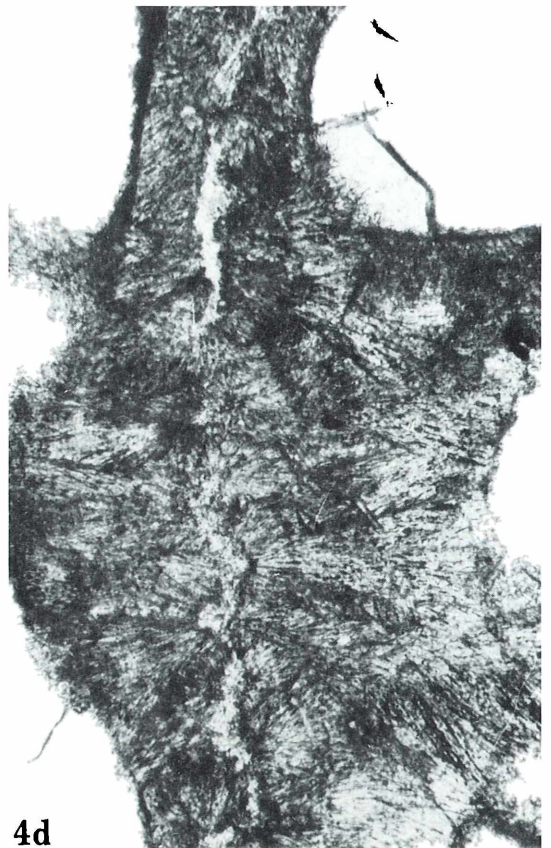
4f



4a



4b



4d

PLATE 24

Figs. 1, 2: Microstructure of *Procycolites triadicus* FRECH, 1890, p. 86

1. GBA 1982/12/216, 1 a – transverse section showing wavy and zigzag mid-septal zones and sections of menianes,  $\times 76$ , 1 b – a detail of the median septal zone (encircled in fig. 1 c) showing trabecular organization of skeleton,  $\times 250$ , 1 c – the same fragment showing laterally extended trabeculae forming a meniane plate (to the left),  $\times 195$ , 1 d – transverse section cutting the septum at the level of meniane plate, note the arrangement of opaque fibre fascicles (arrow) at the distal meniane edge (right),  $\times 195$
2. GBA 1981/12/224, 2 a – oblique section perpendicular to the septal blade showing fibrous structure of well individualized median septal zone and lateral stereome organized into incipient fascicles,  $\times 195$ , 2 b – irregular microornamentation of septal surface produced by protruding tops of fibre fascicles,  $\times 250$

Figs. 1, 2: Fischerwiese



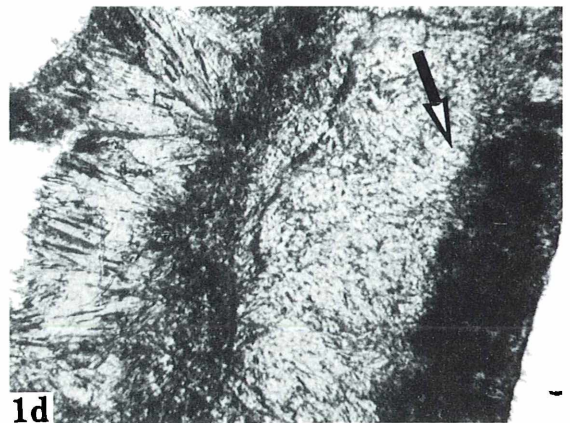
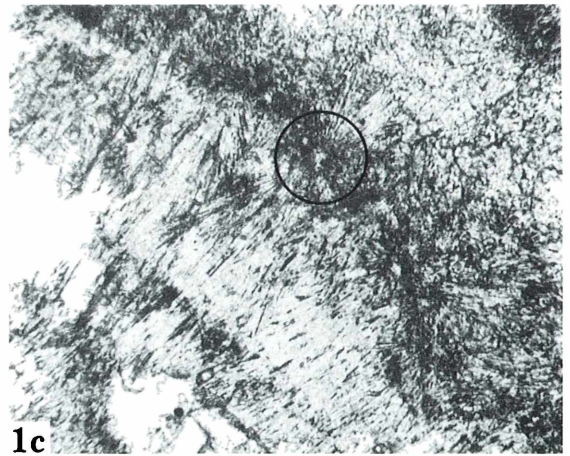
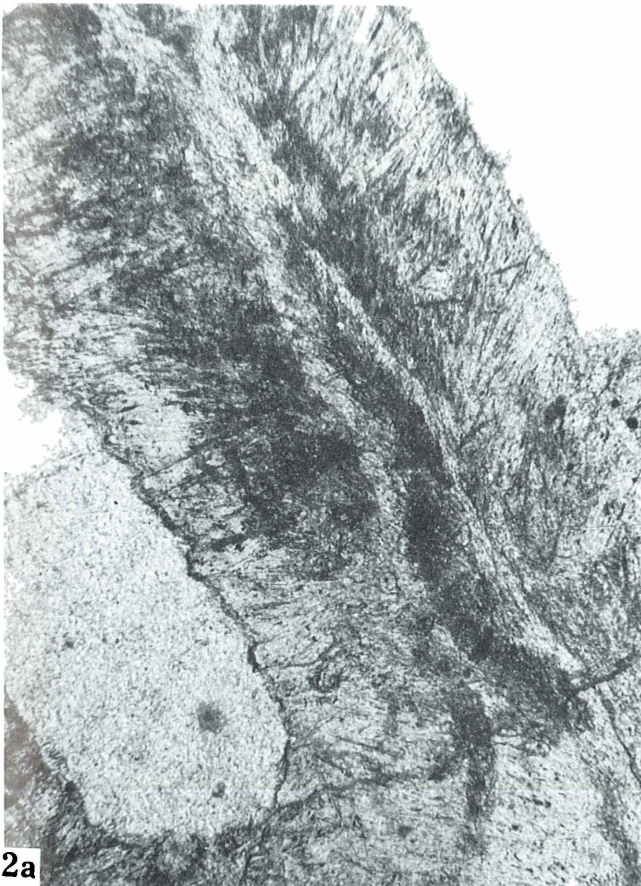
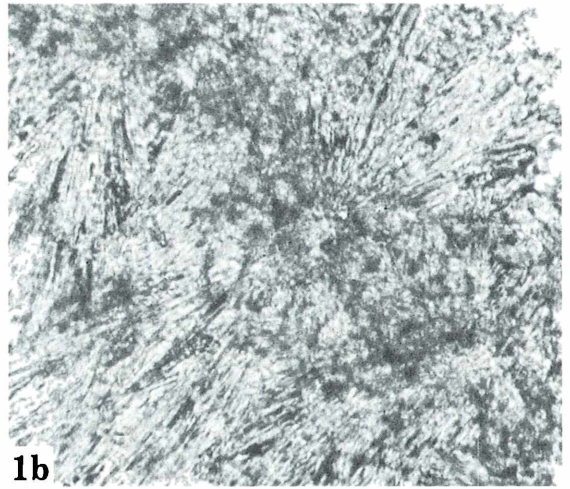
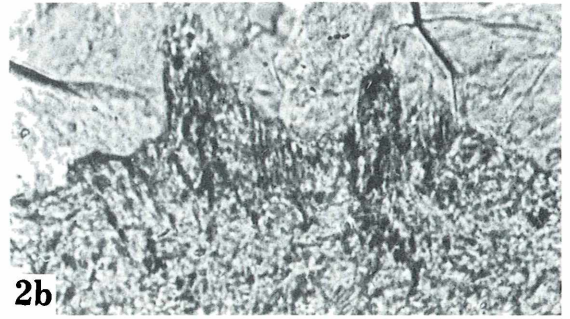
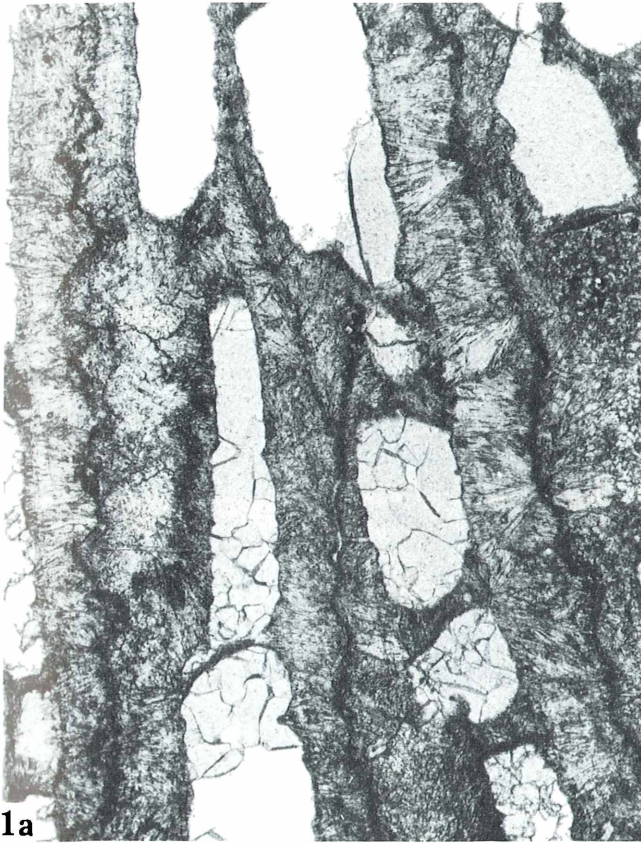


PLATE 25

Figs. 1–3: *Alpinophyllia flexuosa* gen. et sp. n., p. 87

1. NHMW 1982/56/21<sub>1</sub>, holotype, 1 a – transverse section, polished surface,  $\times 1$ , 1 b – longitudinal thin section,  $\times 4.3$ , 1 c – transverse thin section,  $\times 3$
2. NHMW 1982/56/21<sub>2</sub>, paratype, 2 a – a detail of the wall in transverse section showing a synapticular connection of septa,  $\times 84$ , 2 b – transverse section showing a wall built of alternating septa and their synapticular projections,  $\times 52$ , 2 c – septum in transverse section showing arrangement of trabeculae,  $\times 84$ , 2 d – calicular view of the paratype colony,  $\times 1$
3. NHMW 1959/365/58, longitudinal section showing short menianes,  $\times 8$   
See also Pl. 26, figs. 1 and 2

Figs. 4–6: *Stuoresimorpha norica* (FRECH, 1890), p. 89

4. NHMW 1959/361/1, neotype, longitudinal section,  $\times 8$ . See transverse section in Pl. 27, fig. 2
5. NHMW 1982/56/38<sub>3</sub>, transverse section of a colony, polished surface,  $\times 1$
6. NHMW 1982/56/38<sub>1</sub>, calicular colony view,  $\times 1$

Figs. 1–4, 6: Kesselwand-Rohrmoos. Fig. 5: Schneckengraben



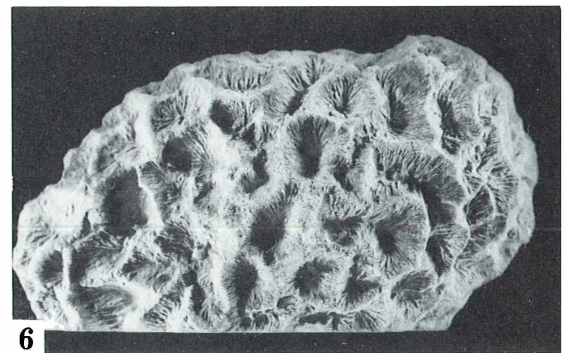
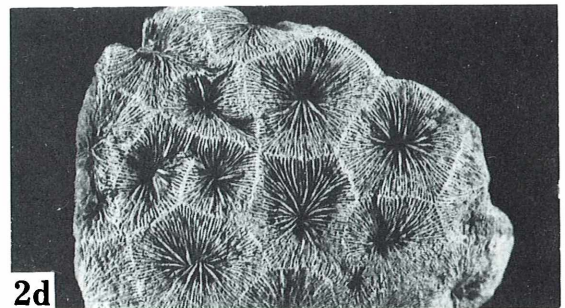
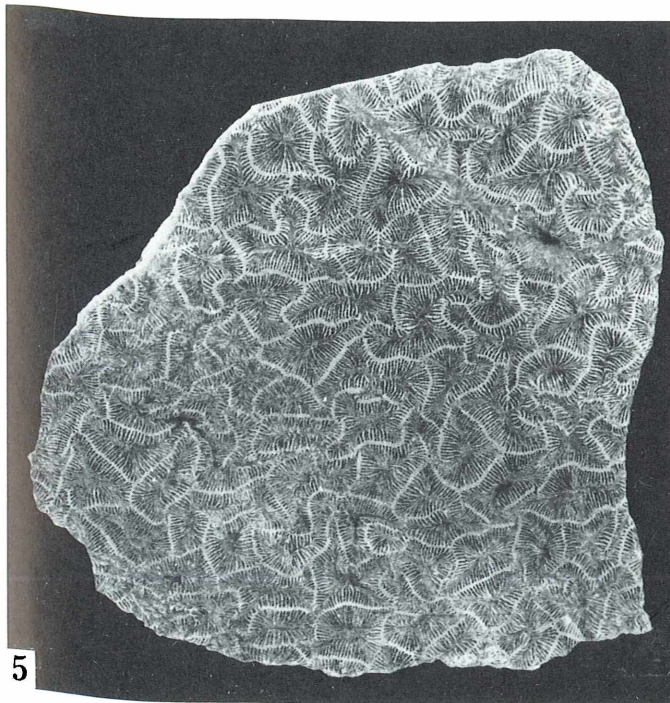
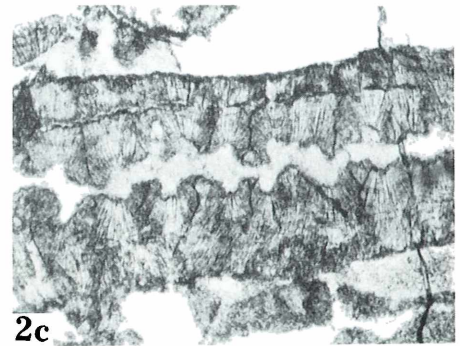
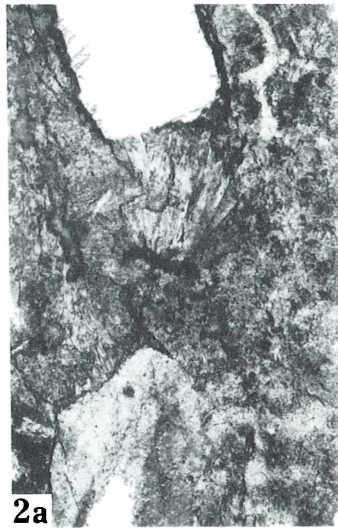
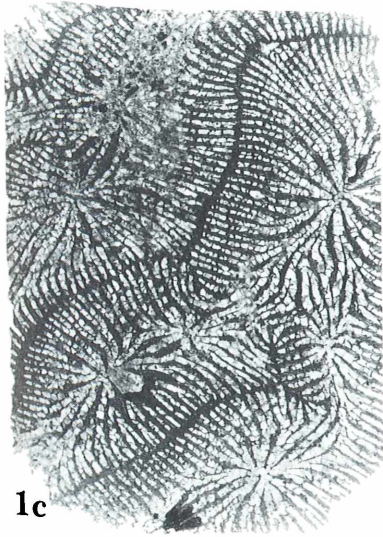
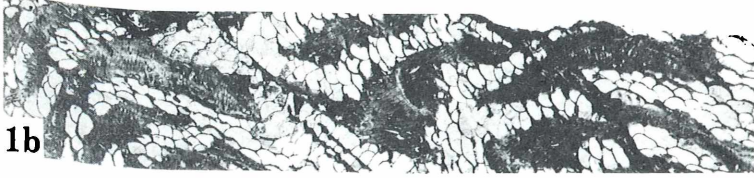
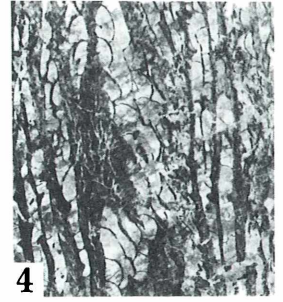
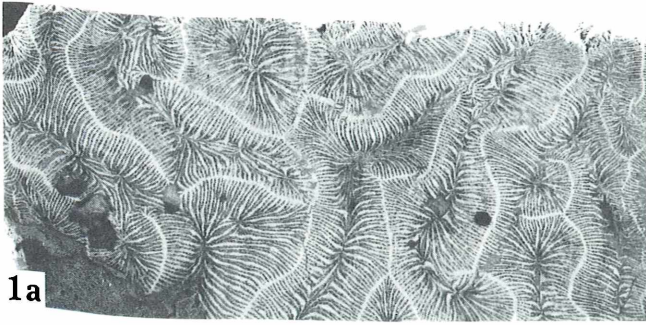




PLATE 26

Figs. 1, 2: Microstructure of *Alpinophyllia flexuosa* gen. et sp. n., p. 88

1. NHMW 1982/56/21, holotype, 1 a – septum in tangential section cutting proximal meniane part and showing well distinguishable lateral trabecular axes,  $\times 123$ , 1 b – transverse section showing trabecular lateral axes forming meniane plate,  $\times 123$ , 1 c – longitudinal radial section showing menianes and dissepiments,  $\times 76$ , 1 d – longitudinal section perpendicular to septal blades, showing axiferous menianes and some dissepiments in the interseptal space,  $\times 76$
2. NHMW 1959/365/58, 2 a – transverse section of septum built of poorly individualised trabeculae resembling in their zigzag arrangement those of the distichophylliid mid-septal zone,  $\times 123$ , 2 b – transverse section showing densely spaced trabeculae extending laterally to produce a short meniane,  $\times 123$ , 2 c – transverse section showing corallite wall region with alternating septa of the neighbouring corallites,  $\times 76$

Figs. 1, 2: Kesselwand-Rohrmoos

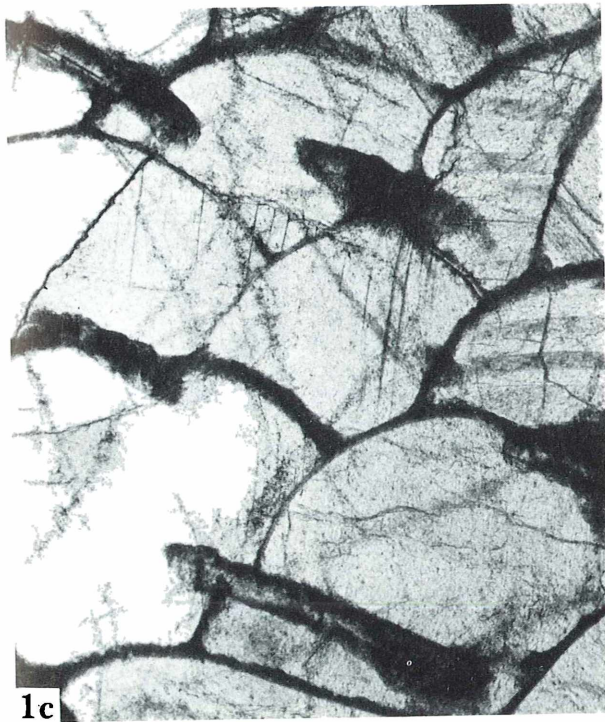
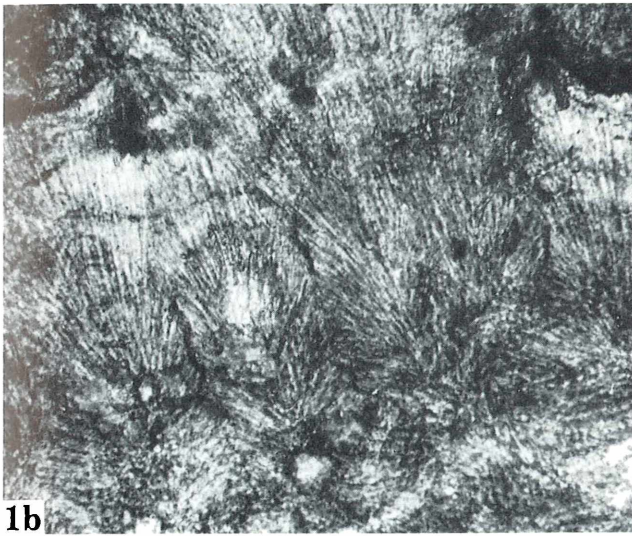
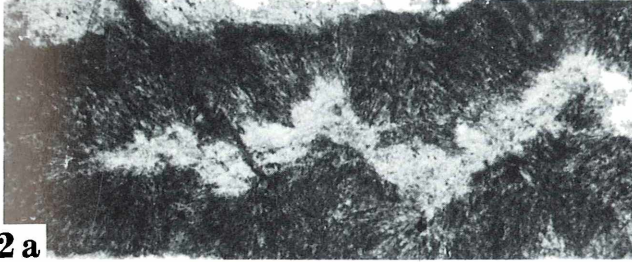
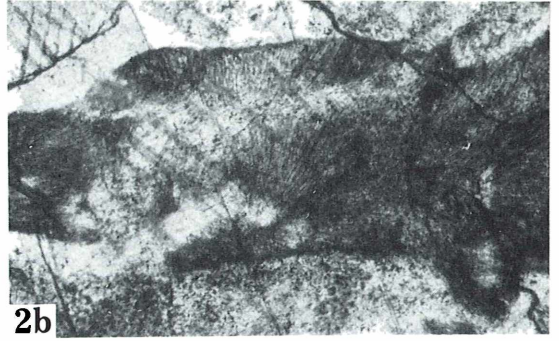
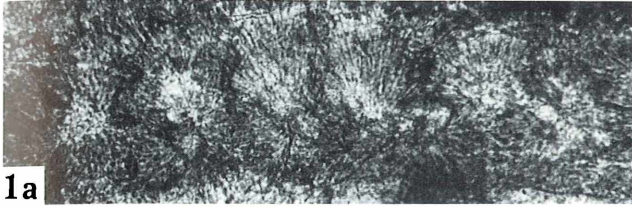


PLATE 27

Fig. 1: *Alpinoseris dendroidea* gen. et sp. n., p. 91

GBA 1982/12/806, holotype, 1 a – transverse section, polished surface,  $\times 1$ , 1 b – longitudinal section, polished surface,  $\times 1$ , 1 c – longitudinal thin section showing menianes and dissepiments,  $\times 4$ , 1 d – transverse thin section, note a branch at the stage of budding,  $\times 4$ , 1 e – menianes and dissepiments in longitudinal radial section,  $\times 20$ , 1 f – longitudinal section perpendicular to septal blades, note meniane edges directed upwards,  $\times 20$ , 1 g – a fragment of fig. 1 f showing coalesced menianes of two opposite septa,  $\times 84$ , 1 h – septum in longitudinal radial section showing fanwise arrangement of trabeculae,  $\times 20$

Fig. 2: *Stuoresimorpha norica* (FRECH, 1890), p. 89

NHMW 1959/361/1, neotype, transverse section,  $\times 4$ . Longitudinal section on Pl. 25, fig. 4

Fig. 1: Schneckengraben. Fig. 2: Kesselwand-Rohrmoos



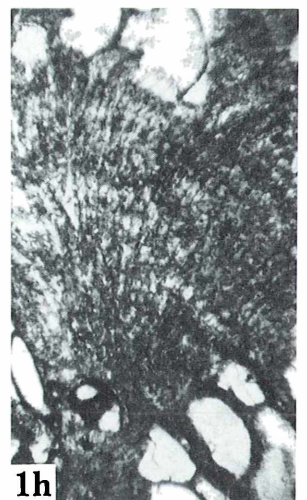
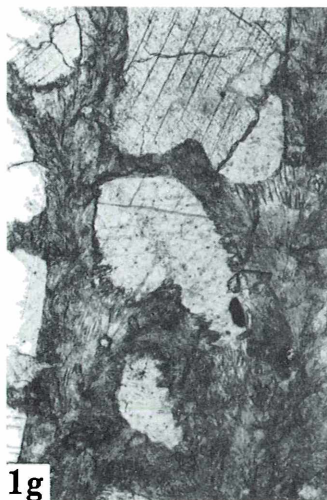
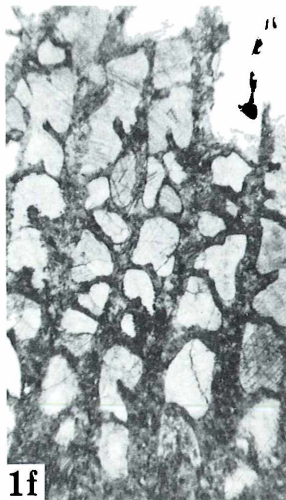
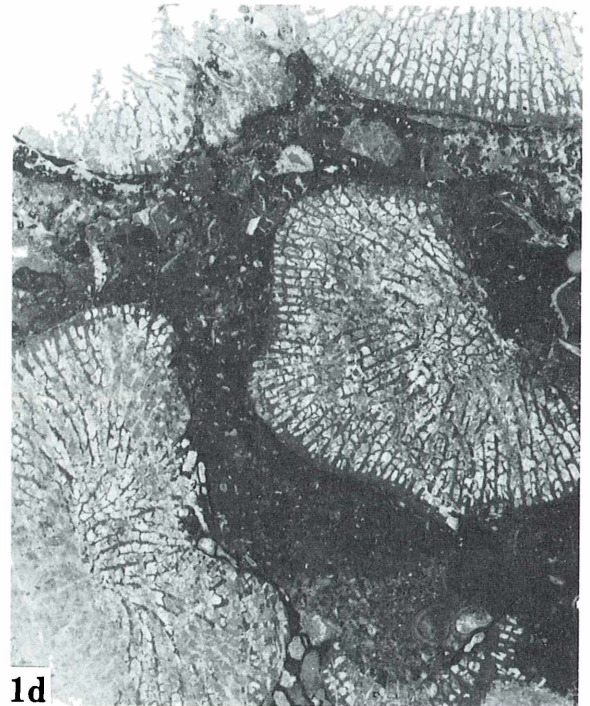
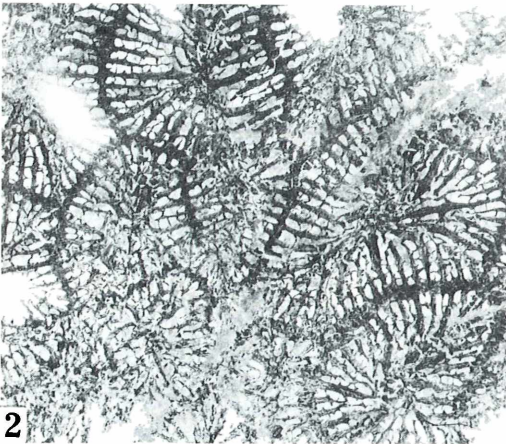
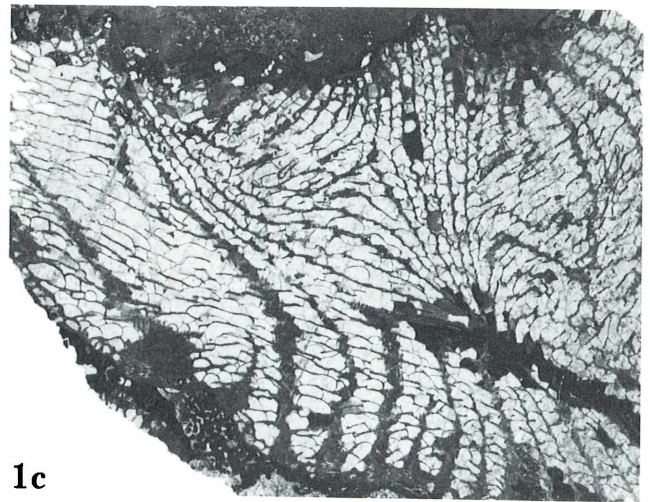
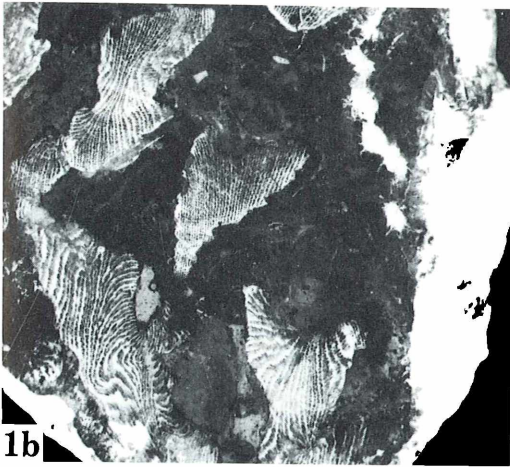
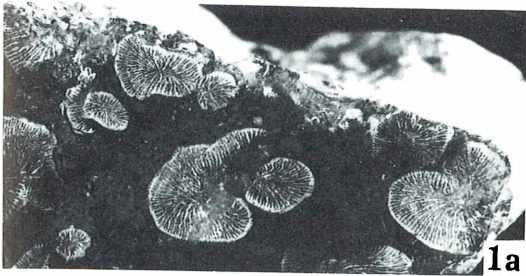


PLATE 28

Figs. 1, 2: *Astraeomorpha confusa* (WINKLER, 1861), p. 96

1. GBA 1982/12/416, colony in upper view, note large pericalicular spaces,  $\times 4$
2. NHMW 1982/56/20, longitudinal section showing axiferous menianes, synapticalae (encircled) and stereome nearly completely filling the interseptal space except rare pores (arrow),  $\times 76$  (continued in Pl. 29, figs. 1 a–d).

See also Pl. 29, figs. 1–3

Figs. 3–5: *Astraeomorpha crassisepta* REUSS, 1854, p. 94

3. GBA 1982/12/426, transverse section showing densely spaced corallites,  $\times 8$
4. NHMW 1982/57/99, longitudinal section of septum showing fanwise arrangement of thin trabeculae,  $\times 195$
5. NHMW 1982/56/37<sub>2</sub>, neotype, longitudinal broken section of colony showing thick menianes and vertical rows of relatively thin synapticalae (arrow),  $\times 8$

Figs. 1, 3, 4: Fischerwiese. Figs. 2, 5: Kesselwand-Rohrmoos



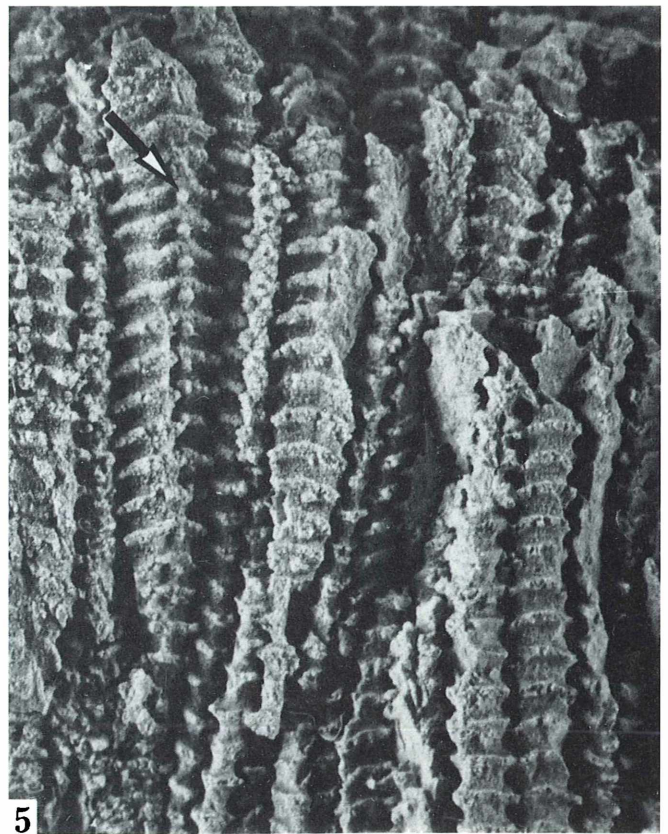
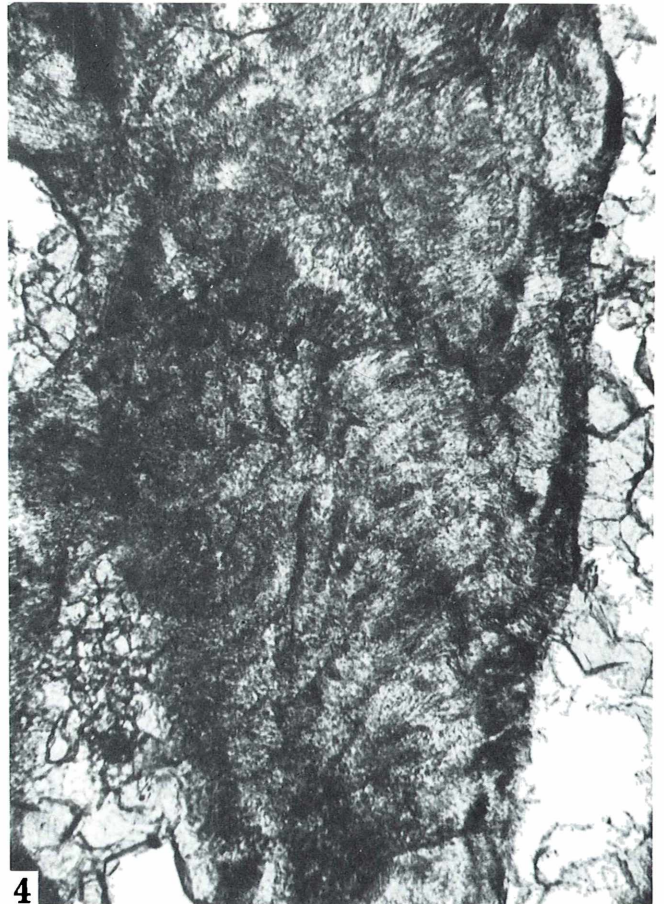
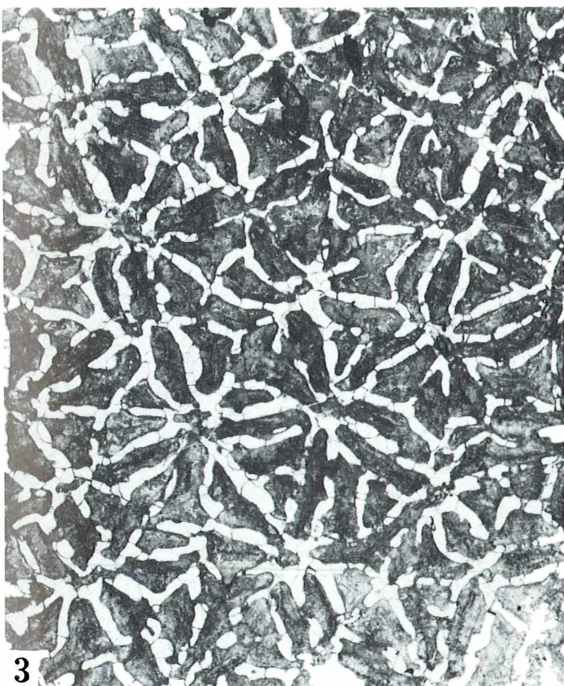
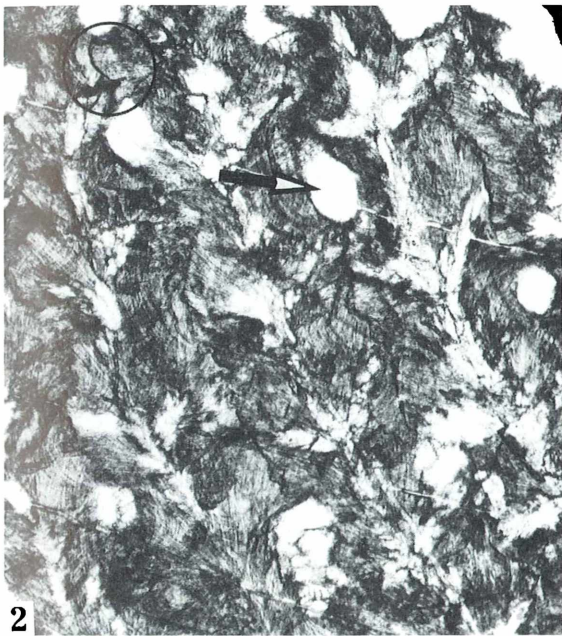
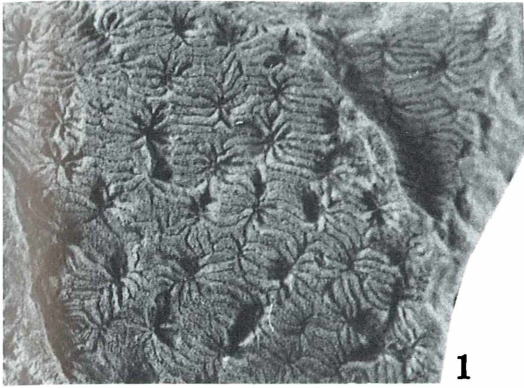




PLATE 29

Figs. 1–3: Microstructure of *Astraeomorpha confusa* (WINKLER, 1861) (continued), p. 97

1. NHMW 1982/56/20, 1 a – meniane in longitudinal section,  $\times 250$ , note the course of fibres and the accretionary layers of stereome, 1 b – transverse section of septum (a fragment of fig. 1 d) with undifferentiated trabeculae,  $\times 195$ , 1 c – transverse section of septa (a fragment of fig. 1 d) with well differentiated trabeculae, the section cuts the septa at the meniane level, 1 d – corallite in transverse section,  $\times 76$
2. GBA 1982/12/415, slightly abraded calicular colony surface with numerous synapticulae in the pericalicular region,  $\times 4$
3. GBA 1982/12/426, transverse section of septum showing well differentiated trabeculae,  $\times 250$   
See also Pl. 28, figs. 1 and 2

Fig. 1: Kesselwand-Rohrmoos. Figs. 2–3: Fischerwiese

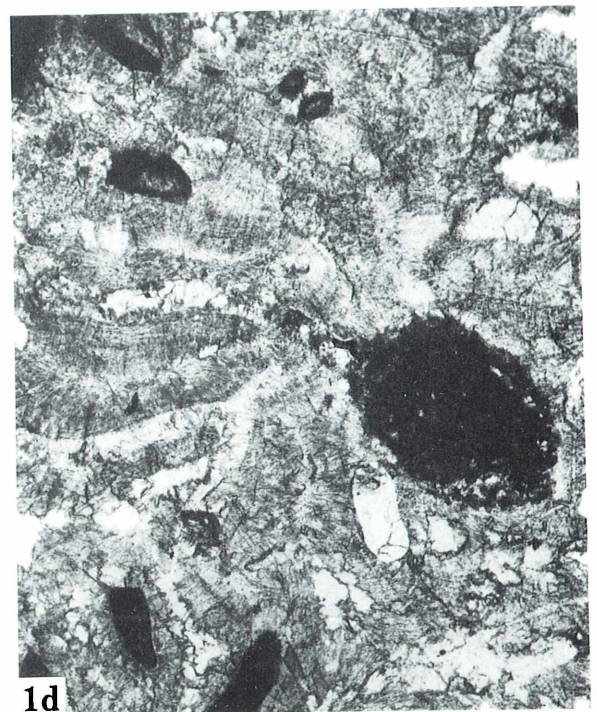
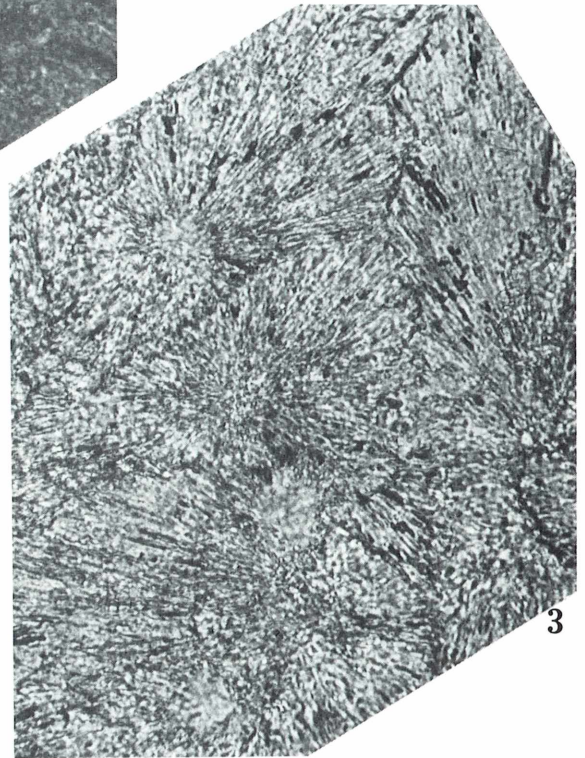
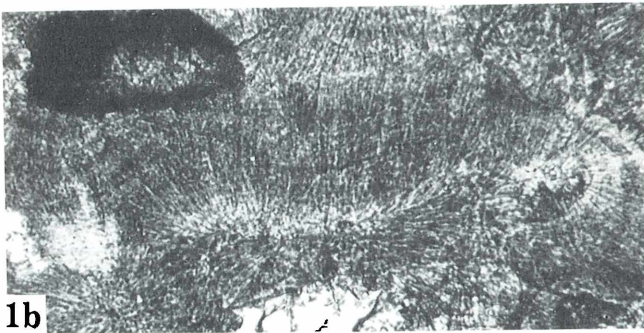
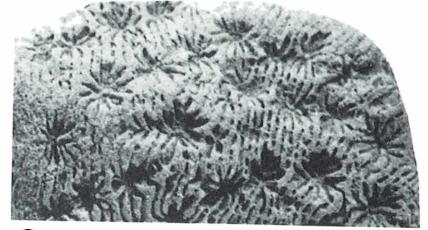
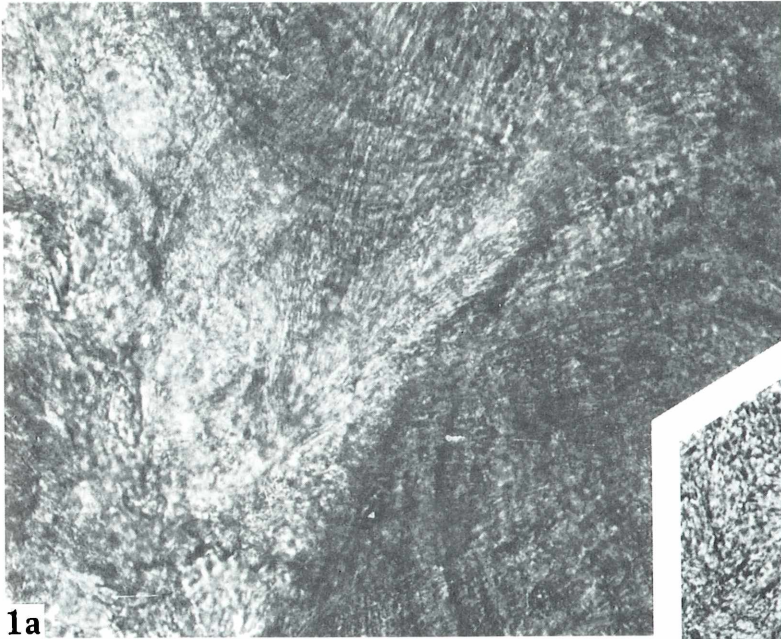


PLATE 30

Figs. 1, 2: *Parastraeomorpha minuscula* gen. et sp. n., p. 98

1. NHMW 1982/57/17, holotype, 1 a – transverse section of a branch,  $\times 8$ , 1 b – a corallite with S2 and S1 septa anastomosing by means of synapticalae developed at the internal edges of S2 septa,  $\times 76$
2. NHMW 1982/57/20, longitudinal section of a branch showing large synapticalae,  $\times 10$ . Note that menianes are lacking.

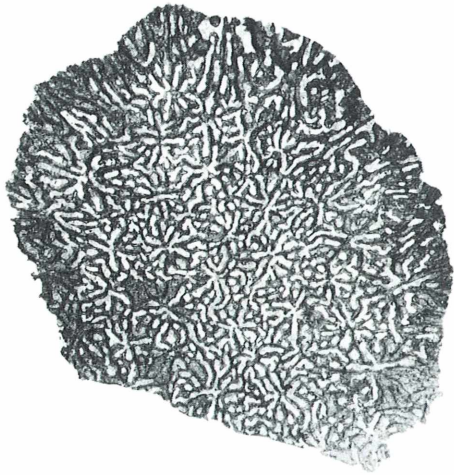
Fig. 3: *Parastraeomorpha similis* gen. et sp. n., p. 99

GBA 1982/12/420, holotype, 3 a – transverse section,  $\times 8$ , 3 b – longitudinal section,  $\times 8$ . Note large and numerous synapticalae and a lack of menianes.

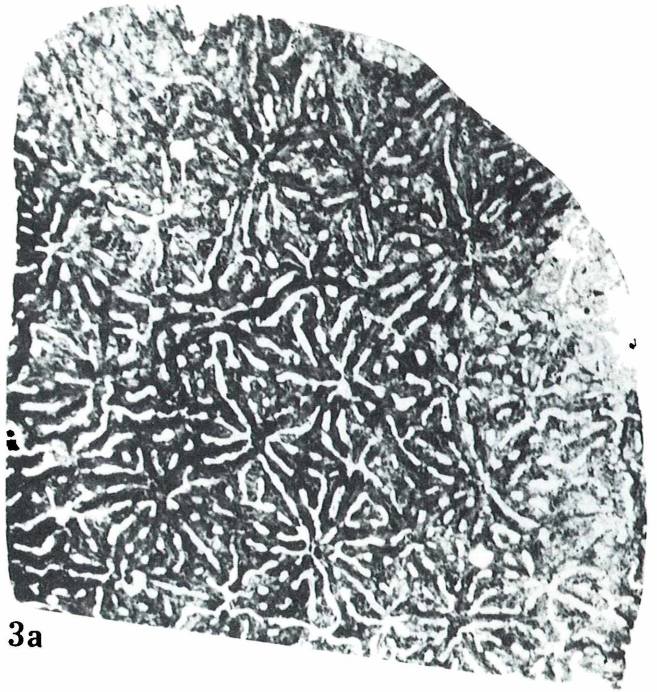
Figs. 1–3: Fischerwiese



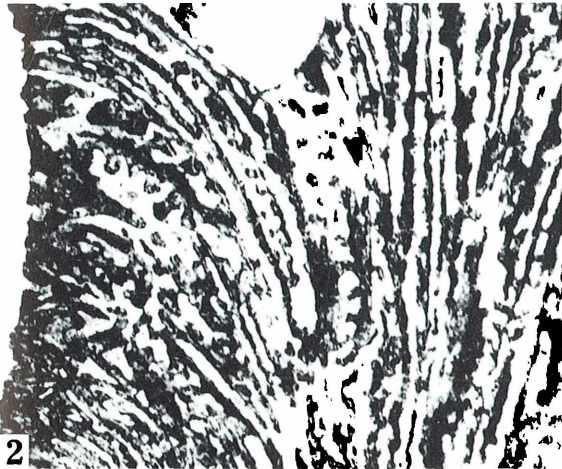
1a



3a



2



3b



1b

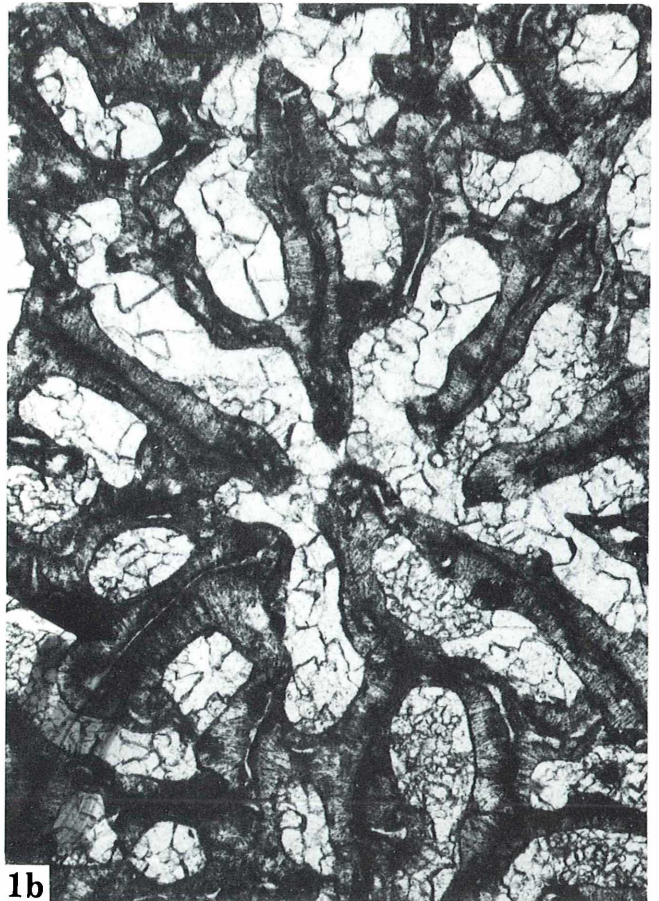


PLATE 31

Fig. 1, 4: *Seriastraea crasssa* sp. n., p. 101

1. NHMW 1982/56/17<sub>2</sub>, 1 a – colony in transverse section showing compact and porous septa,  $\times 8$ , 1 b – longitudinal section,  $\times 8$ , 1 c – transverse section of the septum desintegrating into thick trabeculae of complex structure,  $\times 195$ , 1 d – transverse section showing various stages of individualization of thick trabeculae in the septal blades built of small trabeculae; a straight meniane edge is visible (arrow),  $\times 76$ . Continued in Pl. 32

4. NHMW 1982/56/17<sub>1</sub>, colony in upper view,  $\times 2$

Figs. 2, 3: *Seriastraea multiphylla* SCHÄFER et SENOWBARI-DARYAN, 1978, p. 101

2. GBA 1982/12/747, transverse thin section,  $\times 8$
3. NHMW 1982/56/18, colony in upper view,  $\times 4$

Figs. 1, 3, 4: Kesselwand-Rohrmoos. Fig. 2: Fischerwiese



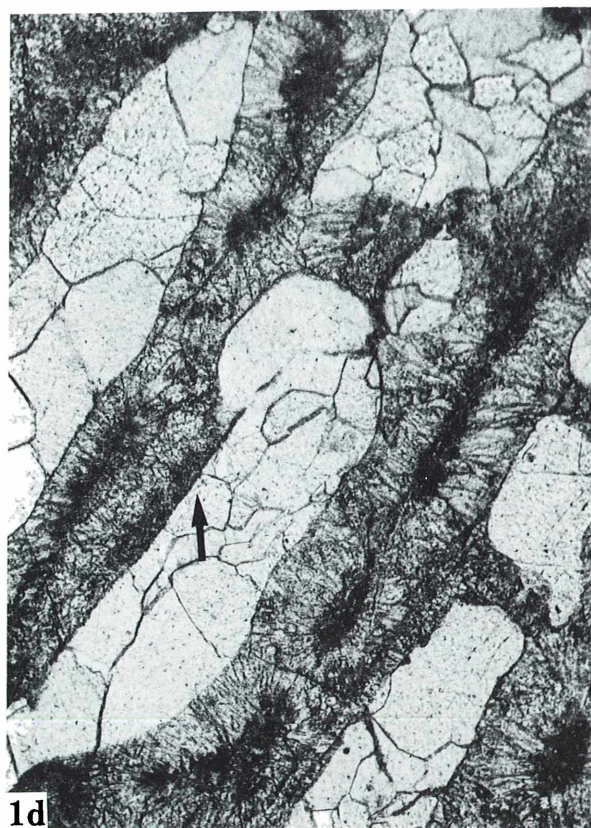
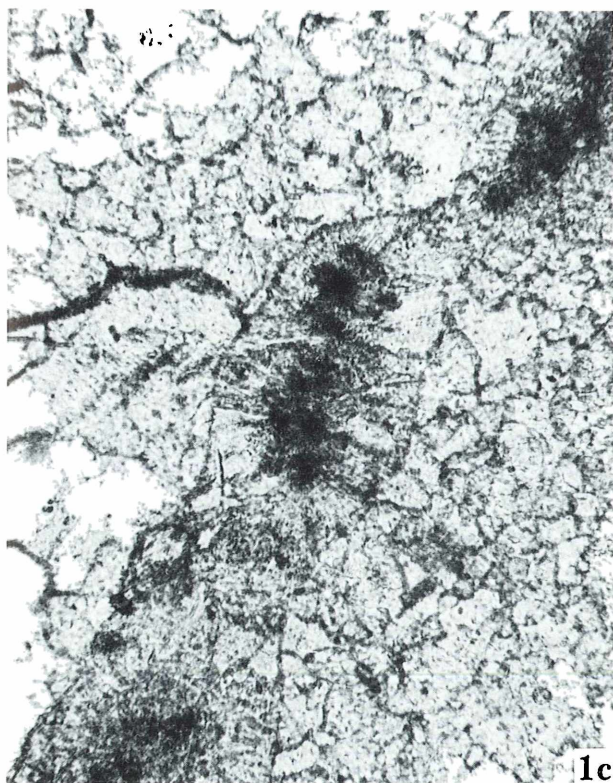
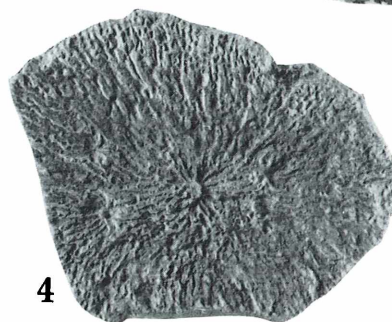
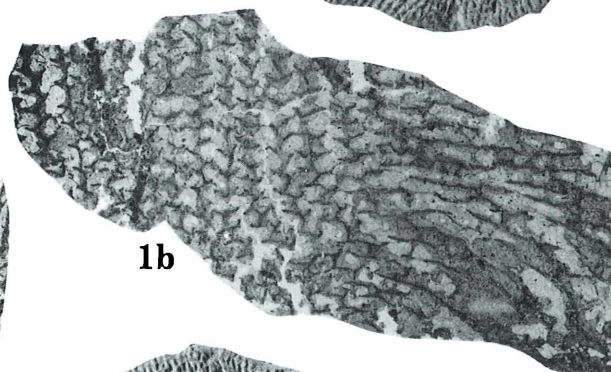
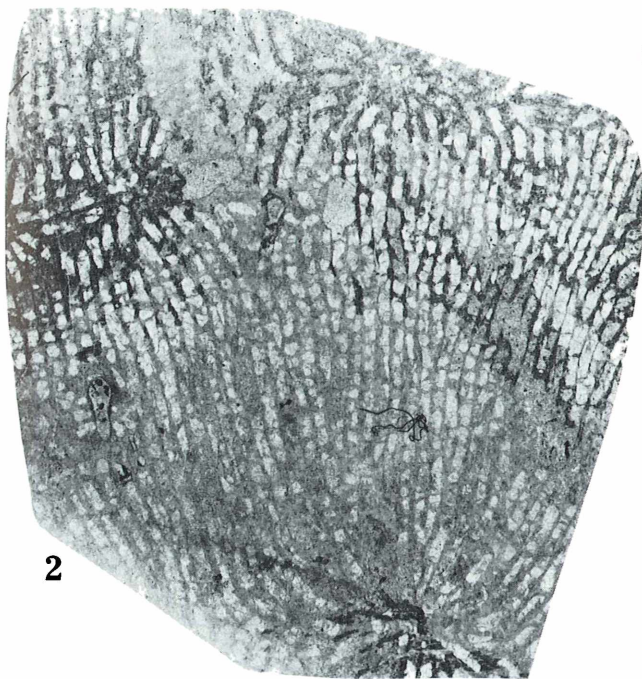
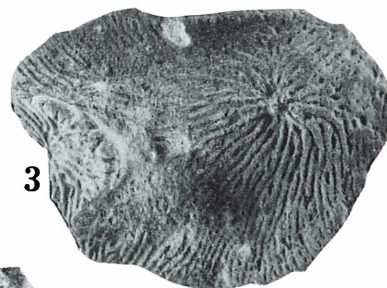
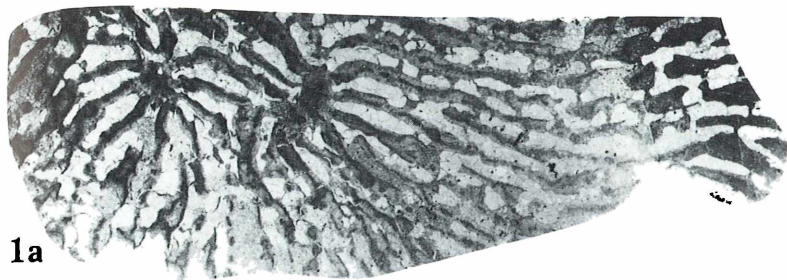


PLATE 32

Fig. 1: Microstructure of *Seriastraea crassa* sp. n. (continued), p. 102

NHMW 1982/56/17<sub>2</sub>, 1 a – isolated thick trabeculae of complex structure,  $\times 195$ , 1 b – thick trabeculae of complex structure individualized in septum,  $\times 195$ , 1 c – septum composed of a single row of small trabeculae,  $\times 195$ , 1 d – a fragment of fig. 1 c showing laterally directed fascicles of fibres constituting menianes,  $\times 250$ . See also Pl. 31, figs. 1 c, d

Kesselwand-Rohrmoos



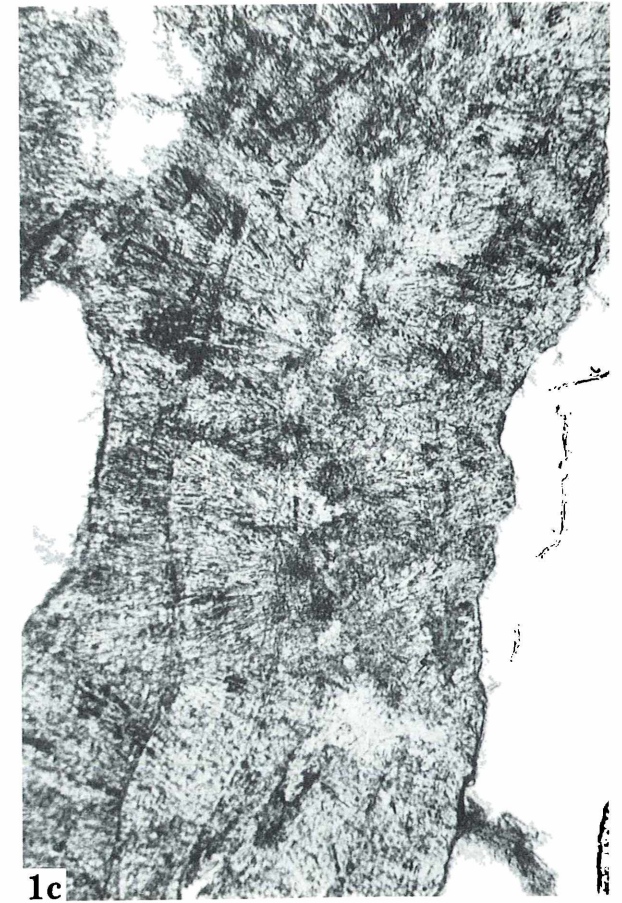
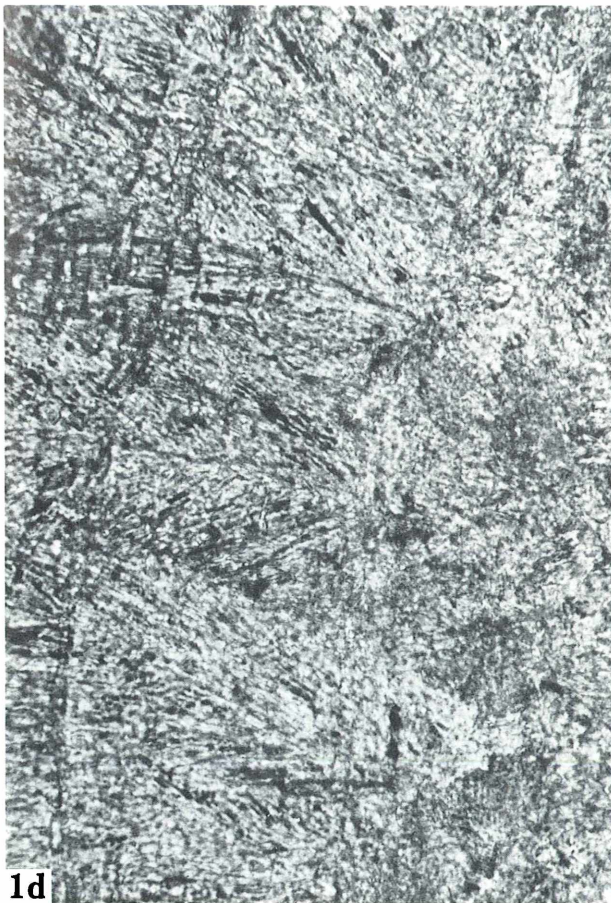




PLATE 33

Figs. 1–3, 5: *Chondrocoenia schafhaeutli* (WINKLER, 1861), p. 104

1. NHMW 1982/56/36<sub>3</sub>, transverse section of atypically developed specimen: note rudimentary peritheca, × 5
2. NHMW 1982/56/36<sub>7</sub>, longitudinal sections of dissepiments and tangential sections of thin lateral septal granules, × 20
3. NHMW 1982/56/36<sub>6</sub>, branching colony in cross section, polished surface, × 1
5. GBA 1982/12/718, abraded surface of subglobular colony, × 4

Fig. 4: *Chondrocoenia* sp. B, p. 108

GBA 1982/12/788, colony surface, × 4

Fig. 6: *Chondrocoenia waltheri* (FRECH, 1890), p. 106

NHMW 1982/57/37, transverse thin section, × 4

Fig. 7: *Chondrocoenia* sp. A, p. 107

NHMW 1982/56/22, 7 a – transverse thin section, × 7, 7 b – longitudinal section, × 6. Note costal trabeculae directed obliquely upwards in fig. 7 b. See also microstructure in Pl. 5, fig. 4

Fig. 8: *Chondrocoenia ohmanni* (FRECH, 1890), p. 106

NHMW 1959/365/42, 8 a – calicular surface, × 4, 8 b – a fragment, × 10. Note paliform projections surrounding the columella (arrow)

Figs. 1–3, 7, 8: Kesselwand-Rohrmoos. Fig. 4: Sommeraukogel. Figs. 5, 6: Fischerwiese

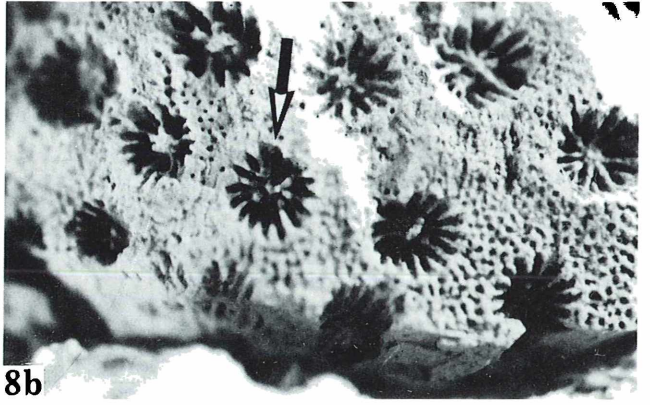
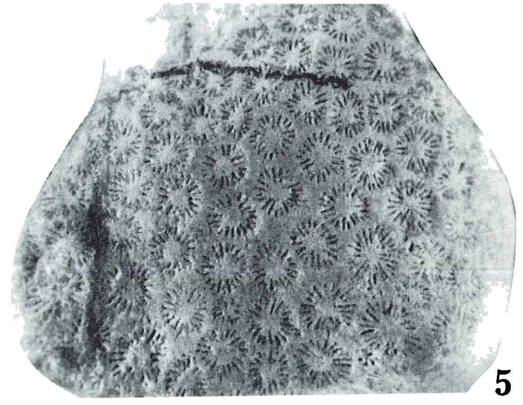
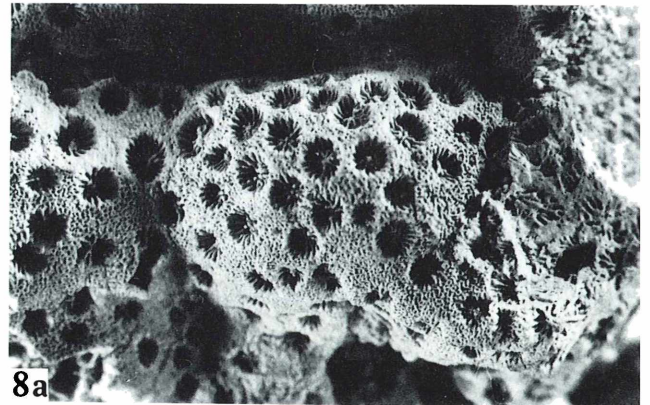
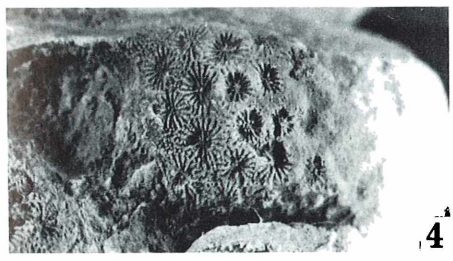
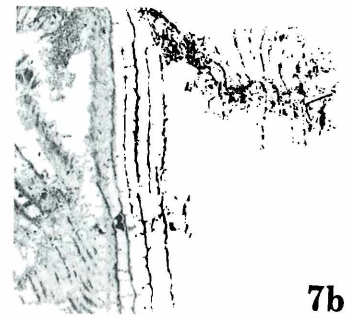
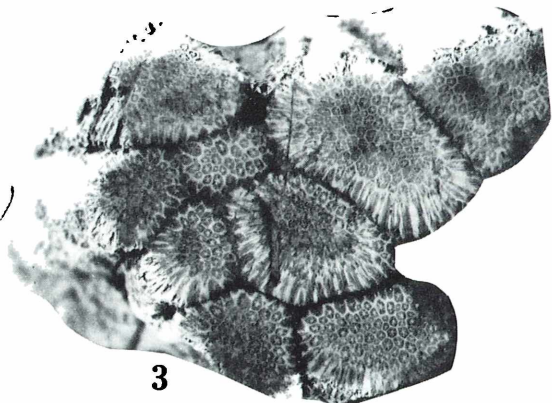
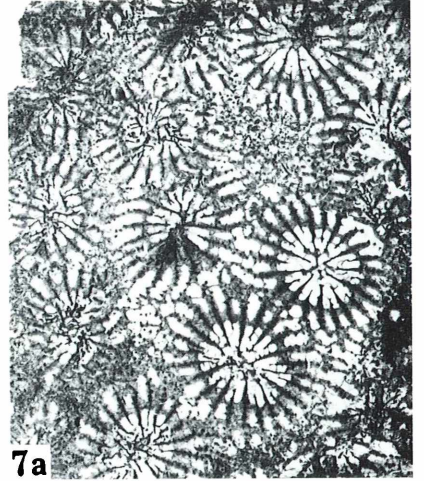
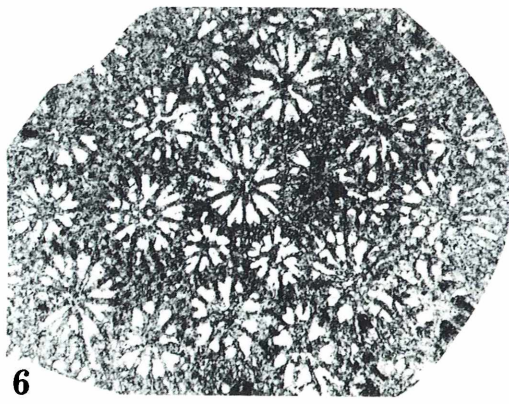
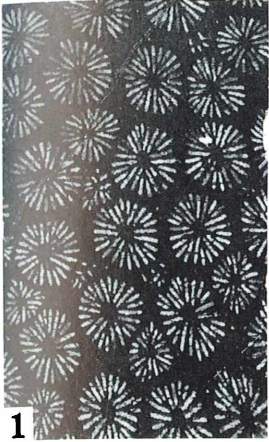




PLATE 34

Figs. 1, 2: *Crassistella juvavica* (FRECH, 1890), p. 113

1. NHMW 1982/56/23<sub>3</sub>, 1 a and 1 b – two fragments of the calicular colony surface with variably shaped walls: tectiform in fig. 1 a and tholiform in fig. 1 b, bisepetal blades well visible,  $\times 6$
2. NHMW 1959/365/23<sub>1</sub>, 2 a and 2 c – transverse thin sections,  $\times 8$  and  $\times 4$  respectively, 2 b – longitudinal section,  $\times 8$

Microstructure in Pl. 35, figs. 1, 2

Figs. 3–5: *Pamiroseris rectilamellosa* (WINKLER, 1861), p. 111

- 3, 4. GBA 1982/12/380 and 382, two specimens with variably thickened septa and columella, both  $\times 4$
5. GBA 1982/12/370, longitudinal section,  $\times 4$

Fig. 1: Schneckengraben. Fig. 2: Kesselwand-Rohrmoos. Figs. 3–5: Fischerwiese

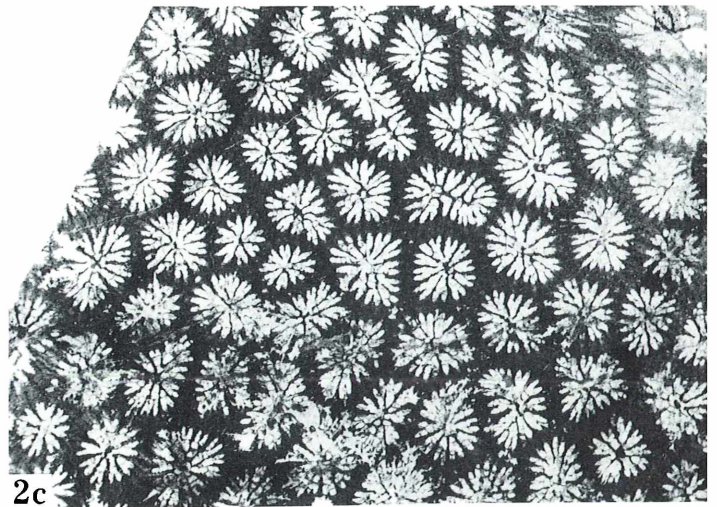
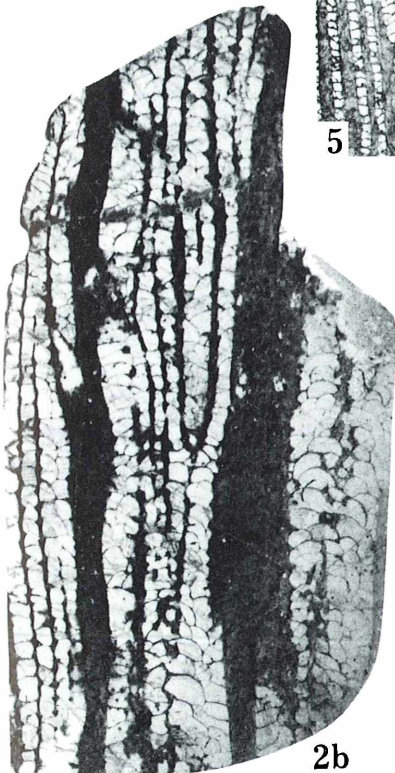
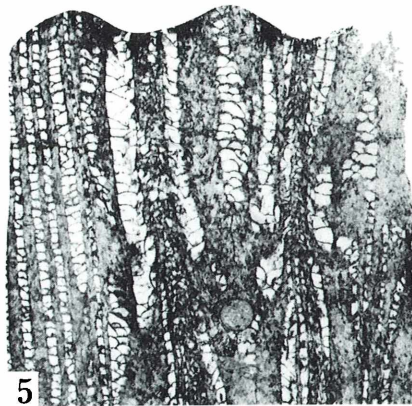
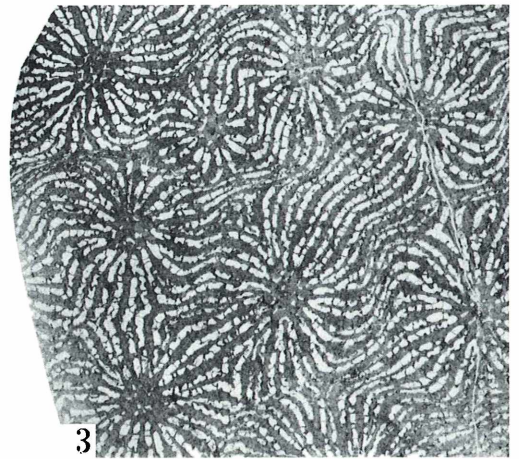
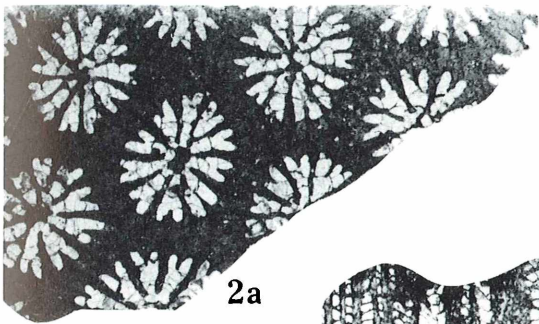
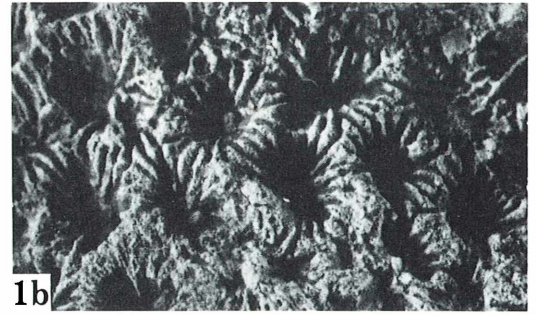
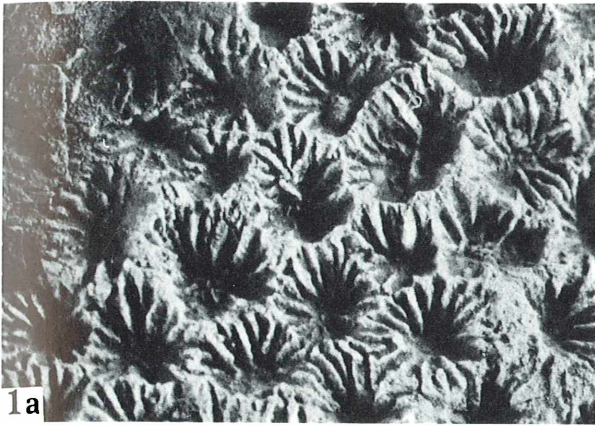


PLATE 35

Figs. 1, 2: Microstructure of *Crassistella juvavica* (FRECH, 1890), p. 114

1. NHMW 1982/56/23<sub>3</sub>, 1 a – transverse section showing thick corallite walls,  $\times 20$ , 1 b – three succeeding trabeculae in a free septal blade,  $\times 134$
2. NHMW 1982/56/23<sub>1,2</sub> a – a fragment of wall in transverse section: bisepthal blade (left) with a boundary between two septa, perfect bisepthal blade (right), two septa apposited to each other with their sides and forming a bisepthal blade with a kinke at its mid-length (middle),  $\times 123$ , 2 b – a fragment showing complex structure of the peripheral septal portion containing lateral irregular outgrowths (L) of the main trabeculae (arrows),  $\times 195$ , 2 c – monotrabeular, thick columella and internal septal edges adjoining to it,  $\times 123$

Fig. 1: Schneckengraben. Fig. 2: Kesselwand-Rohrmoos



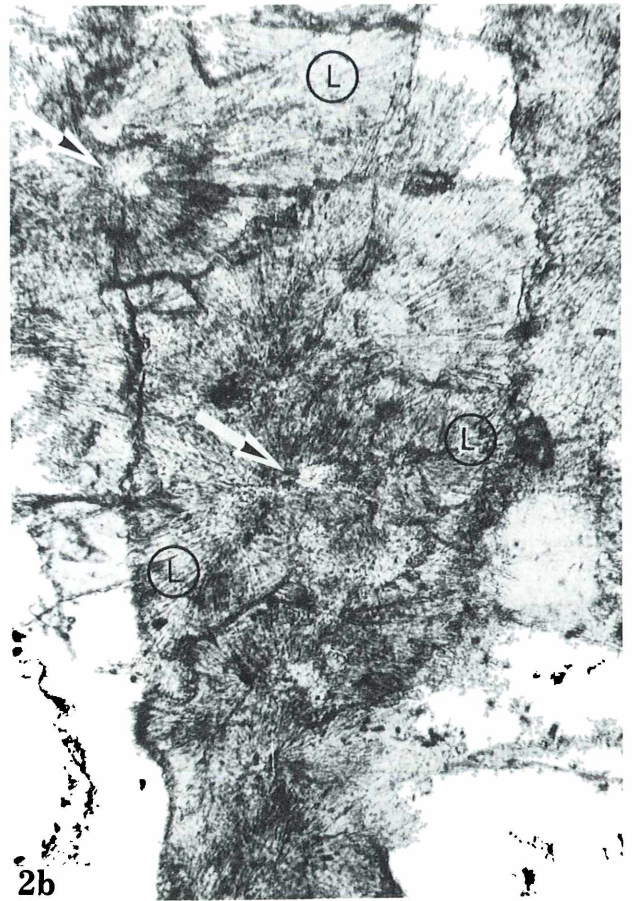
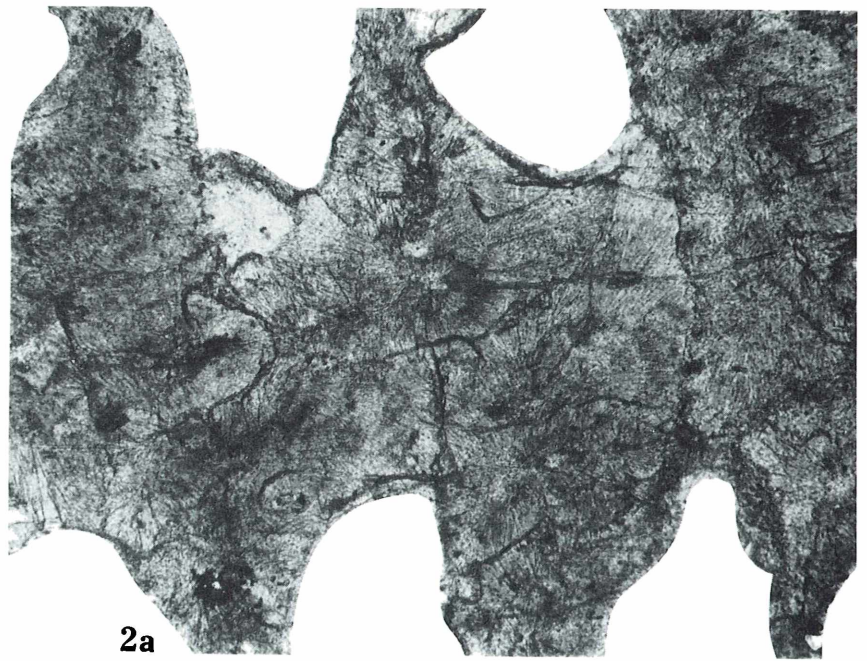
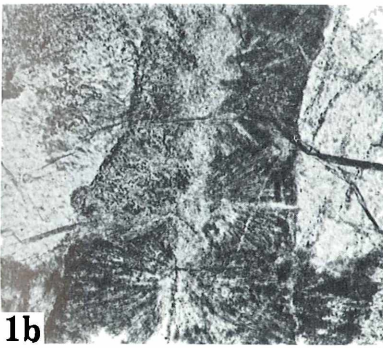
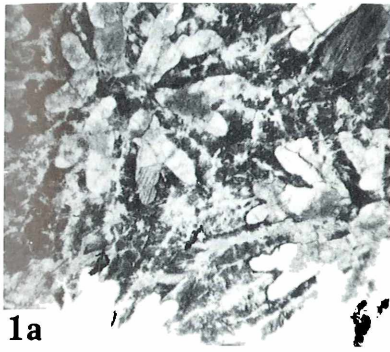


PLATE 36

Fig. 1: *Gigantostylis epigonus* FRECH, 1890, p. 138

NHMW 1982/57/86, proximally abraded corallum,  $\times 1$ . Microstructure in Pl. 42, figs. 1, 2, Pl. 43, figs. 1 a, b

Figs. 2, 5, 10: *Stylophyllum polyacanthum* REUSS, 1854, p. 118

2. NHMW 1982/57/182, small-calicular cerioid colony,  $\times 1$

5. GBA 1982/12/445, large-calicular cerioid colony,  $\times 1$

10. GBA 1982/12/450, 10 a – corallite fragment in transverse section, 10 b – side view, both  $\times 4$ . Note that septal spines penetrating calicular cavity do not correspond to longitudinal rows of wall fibre bundles (fig. 10 b, compare *S. vesiculatum*, Pl. 43, fig. 2 c).

See also Pl. 38, figs. 1–4 and microstructure in Pl. 42, fig. 8

Figs. 3, 4, 8: *Stylophyllum paradoxum* FRECH, 1890, p. 121

3. GBA 1982/12/494, 3 a – thin-skeletal corallum in calicular view, 3 b – side view, both  $\times 1$

4. GBA 1982/12/486, 4 a – thick-skeletal corallum in calicular view, 4 b – side view, both  $\times 1$

8. NHMW 1982/365/48, thick-skeletal morphotype, side view of strongly abraded specimen,  $\times 1$ .

See also Pl. 38, fig. 5 and microstructure in Pl. 42, fig. 9

Figs. 6, 7: *Stylophyllopsis polyactis* FRECH, 1890, p. 124

6. NHMW 1982/56/33<sub>2</sub>, transverse section, polished surface of a corallum with relatively thick and discontinuous septa (compare with Pl. 38, fig. 9).

7. NHMW 1959/364/15<sub>10</sub>, side view of a strongly abraded specimen,  $\times 1$

See also Pl. 37, figs. 1 a, b and Pl. 38, figs. 8, 9

Fig. 9: *Stylophyllum pygmaeum* FRECH, 1890, p. 122

GBA 1982/12/808, bifurcating corallite,  $\times 3$ .

See also Pl. 38, fig. 6

Fig. 11: *Stylophyllum vesiculatum* sp. n., p. 120

NHMW 1982/57/115, calicular view,  $\times 1$ .

See also Pl. 38, figs. 7 and microstructure in Pl. 42, fig. 4 and Pl. 43, fig. 2

Figs. 1–5, 7, 10, 11: Fischerwiese. Figs. 6, 8: Kesselwand-Rohrmoos. Fig. 9: Zlambachgraben



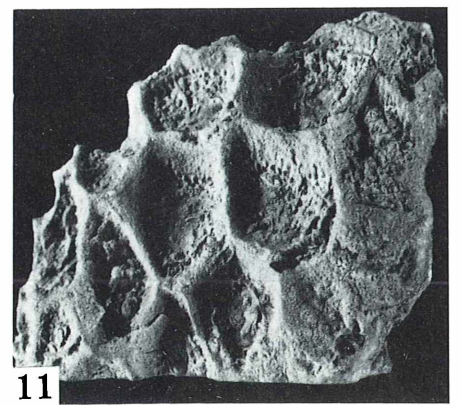
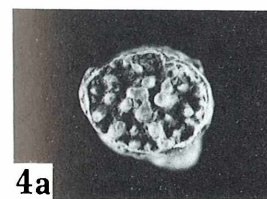
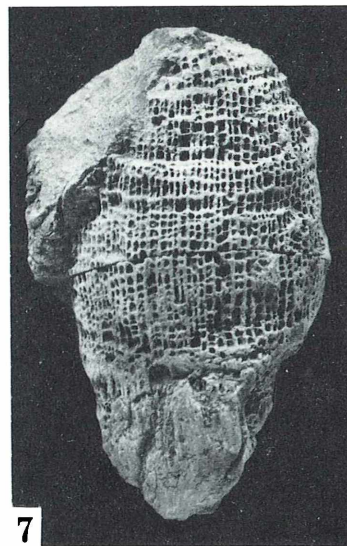
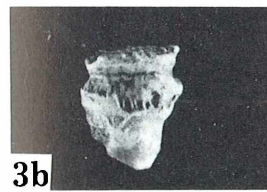
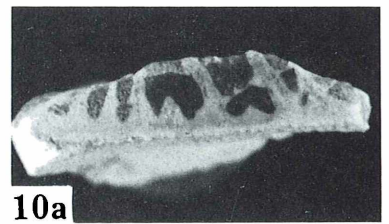
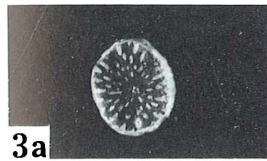
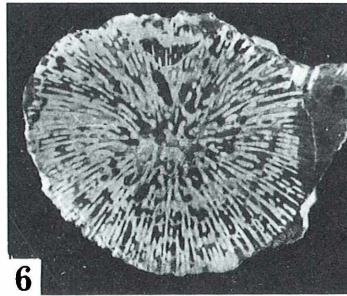
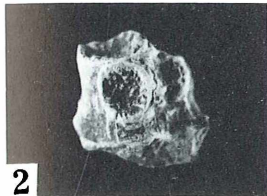
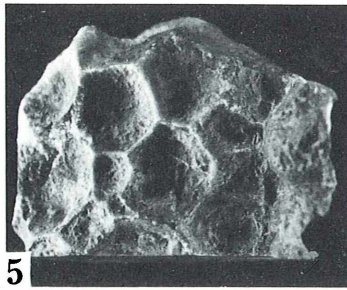
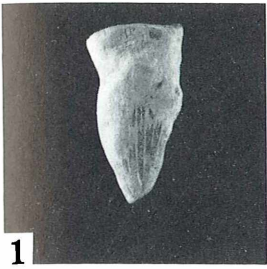


PLATE 37

Fig. 1: *Stylophyllopsis polyactis* FRECH, 1890, p. 124

BSP AS XII 53, lectotype, 1 a – weathered calicular surface showing thin and densely spaced, compact and subcompact septa in transverse section, 1 b – longitudinal broken section showing septa and endotheca, both views  $\times 4$ . Note a subcompact septal blade in side view (1 b, right) built of vertically continuous septal spines which are inclined axialwards and incompletely connected with each other; interspine gaps form large septal pores (arrow), the dissepiments are largely extending and densely packed.

See also Pl. 36, figs. 6, 7 and Pl. 38, figs. 8, 9



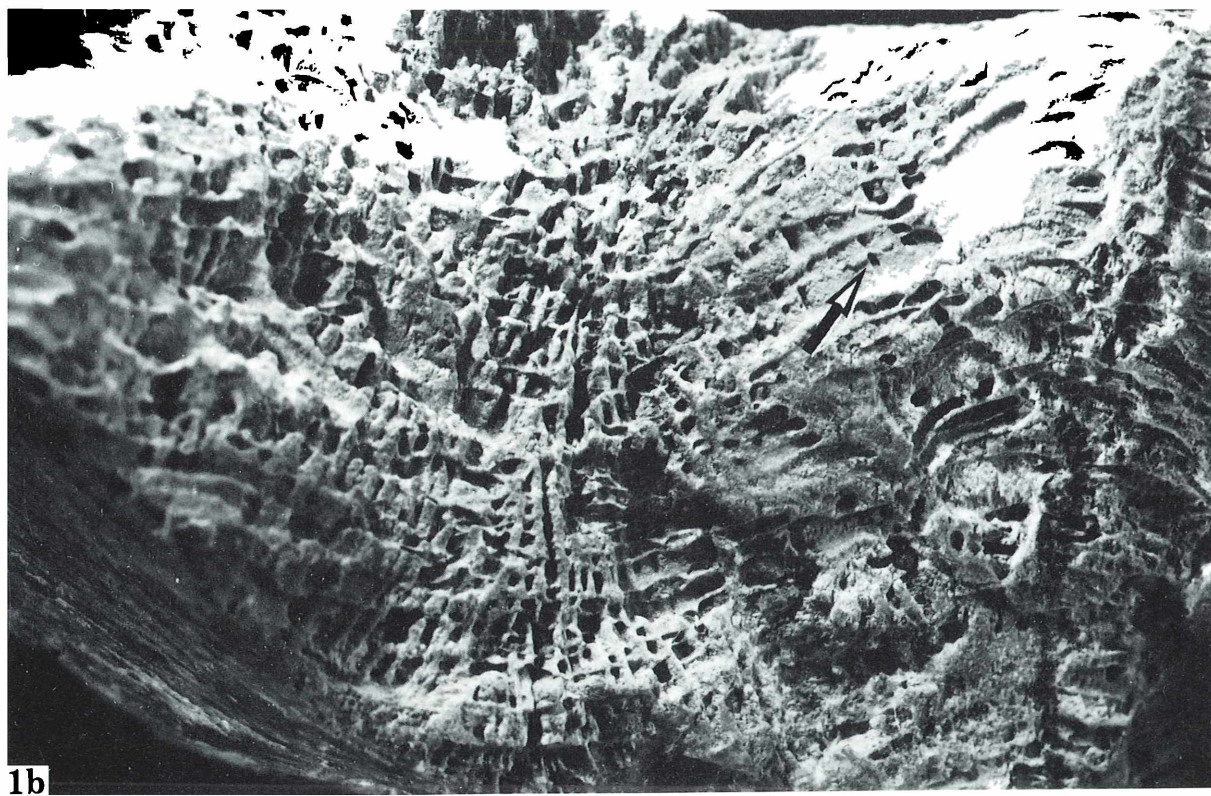
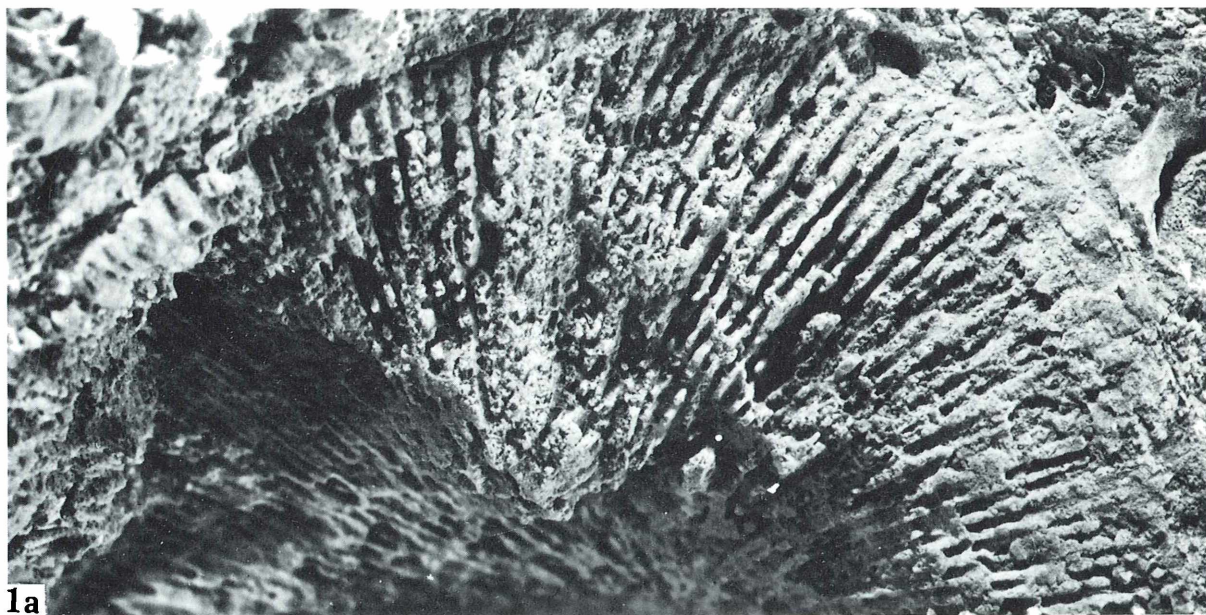


PLATE 38

Figs. 1–4: *Stylophyllum polyacanthum* REUSS, 1854, p. 118

1. GBA 1982/12/445, cerioid colony in transverse section,  $\times 2$ . Note a double wall with a fissure in its middle.
2. NHMW 1982/57/179, 2 a – cerioid colony in transverse section,  $\times 2$ , 2 b – longitudinal section,  $\times 2$ . Note that corallites may be incompletely fused (upper right side); the boundary fissure is usually narrow; the dissepiments are rather large, vesicular or tabuloid and never are densely packed.
- 3, 4. GBA 1982/12/465 and 470, corallites of phaceloid colonies in transverse (3, 4 a) and longitudinal (4 b) sections, all  $\times 4$ .

See also Pl. 36, figs. 2, 5, 10; microstructure in Pl. 42, fig. 8

Fig. 5: *Stylophyllum paradoxum* FRECH, 1890, p. 121

GBA 1982/12/481, transverse section, thin-skeletal morphotype,  $\times 2$

See also Pl. 36, figs. 3, 4, 8 and microstructure in Pl. 42, fig. 9

Fig. 6: *Stylophyllum pygmaeum* FRECH, 1890, p. 122

GBA 1982/12/807, 6 a – transverse and 6 b – longitudinal sections, both  $\times 4$ .

See also Pl. 36, figs. 9

Fig. 7: *Stylophyllum vesiculatum* sp. n., p. 120

NHMW 1982/56/34, 7 a – holotype colony in transverse and 7 b – in longitudinal sections, both  $\times 2$ . Note the difference between this species and *S. polyacanthum* in the septal spines development and structure of endotheca; intracalicular budding is observed in fig. 7 a.

See also Pl. 36, figs. 11 and microstructures in Pl. 42, figs. 4 a–c and Pl. 43, figs. 2 a–c

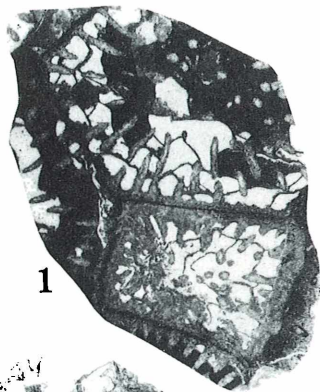
Figs. 8, 9: *Stylophylloopsis polyactis* FRECH, 1890, p. 124

8. GBA 1982/12/654, longitudinal section showing concave endotheca built of large, densely packed subtabuloid dissepiments,  $\times 2$
9. GBA 1982/12/651, transverse section of thin-septate corallum, polished surface,  $\times 2$ . Note the continuous septal blades.

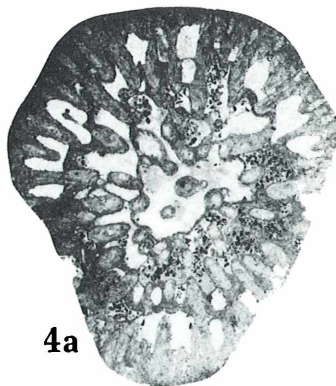
See also Pl. 36, figs. 6, 7 and Pl. 37, fig. 1

Figs. 1–5, 8, 9: Fischerwiese. Fig. 6: Zlambachgraben. Fig. 7: Kesselwand-Rohrmoos

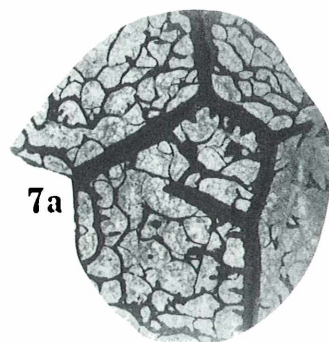




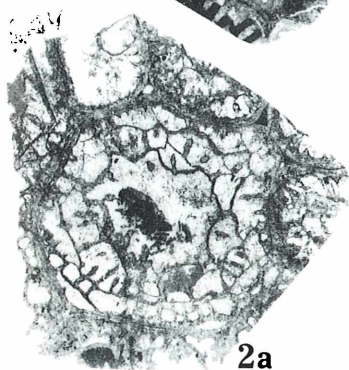
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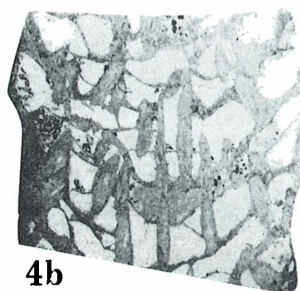
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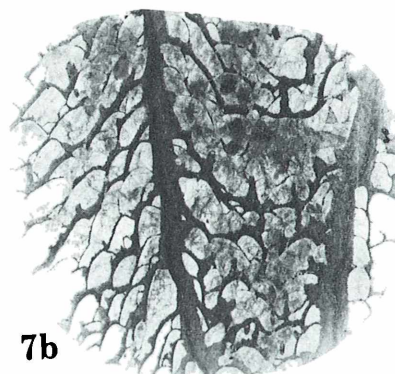
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2a



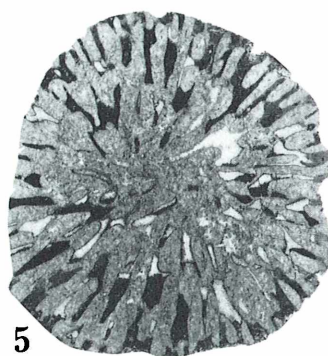
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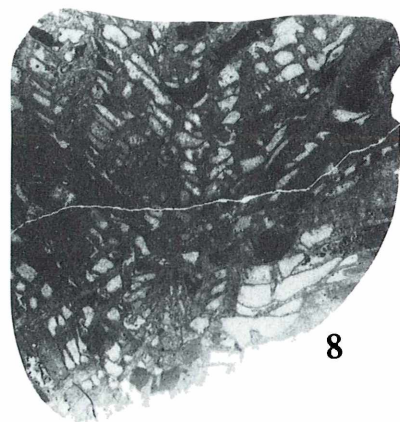
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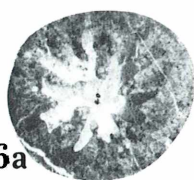
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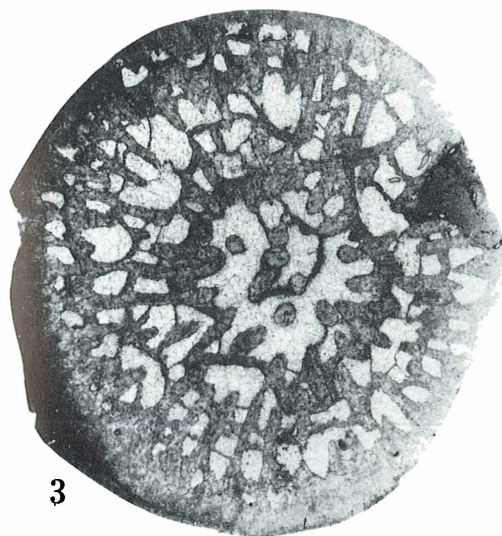
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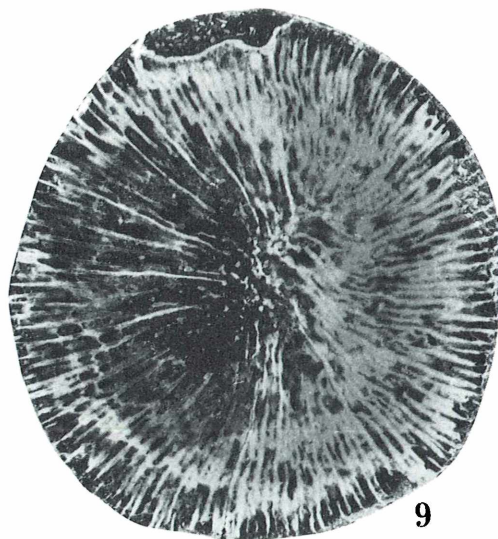
6a



6b



3



9



PLATE 39

Fig. 1: *Stylophyllopsis ramosa* sp. n., p. 130

GBA 1982/12/693, holotype, upper view showing densely spaced corallites,  $\times 1$

Figs. 2–6: *Stylophyllopsis rudis* (EMMRICH, 1853), p. 126

2. BSP AS XII 62, specimen figured by FRECH 1890, Pl. 12, fig. 9,  $\times 1$
  3. BSP AS XII 72, specimen figured by FRECH 1890, Pl. 10, fig. 10,  $\times 1$
  4. BSP AS XII 63, specimen figured by FRECH 1890, Pl. 12, fig. 10,  $\times 1$
  5. NHMW 1982/56/32<sub>2</sub>, paucisepal morphotype,  $\times 1$
  6. NHMW 1982/56/32<sub>1</sub>, multiseptal morphotype, 6 a – calicular view,  $\times 1$ , 6 b – longitudinal section of the proximal corallite part showing horizontal arrangement of vesicular dissepiments,  $\times 1$
- See also Pl. 40, figs. 1, 2 and Pl. 42, fig. 7

Fig. 7: *Stylophyllopsis lindstroemi* FRECH, 1890, p. 128

GBA 1982/12/671, naturally oval calice,  $\times 2$ .

See also Pl. 40, figs. 3, 4

Fig. 8: *Stylophyllopsis zitteli* FRECH, 1890, p. 125

GBA 1982/12/645, corallum with short S3 septa, polished surface,  $\times 2$ .

See also Pl. 40, figs. 5–7

Figs. 9, 10: *Meandrostylis irregularis* FRECH, 1890, p. 131

9. GBA 1982/12/536, thin-septal colony,  $\times 2$
  10. H. ZAPFE's collection, 10 a – thick-septal colony,  $\times 2$ , 10 b – a detail showing septes-de-vallée,  $\times 6$
- See also Pl. 40, figs. 9–11

Fig. 11: *Meandrostylis frechi* HAAS, 1909, p. 132

NHMW 1982/56/40, calicular view,  $\times 1$ .

See also Pl. 40, figs. 8 a-c

Figs. 1, 3, 7–10: Fischerwiese. Figs. 2, 4–6, 11: Kesselwand-Rohrmoos

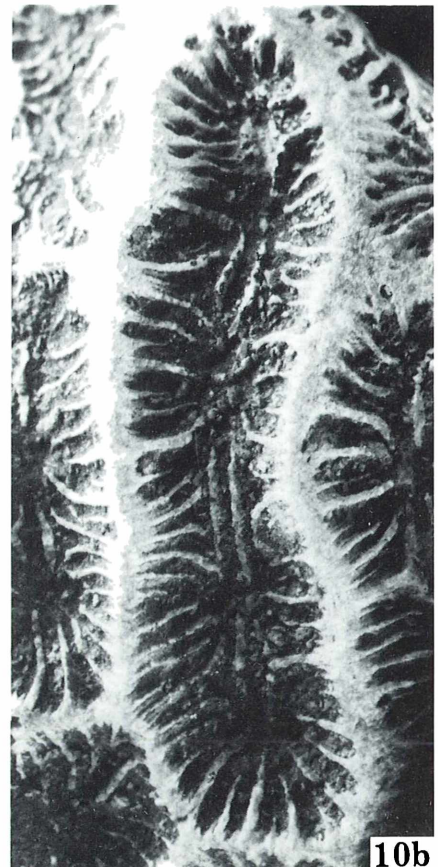
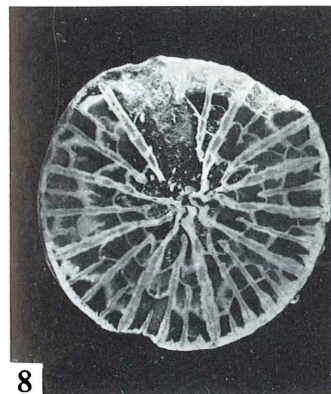
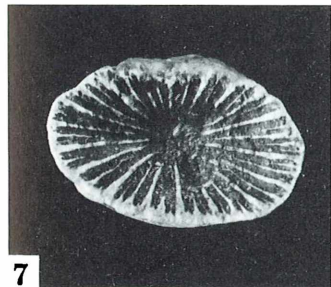
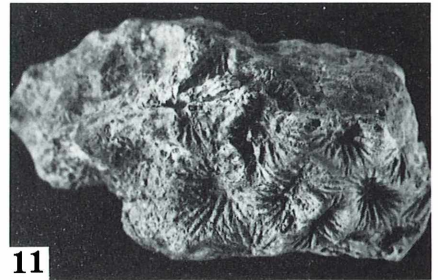
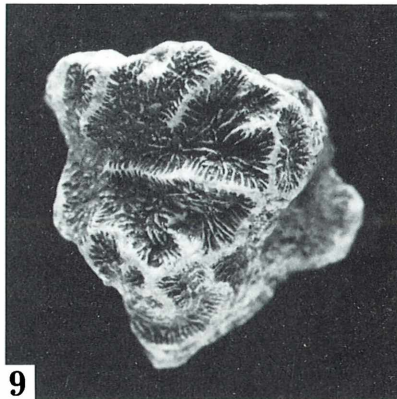
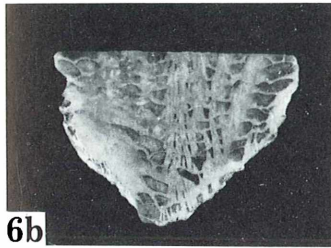
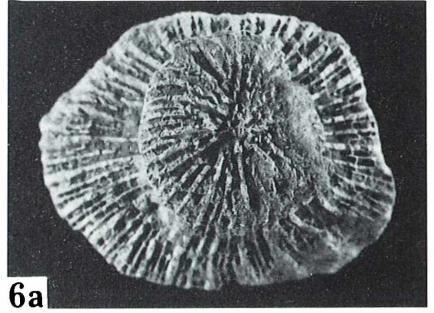
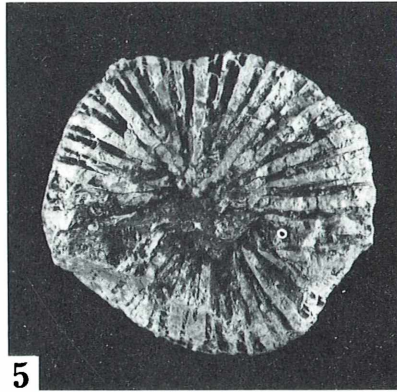
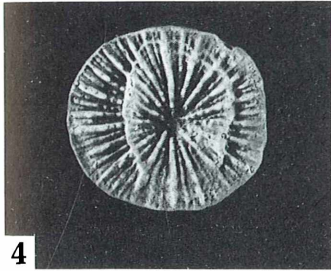
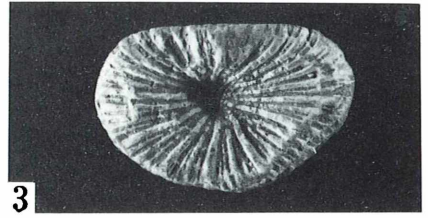
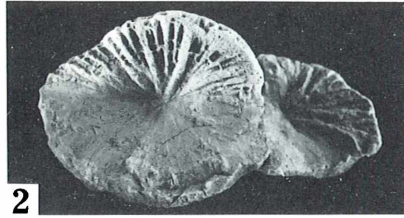
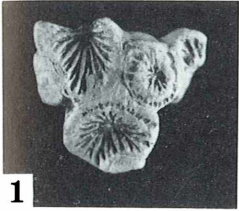


PLATE 40

Figs. 1, 2: *Stylophyllopsis rudis* (EMMRICH, 1853), p. 126

1. NHMW 1982/56/32<sub>3</sub>, multiseptal morphotype, × 2

2. NHMW 1982/56/32<sub>2</sub>, pauciseptal morphotype, × 2

See also Pl. 39, figs. 2–6 and microstructure in Pl. 42, fig. 7

Figs. 3, 4: *Stylophyllopsis lindstroemi* FRECH, 1890, p. 128

3. GBA 1982/12/672, thick-walled corallite, × 4

4. NHMW 1982/57/92, thin-walled corallite, × 6.4

See also Pl. 39, figs. 7

Figs. 5–7: *Stylophyllopsis zitteli* FRECH, 1890, p. 125

5. GBA 1982/12/599, septa numerous, × 2

6. GBA 1982/12/604, longitudinal section showing large-dissepimental endotheca, concave at the corallite axis, × 2

7. GBA 1982/12/645, scarce septa, × 2

See also Pl. 39, fig. 8

Fig. 8: *Meandrostylis frechi* HAAS, 1909, p. 132

GBA 1982/12/520, 8 a – transverse section showing subconfluent septa and an incomplete septotheca, × 4, 8 b – longitudinal section with large, tabuloid dissepiments, × 4, 8 c – septa in transverse section with microornamented surface, × 20

See also Pl. 39, figs. 11

Figs. 9–11: *Meandrostylis irregularis* FRECH, 1890, p. 131

9. GBA 1982/12/528, longitudinal section showing tabuloid organization of endotheca, × 4

10. GBA 1982/12/526, transverse section, × 4

11. GBA 1982/12/529, transverse section at the proximal colony portion showing the protocorallite producing radial series of corallites, × 4

See also Pl. 39, figs. 9, 10

Figs. 1, 2: Kesselwand-Rohrmoos. Figs. 3–11: Fischerwiese



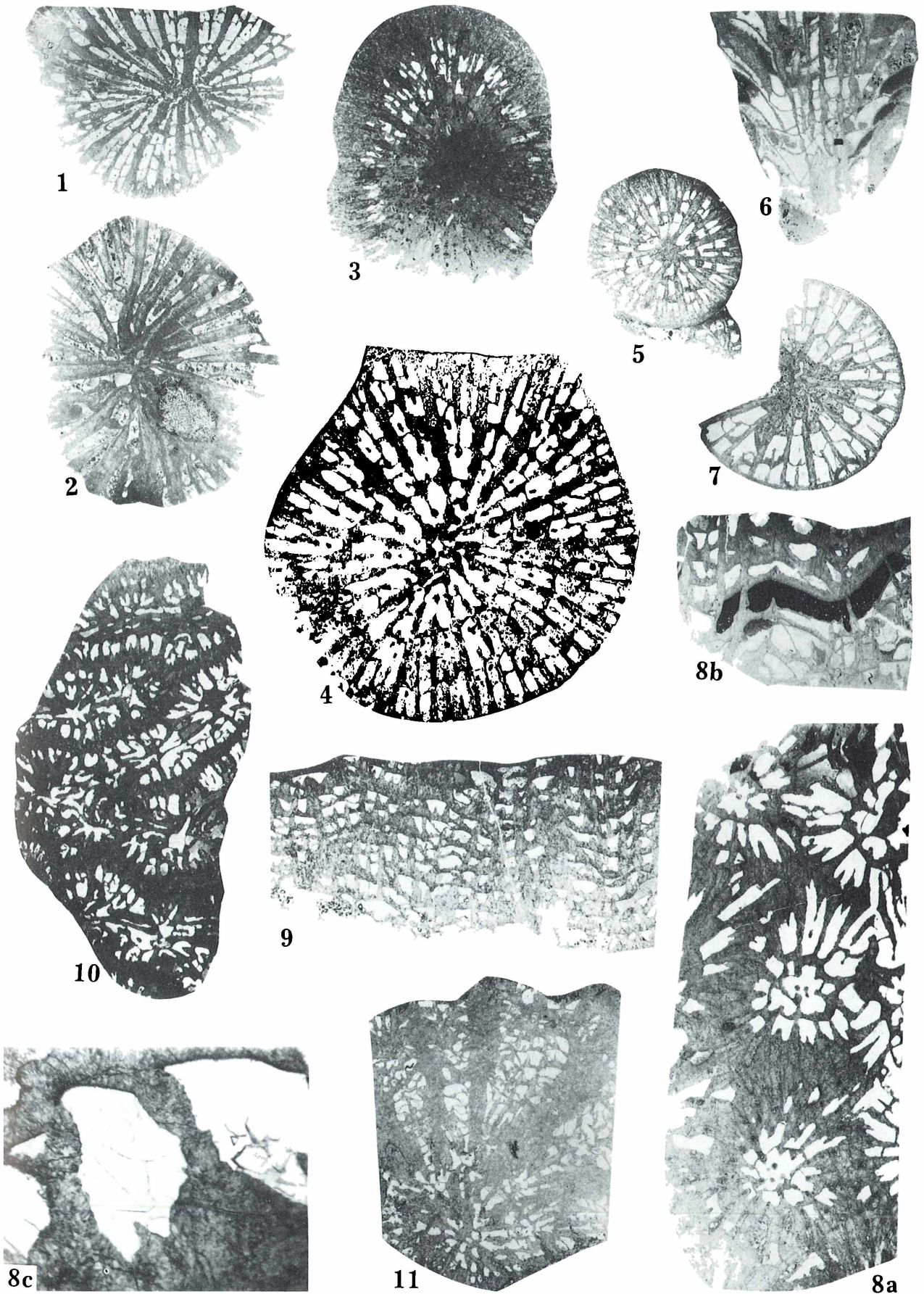


PLATE 41

Figs. 1, 2: *Coccophyllum sturi* REUSS, 1865, p. 134

1. NHMW 1982/56/35<sub>2</sub>, abraded calicular surface of a small-corallite colony,  $\times 1$
2. NHMW 1982/56/35<sub>1</sub>, colony with large-dimensional corallites, 2 a – calicular surface, 2 b – transverse section, polished surface with corallite boundaries visible, 2 c – longitudinal section showing rare tabuloid dissepiments, all  $\times 1$ . Microstructure in Pl. 42, fig. 3

Figs. 3, 4: *Pinacophyllum parallelum* FRECH, 1890, p. 136

3. NHMW 1982/56/19<sub>1</sub>, 3 a – phaceloid colony in transverse thin section,  $\times 1$ , 3 b – longitudinal section, polished surface,  $\times 2$
4. NHMW 1982/56/19<sub>2</sub>, 4 a – cerioid colony in calicular view,  $\times 1$ , 4 b – corallite in longitudinal broken section showing thick septal spines arranged in rows and rare tabular dissepiments,  $\times 10$ . Microstructure in Pl. 42, figs. 5, 6 and Pl. 43, fig. 3

Figs. 5–7: *Anthostylis acanthophora* (FRECH, 1890), p. 133

5. NHMW 1982/57/32, 5 a – transverse and 5 b – longitudinal sections,  $\times 8$
6. GBA 1982/12/737, calicular surface of a small-corallite colony,  $\times 6$
7. GBA 1982/12/732, calicular surface of a large-corallite colony,  $\times 6$

Figs. 1, 2, 4: Kesselwand-Rohrmoos. Fig. 3: Schneckengraben. Figs. 5–7: Fischerwiese



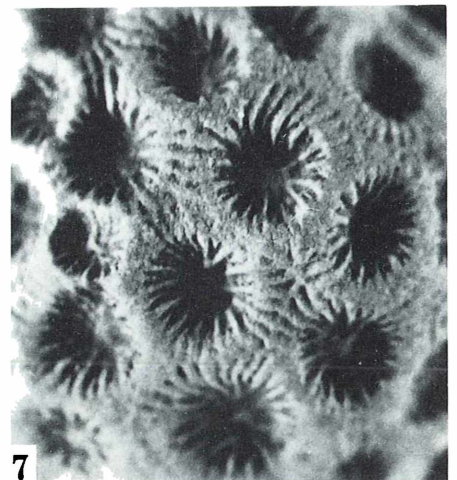
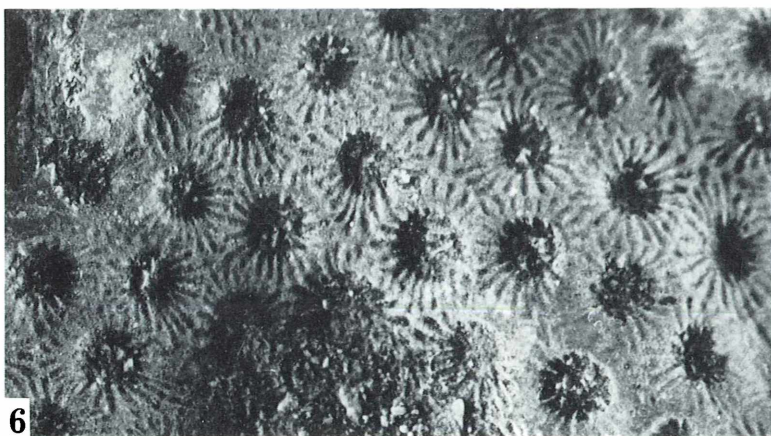
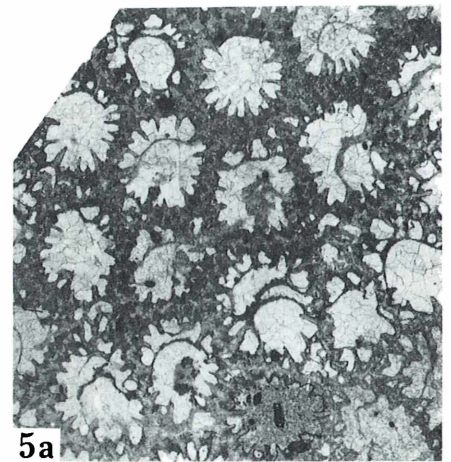
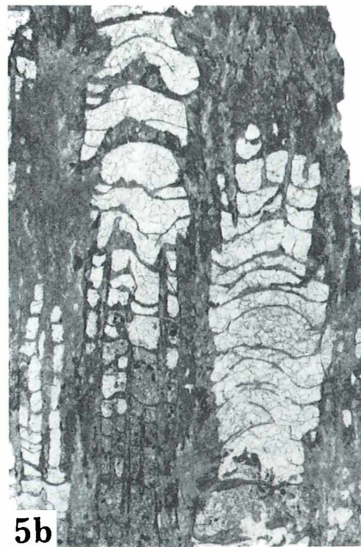
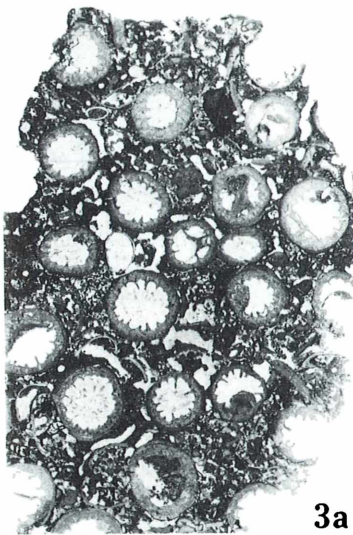
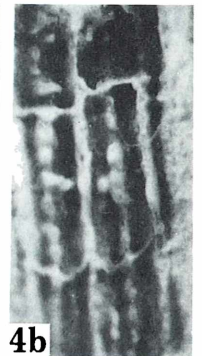
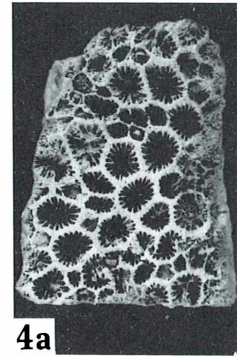
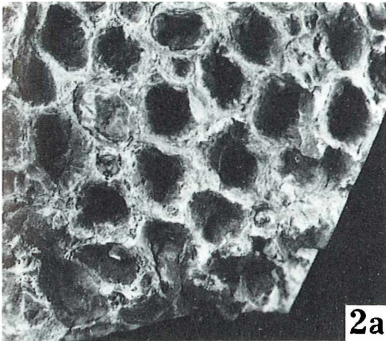
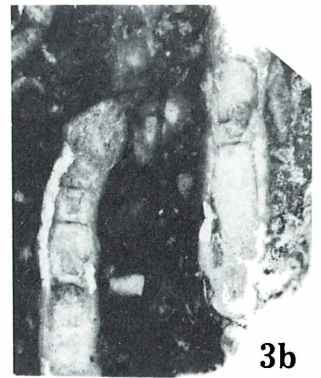
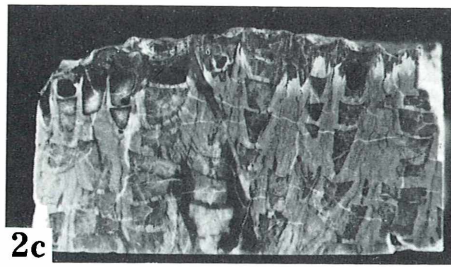
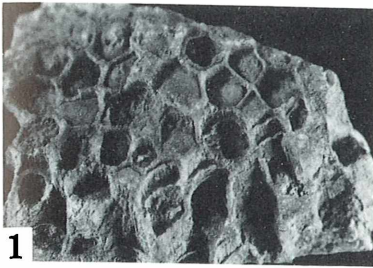


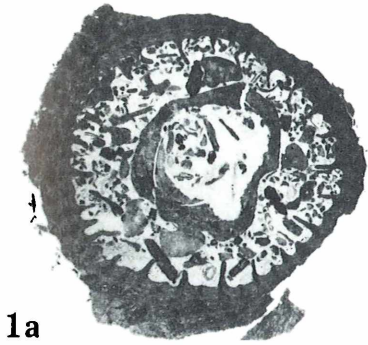
PLATE 42

Figs. 1–9: Stylophyllid microstructure (continued in Pl. 43), p. 117 and pages mentioned below

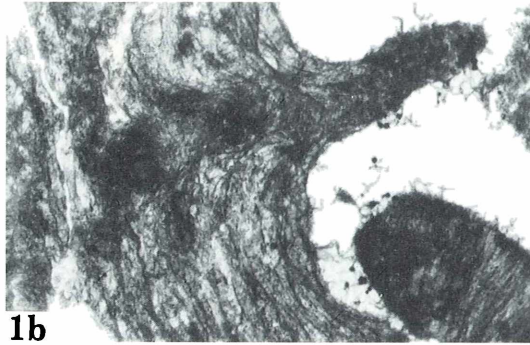
1. *Gigantostylis epigonus* FRECH, 1890, p. 139. GBA 1982/12/582, 1 a – section at the distal portion of the calice showing a thick wall, well developed septa and a columella partially filled with sediment,  $\times 6$ , 1 b – septum growing in structural continuation with the wall,  $\times 84$
2. The same species. GBA 1982/12/543, long-fibrous stereome of the innermost wall layer approaching the collumella (at the upper margin of the picture),  $\times 84$ .  
See also Pl. 43, figs. 1 a, b
3. *Coccophyllum sturi* REUSS, 1865, p. 135. NHMW 1982/56/35<sub>1</sub>, longitudinal section showing structural continuation between the wall and dissepimental stereome,  $\times 52$ . The stereome is organized into bundles of fibres.
4. *Stylophyllum vesiculatum* sp. n., p. 120 NHMW 1982/56/34, 4 a – longitudinal section of the wall (left) and thick dissepiment with two septal spines developed on its upper surface (see Pl. 43, fig. 2 a),  $\times 21$ , 4 b – longitudinal section of the wall and thin dissepiment,  $\times 21$ , 4 c – a detail showing bundles of fibres constituting the wall stereome with tops of the bundles visible on the skeleton surface as its microornamentation,  $\times 134$ . Note the same type of microornamentation on the wall, septal spines and dissepiments.  
See also Pl. 43, figs. 2 a–c
5. *Pinacophyllum parallelum* FRECH, 1890, p. 137. NHMW 1982/56/19<sub>1</sub>, 5 a – phaceloid corallite in transverse section,  $\times 21$ , 5 b – wall fragment showing a thick external layer built of radially arranged fibres and an internal layer built of scales,  $\times 84$ . Note that the wall and septum are in structural continuation.
6. The same species. NHMW 1982/56/19<sub>2</sub>, a fragment of a cerioid colony in transverse section, with a light boundary line between adjacent individuals and scaly structure of the wall stereome,  $\times 84$ .  
See also Pl. 43, figs. 3
7. *Stylophyllopsis rudis* (EMMRICH, 1853), p. 127. NHMW 1982/56/32<sub>2</sub>, transverse section of one of the septal spines showing a sigmoid core blade composed of a row of fibre bundles, now recognizable in traces, and lateral bundles poorly individualized,  $\times 134$
8. *Stylophyllum polyacanthum* REUSS, 1854, p. 119. GBA 1982/12/445, oblique section of the septal spine showing its completely recrystallized, smooth, light core (C) accompanied by elongate bundles of fibres (arrow),  $\times 53$
9. *Stylophyllum paradoxum* FRECH, 1890, p. 121. GBA 1982/12/519, transverse section of the septal spine with a core ornamented with protruding tops of well individualized bundles of fibres (arrows),  $\times 84$

Figs. 1, 2, 8, 9: Fischerwiese. Figs. 3–7: Kesselwand-Rohrmoos

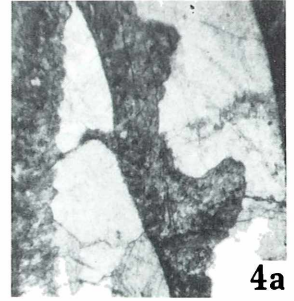




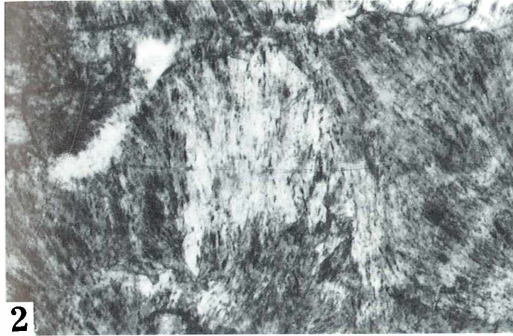
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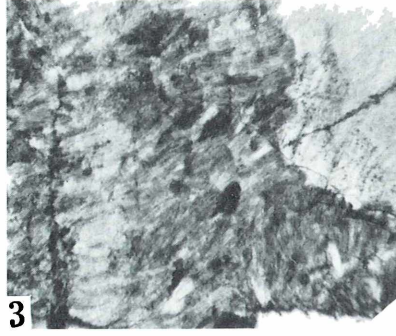
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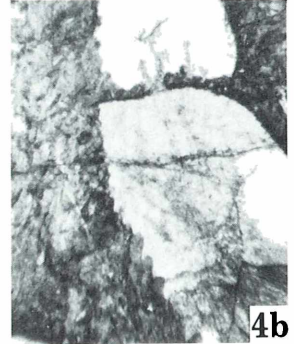
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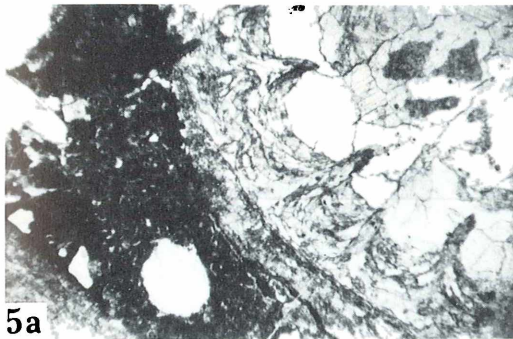
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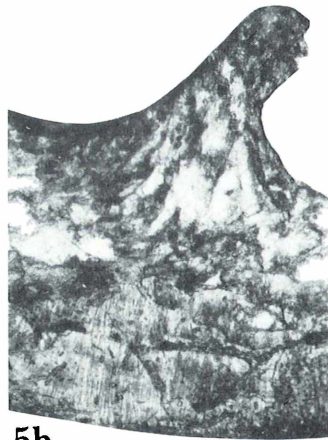
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4b



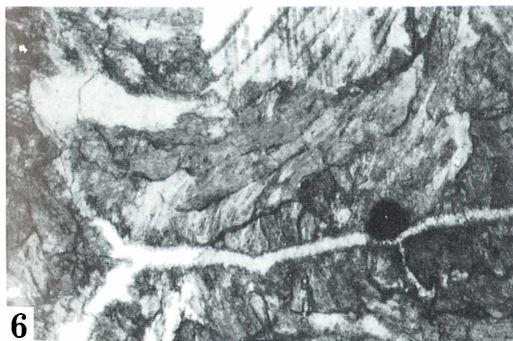
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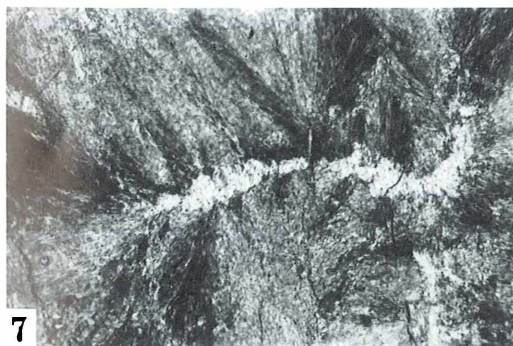
5b



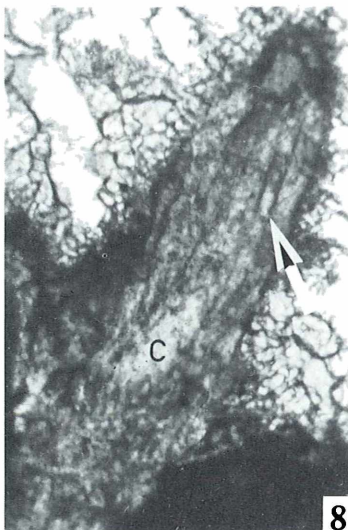
4c



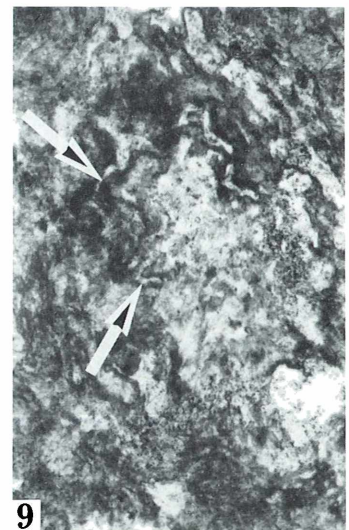
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9

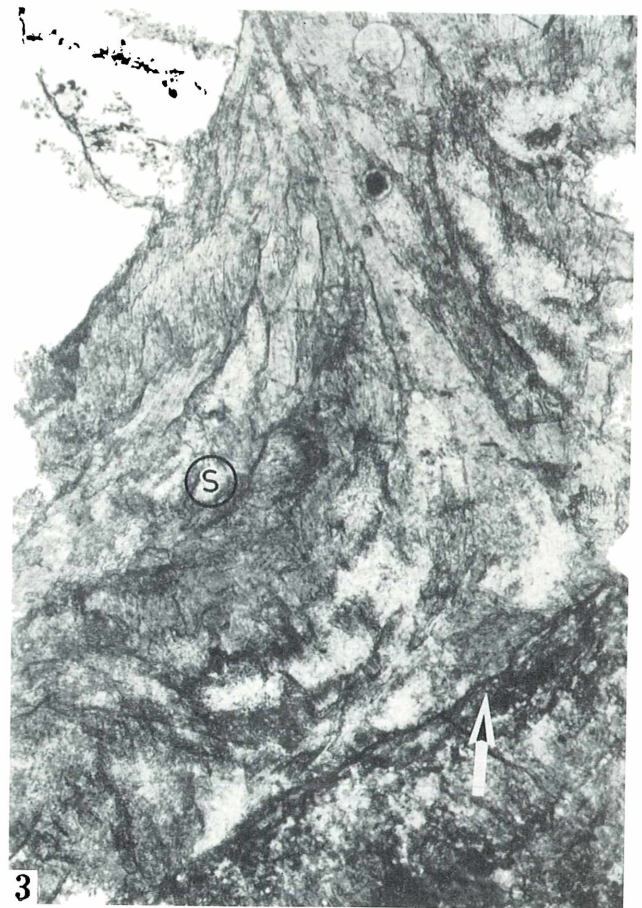
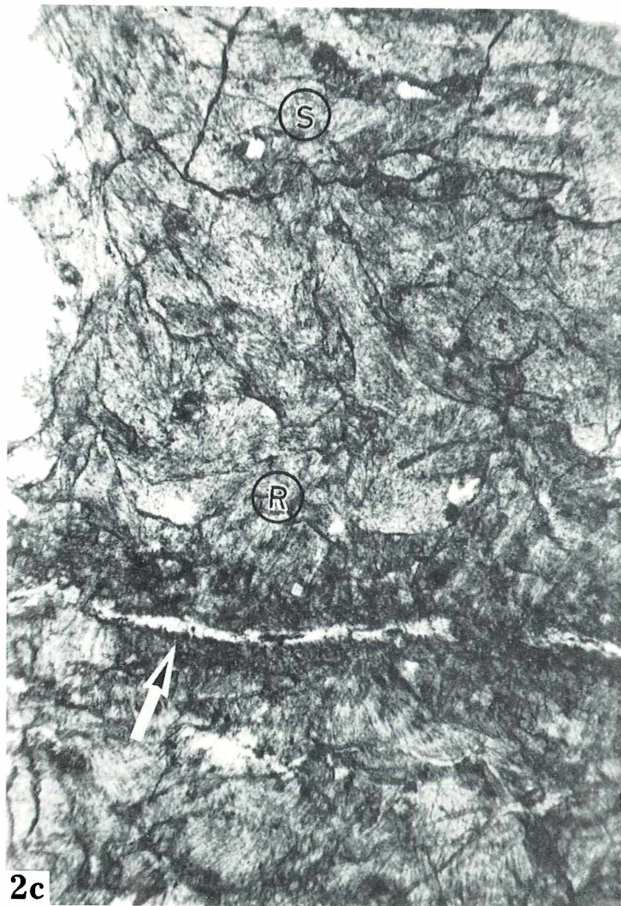
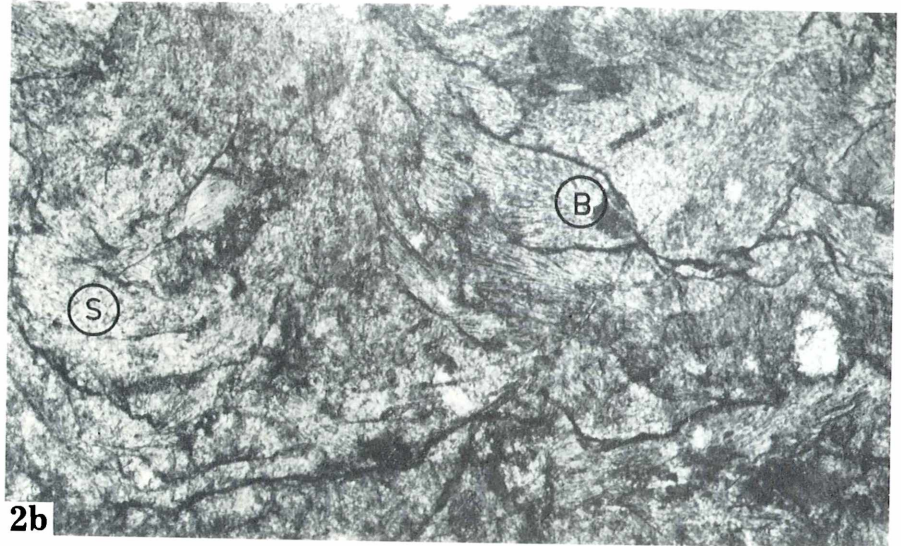
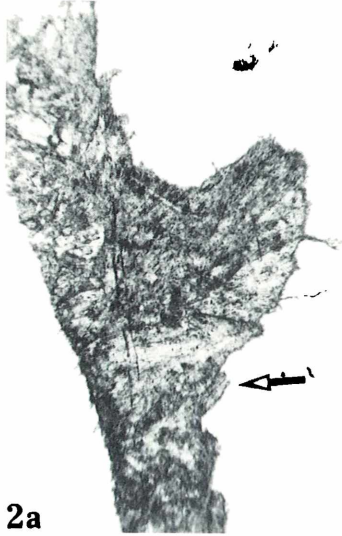
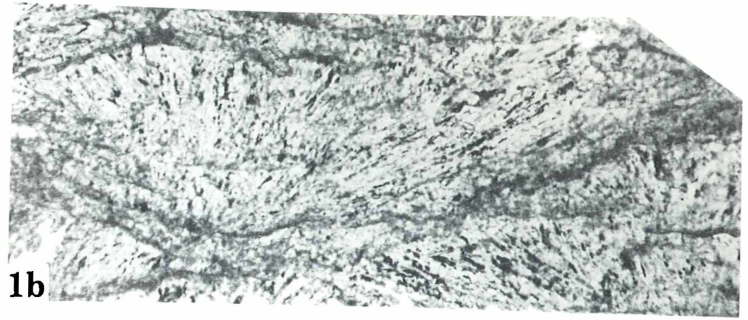
PLATE 43

Figs. 1–3: Stylophyllid microstructure (continued from Pl. 42)

1. *Gigantostylis epigonus* FRECH, 1890, p. 139. GBA 1982/12/543, 1 a – transverse section of the wall showing stereomal squamae built of fanwise arranged fibres,  $\times 134$ , 1 b – a detail,  $\times 228$
2. *Stylophyllum vesiculatum* sp. n., p. 120 NHMW 1982/56/34, 2 a – longitudinal section cutting the septal spine developed on the dissepimental surface; note the characteristic micro-ornamentation of the skeleton surface, produced by tops of fibre bundles (arrow),  $\times 84$ , 2 b – transverse section of the wall showing scaly (S) and bundle-like (B) units of stereome organization,  $\times 142$ , 2 c – transverse section at the wall region with a boundary fissure between corallites (arrow) and a fibrous stereome arranged peripherally into longitudinal ridges (R) and internally – in scaly units (S),  $\times 142$   
See also Pl. 42, figs. 4
3. *Pinacophyllum parallelum* FRECH, 1890, p. 137. NHMW 1982/56/19, transverse section of the wall showing well preserved original structure of the internal wall layer,  $\times 142$ . Note a sharp line between two wall layers (arrow), stereomal squamae (S) and a large septal spine (right) built of a bundle of long, parallel fibres.

Fig. 1: Fischerwiese. Fig. 2: Kesselwand-Rohrmoos. Fig. 3: Schneckengraben











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