Revision of Oligocene Mediterranean meandroid corals in the scleractinian families Mussidae, Merulinidae and Lobophylliidae

Ann F. Budd* and Francesca R. Bosellini

Department of Earth and Environmental Sciences, University of Iowa, 115 Trowbridge Hall, Iowa City, IA 52242 USA; Dipartimento di Scienze Chimiche e Geologiche, Università di Modena e Reggio Emilia, Via Campi 103, 41125 Modena, Italy

(Received 3 February 2015; accepted 27 July 2015; published online 30 November 2015)

Traditional morphology-based systematics indicates close evolutionary relationships between Caribbean and Indo-Pacific ‘faviid’ and ‘mussid’ reef corals. However, molecular phylogenies reveal three distinct family-level clades, which diverged by middle Eocene time: (1) Caribbean faviids + mussids; (2) Indo-Pacific faviids; and (3) Indo-Pacific mussids. During the early Cenozoic, members of these clades also occurred in a third geographical region, the Mediterranean, but became extinct in that region during the Miocene, as the Tethys broke up. We perform morphological phylogenetic analyses including Caribbean, Indo-Pacific and Mediterranean Oligocene and Recent taxa to reconstruct the pattern of divergence between the three regions, and examine how it was related to biogeography. First, fossil specimens were selected from museum collections, and a total of 13 species (three of which are new) were distinguished using nine morphological features. These 13 species were then added to a dataset with taxa consisting of 62 Recent plus one additional extinct species, and with 50 characters. In addition to traditional macromorphology, the characters include new micromorphological and microstructural features observed using electron microscopy and transverse thin sections. Phylogenetic analysis was performed on the dataset using parsimony. The results show that, contrary to traditional systematics, 11 of the 13 Mediterranean extinct coral species group more closely with Indo-Pacific taxa than they do with Caribbean taxa. Recent Caribbean taxa and Indo-Pacific ‘mussids’ form distinct clades; but Indo-Pacific ‘faviids’ form four poorly resolved subclades basal to the Caribbean clade. These results suggest that Mediterranean meandroid corals belong to a cosmopolitan pantropical fauna, from which modern Caribbean meandroid corals diverged as the Caribbean became isolated. Phylogenetic analyses including fossils have higher resolution than analyses including only modern corals. The systematics of the 13 extinct species are formally revised. Two new species Variabilifavia ausuganensis sp. nov. and Echinophyllia sassellensis sp. nov. – and one new genus Paraleptoria gen. nov. – are named, and one undescribed species is left in open nomenclature. Two previously synonymized genera are resurrected.

Keywords: reef corals; Oligocene; Mediterranean; systematics; phylogenetic analysis

Introduction

The biodiversity of modern reef corals differs significantly between the Indo-Pacific and Caribbean regions. In the Indo-Pacific, biodiversity has been estimated as 17 families, 92 genera and >700 species based on traditional taxonomy, whereas in the Caribbean it has been estimated at 11 families, 27 genera and ~60 species (Veron 2000). Traditional taxonomy indicates that only 17% of all modern reef coral genera and none of the 17 modern reef coral families have distributions limited to the Caribbean, whereas 76% of all genera and 39% of families are restricted to the Indo-Pacific (Veron 1995, 2000). These numbers suggest that the Caribbean fauna represents merely a depauperate extension of the Indo-Pacific fauna. However, recent molecular analyses (Fukami et al. 2004, 2008) and studies of micromorphology and microstructure (Budd & Stolarski 2009, 2011; Budd et al. 2010) have found this not to be true. Instead, much of the modern Caribbean fauna appears to be only distantly related to the Indo-Pacific fauna, with the faunas of the two regions diverging during the Palaeogene (Schwartz et al. 2012). These results indicate that the evolutionary histories of the two regions are significantly more complex than previously recognized, and that the differences in biodiversity may have developed in response to different geographical and environmental conditions in the two regions.

In order to trace the evolutionary histories of the two modern regions, we have been performing analyses of the fossil record, not only from Caribbean and Indo-Pacific locations, but also at other intermediate locations within the westward-flowing Tethyan Seaway which extended...
around the globe during the Palaeogene (Berggren & Hollister 1974). One diverse intermediate region is the Mediterranean, where reef corals thrived and constructed large reefs during the Oligocene and Miocene (Bosellini & Perrin 2008; Perrin & Bosellini 2012) but are extinct today (Perrin & Bosellini 2013; Vertino et al. 2014). This region has a long history of palaeontological research dating back to the early 1800s, when the names of species were originally established. Much of our research has therefore concentrated on museum collections. In addition, due to the long history of research on the region, a plethora of scientific names has been assigned to both genera and species, many of which are synonyms or are incorrectly and inconsistently applied. The problems in name usage have necessitated re-examining type specimens and coding sets of morphological characters following recent advances in scleractinian morphological analysis.

In the present study, we focus on a subset of the Palaeogene Mediterranean reef coral fauna consisting of Oligocene meandroid reef corals within three closely related families — Mussidae Ortmann 1890, Merulinidae Verrill 1865 and Lobophylliidae Dai & Horng 2009 — and formally revise their systematics. We focus on meandroid corals because they complement ongoing research comparing the molecular and morphological data in modern members of this group described below. Our eventual goal is to: (1) expand this work to include the Paleocene, Eocene and Miocene, as well as non-meadroid genera (and Hydnotheca) in the three families; (2) compare taxa in the three families with their Caribbean, Middle Eastern and Indo-Pacific counterparts; and (3) reconstruct the phylogeny of the group. This phylogeny will then be analysed to determine how origination and extinction events correspond with long-term changes in climate and biogeography.

Modern representatives of the families Mussidae, Merulinidae and Lobophylliidae are currently being revised in a series of monographs (Budd et al. 2012; Huang et al. 2014), which integrate molecular and morphological data. This revision is based primarily on the molecular tree of Fukami et al. (2008) (Merulinidae (clade XVII), Lobophylliidae (clade XIX) and Mussidae (clade XXI)). Of these three families, Mussidae is currently restricted to the western Atlantic, and Merulinidae (with the exception of the Orbicella annularis complex) and Lobophylliidae are currently restricted to the Indo-Pacific. In this classification system, the family Mussidae consists of the following genera: Mussa, Isophyllia, Mycetophyllia and Scolymia (subfamily Mussinae), and Favia, Colophyllia, Diploria, Manicina, Mussismilia and Pseudodiploria (subfamily Faviinae) (Budd et al. 2012). The Merulinidae consists of Merulina, Australography, Boninastrea, Caulastraeoa, Cyphastrea, Echinopora, Erythastrea, Hydnotheca, Leptoria, Mycedium, Oulophyllia, Paraclavaria, Pectinia, Physophyllia, Platgyra, Scapophyllia, Trachyphyllia, Goniastrea, Coelastrea, Dipsastrea (= Pacific ‘Favia’), Favites (= Pacific ‘Montastrea’ in part), Astrea (= Pacific ‘Montastrea’ in part), Paramontastrea (= Pacific ‘Montastrea’ in part) and Orbicella (Huang et al. 2014). The Lobophylliidae consists of Lobophyllia, Acanthastrea, Cynarina, Echinomorpha, Echinophyllia, Homophyllia (= Pacific ‘Scolymia’ in part), Micromussa, Moseleya, Oxypora, Parascolymia (= Pacific ‘Scolymia’ in part), Sclerophyllia and Symphyllia. This new system is used in the Corallosphere database (http://corallosphere.org) and in WoRMS (http://www.marinespecies.org).

Our approach to the study of fossil corals performs morphological phylogenetic analyses including both modern and fossil corals to assign taxa to families and genera (see also Schwartz et al. 2012; Santodomingo et al. 2014). These analyses are specifically designed to address the following question: are Mediterranean corals more closely related to Caribbean or Indo-Pacific corals? First, we examined fossil meandroid corals in classic and contemporary museum collections, selecting 112 specimens that belong to the families Merulinidae, Lobophylliidae and Mussidae for analysis. Secondly, we grouped the specimens into 13 extinct species by assessing nine different morphological features, including both macromorphology and microstructure. Thirdly, we added one additional extinct species, coded the extinct species using a set of characters modified from Budd et al. (2012), and added 62 living species to create a combined extinct + Recent morphological character matrix (76 taxa × 50 characters). Fourthly, we performed phylogenetic analyses using the character matrix. Finally, we formally revised the systematics of the extinct species based on our results.

**Material**

**Repository abbreviations**

GBA: Geologische Bundesanstalt Wien, Austria; GLAHM: Hunterian Museum and Art Gallery, University of Glasgow, UK; IPUM: Inventario Paleontologia Università di Modena, Italy; MGPUP: Museo di Geologia e Paleontologia dell’Università di Padova, Italy; MNHN: Muséum national d’Histoire naturelle, Paris, France; MPUR: Museo di Paleontologia, Università di Roma ‘La Sapienza’, Rome, Italy; MSNTUP: Museo di Storia Naturale e del Territorio, Università di Pisa, Pisa, Italy; MUSE: Museo delle Scienze di Trento, Italy; NHMUK: Natural History Museum, London, UK (formerly British Museum (Natural History)); NHMW: Naturhistorisches Museum Wien, Austria; SNSB: Staatliche Naturwissenschaftliche Sammlungen Bayerns, Palaeontologisches Museum, München, Germany.
Specimens selected for study

Study specimens consist of Oligocene Mediterranean meandroid corals selected from the following classic museum collections: Catullo (1856) at MGPUP; Reuss (1864, 1868, 1869, 1874) at NHMW and GBA; d’Achiardi (1866, 1868b) at MSNTUP; and Michelotti (Sismonda, 1871) at MPUR. In addition, non-type specimens were selected for study from collections at NHMUK and NHMW made in the 1800s. Finally, we selected specimens from several more recent collections: (1) collections made at Borgo Valsugana by Sergio Boschele (MUSE); (2) collections made at Sassello by Thérèse Pfister and by Francesca Bosellini (IPUM); (3) collections made at Castro and Abesse by Francesca Bosellini (IPUM); and (4) collections made at Gornji Grad by James H. Nebelsick (IPUM).

Over the past 200 years, Oligocene Mediterranean meandroid corals have been assigned to 20 different genera (Supplemental Appendix A) in seven currently recognized scleractinian families (Agariciidae, Calamophylliidae, Euphylliidae, Meandrinidae, Lobophylliidae, Merulinidae, Mussidae). As explained earlier, our revision focuses on only three of these families: Mussidae, Merulinidae and Lobophylliidae. However, we first examined all available museum specimens of meandroid corals in the collections described above and used the macromorphological criteria in Supplemental Appendix A to determine which specimens belonged to three families under consideration. Within the three selected families, we excluded solitary taxa (e.g. Leptomussa, Cricocyathus, Petrophylliella) and members of seven genera: Favia, Dipsastraea, Caulastraea, Lobophyllia, Orbicella, Cyphastrea and Hydnophora. The first six genera were excluded because they are not meandroid (i.e. their corallite series contain ≤3 centres), and Hydnophora was excluded because it was recently revised by Bosellini (1999). Examples of species that were excluded at this initial stage are shown in Figure 1. A list of all included 112 specimens is provided in Supplemental Appendix B.

Next we qualitatively grouped the included specimens into species (a total of 13 species, Supplemental Appendix C) using the following macromorphological and microstructural criteria: corallum (colony shape; development of epitheca), corallite (length, width, and structure of corallite series, ‘valleys’), development of coenosteum, costa continuity, septa (number, relative development), columella (size, structure, linkage), development of paliform lobes, relative abundance of dissepiments, and wall structure. Observations were made on calical surfaces using a stereoscope and on transverse thin-sections using transmitted light. The resulting species comprise the extinct taxa that were analysed in the phylogenetic analysis and are formally described in the systematic account.

Localities

Oligocene fossil specimens used for this study come from seven localities: five are from Italy, one from Slovenia and one from France (Fig. 2). Their updated biostratigraphical ages and palaeoenvironments, together with most recent references, are summarized in Table 1. Of the seven sites, four include some of the most significant coral-bearing units in the Oligocene of the north-western Tethys, and have been known since the nineteenth century from famous monographs and related museum collections: Gornji Grad in Slovenia, the Marostica area and the Eastern Lessini Mountains in the Vicentin Southern Alps, and Sassello in Liguria (Catullo 1856; Reuss 1864; d’Achiardi 1866, 1867, 1868a, b; Reuss 1868, 1869; Michelotti in Sismonda 1871; de Angelis 1894; Osasco 1898, 1902; Prever 1921, 1922). A brief overview of the localities is provided below following the order in Table 1.

Gornji Grad (N Slovenia) (Locality 1). The coral fauna belongs to the Gornji Grad Beds (named Oberburg in the old literature) and was first described by Reuss (1864) with the collection reposited at the NHMW. The Gornji Grad Beds were deposited within the so-called ‘Slovenian Corridor’, located between the northernmost extension of the Tethys to the south and the developing Paratethys. They are represented by brackish to marine marls, sandstones and marine carbonates, with corals found mainly within rudstone carbonates and marly levels (Nebelsick et al. 2000). An early Oligocene age (Rupelian) has been assigned based on the larger benthic foraminiferal association (Biozone SB21 of Cahuzac & Poignant 1997) (Nebelsick et al. 2000). For the coral-rich facies, nearshore turbid-water conditions dominated by sediment-resistant corals have been recently interpreted (Silvestri et al. 2011).

Localities of Veneto and Trentino regions (northern Italy) (Localities 2, 3, 4). All of these localities belong to the Lessini Shelf, a major palaeogeographical unit of the Southern Alps characterized by a well-exposed succession of Palaeogene shallow-water carbonates (Bosellini 1989). The areas of the Eastern Lessini Mountains and Marostica are punctuated by a large number of coral outcrops that represent some of the best-known Cenozoic type localities in the scleractinian systematic literature (Catullo 1856; d’Achiardi 1866, 1867, 1868a, b; Reuss 1868, 1869). The Lessini outcrops belong to the Rupelian Castelgomberto Limestone, a 200m thick unit organized in a number of cycles where well-bedded grainstone units alternate with marly horizons extremely rich in corals (Bosellini & Trevisani 1992). Palaeoenvironmental reconstructions of these sites suggest that scattered coral patches colonized the muddy-unstable substrate of the shallow internal platform or ‘lagoon-like’ setting in low-energy
hydrodynamic conditions (Frost 1981; Bosellini & Trevisani 1992). A very similar depositional environment has been proposed for the coeval coral facies of the Marostica area (Pfister 1980; Frost 1981). Towards the northern margin of the Lessini Shelf, near Borgo Valsugana (Valsugana valley, eastern Trentino Province), the Oligocene shallow-water sedimentary succession involves a series of Rupelian cycles (parasequences) similar to those observed in the Vicentin Lessini Mountains (Luciani & Trevisani 1992), with a rich coral assemblage occurring within marly levels (Boschele et al. 2011).

**Sassello (Liguria, north-western Italy) (Locality 5).** Sassello is another classic locality of the Italian Oligocene, well known from the studies of Michelotti in Sismonda (1871), de Angelis (1894) and Prever (1921, 1922). This area belongs to the southern part of the western Tertiary Piedmont Basin, a thrust-top basin developed during the Cenozoic over the suture zone between the Alps and Apennines and generated by post-collisional subsidence (Mosca et al. 2010). The area is rich in coral localities where small coral build-ups and scattered coral assemblages are associated with the mixed siliciclastic-carbonate sediments of the Molare Formation and
developed in a conglomeratic fan delta to clay-rich prodelta setting (Pfister 1985; Fravega et al. 1987; Silvestri et al. 2008; Quaranta et al. 2009). The age of the Sassello coral facies, determined through the analysis of the larger benthic foraminiferal assemblage, is Upper Rupelian–Lower Chattian (Biozone SB22A-22B of Cahuzac & Poignant 1997) (Quaranta et al. 2009; unpublished data).

**Abesse (Saint-Paul-lès-Dax, Aquitaine, SW France) (Locality 6).** Corals from the Aquitaine Basin are also well known since the nineteenth century and have been extensively studied by Chevalier (1962) and revised more recently by Cahuzac and Chaix (1996), who recognized at the locality of Abesse (near Saint-Paul-lès-Dax) an extraordinary rich coral fauna (up to 100 species). A marginal-coastal depositional setting associated with a mixed carbonate-siliciclastic sedimentation has been suggested for these coral facies, characterized by ‘faluns’ (i.e. shelly facies) and littoral/lagoonal marly sands (Cahuzac & Janssen 2010; unpublished data). These corals were not forming reefs or any sort of framework. As regards their age, the coral deposits have been ascribed to the uppermost Chattian (Cahuzac & Poignant 2002; Cahuzac & Janssen 2010; unpublished data).

**Table 1.** Type and collecting localities for specimens used in this study with their stratigraphical ages and palaeoenvironments. References for ages and palaeoenvironmental setting are also given.

| Locality                              | Age                        | Palaeoenvironment               | References                                      |
|---------------------------------------|----------------------------|---------------------------------|------------------------------------------------|
| Gornji Grad (N Slovenia)              | Oligocene (Rupelian)       | Coral carpets nearshore         | Nebelsick et al. (2000); Silvestri et al. (2011) |
| Marostica area: Crosara, Salcedo, S Luca (Vicenza, Veneto, N Italy) | Oligocene (Rupelian)       | Coral patches inner platform    | Pfister (1980); Frost (1981)                     |
| Eastern Lessini Mountains: Monteviale, Montecchio Maggiore, Castelgomberto (Vicenza, Veneto, N Italy) | Oligocene (Rupelian)       | Patch reefs inner platform       | Frost (1981); Bosellini & Trevisani (1992)       |
| Borgo Valsugana (Trento, Trentino, N Italy) | Oligocene (Upper Rupelian–Lower Chattian) | Coral patches inner platform | Luciani & Trevisani (1992); Boschele et al. (2011) |
| Sassello (Savona, Liguria, NW Italy)  | Oligocene (Upper Rupelian–Lower Chattian) | Coral patches fan delta system  | Fravega et al. (1987); Quaranta et al. (2009)    |
| Abesse (Saint-Paul-lès-Dax, Aquitaine, SW France) | Oligocene (Chattian)       | Coastal protected lagoon        | Cahuzac & Poignant (2002); Cahuzac & Janssen (2010) |
| Castro (Lecce, S Italy)               | Oligocene (Chattian)       | Fringing reef fore reef         | Bosellini & Russo (1992); Bosellini (2006)       |
**Castro (Salento Peninsula, southern Italy) (Locality 7).** Corals analysed from Castro come from the Castro Limestone, one of the rare Oligocene true large reef complexes of the Mediterranean region. This carbonate unit is widely exposed along the eastern coast of the Salento Peninsula and has been interpreted as a fringing reef complex disconformably overlying the tectonically deformed Cretaceous–Eocene eastern margin of the Apulia Platform (Bosellini & Russo 1992; Bosellini et al. 1999). Palaeoenvironmental reconstructions suggest a very well-preserved lateral zonation of reef facies from the back reef towards the reef slope, and reveal changes in coral composition, growth form and fabric within the reef framework (Bosellini & Russo 1992; Bosellini & Perrin 1994; Bosellini 2006). Coral richness is moderately high, consisting of approximately 21 genera and 30 species (Bosellini 2006). The age of the Castro Limestone has been attributed to the early Chattian according to the larger benthic foraminiferal assemblages (Biozone SB22B of Cahuazac & Poignant 1997) (Parente 1994).

**Systematic palaeontology**

**Remarks.** In the systematic account that follows only new species names are considered in synonymies. Question marks are indicated for species whose type specimens are lost and which were figured inadequately or not at all. Only Mediterranean Oligocene species are included in synonymies. Non-Oligocene and non-Mediterranean synonyms are considered in the Remarks sections. Genera are determined based on the phylogenetic analysis shown in the results section; species are based on characters in Supplemental Appendix C. The term ‘non-type’ refers to specimens that are not primary types. For the two species in which we have no thin sections (Variabilifavia ausuganensis, Paraleptoria polygonalis), wall type has been estimated by study of the colony surface.

1973 *Variabilifavia* Barta-Calms: 293, pl. 14, figs 1–4.

**Type species.** *Favia perrandi* Prever, 1922, p. 29, pl. 6, fig. 10.

**Type locality.** Sassello, Upper Rupelian–Lower Chattian.

**Diagnosis.** Meandroid, short uniserial valleys (<5 centres), separated by reduced costate coenosteum; spongy columella with well-developed paliform lobes; reduced epitheca; trabeculothecal wall.

**Remarks.** *Variabilifavia* is distinguished from *Favia* Milne Edwards, 1857 and *Dipsastraea* de Blainville, 1830 by forming series (uniserial) consisting of three or more corallites, and by having equal septal cycles and a trabeculothecal wall. It is also distinguished from *Diploria*, Milne Edwards & Haime, 1848 and *Manicina* Ehrenberg, 1834, which have longer and wider series, unequal septal cycles, and septothecal walls. In addition, *Manicina* has well-developed septal lobes. It differs from *Colpophyllia* Milne Edwards & Haime, 1848 (double-wall) and *Hydnophylla* (no coenosteum) by having a continuous spongy columella with trabecular linkage. Finally, it differs from *Platygyra* Ehrenberg, 1834, which lacks coenosteum. *Variabilifavia* therefore appears to be a distinct genus, as confirmed by the separate clade it forms shown in the phylogenetic analysis section. We assign the name *Variabilifavia* to this genus, because we consider the type species of *Variabilifavia*, *Favia perrandi* Prever, 1922, to be a synonym of *Favia confertissima* Reuss, 1868 as described below.

*Variabilifavia* is similar to the Oligo–Miocene genus *Defrancia* Alloiteau, 1957 (septothecal), described by Chevalier (1962), but has a better-developed coenosteum and a trabeculothecal wall.

*Variabilifavia ausuganensis* sp. nov. (Fig. 3A–C)

**Material.** Twelve specimens, none of which are thin-sectioned (Supplemental Appendix B): all are primary types. Holotype: MUSE 7444 (TOR019), Borgo Valsugana, Upper Rupelian–Lower Chattian. Paratypes: MUSE 7433 (TOR003), MUSE 7434 (TOR004), MUSE 7435 (TOR005), MUSE 7436 (TOR006), MUSE 7437 (TOR007), MUSE 7438 (TOR008), MUSE 7439 (TOR009), MUSE 7440 (TOR016), MUSE 7441 (TOR017), MUSE 7442 (TOR020), MUSE 7443 (TOR021).

**Diagnosis.** Short uniserial valleys (4–5 centres), separated by little or no coenosteum; spongy columella with very strong paliform lobes.

**Description.** Macromorphology: Small colonies, massive in shape, meandroid, intracalicular budding; no polymorphism; short, sinuous uniserial valleys (<5 centres); little or no coenosteum; continuous costosepta; valley width = small (5–10 mm); low calical relief; mostly continuous, equal costosepta; 3 septal cycles, with narrow spacing (12–24 septa per cm, including minor septa); discontinuous, spongy columella (>3 threads), with trabecular linkage and distinct centres; moderate columella, one-quarter to one-half width of corallite; very strong paliform lobes, weak septal lobes; reduced epitheca; moderate endotheca; trabeculothecal wall.
Derivation of name. After ‘Valle di Ausugum’; Ausugum was the old Roman name of the village Borgo Valsugana.

Occurrence. Borgo Valsugana (Upper Rupelian–Lower Chattian).

Remarks. *Variabilifavia ausuganensis* has less coenosteum than *V. confertissima*, and is distinguished by thin septa and very strong paliform lobes.

*Variabilifavia confertissima* (Reuss, 1868)  
(Fig. 3D–I)

*Meandrina cerebriformis* Lamarck: 246 [holotype MNHN-Scle102, ‘mers d’Amérique’].

*Symphyllia crebriformis* Michelotti: 39 [holotype not found; Turin, Miocene].

*Symphyllia multisinuosa* Angelis: 229, pl. 1, fig. 29 [holotype reported in Barta-Calmus, 1973, but not found; Sassello].

*Symphyllia vetusta* Osasco: 140, fig. 1 [holotype not found by Barta-Calmus, 1973; ?Sassello].

Figure 3. Species of *Variabilifavia*. A–C, *Variabilifavia ausuganensis* sp. nov., Borgo Valsugana, Upper Rupelian–Lower Chattian; A, holotype, MUSE 7444 (TOR19), calical surface; B, paratype, MUSE 7435 (TOR5), calical surface; C, paratype, MUSE 7439 (TOR9), calical surface. D–I, *Variabilifavia confertissima* (Reuss); D, holotype, GBA 1868/007/0031, calical surface, Monte Grumi (Castelgomberto), Rupelian; E–I, Sassello, Upper Rupelian–Lower Chattian; E, MPUR 65, holotype of *Favia circumscripta* Michelotti, calical surface; F, MPUR 3700, lectotype of *Meandrina cerebriformis* Michelotti, calical surface; G, hypotype, NHMUK R3485, calical surface; H, hypotype, NHMUK R3485, transverse thin section; I, hypotype, NHMUK R3517, transverse thin section, Sassello. Scale bars: A–G = 10 mm; H, I = 20 mm.

?1838 Meandrina cerebriformis* Lamarck; Lamarck in Michelotti: 154 (in part) [holotype not found].

?1847 *Meandrina bisinuosa* Michelin: 55, pl. 11, fig. 6 [holotype not found; Turin, Miocene].

?1861 *Symphyllia crebriformis* Michelotti: 39 [holotype not found; Turin, Miocene].

1868 *Favia confertissima* Reuss: 152, pl. 8, fig. 5 [holotype GBA 1868/007/0031; Castelgomberto].

1871 *Diploria intermedia* Michelotti in Sismonda: 324, pl. 6, fig. 1 [holotype lost according to Barta-Calmus, 1973; Sassello].

1894 *Symphyllia multisinuosa* Angelis: 229, pl. 1, fig. 29 [holotype reported in Barta-Calmus, 1973, but not found; Sassello].

1898 *Symphyllia vetusta* Osasco: 140, fig. 1 [holotype not found by Barta-Calmus, 1973; ?Sassello].
1921 Symphyllia brevisulcata Prever: 79, pl. 11, fig. 5 [holotype not found in Genoa; Sassello].
1921 Symphyllia obliqua Prever: 81, pl. 12, fig. 1 [holotype not found in Genoa; Sassello].
1921 Symphyllia intermedia Prever: 82, pl. 12, fig. 3 [holotype not found in Genoa; Sassello].
?1921 Symphyllia ruvida Prever: 83 [holotype not found in Genoa; Sassello].
1921 Symphyllia paronai Prever: 84, pl. 12, fig. 4 [holotype not found in Genoa; Sassello].
1921 Symphyllia isseli Prever: 84, pl. 12, fig. 5 [holotype not found in Genoa; Sassello].
1921 Symphyllia irregularis Prever: 84, pl. 12, fig. 6 [holotype not found in Genoa; Sassello].
1921 Symphyllia apennina Prever: 84, pl. 13, fig. 1 [holotype not found in Genoa; Sassello].
1922 Hydnophyllia dalpiazi Prever: 12, pl. 3, figs 4, 5 [holotype not found in Genoa; Sassello].
1922 Favia perrandii Prever: 29, pl. 6, fig. 10 [holotype not found in Genoa; Sassello].
1922 Favia zuffardii Prever: 30, pl. 7, fig. 2 [holotype not found in Genoa; Sassello].
1980 Diploria crebriformis (Michelotti); Pfiester: 82, pl. 5, figs 6–8, pl. 6, figs 1–3, pl. 7, figs 1, 2 [lectotype MPUR 3700; Sassello].

**Material.** Twenty-one specimens, 18 of which are thin-sectioned (Supplemental Appendix B): holotype of *Favia zuffardii*.

**Occurrence.** Castelgomberto (Rupelian); Sassello (Upper Rupelian–Lower Chattian).

**Remarks.** *Variabilifavia confertissima* differs from *Astrea subdentulata* Catullo, 1856 from Montecchio Maggiore (MGPUP 8275C) and *Favia circumscripta* Michelotti in Sismonda, 1871 (MPUR 65) from Sassello, which are mono- and di-centric. It also differs with Eocene *Favia profunda* Reuss, 1874 (GBA 1874/003/023) [= *Favia meneguzzii* d’Achiardi 1868a], which is mono- and di-centric.

Michelotti described *Meandrina cerebriformis* for the first time in 1838 (Michelotti 1838, p. 154) without figuring it, and indicated that it contained both modern Caribbean and fossil (Verona) specimens. He redescribed it as *Symphyllia cerebriformis* in 1861 (Michelotti 1861, p. 39), again without figuring it, and indicated that it occurred in Dego and Sassello. The specific name ‘crebriformis’ appears to be a misspelling of ‘cerebriformis’. The extinct species differs morphologically from Lamarck’s (1816) *Meandrina cerebriformis*, which is modern Caribbean and synonymous with *Diploria labyrinthiformis* (Linnaeus, 1758). Lamarck’s species has larger valleys, more extensive coenosteum, and septotheal walls. Pfiester (1980) erected the lectotype for *Diploria crebriformis* (MPUR 3700) based on Michelotti’s collection in Rome.

Michelotti in Sismonda (1871) described and figured *Diploria intermedia* for the first time on p. 324 and redescribed *Symphyllia crebriformis* without figuring it on p. 326. The holotypes for both species are lost; however, *D. intermedia* and *S. crebriformis* are both from Sassello and appear to be the same species.

Reuss’ (1868) *Favia confertissima* from Castelgomberto is very similar to the Sassello species and differs primarily by having a narrower coenosteum; we therefore synonymize the two species. Frost (1981) considered *Favia confertissima* to be a *Goniastrea*, presumably because he believed it to lack coenosteum.

*Variabilifavia confertissima* appears to be the same as *Meandrina bisinuosa* Michelini, 1842 (p. 51, pl. 11, fig. 6), from the Miocene of Turin (Rivalba).

### Family Merulinidae Verrill, 1865

**Genus Hydnophyllia** Reis, 1889

1889 *Hydnophyllia Reis*: 130, pl. 2, figs 3–6, pl. 4, fig. 29.
1973 *Saepiphylla* Barta-Calmus: 377 [type species: *Meandrina scalaria* Catullo, 1856].
1973 *Sinuosiphylla* Barta-Calmus: 381 [type species: *Laticima dencia macrogyra* Reuss, 1868 = *Hydnophyllia sublabirintica* (Catullo, 1856)].
1973 *Gombertiphylla* Barta-Calmus: 404 [type species: *Meandrina cristata* Catullo, 1856 = *Hydnophyllia serpentinoidei* (Catullo, 1856)].
1889 *Hydnophyllia* Barta-Calmus: 407 [type species: *Coeloria platygyna* Reuss, 1869 = *Hydnophyllia costata* (Catullo, 1856)].

1973 *Fasciatiphyllia* Barta-Calmus: 411 [type species: *Latimaeandra acutijuga* Reuss, 1868 = *Hydnophyllia costata* (Catullo, 1856)].

**Type species.** *Leptoria eocaenica* Reuss, 1864, p. 19, pl. 9, fig. 9; holotype GBA 1864/0002/0032.

**Type locality.** Polschitza (Polisca) near Oberburg in Steiermark (Gornji Grad, Slovenia); Rupelian.

**Diagnosis.** Meandroid, no coenosteum; continuous, subequal costosepta; discontinuous columella with direct linkage (2 or more lamellae); little or no epitheca; trabeculothecal wall; reduced thickening deposits.

**Remarks.** *Hydnophyllia* has long been considered to be a synonym of *Colpophyllia* (Vaughan & Wells, 1943, p. 171; Wells, 1956, p. F403); however, it differs from *Colpophyllia*: (1) by lacking a coenosteum and not forming a distinctive ‘double-wall’ on the calical surface; (2) by sometimes being multiserial and/or having direct linkage (two or more lamellae) between centres; (3) by having a trabeculothecal (not parathecal) wall; and (4) by having little or no epitheca. Its septal cycles are subequal, instead of equal as in *Colpophyllia*, and it lacks the small septal lobes that are characteristic of *Colpophyllia*, instead having paliform lobes. We therefore resurrect *Hydnophyllia*, removing it from synonymy with *Colpophyllia*. *Hydnophyllia* is actually more similar to *Oulophyllia* Milne Edwards & Haime, 1848, as shown by the phylogenetic analysis below, but differs from *Oulophyllia* by forming longer series and lamellar (not trabecular) linkage between centres.

Barta-Calmus (1973, p. 384) reported the holotype of *Leptoria eocaenica* to be lost. She renamed the species *Hydnophyllia oligocenica* and assigned a specimen in the Reis (1889) collection in Munich (SNSB-BSPG AS XXVIII 25; Reis 1889, p.130, pl. 2, fig. 4) to be the holotype. However, Reuss’ original specimen of *Leptoria eocaenica* (GBA1864/0002/0032) has been found at GBA.

**Hydnophyllia collinaria** (Catullo, 1856) (Fig. 4A–F)

1889 *Hydnophyllia mirabilis* Reis: 138, pl. 3, fig. 9 [holotype SNSB-BSPG AS XXVIII 19; Reiter Schichten, Reit im Winkl].

1886 *Meandrina collinaria* Catullo: 69, pl. 9, fig. 5 [syntypes MGPUP 8158, 8206; Crocetta, Monteviale; MGPUP 8158 is selected herein as the lectotype].

1886 *Meandrina infundibuliformis* Catullo: 69, pl. 9, fig. 6 [holotype MGPUP 8226; Crocetta, Monteviale].

1889 *Hydnophyllia mirabilis* Reis: 138, pl. 3, fig. 9 [holotype SNSB-BSPG AS XXVIII 19; Reiter Schichten, Reit im Winkl].

**Material.** Five specimens, two of which are thin-sectioned (Supplemental Appendix B): two syntypes of *Meandrina collinaria*, the holotype of *Meandrina infundibuliformis* and two non-type specimens.

**Diagnosis.** Short, straight multiserial valleys that splay outwards at margins.

**Description.** Macromorphology: Fungiform colony shape, meandroid, intracalicular budding; polymorphic, having a central corallite and radiating valleys; short, straight multiserial valleys of variable width, with terminal forking; no coenosteum; valley width = large (13–28 mm); high calical relief; continuous, subequal costosepta; three septal cycles, with moderate spacing (20–22 septa per cm) and short minor septa; discontinuous, trabecular columella (1–3 threads), with lamellar linkage (2 or more lamellae); small columella, < one-quarter width of corallite; no paliform or septal lobes; little or no epitheca; abundant endothea.

Microstructure: Trabeculothecal wall, containing dissepiments (endotheca); moderate thickening deposits; no carinae or transverse septal crosses; costosepta consisting of weak clusters of fibres, <0.6 mm apart, connected by weak medial lines; columella consisting of clusters of fibres (not aligned).

**Occurrence.** Monteviale and Vicenza (Rupelian); Sassoello (Upper Rupelian—Lower Chattian).

**Remarks.** *Hydnophyllia collinaria* differs from the two modern multiserial genera, *Mycetophyllia* Milne Edwards & Haime, 1848, and *Symphyllia* Milne Edwards & Haime, 1848, by having trabeculothecal walls (Supplemental Appendix A). *Mycetophyllia* has <3 equal septal cycles, a reduced columella, reduced epitheca, and high, widely spaced, spine-shaped septal teeth. *Symphyllia* has very thick and unequal septa with large lobate teeth.

Pfister (1980) interpreted *H. collinaria* as being *Colpophyllia stellata* (Catullo, 1856) forma d (p. 70, pl. 9, fig. 1) and forma e (p. 71, pl. 10, fig. 6); Frost (1981) interpreted *H. collinaria* as being a synonym of *Dimorphophyllia oxylopha* Reuss, 1864. Barta-Calmus (1973) did not mention *H. collinaria*.

**Hydnophyllia costata** (Catullo, 1856) (Fig. 5A–I)

1866 *Symphyllia confusa* Reuss: 146, pl. 4, fig. 3 [holotype not found at GBA or NHMW; Castelgomberto].

1868 *Symphyllia multisimilis* Reuss: 151, pl. 7, figs 1, 3 [holotype MHNW 1868/0030/0025; Castelgomberto].

1868 *Cyathoseris multisinuosa* Reuss: 152, pl. 4, fig. 3 [holotype MHNW 1868/0030/0048; Castelgomberto].
\textit{Ulophyllia irradians} Reuss: 165, pl. 6, fig. 1 [holotype not found at GBA or NHMW; Castelgomberto].

\textit{Ulophyllia} (\textit{?}) \textit{acutijuga} Reuss: 171, pl. 8, fig. 2 [holotype MHNW 1868/0030/0020; Polesella, Montecchio Maggiore].

\textit{Ulophyllia} (\textit{?}) \textit{acutijuga} Reuss: 171, pl. 8, fig. 2 [holotype MHNW 1868/0030/0020; Polesella, Montecchio Maggiore].

\textit{Symphyllia serpentinoides} (Catullo); d’Achiardi: 18, pl. 11, fig. 1 [non-type specimens MSNTUP 441,442,444; Crosara].

\textit{Coeloria} (\textit{?}) \textit{grandis} Reuss: 239, pl. 20, fig. 1 [holotype GBA 1869/0008/0031; Crosara].

\textit{Coeloria} (\textit{?}) \textit{platygyra} Reuss: 239, pl. 19, fig. 2 [holotype not found at GBA or NHMW; Crosara].

\textit{Ulophyllia irradians} Reuss; Reuss: 35, pl. 47, fig. 2 [non-type specimen GBA 1874/003/0068; S. Lorenzo, Monteviale].

\textit{Hydnophyllia italica} Prever: 14, pl. 4, fig. 3 [holotype not found in Genoa; Sassello].

\textbf{Material}. Seventeen specimens, eight of which are thin-sectioned (Supplemental Appendix B): five are holotypes, 12 are non-types.

\textbf{Diagnosis}. Long, wide, sinuous uniserial valleys (>5 centres), which vary in width, spaying outward at the margins, and are V-shaped.

\textbf{Description}. Macromorphology: Fungiform colony shape, meandroid, intracalicular budding; no polymorphism; long, sinuous, V-shaped, uniserial valleys (>5 centres); no coenosteum; valley width = large but variable (10–40 mm); moderate calical relief; continuous,
subequal costosepta; three septal cycles, with moderate spacing (~20 septa per cm); discontinuous, trabecular columnella (1–3 threads), with lamellar linkage (2 or more lamellae); medium columnella, one-quarter to one-half width of corallite; no paliform or septal lobes; little or no epitheca; abundant endotheca.

Microstructure: Trabeculothecal wall; reduced thickening deposits; transverse septal crosses formed by clusters of fibres; costosepta consisting of weak clusters of fibres, <0.6 mm apart, connected by weak medial lines; columnella consisting of clusters of fibres (not aligned).

Occurrence. Crosara, Castelgomberto, Monteviale, Montecchio Maggiore, Vicenza (Rupelian); Castro ( Chattian).

Remarks. Hydnophyllia costata has larger and more variable valley widths than any other species of Hydnophyllia; its series are V-shaped and uniserial, and their margins usually splay outward.

Barta-Calmus (1973) designated a possible synonym of this species as the type of Reussiphyllia Barta-Calmus, 1973, p. 407 (type species: Coeloria (?) platgyra Reuss 1869; holotype not found at GBA or NHMW). Pfister (1980) interpreted H. costata as being Colpophyllia stellata (Catullo, 1856) forma f (p. 71, pl. 9, fig. 2); Frost (1981) interpreted H. costata as a synonym of Dimorphophyllia oxylopha Reuss, 1864.

Hydnophyllia fimbriata (Catullo, 1856)
1856 Meandrina fimbriata Catullo: 72, pl. 16, fig. 3 [holotype MGPUP 8222; S. Urbano, Montecchio Maggiore].
1856 Meandrina filogranaeformis Catullo: 72, pl. 16, fig. 4 [holotype MGPUP 8223; S. Urbano, Montecchio Maggiore].
1868a Mycetophyllia italica d’Achiardi: 21 (part), pl. 12, fig. 2 [syntype MSNTUP 107; Castelgomberto].
1868a Mycetophyllia multilamellosa d’Achiardi: 22, pl. 12, fig. 6 [syntypes MSNTUP 110, 111; Castelgomberto].
1868a Mycetophyllia dubia (Catullo); d’Achiardi: 23, pl. 12, fig. 6 [non-type MSNTUP 109; Castelgomberto].
1868a Ulophyllia ? flexuosa d’Achiardi: 25, pl. 11, figs 2, 3 [holotype MSNTUP 114; Castelgomberto].
1889 Hydnophyllia connectens Reis: 139, pl. 3, figs 1–3, pl. 4, fig. 30 [holotype, SNSB-BSPG AS XXVIII 8; Reiter Schichten, Reit im Winkl].
1921 Trydacnophyllia affinis Prever: 87, pl. 13, figs 3, 4 [holotype not found in Genoa; Sassello].
1921 Trydacnophyllia undans Prever: 88, pl. 13, figs 5, 6 [holotype not found in Genoa; Sassello].

**Material.** Eleven specimens, three of which are thin-sectioned (Supplemental Appendix B): seven are primary types and 4 are non-types.

**Diagnosis.** Short uniserial valleys (4–5 centres); extremely abundant endotheca; well-developed medial lines within costae.
Description. Macromorphology: Fungiform or massive colony shape, meandroid, intracalicular budding; no polymorphism; short, sinuous uniseri al valleys (4–5 centres); no coenosteum; valley width = medium (8–18 mm); high calical relief, V-shaped valleys; continuous, subequal costosepta; >3 septal cycles, with moderate spacing (18–24 septa per cm); discontinuous, trabecular columnella (1–3 threads), with lamellar linkage (2 or more lamellae); medium columnella, one-quarter to half width of corallite; no paliform or septal lobes; little or no epitheca; extremely abundant endotheca.

Microstructure: Trabe clothecal wall; moderate thickening deposits; transverse septal crosses with medial lines; costosepta consisting of weak clusters of fibres, <0.6 mm apart, connected by well-developed medial lines; columnella consisting of clusters of fibres (not aligned).

Occurrence. Gornji Grad, Castelgomberto, and Monteviale (Rupelian); Sassello (Upper Rupelian–Lower Chattian).

Remarks. *Hydnophyllia fimbriata* overlaps with *H. costata* in valley width but differs by having shorter valleys and more abundant dissepiments. Its corallites are larger than *H. stellata*, which also differs from *H. fimbriata* by having paliform lobes.

Barta-Calmus (1973) did not mention *H. fimbriata*. Pfister (1980) interpreted *H. fimbriata* to be *Colpophyllia stellata* (Catullo, 1856) forma h (p. 71, pl. 8, fig. 2). Frost (1981) interpreted *H. fimbriata* as a synonym of *Colpophyllia profunda* (Michelin, 1842).

*Hydnophyllia fimbriata* appears to be the same as *Meandrina stellifera* Michelin, 1842 (p. 54, pl. 11, fig. 4) from the Miocene of Turin (Rivalba). It is similar to the Miocene *Colpophyllia multisepta* Chevalier, 1962 (double wall), but differs in lacking coenosteum and having fewer septa.

*Hydnophyllia scalaria* (Catullo, 1856) (Fig. 7A–I)

1856 *Meandrina scalaria* Catullo: 69, pl. 9, fig. 7 [holotype MGPUP 8228; Creazzo, Monteviale]  
1861 *Maeandrina valleculosa* Günzel: 666 [holotype SNSB-BSPG AS XXVIII 7,14,27; Reiter Schichten, Reit im Winkl].  
?1864 *Myctophyllia interrupta* Reuss: 18, pl. 3, fig. 4 [holotype not found at GBA or MHNW; Oberburg, Gornji Grad].  
1864 *Leptoria eocaenica* Reuss: 19, pl. 9, fig. 9 [holotype GBA 1864/002/032; Oberburg, Gornji Grad]  
1864 *Coeloria (?) cerebriformis* Reuss: 19, pl. 9, fig. 9 [holotype GBA 1864/002/033; Oberburg, Gornji Grad].  
1864 *Hydnophora longicollis* Reuss: 19, pl. 4, figs 2, 4 [holotype GBA 1864/002/034; Oberburg, Gornji Grad].  
1868 *Hydnophora longicollis* Reuss: 168, pl. 5, fig. 1 [non-type specimen GBA 1868/007/0085; Pole sella, Montecchio Maggiore].  
1868a *Myctophyllia italica* d’Achiardi: pl. 12, fig. 3 [syntype MSNTUP 105; Castelgomberto].  
1871 *Ulophylla magnicostata* Michelotti in Sismonda: 324, p. 6, fig. 1 [holotype lost according to Bar- Calmus, 1973; Sassello].  
1874 *Ulophylla (?) acutijuga* Reuss; Reuss: 38, pl. 47, fig. 2 [non-type specimen GBA 1874/003/0075; Monte Sta. Trinità, Montecchio Maggiore].  
1889 *Hydnophyllia curvicollis* Reis: 136, pl. 3, figs 5–8 [SNSB-BSPG AS XXVIII 4; Reiter Schichten, Reit im Winkl].  
1894 *Plerogyra deperdita* Angelis: 224, pl. 1, fig. 25 [holotype could not be found in Rome; Sassello].  
1894 *Plerogyra crassisepta* Angelis: 225, pl. 1, fig. 26 [holotype could not be found in Rome; Sassello].  
1894 *Ulophylla laxa* Angelis: 227, pl. 1, fig. 28 [holotype could not be found in Rome; Sassello].  
1902 *Ulophylla distincta* Osasco: 109, pl. 8, fig. 11 [holotype could not be found by Barta-Calmus (1973); Monte cchio Maggiore].  
?2002b *Diploria* sp. Schuster: 95, pl. 5, figs 3, 4 [NHMW 2000a/208/0036; Doutsiko, Greece].

Material. Eighteen specimens, seven of which are thin sectioned (Supplemental Appendix B): five are primary types, 13 are non-types.

Diagnosis. Long, straight uniserial valleys (>5 centres), which are constant and narrow in width, and V-shaped.

Description. Macromorphology: Fungiform colony shape, meandroid, intracalicular budding; no polymorphism; long, straight, V-shaped uniserial valleys (>5 centres), with sharp collines and terminal forking; no coenosteum; valley width = small (4–12 mm); moderate calical relief; continuous, subequal costosepta; three septal cycles, with moderate spacing (18–24 septa per cm); discontinuous, trabecular columnella (1–3 threads), with lamellar linkage (2 or more lamellae); medium columnella, one-quarter to half width of corallite; weak paliform lobes; little or no epitheca; abundant endotheca.

Microstructure: Trabe clothecal wall; reduced thickening deposits; transverse septal crosses formed by clusters of fibres; costosepta consisting of weak clusters of fibres, <0.6 mm apart, connected by weak medial lines; columnella consisting of clusters of fibres (not aligned).

Occurrence. Gornji Grad, Castelgomberto, Montecchio Maggiore, Monteviale and Vicenza (Rupelian); Sassello (Upper Rupelian–Lower Chattian); Castro (Chattian).

Remarks. *Hydnophyllia scalaria* differs from other species of *Hydnophyllia* by having long, straight, narrow valleys. It has two forms, which may represent separate species. One has valleys that radiate from a central coralite (e.g. Fig. 7A, B, E), and the other has valleys that are more irregularly arranged (e.g. Fig. 7C, D).
Barta-Calmus (1973) described two genera with this species or a synonym as the type species: (1) *Saeptiphyllia* Barta-Calmus, 1973, p. 377 (type species *Meandrina scalaria* Catullo 1856); and (2) *Fasciatiphyllia* Barta-Calmus, 1973, p. 411 (type species *Latimaeandra acutijuga* Reuss, 1868). Pfister (1980) interpreted *H. scalaria* as being *Colpophyllia stellata* (Catullo, 1856) forma a (p. 70, pl. 8, figs 3–5, pl. 10, figs 1–2, 4). Frost (1981) considered *H. scalaria* to be a synonym of *Colpophyllia profunda* (Michelin, 1842).

Schuster (2002b) reported this species as *Colpophyllia longicollis* (Reuss, 1864) and *Colpophyllia eocaenica* (Reuss, 1864) from the Late Oligocene of Abadeh, Iran. This species appears to be the same as *Meandrina meandrinoidea* Michelin, 1842 (p. 57, pl. 11, fig. 9), from the Miocene of Turin (Rivalba).

*Hydnophyllia serpentinoides* (Catullo, 1856)
(Fig. 4G–I)

1856 *Meandrina serpentinoides* Catullo: 70, pl. 9, fig. 8 [holotype MGPUP 8227; Creazzo, Monteviale].

1856 *Meandrina cristata* Catullo: 71, pl. 16, fig. 1 [holotype MGPUP 8160; Valle di Lonte, Castelgomberto].

1869 *Ulophyllia profunda* Milne Edwards & Haime; Reuss: 238, pl. 18, fig. 8 [specimen not found at GBA or NHMW; Crosara].

**Material.** Three specimens, one of which is thin-sectioned (Supplemental Appendix B): holotypes of *Meandrina serpentinoides* and *Meandrina cristata*, and one non-type specimen.
**Diagnosis.** Usually one uniserial valley that forms a continuous series; well-developed paliform lobes and a spongy columella.

**Description.** Macromorphology: Fungiform colony shape, meandroid, intracalicular budding; no polymorphism; mostly mono- to tricentric corallites (short series); no coenosteum; corallite width = small (4 – 11 mm); moderate calical relief, V-shaped valleys; continuous, subequal costosepta; three septal cycles, with narrow spacing (22 – 30 septa per cm); discontinuous, trabecular columella (1 – 3 threads), with lamellar linkage (2 or more lamellae); medium columella, one quarter to half width of corallite; weak paliform lobes; little or no epitheca; abundant endotheca; trabeculothecal wall.

**Occurrence.** Gornji Grad, Castelgomberto, Montecchio Maggiore and Monteviale (Rupelian).

**Remarks.** *Hydnothyllia serpentinoides* is very similar to *H. sublabyrinthica* in valley width and calice shape (U-shaped), but its valleys are not as sinuous, its columella is spongy, and it has more dissepiments. Its colonies are also smaller and they usually form one continuous series.

Barta-Calmus (1973) described the genus *Gombertiophyllia* Barta-Calmus, 1973 (p. 404; type species *Meandrina cristata* Catullo, 1856) with a synonym of *H. serpentinoides* as the type species. Pfister (1980) did not mention *M. serpentinoides*. Frost (1981) interpreted *M. serpentinoides* as a synonym of *Colpophyllia profunda* (Michelin, 1842).

*Hydnothyllia stellata* (Catullo, 1856)
(Fig. 8A–D)

1856 *Meandrina stellata* Catullo: 73, pl. 16, fig. 6 [holotype MGPUP 8205; Monte Pulgo, Castelgomberto].
1856 *Latimaeandra tenera* Reuss: 175, pl. 6, fig. 4 [holotype NHMW 1868/0030/0026; Sangonini, Salcedo].
1921 *Trydacrphyllia variabilis* Prever: 91, pl. 13, fig. 9, pl. 14, figs 1 – 3 [holotype not found in Genoa; Sassello].
1921 *Trydacrphyllia compressa* Prever: 91, pl. 14, fig. 5 [holotype not found in Genoa; Sassello].
1921 *Trydacrphyllia apennina* Prever: 92, pl. 14, fig. 4 [holotype not found in Genoa; Sassello].

**Material.** Four specimens, two of which are thin-sectioned (Supplementary Material Appendix B): holotypes of *Meandrina stellata* and *Latimaeandra tenera*, and two non-types.

**Diagnosis.** Mostly mono- to tricentric corallites (short series), which are narrow in width; closely spaced septa; well-developed medial lines within costosepta.

**Description.** Macromorphology: Fungiform colony shape, meandroid, intracalicular budding; no polymorphism; mostly mono- to tricentric corallites (short series); no coenosteum; corallite width = small (4 – 11 mm); moderate calical relief, V-shaped valleys; continuous, subequal costosepta; three septal cycles, with narrow spacing (22 – 30 septa per cm); discontinuous, trabecular columella (1 – 3 threads), with lamellar linkage (2 or more lamellae); medium columella, one quarter to half width of corallite; weak paliform lobes; little or no epitheca; abundant endotheca; trabeculothecal wall.

Microstructure: Trabeculothecal wall; moderate thickening deposits; transverse septal cross with medial lines; costosepta consisting of weak clusters of fibres, < 0.6 mm apart, connected by well-developed medial lines; columella consisting of clusters of fibres (not aligned).

**Occurrence.** Castelgomberto, Salcedo (Rupelian); Sassello (Upper Rupelian – Lower Chattian); Abesse ( Chattian).

**Remarks.** *Hydnothyllia stellata* is most similar to *H. fimbria*. It is distinguished from all other species of *Hydnothyllia* by having small, short valleys and paliform lobes.

Pfister (1980) interpreted *H. stellata* as *Colpophyllia stellata* (Catullo, 1856) forma b (p. 70, pl. 8, fig. 1, pl. 9, fig. 4, pl. 10, fig. 3); Frost (1981) interpreted it as a synonym of *Colpophyllia profunda* (Michelin, 1842). *Hydnothyllia stellata* was not mentioned by Barta-Calmus (1973).

*Hydnothyllia stellata* is similar to the Miocene species *Coloaria siciliae* Chevalier, 1962, which may be a synonym.

*Hydnothyllia sublabyrinthica* (Catullo, 1856)
(Fig. 8E–I)

1856 *Meandrina subcircularis* Catullo: 73, pl. 15, fig. 2 [holotype MGPUP 8207; Monte Pulgo, Castelgomberto].
1921 *Trydacrphyllia variabilis* Prever: 91, pl. 14, fig. 5 [holotype not found in Genoa; Sassello].
1921 *Trydacrphyllia compressa* Prever: 92, pl. 14, fig. 4 [holotype not found in Genoa; Sassello].

**Material.** Four specimens, two of which are thin-sectioned (Supplementary Material Appendix B): holotypes of *Meandrina stellata* and *Latimaeandra tenera*, and two non-types.

**Diagnosis.** Mostly mono- to tricentric corallites (short series), which are narrow in width; closely spaced septa; well-developed medial lines within costosepta.
Material. Five specimens, one of which is thin-sectioned (Supplemental Appendix B): holotypes of *Meandrina subcircularis* and *Meandrina sublabyrinthica*, and 3 non-types.

Diagnosis. Highly sinuous uniserial valleys (4–5 centres) with bulbous ends, U-shaped; well-developed paliform lobes.

Description. Macromorphology: Fungiform colony shape, meandroid, intracalicular budding; no polymorphism; moderately long, sinuous, U-shaped uniserial valleys (4–5 centres), with bulbous ends; no coenosteum; valley width = medium but variable (8–16 mm); moderate calical relief; continuous, subequal costosepta; three septal cycles, with moderate spacing (18–26 septa per cm); discontinuous, trabecular columella (1–3 threads), with lamellar linkage (2 or more lamellae); medium columella, one-quarter to half width of corallite; well-developed paliform lobes; little or no epitheca; reduced endotheca.

Microstructure: Trabeculothecal wall; reduced thickening deposits; transverse septal crosses formed by clusters of fibres; costosepta consisting of weak clusters of fibres, <0.6 mm apart, connected by weak medial lines; columella consisting of clusters of fibres (not aligned).

Occurrence. Castelgomberto, Monteviale, Crosara, Vicenza (Rupelian).
Remarks. *Hydnophyllia sublabyrinthica* is most similar to *H. serpentinoides*. It distinguished by having sinuous valleys with bulbous lobes at series margins, and a reduced columella.

Barta-Calmus (1973) designated a synonym as the type species of *Sinuosiphyllia* Barta-Calmus, 1973 (p. 381; type species *Latimaeandra macrogyra* Reuss, 1868). Frost (1981) interpreted *H. sublabyrinthica* as being a synonym of *Heterogyra lobata* Reuss, 1868, and he interpreted its synonym *H. subcircularis* as synonymous with *Cyathoseiris hypocrateriformis* (Meneghini in Michelotti, 1861). Pfister (1980) did not mention *H. sublabyrinthica* or its synonyms.

This species appears to be the same as *Meandrina profunda* Michelin, 1842 (p. 54, pl. 11, fig. 3), from the Miocene of Turin (Rivalba).

**Genus** *Merulina* Ehrenberg, 1834

**Type species.** *Madrepora ampliata* Ellis & Solander, 1786, p. 157, pl. 41, figs 1, 2. Recent, “les mers de l’Inde” (Lamarck, 1816, p. 243). Holotype GLAHM 104015.

**Diagnosis.** Meandroid, long uniserial valleys (>5 centres), with no coenosteum; columella with trabecular linkage and well-developed paliform lobes; little or no epitheca; abortive septa.

**Remarks.** Fossil *Merulina isseli* differs from modern *M. ampliata* (the type species) by having larger valleys that predominantly fork laterally (not terminally), and a discontinuous columella. Its abortive septa are less apparent, and it has transverse septal crosses. These differences suggest that it may represent a separate but closely related new genus or subgenus. *Merulina* is superficially similar to *Variabilifavia* but is distinguished from *Variabilifavia* by its long series, its lack of coenosteum and epitheca, its sparse endotheca, and the presence of abortive septa.

**Merulina (?) isseli** (Prever, 1922)  
(Fig. 9A–C)

1922 *Hydnophyllia isseli* Prever: 49, pl. 10, figs 1, 2 [holotype could not be found, Sassello; neotype designated below].

**Material.** Seven specimens, all of which are thin-sectioned (Supplemental Appendix B): IPUM 28555, SAS001, Sassello is designated herein as the neotype; six are non-type specimens.

**Diagnosis.** Long, straight uniserial valleys (>5 centres), which are narrow in width and have continuous, thick costosepta and no coenosteum.

**Description.** Macromorphology: Massive colony shape, meandroid, intracalicular budding; no polymorphism; long, straight uniserial valleys (>5 centres); no coenosteum; valley width = small (5–7 mm); low calical relief;
continuous, thick, equal costosepta; <3 septal cycles, with wide spacing (14–20 septa per cm including minors); discontinuous, trabecular columella (1–3 threads), with trabecular linkage; medium columella, one-quarter to half width of corallite; well-developed paliform lobes; reduced epitheca; sparse endotheca.

Microstructure: Trabeculothecal wall, with some costoseptal thickening (septotheca) and possible abortive septa; moderate thickening deposits; transverse septal crosses formed by clusters of fibres; costosepta consisting of weak clusters of fibres, <0.6 mm apart, connected by weak medial lines; columella consisting of clusters of fibres (not aligned).

Occurrence. Sassello (Upper Rupelian–Lower Chattian)

Remarks. Merulina (?) isseli is similar to Variabilifavia confertissima, but is distinguished by its long, thin valleys, equal septa, and lack of coenosteum. Pfister (1980) considered M. (?) isseli to be a form of Colpophyllia stellata (Catullo, 1856) forma c (p. 70, pl. 9, fig. 5, pl. 10, fig. 5), whereas Frost (1981) interpreted M. (?) isseli to be a synonym of Colpophyllia profunda (Michelin, 1842).

Genus Paraleptoria gen. nov.

Type species. Meandrina polygonalis Catullo, 1856.

Type locality. Castelgomberto (Rupelian).

Additional species. Diploria flexuosissima d’Achiardi, 1868a, p. 22, pl. 11, fig. 4; holotype MSNTUP 576, San Giovanni Ilarione, Lutetian.

Diagnosis. Meandroid, long uniserial valleys (>5 centres); a lamellar columella and T-shaped septa margins; extensive costate coenosteum.

Remarks. Paraleptoria is distinguished from other meandroid genera in this study by its lamellar columella, T-shaped septal margins, and extensive costate coenosteum. Modern Leptoria phrygia (the type species) lacks coenosteum; whereas coenosteum is especially well developed in Paraleptoria. As a result, P. polygonalis does not group with modern Leptoria in the phylogenetic analysis, warranting the description of a new genus. In addition to P. polygonalis, the new genus contains the common early Eocene species P. flexuosissima.

Paraleptoria polygonalis (Catullo, 1856) (Fig. 9D–F)

1856 Meandrina polygonalis Catullo: 72, pl. 16, fig. 5.
1921 Leptoria ambiguа Prever: 93, pl. 14, fig. 7 [holotype not found in Genoa; Sassello].

Material. One specimen, which is not thin-sectioned (Supplemental Appendix B): holotype, MGPUP 8204, Monte Pulgo, Castelgomberto, Rupelian.

Diagnosis. Long sinuous uniseral valleys (>5 centres), separated by extensive costate coenosteum; T-shaped septal margins; lamellar columella.

Description. Macromorphology: Massive colony shape, meandroid, intracalicular budding; no polymorphism; long, sinuous uniserial valleys (>5 centres); extensive costate coenosteum; very small (2–3 mm) valley width; low calical relief; discontinuous, equal costosepta; ≤3 septal cycles, with narrow spacing (~30 major septa per cm), with T-shaped septal margins; continuous, lamellar columella; medium columella, one-quarter to half width of corallite; moderately well-developed paliform lobes; reduced epitheca; sparse endotheca; trabeculothecal wall.

Occurrence. Castelgomberto (Rupelian).

Remarks. This species differs from the Eocene species, Paraleptoria flexuosissima, which has a valley width of 1.5–2 mm and 24–26 major septa per cm. Paraleptoria polygonalis was not reported by Pfister (1980), but Frost (1981) considered it to be a valid species. This species differs from Meandrina phrygia Michelin, 1842 (p. 55, pl. 11, fig. 5), from the Miocene of Turin (Rivalba), which lacks a coenosteum and appears to be more similar to Merulina isseli. It differs from Leptoria bithecata Schuster, 2002b from the Oligocene of NW Greece, which has a valley width of 4.6–6 mm and a distinctive double-wall. It is also not the same as the species identified as Leptoria cf. concentrica (Duncan, 1880) by Schuster (2002a; Oligocene, Iran) or as Leptoria sp. by Schuster (2002b; Oligocene, Greece), which both have valley widths of 6–8 mm.

Family Lobophylliidae Dai & Horng, 2009
Genus Symphyllia Milne Edwards & Haime, 1848

Type species. Meandrina sinuosa Quoy & Gaimard, 1833, p. 227, pl. 18, figs 4, 5; holotype lost.

Type locality. “Habite le havre Carteret de la Nouvelle-Irlande” (Quoy & Gaimard 1833, p. 228); Recent.

Diagnosis. Meandroid, long uniserial or multiserial valleys (>5 centres); no coenosteum; unequal costosepta; discontinuous trabecular columella with direct linkage (2 or more lamellae); no lobes or epitheca; parathecal wall; abundant dissepiments; extensive thickening deposits.

Remarks. Among Palaeogene corals, this genus is most frequently confused with Cyathoseris, which is also multiserial and has columellae with direct linkage (2 or more lamellae). However, Cyathoseris has synapticulae and...
little or no dissepiments; its septa are confluent and its septal cycles are equal.

*Symphyllia* sp.  
(Fig. 10A–C)

**Material.** One specimen, which is thin-sectioned (Supplemental Appendix B).

**Diagnosis.** Multiserial valleys; unequal costosepta; parathecal wall.

**Description.** Macromorphology: Massive colony shape, meandroid, intracalicular budding; no polymorphism; sinuous multiserial valleys of variable width, with terminal forking; no coenosteum; valley width medium (8–15 mm); high calical relief; discontinuous, unequal costosepta; three septal cycles, with moderate spacing (20 septa per cm); discontinuous, spongy columella (>3 threads), with lamellar linkage (2 or more lamellae); medium columella, one-quarter to half width of corallite; no paliform or septal lobes; little or no epitheca; abundant endotheca.

Microstructure: Parathecal wall, with some costoseptal thickening (septotheca); extensive thickening deposits; no carinae or transverse septal crosses; costosepta consisting of well-developed clusters of fibres, >1.2 mm apart, connected by weak medial lines.

**Occurrence.** Vicenza (Rupelian).

**Remarks.** Represented by only one specimen, this species is indicated in open nomenclature.

*Symphyllia* was not reported by Barta-Calmus (1973), Pfister (1980) or Frost (1981). The Eocene species *Pectinia pseudomeandrites* d’Achiardi, 1866 (p. 40, pl. 3, fig. 11) is a synonym.

Genus *Echinophyllia* Klunzinger, 1879

**Type species.** *Madrepora aspera* Ellis & Solander, 1786, p. 156, pl. 39; holotype GLAHM 104004. “Habitat in Oceano Indiae orientalis” (Ellis & Solander, 1786, p.156); Recent.

**Diagnosis.** Meandroid forming series that lack corallite walls; extensive vesicular coenosteum; continuous costosepta; discontinuous columellae, lacking linkages; little or no epitheca.

**Remarks.** *Echinophyllia* differs from other members of Lobophylliidae by having an extensive vesicular coenosteum and lacking corallite walls. It is most frequently confused with the merulinid genus *Pectinia* Blainville, 1825, which also forms series and lacks corallite walls. However, in *Pectinia*, the coenosteum forms high, acute collines.

*Echinophyllia sassellensis* sp. nov.  
(Fig. 10D–F)
**Derivation of name.** After Sassello (Savona, Liguria, Italy).

**Material.** Four specimens, all of which are thin-sectioned and are primary types (Supplemental Appendix B); Sassello, Upper Rupelian–Lower Chattian. Holotype: NHMUK R3525. Paratypes: NHMUK R3499a, R3522, R3524.

**Diagnosis.** Discrete corallites arranged in irregular, sinuous series without corallite walls; <3 septal cycles, with wide spacing (<12 septa per cm).

**Description.** Macromorphology: massive explanate colony shape, meandroid, intracalicular budding; no polymorphism; discrete corallites arranged in irregular, sinuous series without corallite walls; extensive vesicular coenosteum; corallite width = medium (8–12 mm); moderate calical relief; continuous, equal costosepta; <3 septal cycles, with wide spacing (<12 septa per cm); discontinuous, trabecular columella (<3 threads), with no linkages between centres; medium columella, one-quarter to half width of corallite; moderate paliform lobes, no septal lobes; little or no epitheca; moderate endotheca.

Microstructure: Moderate thickening deposits; transverse septal faces formed by clusters of fibres; costosepta consisting of weak clusters of fibres, 0.6–1.2 mm apart, connected by weak medial lines; columella consisting of clusters of fibres (not aligned).

**Occurrence.** Sassello (Upper Rupelian–Lower Chattian).

**Remarks.** *Echinophyllia* was not reported by Barta-Calmus (1973), Pfister (1980) or Frost (1981).

**Analytical methods**

**Characters**

Following Budd & Stolarski (2009, 2011) and Budd et al. (2012), we selected 50 characters for morphological phylogenetic analysis (Supplemental Appendix E), and coded the 14 extinct species (13 species treated herein plus one Oligocene *Hydnophora*). The characters consist of three sets of features: (1) macromorphology (using a stereoscope, at magnifications <50×); (2) micromorphology (using a scanning electron microscope, at magnifications ranging from 50–200×); and (3) microstructure (using transverse thin sections, at magnifications <100×). Micromorphological and microstructural analyses are relatively new to morphological phylogenetic analysis. A glossary of morphological terms that are used in this monograph is provided in Supplemental Appendix D.

Macromorphological features serve as the primary diagnostic characters in traditional classification (Vaughan & Wells 1943; Wells 1956), e.g. Supplemental Appendix A and C. They are architectural in nature, including colony form (corallite budding and integration, the length and shape of calical series); the size and shape of the calice; the structure and development of the septa (number, spacing, relative thickness and length), the columella (and associated internal lobes), the corallite wall, endotheca, and the coenosteum.

Micromorphological features, most notably septal structure, were also included in the traditional definition of families and higher taxonomic levels, but only in a cursory way that did not involve the use of electron microscopy. They focus on the 3D geometry of teeth (dentation) along the upper margins of the costosepta and columella (the septal growing edge), as well as on granulation on septal faces and the sides of teeth. Teeth and granules are surficial projections, which reflect the underlying calcification axes that build the internal structure and framework of the costoseptum. In the present study, micromorphological features could not be examined in extinct taxa due to inadequate preservation, and therefore were coded as missing in the character matrix (Supplemental Appendix F).

With the exception of corallite wall structure, microstructural features were not used in the traditional classification of Vaughan & Wells (1943) and Wells (1956), although they were included in the classification systems of Alloiteau (1952, 1957) and Chevalier & Beauvais (1987). They involve the internal structure (i.e. the arrangement of calcification centres and fibres) within the wall, septa, and columella, and consist of 2D observations made primarily using transmitted light on petrographic thin sections. As in Budd et al. (2012), we focus both on the corallite wall (the skeletal structure uniting the outer edges of septa in a corallite) using the wall types defined by Budd & Stolarski (2011), as well as on the costosepta and columella. In the latter observations, we consider the degree to which calcification centres are clustered, the distinctiveness of costoseptum medial lines, and the presence of transverse structures or clusters of centres crossing medial lines. Despite recrystallization, these features could be observed in extinct taxa for which we have thin sections.

Most of the characters analysed in the phylogenetic analysis (Supplemental Appendix E) are defined as in Budd et al. (2012), with the following exceptions:

1. **five new macromorphological characters** were added: ‘monticules’, ‘series width’, ‘series sinuosity’, ‘series forking/margins’ and ‘columella linkage’;

2. **six macromorphological characters** were redefined: ‘corallite integration’ as ‘corallite series’ (two states added), ‘coenosteum structure’ (one state dropped), ‘corallite centre linkage’ as ‘columella continuity’ (one state dropped), ‘columella size’ (one state added), internal lobes was split into ‘paliform’ and ‘septal lobe/palus’;
one macromorphological character was dropped: ‘free septa’;
(4) one new micromorphological character was added: ‘> 6 teeth per septum’;
(5) two micromorphological characters were redefined: ‘tooth tips’ was split into ‘tooth tips’ and ‘tooth regularity’; ‘granule shape & distribution’ was split into ‘granule distribution’ and ‘granule shape’;
(6) four microstructural characters were redefined: ‘costoseptum centre clusters’ was split into ‘costa/wall centre clusters’ and ‘septum centre clusters’; ‘distance between costoseptum clusters’ was split into ‘distance between costa/wall centre clusters’ and ‘distance between septum centre clusters’; ‘costoseptum medial lines’ was split into ‘costa/wall medial lines’ and ‘septum medial lines’.

These modifications were made to facilitate inclusion of the extinct taxa in the character matrix, and to provide more precise definitions of characters.

Phylogenetic analysis
The phylogenetic dataset was constructed by adding the 14 extinct species (13 species treated herein plus one Oligocene Hydnophora) to a character matrix for 62 living species, making a total of 76 taxa (Supplemental Appendix F). The living species consist of 62 of the 67 species analysed in Budd et al. (2012, figs 2, 8). Five solitary species (Scolymia cubensis, S. wellsi, Cynarina lacrymalis, Parascolymia viensis and Homophylla australis) in Budd et al. (2012) were not included. Diploastrea heliopora — molecular clade XV of Fukami et al. (2008) — was designated as the outgroup. One of the 62 species belongs to molecular clade XVI (Montastraeidae) of Fukami et al. (2008), 31 species belong to molecular clade XVII (Merulinidae), 14 species belong to molecular clade XVIII+XIX+XX (Lobophylliidae), and 16 species belong to molecular clade XX (Mussidae). As mentioned above, of the Fukami et al. (2008) molecular clades, clades XVI (Montastraeidae) and XXI (Mussidae) are exclusively Atlantic today; clade XVII (Merulinidae) (except the Orbicella annularis complex) and clades XVII–XX (Lobophylliidae) are exclusively Indo-Pacific today.

Parsimony analysis was performed on the dataset (76 taxa × 50 characters) using PAUP* 4.0b10 (Swofford 2002). Heuristic searches were conducted with 10,000 random addition replicates on the 76-taxon by 50-character data matrix. Tree bisection and reconnection (TBR) was used as the branch-swapping algorithm. Zero-length branches were collapsed if they lacked support under any of the most parsimonious reconstructions. To assess clad support, heuristic searches were performed on 1000 bootstrap pseudoreplicate datasets (Felsenstein 1985), with 100 random addition sequence replicates for each bootstrap search. In addition, Bremer support values (Bremer 1988) were calculated for each node in the strict consensus of MPTs resulting from each analysis using TreeRot 3 (Sorenson & Franzosa 2007). The number of random addition sequence replicates performed for each constraint analysis was set to 100.

Results
The phylogenetic analysis performed on the character matrix (67 taxa × 50 characters, Supplemental Appendix F) recovered 86 most parsimonious trees (MPTs) of length 93 steps, with a consistency index (CI) of 0.226 and a retention index (RI) of 0.750. The strict consensus tree of the MPTs is shown in Figure 11. Six clades (A–F) are recovered as monophyletic, albeit with low support. Three modern species did not group with any of the six clades: Montastraea cavernosa, Gonastrea stelligera and Astrea curta. In general, the six clades agree with previously defined molecular clades. Clade A corresponds with molecular clade XXI (Mussidae) of Fukami et al. (2008); and clade F corresponds with molecular clades XVIII+XIX+XX (Lobophylliidae) of Fukami et al. (2008), with the exception of two members of the former family Pectiniidae (Oxypora and Echinophyllia). Clades B+C+D+E correspond with molecular clade XVII (Merulinidae) of Fukami et al. (2008), such that clade B corresponds with molecular subclade XVII-C (as defined by Budd & Stolarski 2011 and Huang et al. 2014), clade C with molecular subclades XVII-A+G+H, clade D with molecular subclades XVII-B+D+F, and clade E with molecular subclade XVII-F.

The 14 extinct species group with four of the six clades shown in Figure 11. The two Variabilifavia species group with clade A. Species of Paraleptoria and Merulina and Oligocene Hydnophora group with clade C. The seven Hydnophyllia species group with clade D, and the fossil Echinophyllia groups with the former family Pectiniidae. The seven Hydnophyllia species form a separate subclade within clade D. Assignments of species to families and genera detailed in the Systematic palaeontology section above are based in part on these results.

Discussion
The results of the present study show considerably higher diversity in Oligocene Mediterranean meandroid corals (13 species) than that reported most recently (two species) by Frost (1981) and Pfister (1980), resulting in the resurrection of many of the species originally described by Catullo (1856). Our examination of nineteenth century type species (Catullo 1856; d’Achiardi 1868b; Reuss
1864, 1868, 1869, 1874) indicates that species names correspond among these classic works as shown in Figure 12. Our phylogenetic analysis (Fig. 11) shows that only two of the 13 species group with a modern Caribbean family (Mussidae-XXI), and that 11 species group with modern Indo-Pacific families (Merulinidae-XVII and Lobophylliidae-XVIII-XIX). The overall results reveal six main clades labelled A–F: one (A) consisting of the family Mussidae, four (B–E) consisting of the family Merulinidae and one (F) consisting of the family Lobophylliidae. The one exception is Clade D, which includes a subclade (Oxypora+Echinophyllia, members of the former family Pectiniidae) belonging to the Lobophylliidae.

Figure 11. Strict consensus tree for morphological phylogenetic analysis (maximum parsimony) including modern and extinct species. Species treated herein are with ‘+’. Roman numerals correspond with the molecular clades of Fukami et al. (2008). Numbers above and below nodes are bootstrap values (> 50) and Bremer support values (> 1) respectively.
At the genus level, three distinct fossil genus-level ‘subclades’ occur within the six main clades (Fig. 11), resulting in the resurrection of two fossil genera, *Variabilifavia* (two species) in clade A (Mussidae) and *Hydnophyllia* (seven species) in clade D (Merulinidae), and the description of one new fossil genus, *Paraleptoria* (one species), in clade C (Merulinidae). The remaining three species group with the modern genera *Merulina* (clade C, Merulinidae), *Echinophyllia* (clade D, Lobophylliidae) and *Symphyllia* (clade F, Lobophylliidae). *Variabilifavia*, *Hydnophyllia* and *Paraleptoria* all have a distinctive trabeculothecal wall, similar to modern Indo-Pacific *Leptoria*, *Platygyra* and *Hydnophora*. *Variabilifavia* is morphologically most similar to modern Caribbean *Diplopora* (septothecal) in that it has a well-developed ambulacrum; however, its series are shorter, and its coenosteum is not as well developed. In addition, it has a discontinuous columella and more septal cycles, and differs in wall structure. *Variabilifavia* is also similar to modern Caribbean *Favia* (septothecal), but has longer series and a trabeculothecate wall. By contrast, *Hydnophyllia* is most similar to modern Indo-Pacific *Oulophyllia* (parathecal) in its series dimensions, lack of coenosteum and discontinuous columella. However, it too differs in wall structure. It has frequently been confused with modern Caribbean *Colpophyllia* (parathecal), which unlike *Hydnophyllia* has coenosteum, a double-wall, septal lobes and reduced thickening deposits. *Paraleptoria* is most similar to modern Indo-Pacific *Leptoria*, both genera having trabeculothecal walls and a lamellar columella. However, unlike *Leptoria*, *Paraleptoria* has a well-developed coenosteum. Clearly the patterns in wall structure are noteworthy and require further investigation.

The grouping of Mediterranean extinct species with modern family-level clades in the present study disagrees with previous interpretations that Oligocene Mediterranean and modern Caribbean meandroid corals are more closely related to each other than they are to Indo-Pacific corals (Pfister 1980; Frost 1981). Instead, they suggest that most Mediterranean Oligocene meandroid corals were part of a more cosmopolitan pan-tropical Tethyan fauna, which extended from the Indo-Pacific into the Mediterranean. The seaway between the Eastern Mediterranean Basin and the Mesopotamian Basin narrowed during the Oligocene, but nevertheless marine circulation from the Indian Ocean
to the Atlantic was maintained until the early Miocene (Perrin 2002; Harzhauser et al. 2007). However, few corals with possible Indo-Pacific affinity have been reported to date from Iran and elsewhere on the Arabian shelf (Schuster 2002a, c; Schuster & Wielandt 1999). The close relationship that we have observed between Mediterranean and Indo-Pacific meandroid corals concurs with the ‘hopping hotspot’ theory of Renema et al. (2008), which states that diversity was highest in the Mediterranean during the Eocene and the hotspot shifted in a south-west direction toward South-East Asia, where it has remained since the Miocene (Johnson et al. 2015a, b).

On the western side, our analyses indicate that the Caribbean region may have been more geographically isolated by the widening Atlantic than previously interpreted. Chevalier (1977) and Perrin (2002) have noted that gradual isolation began in the late Oligocene in association with a major change in oceanographic circulation in the central Atlantic. Our results suggest that isolation occurred even earlier, in the early Oligocene or Eocene. Additional comparative work between Caribbean and Mediterranean Eocene–Oligocene reef coral faunas using up-to-date systematics is underway to test this hypothesis. Similarly, previous authors have suggested that many of the Mediterranean reef-building genera and species may have been geographically restricted (Perrin & Bosellini 2012). Further work comparing Caribbean, Mediterranean and Indo-Pacific Eocene–Oligocene reef coral faunas using up-to-date systematics is needed to reassess these geographical ranges.

The addition of fossils to the morphological phylogenetic analysis in the present study, albeit with missing data, has resulted in a significant improvement not only in tree resolution over constructions based only on modern taxa, but also in the agreement between morphological and molecular trees. In a previous modern-only morphological analysis (Budd et al. 2012, fig. 8; 68 taxa × 38 characters), 243 maximum parsimony trees were recovered with a tree length of 200. The Adams consensus tree showed that Indo-Pacific Lobophylliidae (molecular clade XIX) formed a distinct group, and Caribbean Mussidae (molecular clade XXI) formed three distinct groups (two Faviinae, one Mussinae). However, Indo-Pacific Merulinidae (molecular clade XVII) remained for the most part unresolved. In a phylogenetic analysis of modern-only corals based on exactly the same morphological character set as the present study (62 taxa × 50 characters analysed using PAUP*), the analysis found 33,136 maximum parsimony trees with a tree length of 284, compared with 86 trees of length 93 when the 14 fossils are included. Caribbean Mussidae (molecular clade XXI) form a distinct group, and with the exception of Oxypora+Echinophyllia, former members of the Pectiniidae, Indo-Pacific Lobophylliidae (molecular clades XVIII+XIX+XX) form a distinct group. However, Indo-Pacific Merulinidae do not. By contrast, when fossils are included in the morphological analysis, no longer are modern Caribbean meandroid corals (Mussidae: molecular clade XXI) intermixed with modern Indo-Pacific taxa (Merulinidae: molecular clade XVII) as in Budd et al. (2012), but instead the Caribbean taxa form a separate clade. Moreover, as described above, modern Indo-Pacific merulinids form four distinct clades (labelled B–E in Fig. 11), which are congruent with the molecular merulinid clades described by Budd & Stolarski (2011) and Huang et al. (2014).

The improved agreement between morphological and molecular data when fossils are included in the analysis has been found elsewhere in analyses of corals (Santodomingo et al. 2014), as well as in numerous other organisms, including seed plants and amniotes (Donoghue et al. 1989). Improved agreement has been found even when incomplete taxa are added to an analysis (Wiens & Tiu 2012). These results support the notion that limited taxon sampling is equally as problematic as limited character sampling in phylogenetic analysis. Adding extinct taxa has the potential to improve significantly phylogenetic accuracy in groups, such as corals, in which numbers of morphological characters are low, convergences and reversals are high, and branches are relatively long. Fossils have been hypothesized to have a unique combination of primitive and derived character states that can strengthen certain groupings, especially if the included extinct corals are temporally closer to the ancestor (Gauthier et al. 1988; Huelsenbeck 1991; Smith 2010). In the present study, this is the case within the merulinids (clades B–E), as shown in Figure 11. Resolving higher-level relationships among mussids, merulinids and lobophylliids would require including even older fossils in future analyses, dating back to the divergence of the merulinids and lobophylliids in the Cretaceous (Santodomingo et al. 2014). Improved phylogenies in scleractinian systematics will require not only integration of molecular and morphological data, but also the inclusion of extinct taxa.

Conclusions

We have shown that an up-to-date approach to systematics is essential for uncovering evolutionary patterns in reef corals that have long been masked by inadequate phylogenetic analysis. Our work has discovered previously unrecognized faunal differences that are clearly related to biogeography. Most importantly, Oligocene Mediterranean meandroid reef corals are more closely related to modern Indo-Pacific corals than they are to modern Caribbean corals. Mediterranean meandroid corals may have
been part of a more cosmopolitan Tethyan fauna, whereas Caribbean meandroid corals were more isolated, resulting in the development of the genetically unique fauna that occupies the region today. The systematics of additional coral families needs to be similarly analysed to determine how widespread these patterns are and to understand better the role that biogeography has played in the evolution of the modern reef coral fauna.

Acknowledgements

We are grateful to Danwei Huang and Nathan Smith for comments and suggestions on the phylogenetic analysis, and to two anonymous reviewers for comments on the text. For help with museum collections, we thank Irene Zorn (GBA), Mariagabriella Fornasiero (MPUP), Ricardo Manni (MPUR), Marco Avanzini and Massimo Bernardi (MUSE), Jill Darrell (NHMUK), Oleg Mandic (NHMW) and Martin Nose (SNSB). We also thank Sergio Boschele, James Nebelsick and Thérèse Pfister for providing specimens and photos from their collections. We thank Stefano Castelli (MPUP) for making excellent photos of Catullo’s specimens. This work was supported by US National Science Foundation under Grant DEB-1145043 to AFB, and by a grant from MIUR/PRIN 2010-2011 to FRB.

Supplemental material

Supplemental material for this article can be accessed here: http://dx.doi.org/10.1080/14772019.2015.1102171

References

d’Achiardi, A. 1866. Corallari fossili del terreno nummulitico delle Alpi venete. Memorie della Società Italiana di Scienze Naturali, 2(4), 1–53.

d’Achiardi, A. 1867. Corallari fossili del terreno nummulitico dell’Alpi Venete. Catalogo della specie e brevi note. Memorie della Società Italiana di Scienze Naturali, 3, 1–18.

d’Achiardi, A. 1868a. Corallari fossili del terreno nummulitico dell’Alpi Venete. Memorie della Società Italiana di Scienze Naturali, 4(1), 1–31.

d’Achiardi, A. 1868b. Studio comparativo tra i coralli dei terreni terziari del Piemonte e delle Alpi venete. Annali Università toscane, 10(2), 73–144.

Alloiteau, J. 1952. Madrèporaires Post-Paléozoiques. Pp 539–684 in J. Piveteau (ed.) Traité de paléontologie. Masson, Paris.

Alloiteau, J. 1957. Contribution à la systématique des madrèporaires fossiles. Centre National de la Recherche Scientifique, Paris, 1, 462 pp.

Angelis d’Ossat, G. de. 1894. I coralli dei terreni Terziari dell’Italia settentrionale. Collezione Michelotti. Museo Geologico della R. Università di Roma. Roma. Atti della Reale Accademia dei Lincei, 5, 164–280.

Barta-Calmus, S. 1973. Révision de collections de madréporaires provenants du Nummulitique du sudest de la France, de l’Italie et de la Yugoslavie septentrionales. PhD thesis, Université de Paris VI, C.N.R.S., Paris, 694 pp.

Berggren, W. A. & Hollister C. D. 1974. Paleogeography, paleobiogeography and the history of circulation in the Atlantic Ocean. SEPM Special Publication, 20, 12–186.

Blainville, H. M. D. de. 1825. Mollusques, vers et zoophytes. Pp. 1–528 in J. L. M. Defrance (ed) Dictionnaire des sciences naturelles, Volume 38. Levrault, Paris.

Blainville, H. M. D. de. 1830. Zoophytes. Dictionnaire des Sciences Naturelles, 60, 297–364.

Boschele, S., Gatto, R., Bernardi, M. & Avanzini, M. 2011. Fossili cenozoici della Valsugana. Catalogo della collezione Boschele, parte I. Studi Trentini di Scienze Naturali, 88, 219–309.

Rosellini, A. 1989. Dynamics of Tethyan Carbonate Platform. SEPM Special Publication, 44, 3–13.

Bosellini, A., Bosellini, F. R., Colalongo, M. L., Parente, M., Russo, A. & Vescogno, A. 1999. Stratigraphic architecture of the Salento Coast from Capo d’Otranto to S.Maria di Leuca (Apulia, Southern Italy). Rivista Italiana di Paleontologia e Stratigrafia, 105, 397–416.

Bosellini, F. R. 1999. The scleractinian genus Hydnophora (revision of Tertiary species). Paläontologische Zeitschrift, 73, 217–240.

Bosellini, F. R. 2006. Biotic changes and their control on Oligocene-Miocene reefs: a case study from the Apulia Platform margin (southern Italy). Palaeogeography, Palaeoclimatology, Palaeoecology, 241, 393–409.

Bosellini, F. R. & Perrin, C. 1994. The coral fauna of Viti-giano: qualitative and quantitative analysis in a back reef environment (Castro Limestone, Late Oligocene, Salento Peninsula, Southern Italy). Bollettino della Società Paleontologica Italiana, 33, 171–181.

Bosellini, F. R. & Perrin, C. 2008. Estimating Mediterranean Oligocene–Miocene sea-surface palaeotemperatures: an approach based on coral taxonomic richness. Palaeogeography, Palaeoclimatology, Palaeoecology, 258, 71–88.

Bosellini, F. R. & Russo, A. 1992. The Castro Limestone: stratigraphy and facies of an Oligocene fringing reef (Salento Peninsula, Southern Italy). Facies, 26, 145–166.

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

Bremer, K. 1988. The limits of amino-acid sequence data in angiosperm phylogenetic reconstruction. Evolution, 42, 795–803.

Budd, A. F., Fukami, H., Smith, N. D. & Knowlton, N. 2012. Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zoological Journal of the Linnean Society, 166, 465–529.

Budd, A. F., Romano, S. L., Smith, N. D. & Barbeitos, M. S. 2010. Rethinking the phylogeny of scleractinian corals: a review of morphological and molecular data. Integrative and Comparative Biology, 50, 411–427.

Budd, A. F. & Stolarski, J. 2009. Searching for new morphological characters in the systematics of scleractinian reef corals: Comparison of septal teeth and granules between Atlantic and Pacific Mussidae. Acta Zoologica, 90, 142–165.

Budd, A. F. & Stolarski, J. 2011. Corallite wall and septal microstructure in scleractinian reef corals: Comparison of
molecular clades within the family Faviidae. *Journal of Morphology*, 272, 66–88.

Cahuzac, B. & Chaix, C. 1996. Structural and faunal evolution of Chattian-Miocene reefs and corals in western France and the northeastern Atlantic Ocean. Pp. 105–127 in E. K. Franseen, M. Esteban, W. C. Ward & J. M. Rouchy (eds). *Models for Carbonate Stratigraphy from Miocene Reef Complexes of the Mediterranean regions, Concepts in Sedimentology and Paleontology, Volume 5*. SEPM, Tulsa.

Cahuzac, B. & Janssen, A. W. 2010. Eocene to Miocene holoplanktonic Mollusca (Gastropoda) of the Aquitaine Basin, southwest France. *Scripta Geologica*, 141, 1–193.

Cahuzac, B. & Poignant, A. 1997. Essai de biozonation of the Oligo–Miocene in the basins europeens à l’aide des grands foraminifères nériques. *Bulletin de la Société Géologique de France*, 168, 155–159.

Cahuzac, B. & Poignant, A. 2002. Associations of foraminifers benthiques et quelques gisements de l’Oligo-Miocène sud-aquitain. *Revue de Micropaleontologie*, 45, 221–256.

Catullo, T. A. 1838. Die Corallenthiere des rothen Meeres. *Annali Universit a di Ferrara*, 11, 1–110.

Chevalier, J. P. 1981. Oligocene reef coral biofacies of the Vicentin, the northeastern Atlantic Ocean. Pp. 105–21 in A. F. Budd and F. R. Bosellini (eds). *Felsenstein, J.*

Chevalier, J. P. 1987. Recherches sur les madrasiens et les formations récifales miocènes de la Méditerranée occidentale. *Mémoires de la Société Géologique de France*, 93, 1–562.

Chevalier, J. P. 1977. Aperçu sur la faune corallienne récifale du Néogène. *Mémoires du BRGM*, 89, 359–366.

Chevalier, J. P. & Beauvais, L. 1987. Ordre des Scléréactinaires. Pp. 403–764 in P. Grasse (ed.) *Traité de zoologie*, 3 Cnidaires, anthozoaires. Masson, Paris.

Dai, C. F. & Horng, S. 2009. *Scleractinia fauna of Taiwan. II. The robust group*. National Taiwan University, Taipei, 162 pp.

Donoghue, M. J., Doyle, J. A., Gauthier, J., Kluge, A. G., Rowe, T. 1989. The importance of fossils in phylogeny reconstruction. *Annual Review of Ecology and Systematics*, 20, 431–460.

Duncan, P. M. 1880. A monograph of the fossil corals and Alcyonaria of Sind. *Memoirs of the Geological Survey of India*. *Palaeontologia Indica*, Series 14, 1, 1–110.

Ehrenberg, C. G. 1834. Die Corallinhære des rothen Meeres physiologisch Untersucht und systematisch Verzeichnet. Ein Beitrag zur physiologischen Kenntniss der Corallinhære im algeménen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin*, 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*. Benjamin White and Son and Peter Elmsly, London, 206 pp.

Felsenstein, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution*, 39, 783–791.

Fgravea, P., Giammarino, S., Piazza, M., Russo, A. & Vanucci, G. 1987. Significato paleoecologico degli episodi coraligi a nord di Sassello. Nuovi dati per una ricostruzione paleogeografico-evolutiva del margine meridionale del Bacino Terziario del Piemonte. *Atti Società Toscani Scienze Naturali*, 94, 19–76.

Frost, S. H. 1981. Oligocene reef coral biofacies of the Vicentin, northeast Italy. *SEPM Special Publication*, 30, 483–539.

Fukami, H., Budd, A. F., Paulay, G., Sole-Cava, A. M., Chen, C. A., Iwao, K. & Knowlton, N. 2004. Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. *Nature*, 427, 832–835.

Fukami, H., Chen, C. A., Budd, A. F., Collins, A. G., Wallace, C. C., Chuang, Y-Y, Chen, C. A., Dai, C-F, Iwao, K., Sheppard, C. & Knowlton, N. 2008. Mitochondrial and Nuclear Genes suggest that stony corals are monophyletic but most families of stony corals are not (Order Scleractinia, Class Anthozoa, Phylum Cnidaria). *PLoS One*, 3, e3222.

Gauthier, J. A., Kluge, A. G. & Rowe, T. 1988. Amniote phylogeny and the importance of fossils. *Cladistics*, 4, 105–209.

Gregory, J. W. 1900. The corals Jurassic fauna of Cutch. *Palaeontologica Indica, Series 9*, 2, 1–195.

Gümbel, C. W. von. 1861. *Geognostische Beschreibung des Bayerischen Alpengebirges (Teil I) Geognostische Beschreibung des Bayerischen Alpengebirges und seines Vorlandes*. Justus Perthes, Gotha, 950 pp.

Haim J. 1850. *Hydrophora Bronni*. Pp. 229 in A. d’Archiac (ed.) *Histoire des Progrés de la Géologie*. 3. Au lieu des séances de la Société, Paris.

Harzhauser, M., Kroh, A., Mandic, O., Pillar, W. E., Gohl, U., Reuter, M. & Berning, B. 2007. Biogeographic responses to geodynamics: A key study all around the Oligo–Miocene Tethyan Seaway. *Zoologischer Anzeiger*, 246, 241–256.

Huang, D., Benzioni, F., Fukami, H., Knowlton, N., Smith, N. D. & Budd, A. F. 2014. Taxonomic classification of the reef coral families Merulinidae, Montastraeidae and Diplastreaeae (Cnidaria: Anthozoa: Scleractinia). *Zoological Journal of the Linnean Society*, 171, 277–355.

Husseinbeck, J. P. 1991. When are fossils better than extant taxa in phylogenetic analysis? *Systematic Zoology*, 40, 458–469.

Johnson, K. G., Hasibuan, F., Müller, W. & Todd, J. A. 2015a. Biotic and environmental origins of the southeast Asian marine biodiversity hotspot: The Throughflow Project. *Palaios*, 30, 1–6.

Johnson, K. G., Renema, W., Rosen, B. R. & Santodomingo, N. 2015b. Old data for old questions: What can the historical collections really tell us about the Neogene origins of reef-coral diversity in the Coral Triangle. *Palaios*, 30, 94–108.

Klinzinger, C. B. 1879. *Die Korallithiere des Roten Meeres. Dritter Theil: Die Steinkorallen*. Verlag der Guttmann’schen Buchhandlung, Berlin, 188 pp.

Lamareck, J. B. P. de. 1816. *Histoire naturelle des animaux sans vertèbres*. 2. Verdrië, Libraire, Paris, 568 pp.

Linnaeus, C. 1758. *Systema Naturae per regna tria naturae, secundum Classes, Ordines, Genera, Species, cum characteribus, differentiis, synonymis, locis. Tomus I. Regnum Animal. Editio Decima*. Holmiae, Stockholm, 824 pp.

Luciani, V. & Trevisani, E. 1992. Evoluzione paleogeografica del Paleogene della Valsugana. *Annali Università di Ferrara*, 3, 83–99.

Michelin, J. L. H. 1842. *Iconographie zoophytologique. Description par localités et terrains des polypiers fossiles de France*. P. Bertrand, Paris, pp. 41–72.

Michelin, J. L. H. 1847. *Iconographie zoophytologique. Description par localités et terrains des polypiers fossiles de France, et pays environnants*. P. Bertrand, Paris, pp. 307–348.

Michelotti, G. 1838. *Specimen Zoophytologiae diluvianae*. Heredes Sebastian Botta, Torino, 227 pp.

Michelotti, G. 1861. Études sur le Miocène inférieur de l’Italie septentrionale. *Natuurkundige Verhandelingen uitgegeeven door de Hollandsche Maatschappye der Wetenschappen te Haarlem*, 15(2), 183 pp.
Verrill, A. E. 1865. Classification of polyps. (Extract condensed from a synopsis of the polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S.N.). Proceedings of the Essex Institute, 4, 145–152.

Vertino, A., Stolarski, J., Bosellini, F. R. & Taviani, M. 2014. Mediterranean corals through time: from Miocene to Present. Pp. 257–274 in S. Goffredo & Z. Dubinsky (eds) The Mediterranean Sea: its history and present challenges. Springer, Berlin.

Wells, J. W. 1956. Scleractinia. Pp. F328–F443 in R. C. Moore (ed.) Treatise on Invertebrate Paleontology: Coelenterata. Geological Society of America and University of Kansas Press, Boulder and Lawrence.

Wiens, J. J. & Tiu, J. 2012. Highly incomplete taxa can rescue phylogenetic analyses from the negative impacts of limited taxon sampling. PLoS One, 7(8), e42945.