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# Scleractinian corals (Anthozoa) from the lower Oligocene (Rupelian) of the Eastern Alps, Austria

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*ABSTRACT - In the Werlberg Member (Rupelian pro parte) of the Paisslberg Formation (Eastern Alps), an assemblage of colonial corals of eleven species pertaining to eleven genera and eleven families was identified:* Stylocoenia carryensis*,* Acropora lavandulina*, ?*Colpophyllia *sp.,* Dendrogyra intermedia*,* Caulastraea pseudoflabellum*,* Hydnophyllia costata*,* Pindosmilia *cf.* brunni*,* Actinacis rollei*,* Pavona profunda*,* Agathiphyllia gregaria*, and* Faksephyllia faxoensis*. This is the first Oligocene coral assemblage reported from the Paisslberg Formation (Werlberg Member) of the Eastern Alps, consisting exclusively of colonial forms. The assemblage represents the northernmost fauna of reefal corals reported to date for Rupelian time.*

*The Werlberg Member accumulated during marine transgression onto a truncated succession of older carbonate rocks. The corals grew as isolated colonies and in carpets in a protected shoreface setting punctuated by high-energy events. Coral growth forms comprise massive to sublamellar forms, and branched (dendroid, ramose) forms. The coral fauna is dominated by forms with medium- to large size corallites 4 to >10 mm in diameter. The assemblage consists of stress-resistant genera widespread in the Eocene to Miocene of central and southern Europe, Central America, and the Caribbean Islands. On the species level, closest correspondence is with faunas of southern Europe, especially with those of northern Italy (Lessini Shelf). On the genus-level, greatest affinities are with the lower Oligocene faunas of northern Italy (Lessini Shelf). Regarding similarities to other lower Oligocene faunas, seven genera have also been reported from Jamaica, Germany (Reit im Winkel), and Slovenia, and five genera were found in Greece. Ten (91%) of the described Austrian coral taxa from the Paisslberg Formation were found elsewhere in (sub)tropical reefal and peri-reefal settings. The caryophylliine coral* Faksephyllia faxoensis*, however, stands out as the only taxon which, in addition, has been reported from deep-water environments.*

## INTRODUCTION

In the Eastern Alps, Oligocene shallow neritic deposits are very rarely preserved. During the Rupelian, the northern molasse foredeep was connected with the Mediterranean by seaways along both the western and eastern end of the emergent Alpine-Carpathian arc (Popov et al., 2004). Along the southern slope of the Alps and their foreland, Rupelian coral locations are much more common, and range from Slovenia in the East (Nebelsick et al., 2000; Silvestri et al., 2011) via the Lessini Shelf in the center (e.g., Geister & Ungaro, 1977; Frost, 1981; Bosellini & Trevisani, 1992; Bosellini & Stemann, 1996) to Piedmont, Liguria and southern France in the West (e.g., Pfister, 1985; Quaranta et al., 2009; Vannucci et al., 2010).

Scleractinian corals from the lower Oligocene (Rupelian) have been reported from various localities worldwide, most notably from reef structures in the Caribbean/Central America (Duncan, 1863, 1868; Vaughan, 1900, 1919; Frost & Langenheim, 1974; Frost et al., 1983; Stemann, 2004) and from localities throughout the Mediterranean Tethys (northern Italy: Catullo, 1856; d'Achiardi, 1866, 1868; Barta-Calmus, 1973; Reuss, 1868, 1869; Angelis d'Ossat, 1894; Prever, 1922; Pfister, 1980a, b; Frost, 1981; Bosellini, 1988; Bosellini & Trevisani, 1992; Fravega et al., 1994; Budd & Bosellini, 2016; Spain: Álvarez et al., 1993; Libya: Hladil et al., 1992; Slovenia: Reuss, 1864; Silvestri et al., 2008; southern France: Chevalier, 1956, 1962; Hungary: Hegedüs, 1962; Greece: Marcopoulou-Diacantoni et al., 1996; Schuster, 2002c; Kołodziej & Marcopoulou-Diacantoni, 2003; Turkey: Islamoglu, 2008; southern Germany: Reis, 1889).

In addition, lower Oligocene scleractinian coral occurrences that are characterised by either reefal or non-reefal associations have been described from various localities in central, eastern, and western Europe (Germany [excluding southern areas]: Kühn, 1954; Glibert, 1974; Bulgaria: Bontscheff, 1897; Ukraine: Sokolow, 1894; England: Duncan, 1866); Asia (Indonesia: Santodomingo, 2014; Iran: Reuter et al., 2009; Myanmar: Vredenburg, 1921; United Arab Emirates: Gameil & Aly, 2001); the Americas (USA: Vaughan, 1900; Durham, 1942, 1943; Weisbord, 1973; Dockery, 1982; Peru: Wells, 1941); and the Pacific (Marshall Islands: Wells, 1964; New Zealand: Squires, 1958, 1962); Antarctica (Stolarski & Taviani, 2001).

With respect to lower Oligocene scleractinians, no reports were known from the Paisslberg Formation, Eastern Alps. A first documentation of Rupelian corals (Sanders & Baron-Szabo, 2007) was followed by a description of *Faksephyllia faxoensis* (Beck in Lyell, 1837) identified in that assemblage (Baron-Szabo, 2016). The present paper, in turn, provides the first taxonomic description of the entire Rupelian coral fauna collected from the Tyrolian outcrops Wimpissinger and Entfelden.

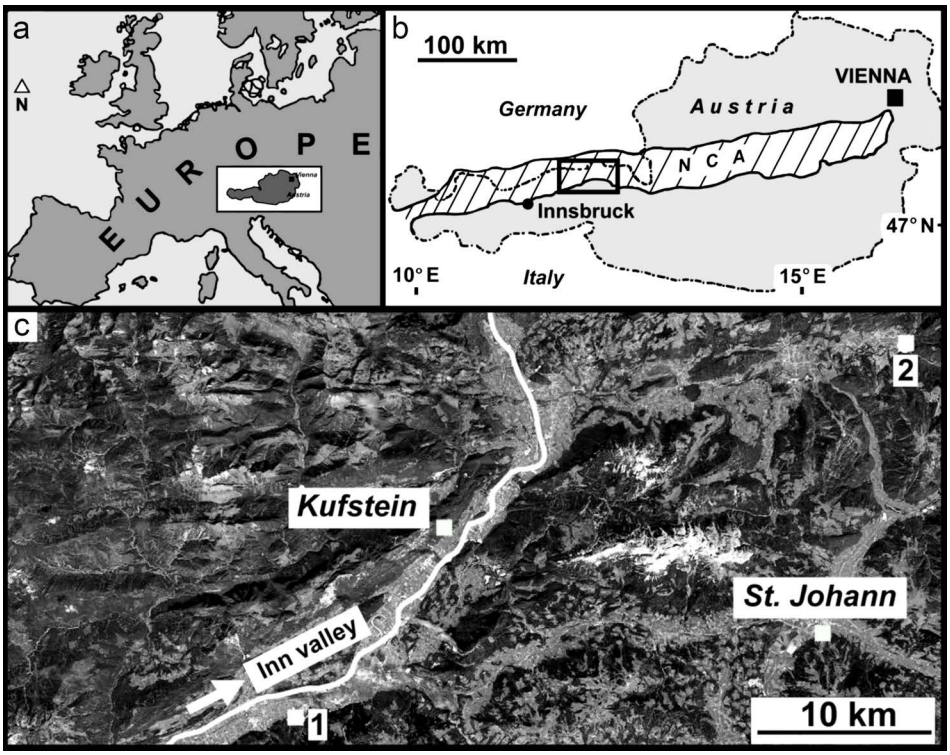



Fig. 1 - a) Location of study area. b) Close-up of Fig. 1a. The two quarries from which the material was collected are in the box. Coordinates of quarry Wimpissinger: 47.467235/12.014900; coordinates of quarry Entfelden: 47.674201/12.492871; coordinates in WGS 1984 decimal notation. NCA = Northern Calcareous Alps. c) Aerial view of study area outlined by box in Fig. 1b (Location 1: Wimpissinger; Location 2: Entfelden).

## MATERIAL, METHODS AND ABBREVIATIONS

The Oligocene succession had been mapped in the field on a scale of 1:10,000 by staff of the Institute of Geology of the University of Innsbruck (Gruber, 1995; Ortner & Stingl, 2001). One of us (DS), in turn, had logged and sampled sections at selected locations (Fig. 1). A total of 80 polished slabs and 61 large thin sections provided documentation of lithologies. For determination of corals, in a total of 34 specimens, structures identified on the upper surface of hand specimens as well as features seen in 19 thin sections were used.

The material used in this work is housed at the Department of Geology, University of Innsbruck, Austria (Institut für Geologie, Universität Innsbruck, Österreich), acronym ICPUIBK.

Symbols used in the synonymies and descriptions are: * = first description of taxon to which the assignment of specimen refers; v = material was studied by author (RBS).

## SETTING

The coral-bearing succession is located in the Northern Calcareous Alps (NCA, part of Eastern Alps), a belt of thrust nappes dominated by Triassic shallow-water carbonate rocks (e.g., Brandner, 1984; Mandl, 1999) (Fig. 1). During the early Oligocene, orogenesis led to surface uplift of the Alpine-Carpathian arc as a peninsula (e.g., Popov et al., 2004; Handy et al., 2015). During the Rupelian, the study area was located on the northern shelf of that peninsula, at ~43°N latitude (Popov et al., 2004). In the study area, marine transgression over subaerially exposed carbonate-rocky terrain resulted in a mixed carbonate-lithic/biogenic nearshore setting inhabited by the corals described herein. The thickness of the corresponding sedimentary succession, the Werlberg Member of the Paisslberg Formation (cf. Ortner & Stingl, 2001), ranges from less than a meter to typically a few meters. A Rupelian age of the Werlberg Member of the Paisslberg Formation is indicated by the co-presence of *Nummulites* ex gr. *vascus* Joly & Leymerie, 1848, *N. fichteli* Michelotti, 1841 and *Amphistegina* (Nebelsick et al., 2001). Above the Werlberg Member, the neritic marls of the Paisslberg Formation are dated into the Rupelian by nannofossils and by benthic foraminifera (e.g., Löffler, 1999; Ortner & Stingl, 2001; Scherbacher et al., 2001). Up-section, the Paisslberg Formation is overlain by the Unterangerberg Formation that was age-dated to the Chattian. Today, the coral-bearing Oligocene deposits are preserved in numerous erosional relicts each a few hundreds of meters to a few kilometers in lateral extent. The transgressive surface along the base of the Werlberg Member is deeply and densely macrobored and colonised by encrusters (e.g., serpulids), to a degree that renders it difficult even in thin section to identify the boundary between Triassic rocks and the overlying Oligocene limestones. In addition, lithoclasts up to boulder-size within the transgressive succession are similarly deeply bored and may show complex encrustations. Branched corals, in turn, typically are coarsely fragmented and toppled. The corals grew as isolated colonies and in

open carpets. Coral growth forms comprise massive-hemispherical to sublamellar-encrusting forms, and branched (dendroid, phaceloid, fasciculate, ?subreproid, ramose) forms (Tab. 1). No coral fabric was observed that would suggest a biohermal development. Together, the evidence suggests that the corals thrived in a rocky to pebbly shoreface environment of overall low energy, and devoid of siliciclastic input, but that was punctuated by episodic high-energy events (Baron-Szabo & Sanders, 2018).

## CORAL FAUNA

*Diversity*

The Werlberg coral fauna consists of 11 species belonging to 11 genera living in a rocky to pebbly shoreface environment of overall low energy that was subjected to episodic high-energy events. Similar environments have been described from various time periods. In the present Florida Bay, depending on location, coral assemblages consist of up to five colonial taxa (*Porites*, *Siderastrea*, *Cladocora*, *Solenastrea*), and the mobile form *Manicina areolata* (Linnaeus, 1758) (Ginsburg, 1972), each of a high resilience to ecostress (cf. Sanders & Baron-Szabo, 2005). In tidal channels between the Florida Bay and the shelf, coral assemblages consist of eight species pertaining to four genera (Abbott, 1975). In Puerto Rico, in Oligocene shelf reefs (thickets, small patch reefs) considered as "sediment-stressed" by Frost et al. (1983, p. 13-15), seven species belonging to five colonial coral genera are present. In the Rupelian of the Lessini Shelf, "pioneer" coral assemblages in areas of substantial terrigenous input consist of nine to eleven genera (two of 11 genera are of questionable affiliation; no species determined) (Frost, 1981). Similarly, within the Castelgomberto Formation

| Austrian species | Polyp integration, polypar size* | Colony shape | Austrian occurrences | | Stratigraphic ranges | Geographic distribution in the lower Oligocene | Distribution outside the lower Oligocene |
|---|---|---|---|---|---|---|---|
| | | | WIM | EN | | | |
| | | | | | | | |
| ***Acropora lavandulina* (Michelin, 1842)** | plocoid, small | columnar, ramose | X | X | Eocene-middle Miocene | Austria, Bulgaria, France, Indonesia | Eocene of Italy, middle Eocene of France, lower Miocene of Egypt, France, and Portugal, lower-middle Miocene of Italy |
| ***Actinacis rollei* Reuss, 1864** | plocoid, small | multicolumnar, submassive, lamellar | X | X | upper Eocene-upper Oligocene | Austria, Germany, Italy, Slovenia | upper Eocene of Hungary and Italy, upper Oligocene of Iran and Libya |
| ***Agathiphyllia gregaria* (Catullo, 1852)** | plocoid, medium to large | massive, small hemispherical | | X | upper Eocene-lower Miocene | Austria, Bulgaria, Germany, Greece, Hungary, Italy, Libya, Slovenia | upper Eocene and lower Miocene of Italy |
| ***Caulastraea pseudoflabellum* (Catullo, 1852)** | phaceloid-subflabellate, medium to large | branching | X | | Eocene- lower Oligocene | Austria, Germany, Bulgaria, Hungary, Italy | Eocene of Italy and Spain, middle Eocene of Slovenia, upper Eocene of Germany and Hungary |
| **?*Colpophyllia* sp.** | meandroid, medium to large | massive | X | | lower Oligocene | Austria | ------- |
| ***Dendrogyra intermedia* Michelotti, in Sismonda, 1871** | meandroid, small to medium | massive | X | | lower Oligocene | Austria, Italy | ------- |
| ***Faksephyllia faxoensis* (Beck in Lyell, 1837)** | phaceloid, subdendroid, fasciculate, small to medium | arborescent, bushy | X | | Paleocene-Oligocene | Austria, Germany, ?Hungary, Italy | Paleocene of Austria, Azerbaijan, Denmark, and Sweden, ?Eocene of Bosnia-Herzegovina |
| ***Hydnophyllia costata* (Catullo, 1856)** | meandroid-subthamnasterioid, medium to large | massive | | X | Oligocene | Austria, Italy | upper Oligocene of Italy |
| ***Pindosmilia* cf. *brunni* Chevalier in Brunn et al., 1955** | subdendroid (-?subreproid), large | branching | | X | Oligocene | Austria, Greece | possibly upper Oligocene of Greece |
| ***Pavona profunda* Reuss, 1868** | thamnasterioid-submeandroid, large | submassive | | X | Oligocene | Austria, Italy | upper Oligocene of France |
| ***Stylocoenia carryensis* Chevalier, 1962** | cerioid, small | massive, encrusting | | X | lower Oligocene-lower Miocene | Austria | lower Miocene of France |

Tab. 1 - Coral species identified in quarries Wimpissinger (WIM) and Entfelden (EN), characteristics of their skeletal elements, and their stratigraphic and geographic ranges; *(corallite size: small = 2 mm or less; medium = >2 to 10 mm; large = >10 mm).

(Rupelian) of the Lessini Shelf, Bosellini & Trevisani (1992) determined a total of 11 genera (species not determined for each genus) of colonial corals. Thus, in view of the shoreface environment inhabited (Sanders & Baron-Szabo, 2018), which represents a comparable high-stress ecosystem to scleractinian corals, the 11/11 genera/species composition of the Werlberg coral fauna ranges near the documented high-diversity end of nearshore assemblages.

*Morphology*

The fauna consists of exclusively colonial forms of three general categories of polyp integration, none of which is dominant: cerioid to plocoid forms (four species), meandroid to thamnasterioid forms (four species), and branching forms (three species) (Tab. 1). With regard to polypar size, the fauna is distinctly dominated by forms with medium to large corallites (4 to >10 mm in diameter), including the meandroid-thamnasterioid and the branching groups as well as the plocoid *Agathiphyllia gregaria* (Catullo, 1852) (73%). In contrast, only corals of the plocoid-cerioid group (with the exception of *Agathiphyllia gregaria*), are characterised by small corallites (~2 mm in diameter) (27%). Coral growth forms are comprised of massive to sublamellar morphotypes, and branched (dendroid, ramose) forms (Tab. 1). With regard to the latter growth forms, comparisons of coral assemblages before and after heavy, prolonged stress from saltation and turbidity indicates that the assemblage became dominated by both massive meandroid forms (Dodge & Vaisnys, 1977) and by ramose-branched forms *Madracis* and *Oculina* (Dryer & Logan, 1978). In environments of intermittently rapid sedimentation mobile meandroid corals (*Manicina, Trachiphyllia*) are also common (Gill & Coates, 1977). Recent *Acropora* shows vertical growth rates of up to about 10 cm/yr, thus preventing choking by sediment, and is able to disperse by fragmentation. The (sub)meandroid corals with polypars of medium to large size (*Pavona*, *Dendrogyra*, *Colpophyllia*) probably were similar to the extant *Diploria* which is an efficient sediment rejecter able to thrive very shallow subtidal habitats. The branched types with small to medium (*Faksephyllia*) and medium to large polypars (*Caulastraea*), respectively, closely correspond to recent *Cladocora* and similar forms (Baron-Szabo, 2016, tab. 2), i.e., rapidly-growing pioneer corals colonising new substrata (Barnes & Hughes, 1988). The subdendroid *Pindosmilia* with closely adjacent, medium to large polypars corresponds to recent genera such as *Astroides*, *Balanopsammia*, and *Dichopsammia*, which typically thrive in waters less than 30 m in depth (Cairns, 2001; Baron-Szabo & Cairns, 2019). Finally, with its very "plastic" skeleton and high tolerance to sediment input, the extinct *Actinacis* was among the most ecoresilient corals ever (cf. Sanders & Baron-Szabo, 2005). From that it can be concluded that the determined coral genera were forms resilient to ecostress.

*Stratigraphic and paleobiogeographic distribution*

The colonial coral assemblage described herein is the first one from the Paisslberg Formation, which belongs to the northern shelf of the emerging Alpine-Carpathian arc. The assemblage represents the northernmost coral fauna reported to date for Rupelian time (cf. Perrin & Bosellini, 2012, fig. 7). As mentioned, the location corresponds to a paleolatitude of ~43°N. Today, the northernmost assemblage of colonial corals thrives at 34°N (Tateyama, Japan) (Veron, 1992); this non-reefal assemblage, as well as coral reefs growing to > 30°N, are sustained by northward flow of warm oceanic surface waters in the Kuroshio western boundary current (Veron & Michin, 1992; Ikeda et al., 2006). This indicates that, although the Rupelian is characterised by global cooling relative to the late Eocene, colonial corals still could range to distinctly higher northern latitudes than today.

All of the Austrian species had their first appearance in the Paleogene (Tab. 1). Five of the 11 taxa (= 45%) had their first appearance before the Oligocene (Paleocene or Eocene); six taxa (= 55%) are new in the lower Oligocene (Tab. 1). The majority of the species (eight taxa = 73%) did not cross the Paleogene-Neogene boundary. Only three species (27%) had their last occurrence in the Miocene, two of which first appeared during pre-Oligocene time periods (the plocoid species *Acropora lavandulina* [Michelin, 1842] and *Agathiphyllia gregaria*), and the third, the cerioid taxon *Stylocoenia carryensis* Chevalier, 1962, which had its first appearance in the lower Oligocene. None of the Austrian species are known from strata younger than the Miocene.

With respect to their geographic distribution in the Oligocene, the Austrian taxa belong to species that are subcosmopolitan (*Acropora lavandulina*), geographically restricted to the Mediterranean Tethys (eight species = 73%), or endemic and restricted to the Austrian localities described in the current paper (two species = 18%), (= the meandroid ?*Colpophyllia* sp., reported from quarry Wimpissinger, and the single one cerioid taxon *Stylocoenia carryensis*, found at quarry Entfelden) (Tab. 1). Closest correspondence is with faunas of southern Europe, especially with the ones of northern Italy (Lessini Shelf; eight species = 73%) (Tab. 1). The species of the Paisslberg Formation with the largest geographic distributions in the Oligocene all belong to plocoid species *Acropora lavandulina, Actinacis rollei* Reuss, 1864, and *Agathiphyllia gregaria* (three species = 27%), followed by the branching *Faksephyllia faxoensis* and *Caulastraea pseudoflabellum* (Catullo, 1852) (two species = 18%). Four species (36%) are known only from one additional lower Oligocene southern European locality: the branching species *Pindosmilia* cf. *brunni* Chevalier in Brunn et al., 1955, and the (sub-)thamnasterioid to meandroid taxa *Dendrogyra intermedia* Michelotti, in Sismonda (1871), *Hyndophyllia costata* (Catullo, 1856), and *Pavona profunda* Reuss, 1868 (Tab. 1).

With regard to their stratigraphic distributions, seven species (= 64%) either occurred only during the Eocene-Oligocene or were restricted to the Oligocene (*Actinacis rollei*, *Caulastraea pseudoflabellum*, ?*Colpophyllia* sp., *Dendrogyra intermedia*, *Hydnophyllia costata*, *Pindosmilia* cf. *brunni*, *Pavona profunda*) (Tab. 1). The branching *Faksephyllia faxoensis* (Paleocene-Oligocene) and the plocoid-ramose *Acropora lavandulina* (Eocene-middle Miocene) have by far the largest stratigraphic distributions as both species have been reported from strata spanning a time range of around 40 My. The meandroid species ?*Colpophyllia* sp. and *Dendrogyra intermedia* have the shortest stratigraphic distribution. Their occurrence is restricted to the lower Oligocene (Tab. 1).

| Austrian species | Environmental occurrences | References* |
|---|---|---|
| | | |
| ***Acropora lavandulina*** | shallow subtidal, carpet, small coral patch or fringing reefs | Cahuzac & Chaix (1993); Wilson (1995); Schuster (2002b) |
| ***Actinacis rollei*** | reef, buildup, carpet, or bioherm, shallow subtidal, lagoonal | Pfister (1980, 1985); Frost (1981); Bosellini & Russo (1988); Bosellini & Trevisani (1992); Nebelsick et al. (2000) |
| ***Agathiphyllia gregaria*** | reef, buildup, bioherm, carpet, shallow subtidal, lagoonal | Pfister (1980); Frost (1981); Bosellini & Trevisani (1992); Nebelsick et al. (2000); Silvestri et al. (2011) |
| ***Caulastraea pseudoflabellum*** | mainly reef, buildup, or bioherm, carpet, shallow subtidal | Pfister (1980, 1985); Frost (1981); Bosellini & Trevisani (1992) |
| ***?Colpophyllia* sp.** | genus occurs mainly in reef, buildup, carpet, or bioherm, shallow subtidal | Pfister (1980); Bosellini & Trevisani (1992); Schuster (2002c); Johnson (2007) |
| ***Dendrogyra intermedia*** | coral carpets, fan delta systems | Pfister (1980); Silvestri et al. (2008) |
| ***Faksephyllia faxoensis*** | shallow (incl. lagoonal)- to deep-water (300 m depth); often in coral thickets, bioherms, carpets | Floris (1972); Frost (1981); Bernecker & Weidlich (1990, 2005); Bosellini & Trevisani (1992); Baron-Szabo (2016) |
| ***Hydnohyllia costata*** | carpet, patch reefs, inner platform | Budd & Bosellini (2016) |
| ***Pindosmilia* cf. *brunni*** | reef, buildup, carpet, bioherm, shallow subtidal | Brunn et al. (1955) |
| ***Pavona profunda*** | reef, buildup, carpet, bioherm, subreefal structure with hermatypic and ahermatypic corals | Frost (1981); Bosellini & Trevisani (1992); Cahuzac & Chaix (1993); Chaix & Cahuzac (2001) |
| ***Stylocoenia carryensis*** | reef, buildup, carpet, shallow subtidal | Chevalier (1962) |

Tab. 2 - Environmental occurrences of the Austrian species, *including environmental information concerning the Austrian localities of the current paper (unpublished data; and herein).

With regard to the distributional pattern in the lower Oligocene, on the genus-level, the Austrian corals belong to mainly subcosmopolitan genera (*Acropora*, *Actinacis*, *Agathiphyllia*, *Caulastraea*, *Colpophyllia*, *Pavona*, and *Stylocoenia*; seven genera = 64%), and, to a minor extent, taxa that are very restricted geographically (*Dendrogyra*, *Faksephyllia*, *Hydnophyllia*, and *Pindosmilia*; four genera = 36%) (Tab. 3). Greatest affinities are with the faunas of northern Italy (Lessini Shelf) (ten genera = 91%). Regarding similarities to other lower Oligocene faunas, eight genera (= 73%) were also described from Germany (Reit im Winkel) and Slovenia, seven genera (= 64%) were reported from Jamaica, and five genera (= 46%) were found in Greece (Tab. 3).

| | Caribbean/ Central America | | | | Europe | | | | | | | | | | | Africa | | Asia | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Coral genera** | **Antigua & Barbuda** | **Haiti** | **Jamaica** | **Mexico** | **Austria** | **Bulgaria** | **England** | **France** | **Germany** | **Greece** | **Hungary** | **Italy** | **Slovenia** | **Spain** | **Turkey** | **Libya** | **Somalia** | **Indonesia** | **Iran** |
| ***Acropora*** | X | X | X | | X | X | X | X | X | | | X | X | | X | | | X | |
| ***Actinacis*** | | X | X | | X | | | | X | X | | X | X | X* | | | X* | | |
| ***Agathiphyllia*** | | | X | X | X | X | | | X | X* | | X | X | | X | X | | | |
| ***Caulastraea*** | X | | X | | X | X | | | X | | X | X | X | | | | | | X |
| ***Colpophyllia*** | | | X | X | X | | | | | X | | X | X | | | | | | |
| ***Dendrogyra*** | | | | | X | | | | | | | X | | | | | | | |
| ***Faksephyllia*** | | | | | X | | | | X | | ? | X | | | | | | | |
| ***Hydnophyllia*** | | | | | X | | | | X | | | X | X | | | | | | |
| ***Pindosmilia*** | | | | | X | | | | | X* | | | | | | | | | |
| ***Pavona*** | | | X | | X | | | | X | X | | X | X | | | | | | |
| ***Stylocoenia*** | | | X | | X | | | X | X | | X | X | X | X | X | X | X | | X |

Tab. 3 - Distribution in the lower Oligocene of the coral genera found in Austria. *might also include upper Oligocene sediments at this location (data from Paleobiology Database: https://paleobiodb.org/#/ current paper; and unpublished data from database RBS).

With respect to phylogenetic ancestry, the fauna consists of a mix of mainly genera that appeared during the Paleogene (*Acropora*, *Agathiphyllia*, *Caulastraea*, *Dendrogyra*, *Faksephyllia*, *Hydnophyllia*, *Pindosmilia*, *Pavona*, and *Stylocoenia*) with a small number of Mesozoic hold-over taxa (*Actinacis* and *Colpophyllia*).

With regard to their environmental occurrences, all of the taxa have been found elsewhere in shallow-water, (sub) tropical reefal and peri-reefal settings. The caryophylliine coral *Faksephyllia faxoensis,* however, stands out as the only taxon which, in addition, has been reported from deep-water environments (Tab. 2).

As mentioned, the Werlberg coral fauna is most similar to faunas of the Lessini Shelf. In view of the paleogeographic distribution of land and seaways, this suggests that the carbonate environments along the southern fringe of the Alpine edifice were the crucial reservoir for coral recruitment to the northern shelf.

## SYSTEMATIC PALEONTOLOGY

*Taxonomic framework*

The taxonomic framework followed here is based on the works by Milne Edwards & Haime (1857), Vaughan & Wells (1943), Beauvais (1981), and Baron-Szabo (2014, 2018; and new herein) for higher-level taxa (family), with updates on individual genera and species by Pfister (1980a), Beauvais (1982), Bosellini (1988, 1998), Cahuzac & Chaix (1993), Wallace (2008), Budd & Bosellini (2016), and Baron-Szabo (2003, 2016).

### Order Scleractinia Bourne, 1900
### Family Acroporidae Verrill, 1902

#### Genus *Acropora* Oken, 1815

Type species *Millepora muricata* Linnaeus, 1758, Recent, Moluccas, subsequent designation by Verrill (1901).

*Diagnosis* - See Wallace (2008).

#### *Acropora lavandulina* (Michelin, 1842)
(Pl. 1, figs 1-3)

v *1842 *Madrepora lavandulina*, N. - Michelin, p. 67, Pl. 14, fig. 2a-b [chronotypic material from this location studied].
1927 *Acropora lavandulina* Michelin n. sp. 1842 - Felix, pars 33, p. 464 (cum syn.).
2008 *Acropora lavandulina* (Michelin, 1840) - Wallace, p. 327, Fig. 12.1-3.
2014 *Acropora lavandulina* (Michelin, 1840) - Santodomingo, p. 105-107, Fig. 21A-E (cum syn.).

*Dimensions* - Diameter (lumen) of radial corallites: up to 0.8 mm; diameter (lumen) of axial corallites: 1-1.8 mm; distance of corallite centers: 1-2.2 mm; septa/corallite: 12-24.

*Description* - Corallum ramose (corymbose), branches generally circular; plocoid; radial corallites tubular, protuberant, circular in outline, embedded in a porous to reticulate coenosteum; septa arranged in two to three cycles in six systems.

*Type locality* - Middle Eocene of France.

*Distribution* - Eocene of Italy, middle Eocene-lower Miocene of France, lower Oligocene of Austria (quarries Entfelden and Wimpissinger; this paper), Bulgaria (Haskovo), and Indonesia, lower Miocene of Egypt and Portugal, lower-middle Miocene of Italy.

*Material* - ICPUIBK-EN 8-VI; -WIM 1; -WIM 6/6-III; -WIM 6/10-II; -WIM 6/11-III; -WIM 6/12-II; -WIM 6/14-II; -WIM 6/23-II.

### Family Astrocoeniidae Tomes, 1883
(= Stylocoeniidae Alloiteau, 1952)

*Remarks* - In general, authors have credited the authorship of the family Astrocoeniidae to Koby (1889). However, the fact has been largely overlooked that Tomes (1883) already used the genus *Astrocoenia* to create the family-level taxon Astrocoeniinae, giving him priority of authorship of each family-level taxon based on this type genus.

#### Genus *Stylocoenia* Milne Edwards & Haime, 1848

Type species *Astrea emarciata* Lamarck, 1816, Eocene of France (designation by Milne Edwards & Haime, 1848a).

*Diagnosis* - See Álvarez Perez (1993).

*Synonyms* - *Hydnoseriatopora* Reig Oriol, 1990 (type species *Hydnoseriatopora viai* Reig Oriol, 1990; fide Álvarez Perez, 1993); *Stylophoropsis* Reig Oriol, 1988 (type species *Stylophoropsis renzii* Reig Oriol, 1988, Tertiary of northeastern Spain; fide Álvarez Perez, 1993); *Triphyllocoenia* d'Orbigny, 1849 (type species *Triphyllocoenia excavata* d'Orbigny, 1849, Eocene of France, Hautes-Alpes).

*Remarks* - According to Álvarez Perez (1993), the type material of the type species of the genera *Hydnoseriatopora* Reig Oriol, 1990 (= *Hydnoseriatopora viai* Reig Oriol, 1990) and *Stylophoropsis* Reig Oriol, 1988 (= *Stylophoropsis renzii* Reig Oriol, 1988) closely corresponds to *Stylocoenia taurinensis* (Michelin, 1842).

#### *Stylocoenia carryensis* Chevalier, 1962
(Pl. 2, fig. 4)

v *1962 *Stylocoenia carryensis* nov. sp. Chevalier, p. 126-127, Pl. 1, figs 1 and 6 [topotypes studied].

*Dimensions* - Corallite diameter (max, lumen): 1.2-1.5 mm, in areas of intense budding around 0.6 mm; corallite diameter (min, lumen): 0.8-1.2 mm, in areas of intense budding around 0.4 mm; septa/corallite: 12+s3.

*Description* - Massive to encrusting colony, cerioid; costosepta developed in two complete cycles in six systems, regularly alternating in length; a small number of S3 present in some corallites.

*Type locality* - Lower Miocene of France (Chainon de La Nerthe, Bouches-du-Rhône).

*Distribution* - Lower Oligocene of Austria (quarry Entfelden; this paper), lower Miocene of France.

*Material* - ICPUIBK-EN 8-V.

Family Faviidae Milne Edwards & Haime, 1857
(= Hemiporitidae Alloiteau, 1952, p.p.)

*Remarks* - Many authors have credited the authorship of the family Faviidae to Gregory (1900) who used the genus *Favia* at this family-level. It has been largely overlooked that Milne Edwards & Haime (1857) erected the taxon Faviacées (including its Latinised version of Faviaceae), which had been immediately accepted as a lower family-level taxon by subsequent authors (e.g., Étallon, 1859, Faviacées; d'Achiardi, 1866, Faviaceae; Duncan, 1884, Favioida; Solomko, 1888, Favioida). In addition, it was de Fromentel (1861) who first used the family-level Faviidae (in the French version of "Famille - Faviens"), clearly referring to the work by Milne Edwards & Haime (for discussion on the Faviidae and designation of its type genus *Favia*, see Baron-Szabo, 2018).

Genus *Colpophyllia* Milne Edwards & Haime, 1848

Type species *Madrepora gyrosa* Ellis & Solander, 1786 (= *Meandrina gyrosa* Lamarck, 1816), Recent, West Indies (genus designation by Milne Edwards & Haime, 1848b).

*Diagnosis* - See Budd & Johnson (1999).

?*Colpophyllia* sp.
(Pl. 1, fig. 4)

*Dimensions* - Diameter of corallite series (wall to wall): 3.5-11 mm; septa/mm: 11-13/5.

*Description* - Fragment of a massive, meandroid colony; septa developed in four-five size orders.

*Material* - ICPUIBK-WIM 6/11-II; -WIM 6/13-II; ?-WIM 6/25-I (all from the lower Oligocene of Austria; quarry Wimpissinger).

*Remarks* - Because the specimens represent colony fragments, the identification is provisional.

Genus *Hydnophyllia* Reis, 1889

Type species *Leptoria eocaenica* Reuss, 1864, Polschitza/Polšica near Oberburg, Steiermark/Gornji Grad, Slovenia, lower Oligocene (Rupelian).

*Diagnosis* - See Budd & Bosellini (2016).

*Hydnophyllia costata* (Catullo, 1856)
(Pl. 2, figs 9-10)

v *1856 *Meandrina costata* Cat. Catullo, p. 70, Pl. 15, fig. 1 [chronotypic material from this location studied].
v 2016 *Hydnophyllia costata* (Catullo, 1856) - Budd & Bosellini, p. 779-781, Fig. 5A-I [chronotypic material from this location studied] (cum syn.).

*Dimensions* - Diameter of corallite series (wall to wall): 10-14 mm, in areas of intense budding around 6 mm; septa (isolated corallites): 20-24; septa/mm: 11-14/10.

*Description* - Massive, meandroid colony; corallite centers distinct, connected by up to four lamellar linkages; small number of isolated corallites present; costosepta developed in three size orders, irregularly alternating in length and thickness.

*Type locality* - Oligocene of Italy (Castelgomberto).

*Distribution* - Oligocene of Italy (Crosara, Castelgomberto, Monteviale, Montecchio Maggiore, Vicenza: Rupelian; Castro: Chattian).

*Material* - ICPUIBK-EN 8-I.

Family Meandrinidae Gray, 1847

Genus *Dendrogyra* Ehrenberg, 1834

Type species *Maeandra (Dendrogyra) cylindrus* Ehrenberg, 1834, Antilles, Holocene (originally described as subgenus, raised to genus-level by Milne Edwards & Haime, 1848a).

*Diagnosis* - Genus is in need of revision. Here, genus characterisation by Milne Edwards & Haime (1857) is followed.

*Dendrogyra intermedia* Michelotti in Sismonda, 1871
(Pl. 1, figs 5-6)

*1871 *Dendrogyra intermedia* Michttl. Michelotti in Sismonda, p. 73, Pl. 6, fig. 2.
1925 *Dendrogyra intermedia* Sismonda, 1871 - Felix, pars 28, p. 36.

*Dimensions* - Corallite diameter (arranged in meandroid series): 3-6.5 mm; corallite diameter (isolated corallites): 2-3 mm; septa/mm: 6-8/5.

*Description* - Massive, meandroid colony with corallites arranged mainly in sinuous series; isolated corallites very rare; costosepta developed in six size orders, arranged highly irregularly.

*Type locality* - Lower Oligocene of Italy (Sassello).

*Distribution* - Lower Oligocene of Austria (quarry Wimpissinger; this paper) and Italy.

*Material* - ICPUIBK-WIM 6/18.

Family Merulinidae Milne Edwards & Haime, 1857

Genus *Caulastraea* Dana, 1846

Type species *Caulastraea furcata* Dana, 1846, Recent, Fiji.

*Diagnosis* - See Pfister (1980a).

*Remarks* - Recently, *Caulastraea* was compared with genera that are closely related morphologically (Baron-Szabo, 2016, tab. 2).

*Caulastraea pseudoflabellum* (Catullo, 1852)
(Pl. 1, fig. 7)

v *1852 *Lithodendron pseudoflabellum*, nob. Catullo, p. 21-22, Pl. 2, fig. 3a-c [topotypes studied].
v 1852 *Lithodendron fusinieri*, nob. Catullo, p. 22, Pl. 3, fig. 2 [topotypes studied].
1966 *Calamophyllia pseudoflabellum* Catullo - Kolosváry, p. 194-195, Figs 9-10.
v 1980a *Caulastraea pseudoflabellum* (Catullo, 1852) - Pfister, p. 65-67, Pl. 5, figs 1-3 (cum syn.).
v 1988 *Caulastrea pseudoflabellum* (Catullo) - Bosellini, p. 132, Pl. 3, fig. 2 [chronotypic material from this location studied] (cum syn.).
non 2002c *Caulastraea pseudoflabellum* (Catullo, 1852) - Schuster, p. 94, Pl. 4, fig. 3.

*Dimensions* - Great diameter of corallites: 7-9 mm; small diameter of corallites: 5-6 mm; septa/corallite: 32-48.

*Description* - Fragments of phaceloid colony; corallites are subcircular to subflabellate in outline; septa slightly wavy to sinuous, developed in three to four size orders, regularly alternating in length and thickness; up to around 15 septa reach corallite center where their axial ends often fuse with columella.

*Type locality* - Lower Oligocene of Italy (Vicenza).

*Distribution* - Eocene of Italy, middle Eocene of Slovenia, upper Eocene of Germany (Eisenrichterstein), Hungary, and Italy (Nago Limestone), lower Oligocene of Austria (quarry Wimpissinger; this paper), Bulgaria (Haskovo), Germany, Hungary, and Italy.

*Material* - ICPUIBK-WIM 6/6-I; -WIM6/10-I; -WIM-6/17-I.

*Remarks* - In having corallite diameters of up to 17 mm and septa developed in up to five (or ?six) size orders, the material described from the lower Oligocene of Greece (Schuster, 2002c, pl. 4, fig. 3) differs from *C. pseudoflabellum* but closely corresponds to *C. farsis* Schuster, 2002a (pl. 6, figs 1-4) from the upper Oligocene of Iran. Therefore, it is excluded here.

Family Stylophyliidae Frech, 1890

Genus *Pindosmilia* Chevalier in Brunn et al., 1955

Type species *Pindosmilia brunni* Chevalier in Brunn et al., 1955, Oligocene of Greece.

*Diagnosis* - See Chevalier, in Brunn et al. (1955).

*Remarks* - According to Chevalier, in Brunn et al. (1955), the genus *Pindosmilia* is characterised by

EXPLANATION OF PLATE 1

Lower Oligocene corals from the Paisslberg Formation, Austria (quarries Wimpissinger and Entfelden) (color online).

Figs 1-3 - *Acropora lavandulina* (Michelin, 1842).
1 - Upper surface of colony, longitudinal view; quarry Entfelden, ICPUIBK-EN 8-VI; scale bar: 5 mm.
2 - Oblique view of branch, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/6-III; scale bar: 2.5 mm.
3 - Longitudinal view of branch, thin section; quarry Wimpissinger, ICPUIBK-WIM-6-/1-IV; scale bar: 1.5 mm.

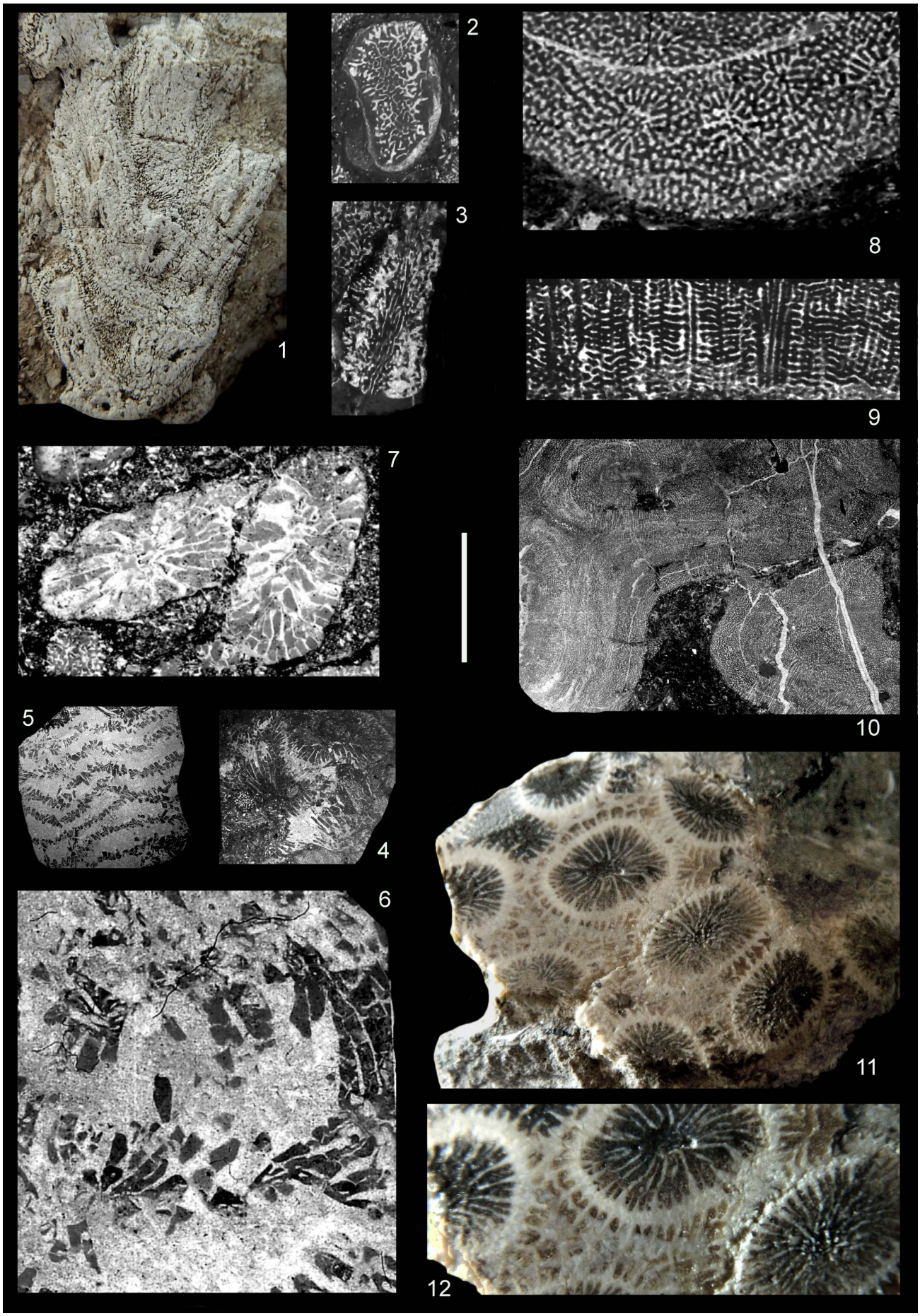
Fig. 4 - ?*Colpophyllia* sp.; cross view of colony, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/13-II; scale bar: 5 mm.

Figs 5-6 - *Dendrogyra intermedia* Michelotti in Sismonda, 1871.
5 - Cross view of colony, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/18; scale bar: 6 mm.
6 - Close-up of fig. 5; scale bar: 2.5 mm.

Fig. 7 - *Caulastraea pseudoflabellum* (Catullo, 1852); calicular view of colony fragment, slightly oblique, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/17-I; scale bar: 3 mm.

Figs 8-10 - *Actinacis rollei* Reuss, 1864.
8 - Calicular view of colony, thin section, close-up of fig. 10; scale bar: 1.5 mm.
9 - Longitudinal view of colony, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/6-II; scale bar: 2.5 mm.
10 - View of ramose to incrusting colony, thin section; quarry Wimpissinger, ICPUIBK-WIM-6/20; scale bar: 6.5 mm.

Figs 11-12 - *Agathiphyllia gregaria* (Catullo, 1852).
11 - Calicular view of colony, partially polished; quarry Entfelden, ICPUIBK-RIW; scale bar: 7 mm.
12 - Close-up of fig. 11; scale bar: 3 mm.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extracalicular budding and plocoid polyp integration. However, based on the original illustrations of the type specimen (Brunn et al., 1955, pl. 9, figs 1-3), both lamellar linkages and remains of a common wall formerly enclosing at least two corallites are present typical of corallites that formed by intracalicular budding (see Brunn et al., 1955, pl. 9, fig. 1). In addition, the longitudinal view of the type material (Brunn et al., 1955, pl. 9, fig. 2) clearly shows some corallites in branching (subdendroid and ?reptoid) arrangement.

*Pindosmilia* cf. *brunni* Chevalier in Brunn et al., 1955
(Pl. 2, figs 5-7)

*1955 *Pindosmilia brunni* nov. sp. Chevalier in Brunn et al., p. 200-201, Pl. 9, figs 1-3.
non 2002c *Pindosmilia brunni* nov. sp. Chevalier, 1955 - Schuster, p. 93-94, Pl. 4, figs 1-2.

*Dimensions* - Great diameter of corallite: 11-15 mm; small diameter of corallite (min): 8-11 mm; distance of corallite centers: 15 mm; septa/corallite: 48 to around 60.

*Description* - Fragment of subdendroid (-?subreptoid) colony, produced by extracalicular budding; septa arranged in four complete cycles in six systems; S5 present to absent; up to 12 septa reach corallite center; corallites stand off of each other at angles of up to 90°.

*Type locality* - Oligocene of Greece (Pentalofon).

*Distribution* - Oligocene of Greece, lower Oligocene of Austria (quarry Entfelden; this paper).

*Material* - ICPUIBK-EN 8-III.

*Remarks* - In the original description of the type material by Chevalier in Brunn et al. (1955), the corallite diameter is given as 20-30 mm. However, as can be seen in the original illustrations of the type specimen (Brunn et al., 1955, pl. 9, figs 1-3), the range given by Chevalier does not include (?juvenile) corallites of around 10-15 mm. Because the Austrian material is a colony fragment, the total dimensions of its skeletal elements cannot be determined. Its range of corallite diameters corresponds to the small (?juvenile) corallites seen in the type material of *Pindosmilia brunni.*

In forming a solitary corallum that has a septotheca, the material described from the upper Oligocene of Greece (Doutsiko) in Schuster (2002c) rather corresponds to the genus *Syzygophyllia* Reuss and is, therefore, excluded here. The reasons for the author to assume that it could be a part of a colonial form remain unclear. Nevertheless, the presence of a septothecal wall in the material from Doutsiko excludes it from *Pindosmilia* which is characterised by a wall that is mainly parathecal.

Family Actinacididae Vaughan & Wells, 1943

Genus *Actinacis* d'Orbigny, 1849

Type species *Actinacis martiniana* d'Orbigny, 1849, upper Santonian of France (Figuères).

*Diagnosis* - See Beauvais (1982) and Baron-Szabo (2003).

*Actinacis rollei* Reuss, 1864
(Pl. 1, figs 8-10)

v *1864 *Actinacis Rollei* Reuss, p. 27-28, Pl. 8, fig. 6a-b [topotypes studied].
non 1874 *Porites polystyla* nov. sp. - Reuss, p. 40-41, Pl. 56, figs 1-3.
non 1914 *Actinacis Rollei* Reuss - Oppenheim, p. 164-170, Pl. 3, fig. 4.
non 1937 *Actinacis* n. sp. cfr. *delicata* Rss - Zuffardi-Comerci, p. 289-290, Pl. 26, fig. 6.
v 1967 *Actinacis rollei* Reuss - Kolosváry, p. 211, Fig. 7 [chronotypic material from this location studied].
non 1992 *Actinacis rollei* Reuss, 1864 - Darga, p. 76, Pl. 7, fig. 5; Pl. 15, fig. 4.
1992 *Actinacis* cf. *rollei* Reuss, 1864 - Hladil, Otava & Galle, p. 1403 and p. 1407, Pl. 1, figs 1-2.
v 1995 *Actinacis rollei* Reuss, 1864 - Bosellini & Russo, p. 120-123, 125, Pl. 2, figs 1-6; Pl. 3, fig. 1; Text-figs 2-3 [chronotypic material from this location studied] (cum syn.).
non 2001 *Actinacis rollei* Reuss, 1864 - Gameil & Aly, p. 164-167, Fig. 6.1-3.
2002a *Actinacis rollei* Reuss, 1864 - Schuster, p. 18-19.

*Dimensions* - Diameter of corallite: 1-1.5 mm; distance of corallite centers: 1.2-2 mm; septa/corallite: 14-22.

*Description* - Knobby, columniform, and encrusting colonies; corallites circular in outline, regularly disposed over the colony; septa equal in thickness, developed in unclear systems.

*Type locality* - Lower Oligocene of Slovenia (Gornji Grad/Oberburg; Gornji Grad Formation/Oberburg Beds).

*Distribution* - Upper Eocene of Hungary and Italy (Nago Limestone), lower Oligocene of Austria (quarry Wimpissinger; this paper), Germany (Reit im Winkel), Italy, and Slovenia, upper Oligocene of Iran and Libya.

*Material* - ICPUIBK-WIM-6/6-II; -WIM 6/10-II; -WIM 6/14-I; - WIM 6/17-II; -WIM 6/20; -WIM 6/26-I.

*Remarks* - In having cerioid to cerio-plocoid polyp integration and up to 24 septa, the material described from the Oligocene of southern France by Oppenheim (1914, pl. 3, fig. 4) differs from both the genus *Actinacis* (rather resembling a *Goniopora*) and the species *rollei*. In having 24 septa in corallites throughout the colony, the material described from the upper Eocene of Germany in Darga (1992, pl. 7, fig. 5; pl. 15, fig. 4) differs from *A. rollei*. In having corallite diameters of up to 2 mm and up to 24 septa (in contrast to the information given in the description [18-20 septa] but seen in the illustrations) the material described from the lower Oligocene of the United Arab Emirates in Gameil & Aly (2001, fig. 6.1-3) differs from *A. rollei*. The material described as *Porites polystyla*

Reuss from the Oligocene of Italy which was grouped with *A. delicata* (here considered as a junior synonym of *A. rollei*) in Oppenheim (1914) and also was included in the list of synonyms of *A. rollei* by subsequent authors (e.g., Felix, 1925; Bosellini & Russo, 1995), differs from *A. rollei* in having both generally 24 septa and corallites that are 1.5-2 mm in diameter (dimensions as provided in the original description and illustrations in Reuss, 1874). In having 24 septa and corallites that are 1 mm in diameter, the material described as *Actinacis* cf. *delicata* from the Oligocene of Somalia (Zuffardi-Comerci, 1937) (*A. delicata* is here considered as a junior synonym of *A. rollei*) differs from *A. rollei*. Therefore, they are excluded from the synonymy of *A. rollei*.

Family Agariciidae Gray, 1847
(= Lamellofungiidae Alloiteau, 1957)

Genus *Pavona* Lamarck, 1801

Type species *Madrepora cistata* Ellis & Solander, 1786, Red Sea, Holocene
(subsequent designation Vaughan, 1918).

*Diagnosis* - See Pfister (1980a).

*Pavona profunda* (Reuss, 1868)
(Pl. 2, figs 3-4)

*1868 *Mycedium profundum* nov. sp. Reuss, p. 179, Pl. 16, fig. 2a-b.
2001 *Pavona (Pavona) profunda* (Reuss, 1868) - Chaix & Cahuzac, p. 22-23, Pl. 4, fig. 1.

*Dimensions* - Width of corallite series: 7-10 mm; diameter of isolated corallites: 4-7 mm; distance of corallite centers (same series): 6-10 mm, in areas of intense budding the distance is around 3 mm; septa/mm: 10-12/5.

*Description* - Submassive, thamnasterioid-submeandroid colony with mainly distinct to subdistinct corallites; isolated corallites sparse; septa developed in four to five size orders, alternating in length and thickness; up to around 12 septa reach corallite center; columella small, usually fused with axial ends of septa.

*Type locality* - Lower Oligocene of Italy (Castelgomberto Formation).

*Distribution* - Lower Oligocene of Italy (Castelgomberto Formation) and Austria (quarry Entfelden; this paper), upper Oligocene of southern France.

*Material* - ICPUIBK-EN 8-II.

Family Agathiphylliidae Vaughan & Wells, 1943

Genus *Agathiphyllia* Reuss, 1864

Type species *Agathiphyllia explanata* Reuss, 1864, lower Oligocene of Slovenia (subsequent designation by Vaughan, 1919).

*Diagnosis* - See Pfister (1980a).

*Agathiphyllia gregaria* (Catullo, 1852)
(Pl. 1, figs 11-12)

v *1852 *Lobophyllia gregaria*, nob. Catullo, p. 27, Pl. 2, fig. 5a-b [topotypes studied].
v 1871 *Heliastraea apenninica* d'Ach. - Michelotti, in Sismonda, p. 49.
v 1889 *Cyathomorpha Rochettina* Michelin sp. - Reis, p. 147-150, Pl. 3, figs 17-19.
v 1980a *Agathiphyllia gregaria* (Catullo, 1852) - Pfister, p. 80-82, Pl. 13, fig. 1; Pl. 14, fig. 7 (cum syn.).
v 1988 *Agathiphyllia gregaria* (Catullo, 1852) - Bosellini, p. 150-153, Pl. 5, fig. 3a-b [chronotypic material from this location studied].
1992 *Agathiphyllia gregaria* (Catullo, 1852) - Hladil, Otava & Galle, p. 1403 and 1407, Pl. 2, Fig. 2.
non 2001 *Agathiphyllia gregaria* (Catullo, 1852) - Gameil & Aly, p. 175-178, Fig. 9.4-6.
2002c *Agathiphyllia gregaria* (Catullo, 1852) - Schuster, p. 98, Pl. 11, figs 1-2; Pl. 12, figs 1-4.

*Dimensions* - Great diameter of corallites (lumen): 7.5-14 mm; small diameter of corallites (lumen): 4.5-9 mm; distance of corallite centers: 7.5-20 mm; septa/corallite: 30 to around 60.

*Description* - Small (around 60 mm in diameter) submassive colony; corallites subcircular to very elongate in outline; septa developed in three to four complete cycles in six systems; some septa of S5 present in corallites having a great diameter (lumen) of around 9 mm or larger.

*Type locality* - Oligocene of Italy (Montecchio Maggiore).

*Distribution* - Upper Eocene (Nago Limestone)-lower Miocene of Italy (Montecchio Maggiore, Castelgomberto Limestone, Sassello, Dego, Colli Torino), lower Oligocene of Austria (quarry Entfelden, this paper), Bulgaria (Haskovo), Germany (Reit im Winkel), Hungary, Libya, and Slovenia, Oligocene of Greece (Mesolouri, Doutsiko).

*Material* - ICPUIBK-RIW.

*Remarks* - In having corallite diameters of up to 25 mm and a distance of corallite centers of up to 40 mm, the material described from the lower Oligocene of the United Arab Emirates in Gameil & Aly (2001, fig. 9.4-6) differs from *A. gregaria*. In having cerio-plocoid corallites with diameters ranging between 4 and 10 mm, and pennular structures, the material described as *Agathiphyllia rochettina* (here considered as a junior synonym of *A. gregaria*) from the lower Oligocene of the United Arab Emirates in Gameil & Aly (2001) differs from both the genus *Agathiphyllia* and the species *A. gregaria*. Therefore, these specimens are excluded here.

Family Caryophylliidae Dana, 1846
(= Caryophylliinae Milne Edwards & Haime, 1857; = Desmophylliinae Vaughan & Wells, 1943; = Parasmiliinae Vaughan & Wells, 1943; = Parasmiliidae Alloiteau, 1952)

*Remarks* - The classification system of the caryophylliids has long been discussed. Vaughan & Wells (1943) and Wells (1956) divided the Family Caryophylliidae into the six subfamilies Caryophylliinae, Turbinoliinae, Thecocyathinae, Desmophylliinae, Parasmiliinae, and Eusmiliinae. Chevalier & Beauvais (1987) treated these as distinct families, even adding a seventh family (Dasmiidae; type genus *Dasmia* Milne Edwards & Haime, 1848c, grouped with the Desmophylliinae in Vaughan & Wells, 1943). Cairns (1994; also see discussion in Cairns, 1997) elevated the subfamily Turbinoliinae to the family level but did not recognise the distinction of the other families or subfamilies, respectively. Likewise, Stolarski (1995) elevated the Thecocyathinae to family status. Recent molecular studies (Romano & Cairns, 2000) imply that the Caryophylliidae is an unnatural, or polyphyletic, family. Therefore, the recognition of subfamilies cannot be supported until further research is conducted. Based on the current understanding of this group, the genus *Faksephyllia* would be grouped with the Parasmiliinae (Baron-Szabo, 2016).

Genus *Faksephyllia* Floris, 1972

Type species *Caryophyllia faxoensis* Beck in Lyell, 1837, middle Danian of Denmark (Fakse limestone); neotype designation by Floris (1972).

*Diagnosis* - See Baron-Szabo (2016).

*Remarks* - From the Nielsen collection, Floris (1972, pl. 4, fig. 11) chose specimen MMH 2043 as the neotype of the type species *Faksephyllia faxoensis* (Beck in Lyell, 1837). This specimen was originally figured as a sketch in Nielsen (1922, pl. 1, fig. 1). Later, Floris (1972, pl. 4, fig. 11) presented the same specimen as a photograph. Recently, reproductions of both images were presented (Baron-Szabo, 2016, pl. 1, figs 1-2).

Floris (1972) mentioned that considerable effort was made to track down the original Beck/Lyell (Mineralogical Museum of Copenhagen University) material but without success.

Based on the presence of a sparsely developed endotheca; dendroid, fasciculate or phaceloid colony formation; compact costosepta that are smooth or have small (<50 µm) granules laterally; costae that are short or absent; and a corallite wall that can be a very thick septotheca, the genus *Faksephyllia* was grouped with the family Caryophylliidae (Baron-Szabo, 2016).

*Faksephyllia faxoensis* (Beck in Lyell, 1837)
(Pl. 2, figs 1-2)

| | | |
|---|---|---|
| *v | 1837 | *Caryophyllia faxoensis* Beck in Lyell, p. 249, Fig. 4 [topotypes studied]. |
| parsv | 1868 | *Rhabdophyllia tenuis* nov. sp. Reuss, p. 144, Pl. 2, fig. 4a-b (non figs 3 and 5). |
| | ? 1896 | *Rhabdophyllia tenuis* Reuss - Oppenheim, p. 262. |
| | ? 1912 | *Calamophyllia rosicensis* n. sp. - Oppenheim, p. 124, Pl. 16, fig. 7-7c. |
| v | 1972 | *Faksephyllia faxoensis* gen. n. & Beck, in Lyell, 1837 sp.- Floris, p. 73-80, Pl. 4, figs 7-11; Pl. 5, figs 1-5 [topotypes studied] (cum syn). |
| v | 2016 | *Faksephyllia faxoensis* (Beck, in Lyell, 1837) - Baron-Szabo, p. 529-533, Pl. 1, figs 1-13; Pl. 2, figs 1-15 (cum syn.). |

*Dimensions* - Diameter of corallite (monocentric): 2-6 mm, mainly ranging between 3.5-6 mm, in late budding stages often up to 8 mm, maximum size in a few places 10 mm; septa/corallite 18-52; height of branches: 10 to around 30 mm.

EXPLANATION OF PLATE 2

Lower Oligocene corals from the Paisslberg Formation, Austria (quarries Wimpissinger and Entfelden) (color online).

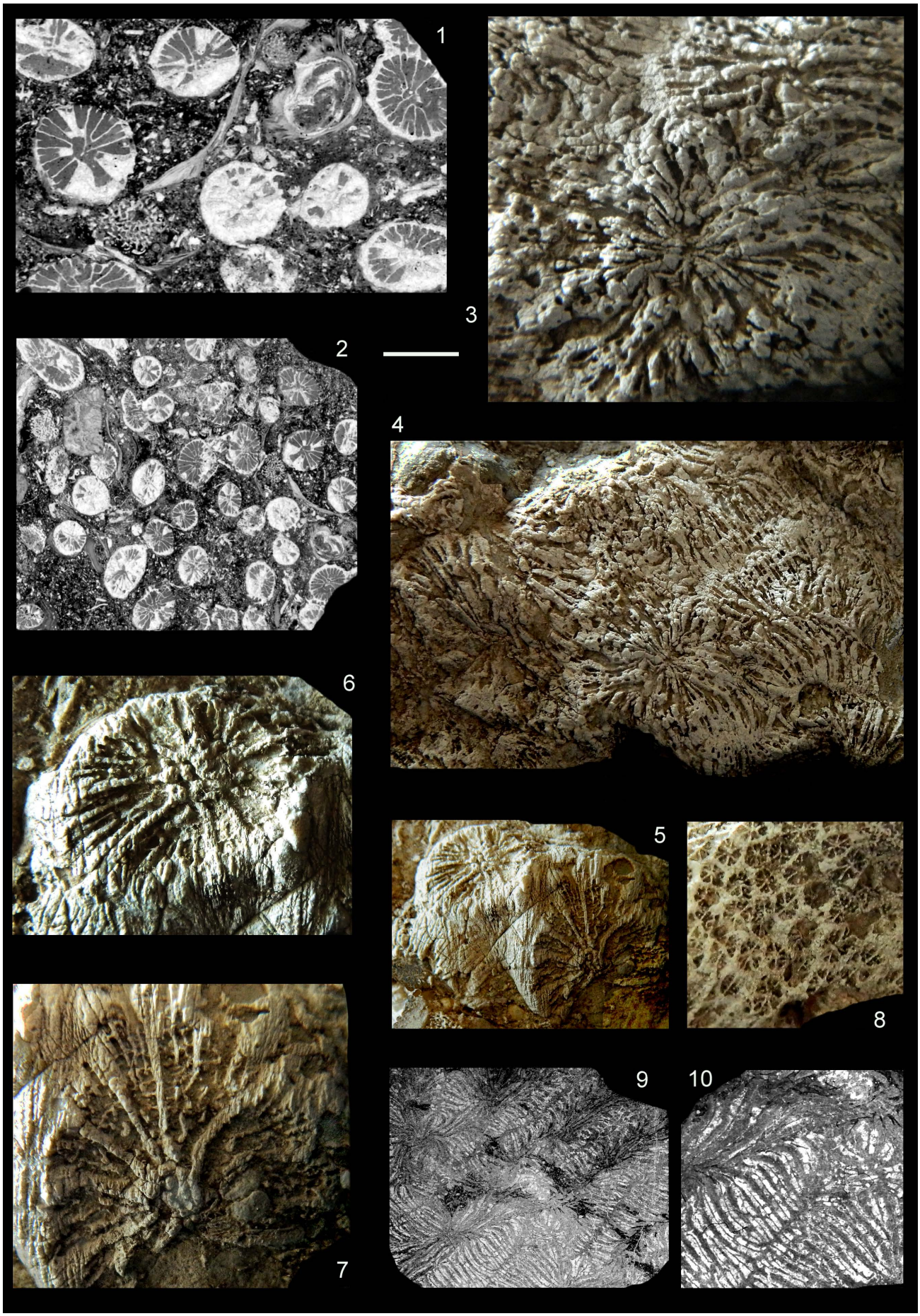
Figs 1-2 - *Faksephyllia faxoensis* (Beck in Lyell, 1837).
1 - Calicular view of colony, thin section, close-up of fig. 2, scale bar: 3.5 mm.
2 - Calicular view of colony; quarry Wimpissinger, ICPUIBK-WIM-6/12-I; scale bar: 8.5 mm.

Figs 3-4 - *Pavona profunda* Reuss, 1868.
3 - Calicular view of colony, close-up of fig. 4; scale bar: 3 mm.
4 - Upper surface of colony, calicular view; quarry Entfelden, ICPUIBK-EN 8-II; scale bar: 5.5 mm.

Figs 5-7 - *Pindosmilia* cf. *brunni* Chevalier in Brunn et al., 1955.
5 - Calicular view, close-up of fig. 7; scale bar: 3.5 mm.
6 - Calicular view, close-up of fig. 7; scale bar: 3.5 mm.
7 - Upper surface of colony, calicular view; quarry Entfelden, ICPUIBK-EN 8-III; scale bar: 6.5 mm.

Fig. 8 - *Stylocoenia carryensis* Chevalier, 1962; upper surface of colony, calicular view; quarry Entfelden, ICPUIBK-EN 8-V-II; scale bar: 3.5 mm.

Figs 9-10 - *Hydnophyllia costata* (Catullo, 1856).
9 - Cross view of colony, thin section; Entfelden, ICPUIBK-EN 8-I; scale bar: 9 mm.
10 - Close-up of fig. 9; scale bar: 5.5 mm.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*Description* - Phaceloid to subdendroid and fasciculate colony. Corallites circular to irregularly elliptical in outline. In corallites that are not influenced by budding, costosepta developed in two-four cycles in six systems. In corallites of 4 mm in diameter, around 40 septa are present. Septa straight or wavy, oldest of which reach corallite center where they sometimes fuse. Septa are equally thin or, in some corallites, oldest septa significantly increase in thickness towards the corallite wall, becoming up to around ten times as thick as youngest septa. Branching angle often between 30°-45°, can be up to 90°. Columella weakly to well developed, 1-2 mm in length, spongy-papillose or formed by a small number of twisted segments, or absent.

*Type locality* - Middle Danian of Denmark (Fakse limestone).

*Distribution* - Paleocene of Austria (Kambühel limestone, Styria), Azerbaijan (Dash-Salakhly), and Denmark (Greenland, Kangilia and Nugssuaq areas), Danian of Denmark (Fakse), Kazakhstan (Mangyshlag), and Sweden (Limhamn), ?Eocene of Bosnia-Herzegovina (Rošići area), lower Oligocene of Italy (Monte Pulgo and Castelgomberto, Vicenza area), Austria (quarry Wimpissinger), Germany (Reit im Winkel, Bavaria, Reiter beds), and ?Hungary.

*Material* - ICPUIBK-WIM 5; -WIM 6/2-II; -WIM 6/10-I and -IV; -WIM 6/12-I; -WIM 6/13-I; -WIM 6/23-I; -WIM 6/25.

*Remarks* - In forming phaceloid to subdendroid colonies and having corallite diameters ranging between 3 and 5 mm; number of septa between 20 and 30 that sometimes fuse in a way resembling the dendrophylliid and micrabaciid septal arrangements; trabecular extensions of axial ends of septa that form a pseudo-columella; and sparsely developed endotheca, the material described by Oppenheim (1912, pl. 16, fig. 7-7c) as *Calamophyllia rosicensis* from the Eocene of Bosnia-Herzegovina shows close affinities to *Faksephyllia faxoensis* (Beck). Because information regarding the budding mode is missing, the grouping of this taxon with *Faksephyllia* is only provisional. Oppenheim (1896) assigned material to *Rhabdophyllia tenuis* Reuss from the lower Oligocene of Hungary. Because the Reuss' material represents a mix of specimens that belong to various genera, it remains unclear whether or not the Hungarian material corresponds to *Faksephyllia*.

Based on the current taxonomic model (visit: www.corallosphere.org), *Faksephyllia* represents the earliest colonial caryophylliid (also see Baron-Szabo, 2016, tab. 1).

## CONCLUSIONS

The described Austrian coral fauna consists of at least eleven species from eleven genera of eleven families. Considering that approximately 20% of the coral fragments that could not be taxonomically assigned due to poor preservation, seemed to differ from the identified taxa (based on corallite integration and other skeletal elements), it is suggested that the actual taxonomic diversity of this lower Oligocene fauna is higher.

The fauna is represented only by colonial forms of three types of polyp integration, none of which is dominant: cerioid to plocoid; meandroid to thamnasterioid; and branched forms. Most of the species (73%) are characterised by medium- to large-size corallites 4 to >10 mm in diameter, including all of the meandroid-thamnasterioid and the branching groups, as well as the plocoid *Agathiphyllia gregaria*.

The corals grew as isolated colonies and in carpets in a low-energy shoreface seaward of a rocky to pebbly beach that was punctuated by high-energy events. Despite stressors typical of such habitats (e.g., seasonal temperature changes, salinity fluctuations), the fauna is quite diverse compared to both fossil and extant coral faunas reported from similar environments.

All of the described species first appeared in the Paleogene, but the majority (eight taxa = 73%) did not cross the Paleogene-Neogene boundary. None of the species is known from strata younger than the Miocene. On the species level, closest correspondence is with faunas of southern Europe, in particular with those of the Lessini Shelf (seven species = 64%). The species of the Paisslberg Formation with the largest lower Oligocene biogeographic distribution are plocoid (*Acropora lavandulina*, *Actinacis rollei*, and *Agathiphyllia gregaria*) and branching (*Caulastrea*, *Faksephyllia*).

On the genus-level, greatest paleobiogeographic affinity again is with the coral faunas of northern Italy: except for *Pindosmilia,* ten genera (91%) are also known from the Italian Lessini Shelf. Regarding similarities to other lower Oligocene faunas, eight genera (= 73%) were also described from both Germany (Reit im Winkel) and Slovenia, seven genera (= 64%) were reported from Jamaica, and five genera (= 46%) were found in Greece (Tab. 3). In view of the paleogeographic distribution of land and seaways, this suggests that the carbonate environments along the southern fringe of the Alpine edifice were the crucial reservoir for coral recruitment to the northern shelf.

With regard to their environmental occurrences, all of the taxa have been found elsewhere in shallow-water, (sub) tropical reefal and peri-reefal settings. The caryophylliine coral *Faksephyllia faxoensis,* however, stands out as the only taxon which, in addition, has been reported from deep-water environments.

The assemblage represents the northernmost coral fauna found in reefal and peri-reefal settings reported to date for Rupelian time.

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## REFERENCES

Abbott B.M. (1975). Implications for the fossil record of modern carbonate bank corals. *Geological Society of America Bulletin*, 86: 203-204.

Achiardi A. d' (1866). Corallarj fossili del terreno nummulitico dell'Alpi venete. *Memorie della Società Italiana di Scienze Naturali*, 2: 1-53.

Achiardi A. d' (1868). Corallarj fossili del terreno nummulitico dell'Alpi venete. Parte Seconda. *Memorie della Società Italiana di Scienze Naturali,* 4: 1-31.

Alloiteau J. (1952). Embranchment des Coelentérés. II. Madréporaires post-paléozoïques. *In* Piveteau J. (ed.), Traité de Paléontologie, 1: 539-684.

Alloiteau J. (1957). Contribution à la systématique des madréporaires fossiles. 462 pp. Centre National Recherche Scientifique, Paris.

Álvarez Perez G. (1993). Cnidaria Fòssils de la Conca d'Igualda. 261 pp. Universitat de Barcelona, Barcelona.

Álvarez Perez G., Busquets P., Vilaplana M. & Ramos-Guerrero E. (1993). Fauna coralina paleógena de las Islas Baleares (Mallorca y Cabrera, España). *Batalleria*, 3 [for 1989]: 61-63.

Angelis d'Ossat G. de (1894). I Corallarj dei terreni terziari dell'Italia settentrionale. Collezione Michelotti. Museo Geologico della R. Università di Roma. *Atti della Reale Accademia dei Lincei,* 5: 164-280.

Barnes R.S.K. & Hughes R.N. (1988). An Introduction to Marine Ecology. 351 pp. Blackwell Scientific, Oxford.

Baron-Szabo R.C. (2003). Taxonomie und ontogenie von scleractinen Korallen der ostalpinen Oberkreide (Hochmoos- und Grabenbachschichten, Gosau-Gruppe, Santon). *Jahrbuch der Geologischen Bundesanstalt,* 143: 107-201.

Baron-Szabo R.C. (2014). Scleractinian Corals from the Cretaceous of the Alps and Northern Dinarides (Helvetic Unit; Austro-Alpine Units; Rhenodanubian Unit; N Dinaric Platform; Inner Dinarides), with remarks on related taxa. *Abhandlungen der Geologischen Bundesanstalt Wien*, 68: 1-297.

Baron-Szabo R.C. (2016). New taxonomic, stratigraphic, and geographic information on the genus *Faksephyllia* Floris, 1972 (Scleractinia; Caryophylliidae); first records from the Oligocene of Austria, Germany, and Italy. *Zootaxa*, 4154: 526-540.

Baron-Szabo R.C. (2018). Nomenclatural notes on the genus *Favia* (Anthozoa: Scleractinia: Faviina: Faviidae). *Proceedings of the Biological Society of Washington*, 131: 197-201.

Baron-Szabo R.C. & Cairns S.D. (2019). Part F, Revised, Volume 2, Chapter 14: Systematic Descriptions of the Scleractinia Family Dendrophylliidae. *Treatise Online*, 119: 1-33.

Baron-Szabo R.C. & Sanders D. (2018). Scleractinian corals from the Lower Oligocene of the Eastern Alps, Austria: taxonomic composition, palaeoecology and palaeobiogeography - preliminary results. PANGEO Austria 2018, Vienna (Austria), 26.09.2018, Abstract: 6.

Barta-Calmus S. (1973). Revision de collections de madréporaires provenants du nummulitique du sudest de la France, de l'Italie et de la Yugoslavie septentrionales. 694 pp. PhD thesis, Université de Paris.

Beauvais L. (1981). Sur le taxinomie des Madréporaires mésozoïques. *Acta Pa1aeontologica Polonica*, 25: 345-360.

Beauvais M. (1982). Révision systématique des Madréporaires des couches de Gosau (Crétacé supérieur, Autriche). *Travaux du Laboratoire de Paléontologie des Invertébrés*, 2: 1-278.

Bernecker M. & Weidlich O. (1990). The Danian (Paleocene) coral limestone of Fakse, Denmark, a model for ancient aphotic, azooxanthellate coral mounds. *Facies*, 22: 103-138.

Bernecker M. & Weidlich O. (2005). Azooxanthellate corals in the Late Maastrichtian-early Paleocene of the Danish basin, bryozoan and coral mounds in a boreal shelf setting. *In* Freiwald A. & Roberts J.M. (eds), Cold-water Corals and Ecosystems, Springer-Verlag, Berlin-Heidelberg: 3-25.

Bontscheff St. (1897). Das Teriärbecken von Haskovo (Bulgarien). *Jahrbuch der Kaiserlich Königlichen Geologischen Reichsanstalt*, 46: 309-384.

Bosellini F.R. (1988). Oligocene corals from Monte Bastia (Vicentin Lessini Mountains, N Italy). *Atti e Memorie della Accademia Nazionale di Scienze Lettere e Arti di Modena*, serie VII, 5: 111-157.

Bosellini F.R. (1998). Diversity, composition and structure of Late Eocene shelf-edge associations (Nago Limestone, northern Italy). *Facies*, 39: 203-226.

Bosellini F.R. & Russo A. (1988). The Oligocene *Actinacis* coral community of the Southern Alps (Italy): Temperature vs. terrigenous control. *In* Choat J.H., Barnes D., Borowitzka M.A., Coll J.C., Davies P.J., Flood P., Hatcher B.G., Hopley D., Hutchings P.A., Kinsey D., Orme G.R., Pichon M., Sale P.F., Sammarco P., Wallace C.C., Wilkinson C., Wolanski E. & Bellwood O. (eds), Contributed Papers. *Proceedings of the 6th International Coral Reef Symposium*, 3: 385-391.

Bosellini F.R. & Russo A. (1995). The scleractinian genus *Actinacis*: systematic revision and stratigraphic record of the Tertiary species with special regard to Italian occurrences. *Rivista Italiana di Paleontologia e Stratigrafia*, 101: 215-230.

Bosellini F.R. & Stemann T. (1996). Autecological significance of growth form in the scleractinian *Actinacis rollei* Reuss (Oligocene, Lessini Mountains, Northern Italy). *In* Cherchi A. (ed.), Autecology of selected fossil organisms: Achievements and problems. *Bollettino della Società Paleontologica Italiana,* Special Volume 3: 31-43.

Bosellini F.R. & Trevisani E. (1992). Coral facies and cyclicity in the Castelgomberto Limestone (Early Oligocene, Eastern Lessini Mountains, Northern Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 98: 339-352.

Bourne G.C. (1900). Anthozoa. *In* Lankester E.R. (ed.), Treatise on Zoology, Volume 2, Adam & Charles Black, London: 1-84.

Brandner R. (1984). Meeresspiegelschwankungen und Tektonik in der Trias der NW-Tethys. *Jahrbuch der Geologischen Bundesanstalt*, 126: 435-475.

Brunn J.H., Chevalier J.-P. & Marie P. (1955). Quelques formes nouvelles de polypiers et de foraminiféres de l'Oligocène et du Miocène du NW de la Grèce. *Bulletin de la Société Géologique de France, 6e série*, 5: 193-202.

Budd A.F. & Bosellini F.R. (2016). Revision of Oligocene Mediterranean meandroid corals in the scleractinian families Mussidae, Merulinidae and Lobophylliidae. *Journal of Systematic Palaeontology*, 14: 771-798.

Budd A.F. & Johnson K.G. (1999). Neogene paleontology in the northern Dominican Republic 19. The family Faviidae (Anthozoa: Scleractinia). Part II. The genera *Caulastraea, Favia, Diploria, Thysanus, Hadrophyllia, Manicina*, and *Colpophyllia*. *Bulletins of American Paleontology*, 356: 1-83.

Cahuzac B. & Chaix C. (1993). Les faunes de coraux (Anthozoaires Scléractiniaires) de la façade atlantique française au Chattien et au Miocène. *Ciências da Terra*, 12: 57-69.

Cairns S.D. (1994). Scleractinia of the temperate North Pacific. *Smithsonian Contributions to Zoology*, 557: 1-150.

Cairns S.D. (1997). A generic revision and phylogenetic analysis of the Turbinoliidae (Cnidaria, Scleractinia). *Smithsonian Contributions to Zoology*, 591: 1-55.

Cairns S.D. (2001). A generic revision and phylogenetic analysis of the Dendrophylliidae (Cnidaria: Scleractinia). *Smithsonian Contributions to Zoology*, 615: 1-75.

Catullo T.A. (1852). Cenni sopra il terreno di sedimento superiore delle Provincie Venete e descrizione di alcune specie di polipai fossili ch'esso racchiude. *Memorie del Reale Istituto Veneto di Scienze, Lettere ed Arti,* 4: 1-44.

Catullo T.A. (1856). Dei terreni di sedimento superiore della Venezie e dei fossili Bryozoari, Antozoari e Spongiari. Angelo Sicca, Padova: 1-88.

Chaix C. & Cahuzac B. (2001). Une faune inédite de coraux scléractiniaires dans le gisement chattien d'Escornebéou (Landes, SW France); stratigraphie, systématique et paléoécologie. *Annales de Paléontologie*, 87: 3-47.

Chevalier J.-P. (1956). Les polypiers anthozoaires du Stampien de Gaas (Landes). *Bulletin de la Societe d'Histoire Naturelle de Toulouse*, 90: 375-410.

Chevalier J.-P. (1962). Recherches sur les Madréporaires et les Formations Récifales Miocènes de la Méditerranée Occidentale. *Mémoires de la Société Géologique de France*, 40: 1-562.

Chevalier J.-P. & Beauvais L. (1987) Systématique. *In* Grassé P.-P. & Doumenc D. (eds), Ordre des scléractiniaires, XI, Masson, Paris: 679-764.

Dana J.D. (1846). United States Exploring Expedition during the years 1838-1842 under the command of Charles Wilkes, U.S.N. Volume 7: Zoophytes. 740 pp. Sherman, Philadelphia.

Darga R. (1992). Geologie, Paläontologie und Palökologie der südostbayerischen unter-priabonen (Ober-Eozän) Riffkalkvorkommen des Eisenrichtersteins bei Hallthurm (nördliche Kalkalpen) und des Kirchbergs bei Neubeuern (Helvetikum). *Münchner Geowissenschaftliche Abhandlungen Reihe A: Geologie und Paläontologie,* 23: 1-166.

Dockery D.T. (1982). Lower Oligocene Bivalvia of the Vicksburg Group in Mississippi. *Mississippi Department of Natural Resources Bureau of Geology*, 123: 1-261.

Dodge R.E. & Vaisnys J.R. (1977). Coral populations and growth patterns: responses to sedimentation and turbitity associated with dredging. *Journal of Marine Research*, 35: 715-730.

Dryer S. & Logan A. (1978). Holocene reefs and sediments of Castle Harbour, Bermuda. *Journal of Marine Research*, 36: 399-425.

Duncan P.M. (1863). On the fossil corals of the West Indian Islands, Part I. *Quarterly Journal of the Geological Society of London,* 19: 406-458.

Duncan P.M. (1866). A Monograph of the British fossil corals, 2nd Series. VII. Corals from the Tertiary Formations. I. Corals from Brackenhurst and Roydon. *Palaeontographical Society,* Volume for 1865: 40-66.

Duncan P.M. (1868). On the fossil corals (Madreporaria) of the West-Indian Islands, Part IV, Conclusions. *Quarterly Journal of the Geological Society of London,* 24: 9-33.

Duncan P.M. (1884). A revision of the families and genera of the sclerodermic Zoantharia, Ed. and H., or Madreporaria (M. Rugosa excepted). *Journal of the Linnean Society of London, Zoology*, 18: 1-204.

Durham J.W. (1942). Eocene and Oligocene coral faunas of Washington. *Journal of Paleontology,* 16: 84-104.

Durham J.W. (1943). Pacific coast Cretaceous and Tertiary corals. *Journal of Paleontology,* 17: 196-202.

Ehrenberg C.G. (1834). Die Corallenthiere des rothen Meeres physiologisch Untersucht und systematisch Verzeichnet. Beiträge zur physiologischen Kenntniss der Corallenthiere im allegemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, volume for 1832: 225-380.

Ellis J. & Solander D.C. (1786). The Natural History of Many Curious and Uncommon Zoophytes Collected from Various Parts of the Globe. 208 pp. Benjamin White and Son and Peter Elmsly, London.

Étallon A. (1859). Études paléontologiques sur le Haut-Jura. Rayonnés du Corallien. *Mémoires de la Société d'Émulation du Département du Doubs, 3e série*, 6: 53-260.

Felix J.P. (1925). Anthozoa eocaenica et oligocaenica. Fossilium Catalogus I: Animalia, pars 28. 296 pp. Junk, Berlin.

Felix J. (1927). Anthozoa miocaenica. Fossilium Catalogus I: Animalia, pars 33, Junk, Berlin: 297-488.

Floris S. (1972). Scleractinian corals from the Upper Cretaceous and Lower Tertiary of Nugssuaq, West Greenland. *Muséum de Minéralogie et de Géologie de l'Université de Copenhague, Communications paléontologiques*, 183: 1-132.

Fravega P., Piazza M., Stockar R. & Vannucci G. (1994). Oligocene coral and algal reef and related facies of Valzemola (Savona, NW Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 100: 423-456.

Frech F. (1890). Die Korallenfauna der Trias. *Palaeontographica,* 37: 1-116.

Fromentel L.É.G. de (1861). Introduction à l'étude des Polypiers fossiles. *Mémoires de la Société d'Émulation du Département du Doubs*, 5: 1-357.

Frost H. (1981). Oligocene reef coral biofacies of the Vicentin, northeast Italy. *In* Toomey D.F. (ed.), European fossil reef models. *Society of Economic Paleontologists and Mineralogists, Special Publication,* 30: 483-539.

Frost S.H., Harbour J.L., Beach D.K., Realini M.J. & Harris P.M. (1983). Oligocene reef tract development, southwestern Puerto Rico. *Sedimenta*, 11: 1-107.

Frost S.H. & Langenheim R.L. (1974). Cenozoic Reef Biofacies. 388 pp. Northern Illinois Press, Dekalb.

Gameil M. & Aly M.F. (2001). Paleontological studies on some Oligocene colonial corals from Gabal Hafit (Al Ain area, UAE). *Middle East Research Center, Ain Shams University, Earth Science Series*, 15: 156-183.

Geister J. & Ungaro S. (1977). The Oligocene formations of the Colli Berici (Vicenza, northern Italy). *Eclogae Geologicae Helvetiae*, 70: 811-823.

Gill G.A. & Coates A.G. (1977). Mobility, growth patterns and substrate in some fossil and Recent corals. *Lethaia,* 10: 119-134.

Ginsburg R.N. (1972). South Florida Carbonate Sediments. *Sedimenta,* 2: 1-71.

Glibert M. (1974). Quelques Turbinoliidae Cenozoiques des collections de l'Institut Royal des Sciences Naturelles de Belgique, I: Genre *Turbinolia* Lamarck, 1816. *Bulletin Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre,* 50: 1-27.

Gray J.E. (1847). An outline of an arrangement of stony corals. *Annals and Magazine of Natural History, Series 1*, 19: 120-128.

Gregory J.W. (1900). The corals. *In* The Jurassic fauna of Cutch. *Memoirs of the Geological Survey of India, Palaeontologia Indica, Series IX*, 2: 1-195.

Gruber A. (1995). Öffnung und Schliessung von Tertiärbecken im Bereich des Eiberger Beckens (Unterinntal, Tirol). Ein strukturgeologischer Beitrag zur Unterinntaler Scherzone. 144 pp. Unpublished Diploma thesis, University of Innsbruck.

Handy M.R., Ustaszewski K. & Kissling E. (2015). Reconstructing the Alps-Carpathians-Dinarides as a key to understanding switches in subduction polarity, slab gaps and surface motion. *International Journal of Earth Sciences*, 104: 1-26.

Hegedüs G. (1962). Magyarorszägi oligocen korallok (Oligocene corals of Hungary). *Annual Report of the Hungarian Geological Instistute, from the year 1959*: 231-261.

Hladil J., Otava J. & Galle A. (1992). Oligocene Carbonate Buildups of the Sirt Basin, Libya. *Geology of Libya,* 4: 1401-1420.

Ikeda E., Iryu Y., Sugihara K., Ohba H. & Yamada T. (2006). Bathymetry, biota and sediments on the Hirota Reef, Tane-ga-shima — the northernmost coral reef in the Ryukyu Islands. *Island Arc*, 15: 407-419.

Islamoglu Y. (2008). Molluscan biostratigraphy and paleoenvironmental reconstruction of Oligocene deposits in the Denizli and Kale-Tava subbasinbs (SW Turkey). *Geodiversitas*, 30: 261-285.

Johnson K.G. (2007). Reef-coral diversity in the Late Oligocene Atigua Formation and temporal variation of local diversity

on Caribbean Cenozoic Reefs. *In* Hubmann B. & Piller W.E. (eds), Fossil Corals and Sponges. Proceedings of the 9th International Symposium on Fossil Cnidaria and Porifera. Österreichische Akademie der Wiisenschaften, Schritenreihe der Erdwissenschaftlichen Kommission, 17: 471-491.

Joly N. & Leymerie A. 1848. Memoire sur les *Nummulites*, considerees zoologiquement et geologiquement. *Memoire de l'Academie des Sciences de Toulouse* (3), 4: 149-218.

Koby F. (1889). Monographie des polypiers jurassiques de la Suisse (9). *Mémoires de la Société Paléontologique Suisse (=Abhandlungen der Schweizerischen Paläontologischen GesellIschaft),* 16: 457-586.

Kołodziej B. & Marcopoulou-Diacantoni A. (2003). Late Eocene-Oligocene corals from Evros (Thrace Basin, NE Greece). Abstracts of the 8th International Symposium on Fossil Cnidaria and Porifera, Graz, August 3-7, 2003. *Berichte des Institutes für Geologie und Paläontologie der Karl-Franzens-Universität Graz*, 7: 45.

Kolosvary G. (1966). Lutetian corals from Crni Kal in Yugoslavia. *Geologjia*, 10: 189-204.

Kolosvary G. (1967). Korallen und Balaniden aus den paläogenen Schichten Jugoslawiens [Corals and balanids from Paleogene beds of Yugoslavia]. *Geologija*, 10: 205-218.

Kühn O. (1954). Korallen des mitteldeutschen Mitteloligozäns. *Notizblatt des hessischen Landesamtes, Bodenforschung*, 82: 50-56.

Lamarck J.B.P. de (1801). Système des animaux sans vertèbres. 423 pp. Lamarck et Deterville, Paris.

Lamarck J.B.P. de (1816). Histoire naturelle des animaux sans vertèbres. 568 pp. Verdiére, Paris.

Linnaeus C. von (1758). Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 1, 10th edition. 824 pp. Holmiae, Stockholm.

Löffler S.-B. (1999). Systematische Neubearbeitung und paläoökologische Aspekte der unteroligozänen Molluskenfauna aus den Zementmergeln von Bad Häring (Unterinntal, Tirol). *Tübinger geowissenschaftliche Arbeiten A*, 54: 1-207.

Lyell C. (1837). On the Cretaceous and Tertiary Strata of the Danish Islands of Seeland and Möen. *Transactions of the Geological Society, London, series 2*, 5: 243-257.

Mandl G.W. (1999). The Alpine sector of the Tethyan shelf - Example of Triassic to Jurassic sedimentation and deformation from the Northern Calcareous Alps. *Mitteilungen der Österreichischen Geologischen Gesellschaft*, 92: 61-77.

Marcopoulou-Diacantoni A., Fountoulis J. & Lekkas E. (1996). The occurrence of Oligocene (Rupelian) corals in west-central Peloponnesus (Greece), paleoecological and paleobiogeographic significance. *Geologie Mediterraneenne*, 23: 11-25.

Michelin H. (1842). Iconographie zoophytologique. Description par localités et terrains des polypiers fossiles de France. Volume 2, Bertrand, Paris: 41-72.

Michelotti G. (1841). Saggio storico dei rizopodi caratteristici dei terreni sopracretacei. *Memorie di matematica e di fisica della Società Italiana delle Scienze Residente in Modena*, 22: 253-302.

Milne Edwards H. & Haime J. (1848a). Observations sur les polypiers de la famille des astréides. *Comptes Rendus de l'Académie des Sciences*, 27: 465-469.

Milne Edwards H. & Haime J. (1848b). Note sur la classification de la deuxième tribu de la famille des astréides. *Comptes Rendus de l'Académie des Sciences*, 27: 490-497.

Milne Edwards H. & Haime J. (1848c). Recherches sur les polypiers (2). Monographie des turbinolides. *Annales de Sciences Naturelles, Série 3, Zoologie*, 9: 211-344.

Milne Edwards H. & Haime J. (1857). Histoire naturelle des Coralliaires ou polypes proprement dits. Volume 2. 560 pp. Librairie Encyclopédique de Roret, Paris.

Nebelsick J., Bassi D. & Drobne K. (2000). Microfacies analysis and palaeoenvironmental interpretation of Lower Oligocene, shallow-water carbonates (Gornji Grad beds, Slovenia). *Facies*, 43: 157-176.

Nebelsick J., Rasser M. & Stingl V. (2001). Autochthonous facies and debris flows compared: Lower Oligocene carbonates of the Lower Inn Valley (Tyrol, Austria). *Facies*, 44: 31-45.

Nielsen F. (1922). Zoantharia from Senon and Paleocene in Denmark and Skaane. *Biologiske skrifter*, 8: 199-233.

Oken L. (1815). Lehrbuch der Naturgeschichte. III Zoologie. 850 pp. August Schmid und Comp., Leipzig-Jena.

Oppenheim P. (1896). Die oligocäne Fauna von Polschitza in Krain. *Bericht über die Senckenbergische Naturforschende Gesellschaft in Frankfurt am Main,* 1896: 259-283.

Oppenheim P. (1912). Neue Beiträge zur Eozänfauna Bosniens. *Beiträge zur Paläontologie und Geologie Österreich-Ungarns und des Orients*, 25: 87-149.

Oppenheim P. (1914). Über *Porites polystyla* Reuss und die Gattung *Actinacis*. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 65 [for 1913]: 159-180.

Orbigny A. d' (1849). Note sur des polypiers fossiles. 12 pp. Victor Masson, Paris.

Ortner H. & Stingl V. (2001). Facies and basin development of the Oligocene in the Lower Inn Valley, Tyrol/Bavaria. *In* Piller W.E. & Rasser M.W. (eds), Paleogene of the Eastern Alps. Österreichische Akademie der Wissenschaften, Schriftenreihe der Erdwissenschaftlichen Kommission, 14: 153-196.

Perrin C. & Bosellini F.R. (2012). Paleobiogeography of scleractinian reef corals: Changing patterns during the Oligocene–Miocene climatic transition in the Mediterranean. *Earth-Science Reviews*, 111: 1-24.

Pfister T. (1980a). Systematische und paläoökologische Untersuchungen an oligozänen Korallen der Umgebung von San Luca (Provinz Vicenza, Norditalien). *Schweizerische Paläontologische Abhandlungen (Mémoires Suisses de Paléontologie),* 103: 1-121.

Pfister T. (1980b). Paläoökologie des oligozänen Korallenvorkommens von Cascine südlich Acqui (Piemont, Norditalien). *Jahrbuch des Naturhistorischen Museums der Stadt Bern*, 7: 247-262.

Pfister T. (1985). Coral fauna and facies of the Oligocene fringing reef near Cairo Montenotte (Liguria, northern Italy). *Facies*, 13: 175-226.

Popov S.V., Rögl F., Rozanov A.Y., Steininger F.F., Shcherba I.G. & Kovac M. (2004). Lithological-paleogeographic maps of Paratethys, 10 maps late Eocene to Pliocene. *Courier Forschungsinstitut Senckenberg*, 250: 1-46.

Prever P.L. (1922). I coralli Oligocenici di Sassello nell'Appenino Ligure. Continuazione parte I. Corallari a calici confluenti. *Palaeontographia Italica,* 28: 1-40.

Quaranta F., Piazza M. & Vannucci G. (2009). Climatic and tectonic control on the distribution of the Oligocene reefs of the Tertiary Piedmont Basin (NW Italy). *Bollettino della Società Geologica Italiana*, 128: 587-591.

Reig Oriol J.M. (1988). Dos nuevos géneros de corales cretácicos. *Batalleria*, 1: 39-45.

Reig Oriol J.M. (1990). Madreporarios eocénicos de Castellolo y de la Sierra de Malvals. 71 pp. Reig Oriol, Barcelona.

Reis O.M. (1889). Die Korallen der Reiter Schichten. *Geognostische Jahreshefte*, 2: 91-162.

Reuss A.E. von (1864). Die fossilen Foraminiferen, Anthozoen und Bryozoen von Oberburg in Steiermark. Ein Beitrag zur Fauna der oberen Nummulitenschichten. *Denkschriften der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe,* 23: 1-36.

Reuss A.E. von (1868). Palaeontologische Studien über die altern Tertiärschichten der Alpen. 1. Theil. Die fossilen Anthozoen und Bryozoen der Schichtengruppe von Crosara. *Denkschriften der kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe*, 28: 129-184.

Reuss A.E. von (1869). Zur fossilen Fauna der Oligocänschichten von Gaas. *Sitzungsberichte der Kaiserlichen Akademie der*

*Wissenschaften. Mathematisch Naturwissenschaftliche Classe,* 59: 446-488.

Reuss A.E. von (1874). Paläontologische Studien über die älteren Tertiärschichten der Alpen. III. Abtheilung. Die fossilen Anthozoen der Schichtengruppe von S. Giovanni Ilarione und von Ronca. *Denkschriften der Österreichischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe,* 33: 1-60.

Reuter M., Piller W.E., Harzhauser M., Mandic O., Berning B., Rögl F., Krog A., Aubry M.-P., Wieland-Schuster U. & Hamedani A. (2009). The Oligo/Miocene Qom Formation (Iran): evidence for an early Burdigalian restriction of the Tethyan Seaway and closure of its Iranian gateways. *International Journal of Earth Sciences,* 98: 627-650.

Romano S.L. & Cairns S.D. (2000). Molecular phylogenetic hypotheses for the evolution of scleractinian corals. *Bulletin of Marine Science*, 67: 1043-1068.

Sanders D. & Baron-Szabo R.C. (2005). Scleractinian assemblages under sediment input: their characteristics and relation to the nutrient input concept. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 216: 139-181.

Sanders D. & Baron-Szabo R.C. (2007). First Oligocene coral fauna of the Eastern Alps. Sediment 2007, Brixen/Bressanone (Italy), 12.9.2007, Abstract: 1 p.

Santodomingo N. (2014). Miocene reef-coral diversity of Indonesia: unlocking the murky origins of the Coral Triangle. *Utrecht Studies in Earth Sciences*, 63: 1-336.

Scherbacher M., Schmiedl G. & Hemleben C. (2001). Early Oligocene benthic foraminifera from the Lower Inn Valley area, Austria: Implications for the paleoenvironmental evolution of the Inneralpine Molasse. *In* Piller W. & Rasser M. (eds), Paleogene in Austria, *Schriftenreihe der Erdwissenschaftlichen Kommissionen*, 14: 611-640.

Schuster F. (2002a). Scleractinian corals from the Oligocene of the Qom formation (Esfahan-Sirjan fore-arc basin, Iran). *Courier Forschungsinstitut Senckenberg*, 239: 5-55.

Schuster F. (2002b). Early Miocene corals and associated sediments of the northwestern Gulf of Suez, Egypt. *Courier Forschungsinstitut Senckenberg*, 239: 57-81.

Schuster F. (2002c). Oligocene scleractinian corals from Doutsiko (Mesohellenic Basin, northwestern Greece). *Courier Forschungsinstitut Senckenberg*, 239: 83-127.

Silvestri G., Bosellini F.R. & Morsilli M. (2008). Turbid-water coral assemblages: A case study from the Oligocene Tertiary Piedmont Basin (N Italy). *Rendiconti online Società geologica Italiana,* 2: 177-180.

Silvestri G., Bosellini F.R. & Nebelsick J.H. (2011). Microtaphofacies analysis of lower Oligocene turbid-water coral assemblages. *Palaios,* 26: 805-820.

Sismonda E. (1871). Matériaux pour servir a la paléontologie du terrain tertiaire de Piémont. *Memorie della Reale Accademia delle Scienze di Torino (serie 2),* 25: 21-107.

Sokolow N. (1894). Die unteroligocäne Fauna der Glaukonitsande bei der Einsenbahnbrücke von Jekaterinoslaw. *Mémoires of the geological Commission, Russia*, 9: 1-138.

Solomko E. (1888). Die Jura- und Kreidekorallen der Krim. *Verhandlungen der Russisch-Kaiserlichen Mineralogischen Gesellschaft zu St. Petersburg (2)*, 24: 67-231.

Squires D.F. (1958). The Cretaceous and Tertiary corals from New Zealand. *New Zealand Geological Survey Palaeontological Bulletin,* 29: 1-107.

Squires D.F. (1962). Additional Cretaceous and Tertiary corals from New Zealand. *Transactions of the Royal Society of New Zealand (Geology),* 1: 133-150.

Stemann T.A. (2004). Reef corals of the White Limestone Group of Jamaica. *In* Donovan S.K. (ed.), The Mid-Cainozoic White Limestone Group of Jamaica. *Cainozoic Research*, 3: 83-107.

Stolarski J. (1995). Ontogenetic development of the thecal structures in caryophylliine scleractinian corals. *Acta Geologica Polonica*, 40: 19-44.

Stolarski J. & Taviani M. (2001). Oligocene scleractinian corals from CRP-3 drillhole, McMurdo Sound (Victoria Land Basin, Antarctica). *Terra Antartica,* 8: 1-4.

Tomes R.F. (1883). On some new or imperfectly known Madreporaria from the Coral Rag and Portland Oolite of the counties of Wilts, Oxford, Cambridge, and York. *Quarterly Journal of the Geological Society*, 39: 55-65.

Vannucci G., Testa M., Piazza M. & Pastorino P. (2010). *Subterraniphyllum* and free-living *Neogoniolithon* (coralline algae) from the Oligocene reef facies of Costa d'Ovada (Tertiary Piedmont Basin, Alessandria, NW Italy). *Italian Journal of Geosciences*, 129: 4-14.

Vaughan T.W. (1900). The Eocene and Lower Oligocene coral faunas of the United States with descriptions of a few doubtfully Cretaceous species. *Monographs of United States Geological Survey*, 39: 1-263.

Vaughan T.W. (1918). Some shoal-water corals from Murray Island (Australia), Cocos-Keeling Islands, and Fanning Island. *Papers from the Department of Marine Biology of the Carnegie Institution of Washington*, 9: 49-234.

Vaughan T.W. (1919). Fossil corals from Central America, Cuba, and Porto Rico, with an account of the American Tertiary, Pleistocene, and Recent coral reefs. *United States National Museum Bulletin*, 103: 189-524.

Vaughan T.W. & Wells J.W. (1943). Revision of the suborders, families and genera of the Scleractinia. *Geological Society of America, Special Paper*, 44: 1-363.

Veron J.E.N. (1992). Conservation of biodiversity: A critical time for the Hermatypic Corals of Japan. *Coral Reefs*, 11: 13-21.

Veron J.E.N. & Michin P.R. (1992). Correlations between sea surface temperature, circulation patters and the distribution of hermatypic corals of Japan. *Continental Shelf Research*, 12: 835-857.

Verrill A.E. (1901). Variations and nomenclature of Bermudian, West Indian, and Brazilian reef corals, with notes on various Indo-Pacific corals. *Transactions of the Connecticut Academy of Arts and Sciences,* 11: 63-168.

Verrill A.E. (1902). Notes on corals of the genus *Acropora* (Madrepora Lam.) with new descriptions and figures of types, and of several new species. *Transactions of the Connecticut Academy of Arts and Sciences*, 11: 207-266.

Vredenburg E. (1921). Comparative diagnoses of Pleurotomidae from the Tertiary formations of Burma. *Records of the Geological Survey of India*, 53: 83-129.

Wallace C.C. (2008). New species and records from the Eocene of England and France support early diversification of the coral genus *Acropora*. *Journal of Paleontology*, 82: 313-328

Weisbord N.E. (1973). New and little-known corals from the Tampa Formation of Florida. *Bulletin State of Florida Department of Natural Resources Division of Interior Resources Bureau of Geology*, 56: 1-146.

Wells J.W. (1941). Cretaceous and Eocene corals from northwestern Peru. *Bulletins of American Paleontology*, 26: 301-326.

Wells J.W. (1956). Part F, Coelenterata. *In* Moore R.C. (ed.), Treatise on Invertebrate Paleontology, Lawrence, Kansas: F328-F444.

Wells J.W. (1964). Fossil Corals from Eniwetok Atoll. *United States Geological Survey Professional Paper*, 260-DD: 1101-1111.

Wilson M.E.J. (1995). The Tonasa Limestone Formation, Sulawesi, Indonesia: Development of a Tertiary Carbonate Platform. 520 pp. PhD Thesis, University of London.

Zuffardi-Comerci R. (1937). Corallari oligocenici e miocenici della Somalia. *Palaeontographia Italica*, 32: 265-301.

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