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Acropora (Scleractinia) from the Oligocene and Miocene of Europe: species longevity, origination and turnover following the Eocene–Oligocene transition

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Four new species and new records for six species of the highly successful reef-building coral genus *Acropora* are described from Oligocene and Early Miocene (Rupelian to Burdigalian) localities in Europe. *Acropora slovenica* sp. nov. is described from Slovenia (Gornji Grad beds); *A. piedmontensis* sp. nov. and *A. macrocalyx* sp. nov. from the Torino Hills (Piedmont), and *A. salentina* sp. nov. from the Salento Peninsula (Apulia) of Italy. The remaining six species have an Eocene lineage. From south-west France, *A. anglica* and *A. bartonensis*, previously known from England (Priabonian and Bartonian), are recorded: *A. anglica* in Oligocene (Chattian) and both in Miocene (Aquitanian) deposits, indicating their persistence in the western Tethys for up to 17 and 20 million years respectively. Also recorded from Aquitaine is *A. wilsonae* (type locality Eocene Paris Basin), indicating persistence in western France for up to 28 Ma. Italian material includes *A. proteacea*, also known from the Lower Bartonian of France and *A. lavandulina*, already known from Italy and the Eocene of France. From Slovenia (Oligocene, Rupelian), *A. haidingeri* is recorded, including from the type locality. The species are interpreted as representing seven extant species groups previously documented from the Eocene of Europe and the first records for two further extant groups. These results complement a previous finding of Eocene diversification of *Acropora* into the beginnings of up to 10 of the 20 recognized modern species groups in England and France. They indicate that the longevity of some Eocene taxa was extended into the Oligocene to Early Miocene of Europe and allowed some turnover, probably associated with changes in configuration of the western Tethys Sea. This information is important for interpreting molecular phylogenies and the evolution of modern *Acropora* diversity, by providing extended stratigraphical ranges for species groups with Eocene origins and dates of origination for two groups previously unrecorded in the early fossil record.

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Keywords: coral reefs; palaeoecology; palaeobiogeography; Eocene–Oligocene transition; western Tethys

Introduction

The fossil record is a valuable source of information on the history and palaeobiogeography of modern reef-building corals (order Scleractinia). Particularly important is the record relating to *Acropora*, the most diverse extant genus with up to 150 living species in the present-day centre of diversity in the Indo-Pacific, and two in the Atlantic (Wallace 1999; Veron 2000; Wallace *et al.* 2012). The record shows early occurrences of *Acropora* immediately after the K–Pg event, in the Palaeocene of Somalia and Austria (Carbone *et al.* 1994; Baron-Szabo 2006). Following this, *Acropora* is seen to diversify in terms of species, with the beginnings of up to 10 of the 20 currently recognized species groups in high palaeolatitudes (up to 48° N) in the Eocene of England and France (Wallace & Rosen 2006; Wallace 2008; White *et al.* 2010). Other Eocene species from Spain (Álvarez Pérez *et al.* 1989; Álvarez Pérez 1997) indicate the presence of additional lineages, not as yet identified.

During the Eocene–Miocene time interval, the evolution of scleractinian corals was strongly controlled by the global climatic transition from greenhouse to icehouse conditions and, biogeographically, by gradual change from a pan-tropical Tethyan Province in the Eocene to the onset of the three reef coral provinces of the western Atlantic-Caribbean, Indo-Pacific and Mediterranean. These corals expanded their role as reef builders in the Oligocene when luxuriant coral reefs emerged on a global scale (Perrin 2002) with high generic richness (Bosellini & Perrin 2008). Floatstone and rudstone *Acropora*-rich deposits are recorded from the Oligocene and Early Miocene of northern Italy, Slovenia, Greece and Egypt (Pfister 1980a; Schuster 2002; Silvestri *et al.* 2008, 2011). These facies suggest that suitable conditions existed for the formation of some localized *Acropora*-dominated

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assemblages, such as those described by Schuster (2002) from the Late Oligocene Mesohellenic Basin of north-west Greece and interpreted as dense thickets growing in a calm lagoon environment. Following this in the Miocene of the Mediterranean, the geodynamic and climatic context gradually changed, leading to the decline of coral richness and almost complete disappearance of zooxanthellate corals near the end of the Miocene (Perrin 2002; Bosellini 2006; Perrin & Bosellini 2012, 2013). Within this palaeobiogeographical framework, we know from recent studies that *Acropora* had already diversified prior to the Eocene–Oligocene Transition (EOT), as indicated by the Eocene records mentioned above. In contrast, there is a lack of recent knowledge about the systematics of Oligocene and Miocene *Acropora* from Europe, although some species are known from brief accounts of (usually) single specimens in the works of Michellotti (1838), Michelin (1840–1847), Reuss (1864), Reis (1889) and Chevalier (1956, 1962). These and other early references form part of the background to the systematic palaeontology in the present study and are responsible for up to seven Oligo-Miocene species, with *A. lavandulina* and *A. haidingeri* being the best known. The very small amount of material available to these authors (with the exception of Reuss 1864), and absence of an emphasis on *Acropora* in the selection of samples, restrict them to only hinting at the overall role of *Acropora* in the diversification of Scleractinia in Europe during this time.

Resolving the fauna of the Oligo-Miocene interval in the reef-bearing history of Europe has the potential to enhance the known fossil diversity of *Acropora* and extend its value as an indicator of both change and continuity in scleractinian coral populations (Wallace 2008). This exercise can also be complemented by information contained in stratigraphical studies and revisions from several coral-bearing localities (Bosellini & Russo 1992; Nebelsick *et al.* 2000; Bosellini 2006; Bosellini & Perrin 2008; Silvestri *et al.* 2011; Perrin & Bosellini 2012). In this paper we examine collections of *Acropora* from five Oligocene and two Miocene localities in Italy, France and Slovenia, to provide more information on the *Acropora* fauna of these sites and its relationship to that published for Eocene sites.

Material and methods

Locations

The specimens described come from seven main localities in Italy, France and Slovenia, representing five Oligocene and two Miocene sites (Fig. 1). Updated biostratigraphical ages of the locations, together with the most recent references concerning stratigraphy and coral facies are summarized in Table 1.

Specimen repositories

Types and all specimens described are lodged in the Inventario Paleontologia Università di Modena e Reggio Emilia (**IPUM**). Types and comparative specimens referenced are from the Natural History Museum, London (**NHMUK**), the Museum of Paleontology, University of Rome (**MPUR**), and the Museum of Tropical Queensland, Townsville (**MTQ**).

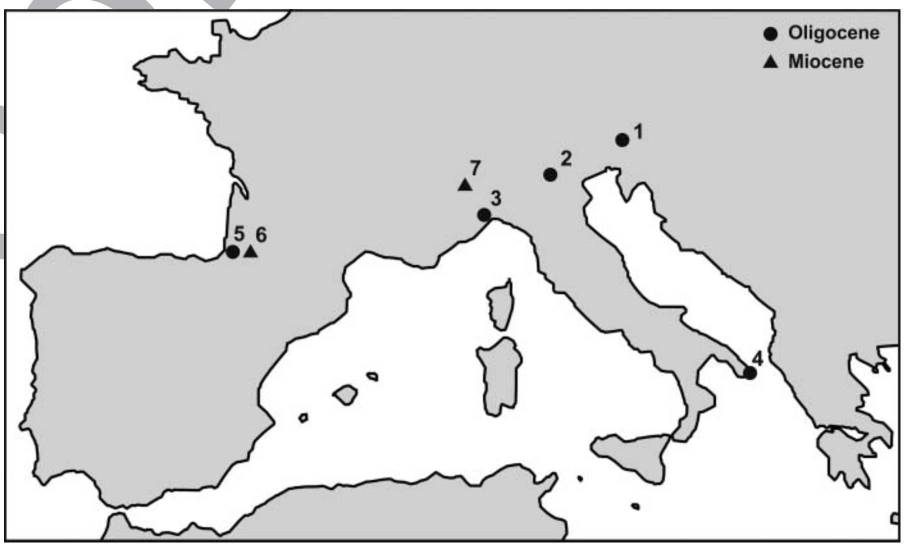

Figure 1. Map of Europe indicating localities from which the fossils described in this paper were collected. Localities are indicated by the same numbers in Table 1. Deposit ages indicated with locality number, as per legend on figure.

Table 1. Localities from which the Oligocene and Early Miocene *Acropora* fossils in this study were collected. Features of the palaeoenvironments and references used for ages and /or coral facies are indicated.

Locality	Country	Biostratigraphical age	Palaeoenvironment	References
1 Dol (Gornji Grad)	N Slovenia	Oligocene (Rupelian; SB21, P18-19)	Coral carpets nearshore	Nebelsick *et al.* 2000; Silvestri *et al.* 2011
2 San Luca (Vicenza)	NE Italy	Oligocene (Rupelian; SB21, P18-19)	Coral patches inner platform	Pfister 1980a
3 Cascine (Aqui Terme, Piedmont)	NW Italy	Oligocene (Upper Rupelian-Lower Chattian; SB22A-22B)	Coral patches fan delta system	Pfister 1980b; Silvestri *et al.* 2008; unpublished data
4 Castro (Lecce), S Italy	S Italy	Oligocene (Chattian; SB22B, P21)	Fringing reef front-fore reef	Bosellini & Russo 1992; Bosellini 2006
5 Abesse (Saint-Paul-lès-Dax)	SW France	Oligocene (Chattian; SB23, P22)	Coastal protected lagoon	Cahuzac & Poignant 2002; Cahuzac & Janssen 2010
6 Carrière Vives (Saint-Paul-lès-Dax)	SW France	Miocene (Aquitanian; SB24, N4)	Coastal protected lagoon	Cahuzac & Janssen 2010
7 Valle Ceppi, Valle Vergnana, Torino Hills (Torino)	NW Italy	Miocene (Burdigalian, N7)	Unknown	Festa *et al.* 2010; Zunino 2007

Abbreviations: N and P refer to Planktonic Foraminiferal Biozonation after Berggren *et al.* (1995); SB refers to the Shallow Benthic Biozonation of Cahuzac & Poignant (1997).

Morphological characters

Wallace (2008, pp. 314–315) noted that various morphological characters, commonly used for modern *Acropora* material, have been overlooked in fossils. *Acropora* species are characterized by the presence of a single axial corallite that forms the centre of each branch. Although occasionally present in other genera of Acroporidae (Wallace *et al*. 2007, 2011), this character, combined with differentiated radial corallites and the synapticulothecal skeletal microstructure common to all Acroporidae, uniquely identifies *Acropora*. The fossils were examined, using a Wild binocular microscope with eyepiece graticule, for the presence of diagnostic *Acropora* features, including branching type, radial corallite structure and coenosteal structure (see Wallace 1999; Wolstenholme *et al.* 2003). Examples of morphological characters were photographed using an Olympus E410 camera. The most likely species group membership for each species was determined by comparing the fossils with modern material in the MTQ (Wallace *et al*. 2012) to ascertain the most similar modern species and its putative species group, as outlined in Wallace (2008).

Thin sections (longitudinal and transverse) were made by Petrographic International. These were used to confirm the presence of an axial corallite and the relative contribution of this and the radial corallites to the branch diameter, and to compare specimens in terms of positioning and details of corallites and coenosteum. All specimens described are known to have an axial corallite by the presence of a central axis, even when the terminal part of the branch is missing.

To infer phylogenetic positions of the fossil species, they were aligned against their putative species group in a previously published morphological phylogeny of the genus, which followed transitions of skeletal characters within a composite tree (Fig. 2; Wallace 1999, pp. 72–102). This allowed the results to be compared with those found for a group of Eocene specimens of *Acropora* by Wallace & Rosen (2006; see Wallace 2008).

Terminology

Terminology used for *Acropora* structures is as detailed in Wallace (1999, including glossary pp. 407–410) and revised layout in Wallace *et al.* (2012). Descriptions of species groups in the systematic palaeontology section were taken from Wallace (1999).

Systematic palaeontology

Phylum **Cnidaria** Hatschek, 1888
Class **Anthozoa** Ehrenberg, 1834
Subclass **Hexacorallia** Haekel, 1896
Order **Scleractinia** Bourne, 1900
Family **Acroporidae** Verrill, 1902

Diagnosis. Massive or ramose colonies by extratentacular budding; corallites small, synapticulothecate, pseudocostate, slightly differentiated from coenosteum. Septa non-exert, in two cycles, formed by simple spiniform trabeculae projecting inward and upward from vertical mural trabeculae, commonly fusing to form laminae. Columella absent or trabecular and weak. Dissepiments thin and tabular when developed. Coenosteum extensive, light reticulate, flaky, generally spinose or striate on surface.

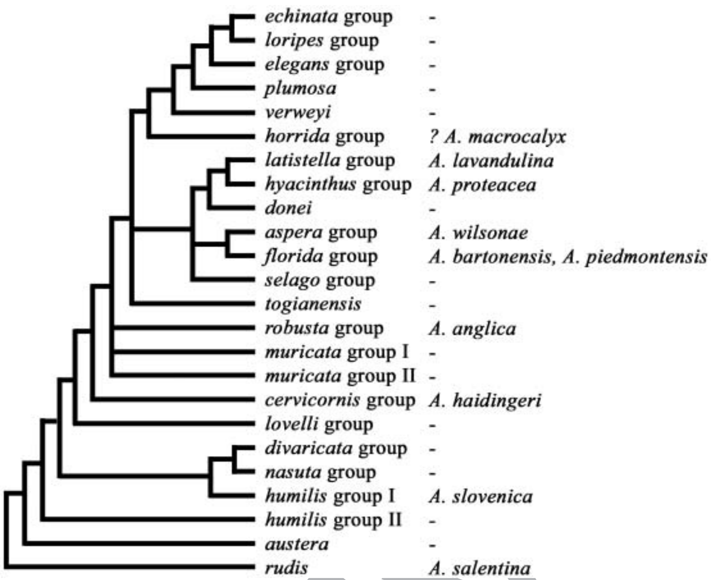

Figure 2. Species described in this paper, displayed against species groups to which they are attributed, in the morphological phylogeny of Wallace (1999). Question mark indicates degree of uncertainty in assigning species to species group.

Occurrence. Late Cretaceous to Recent.

Genus ***Acropora*** Oken, 1815

1815 *Acropora* Oken: 66 (validated in 1963: Boschma 1961; China 1963).

Type species. *Acropora muricata* (Linnaeus, 1758). Recent, Indonesia, Ambon. Neotype: MTQ G49167.

Diagnosis. Acroporidae that are ramose, rarely massive or encrusting, branching with a single axial corallite that forms axis of branch and opens at its tip; more numerous radial corallites budded from the branch tip; radial corallites connected by light, reticulate, spinose, costate or pseudocostate coenosteum which is also the wall of the axial corallite; columella and dissepiments absent.

Occurrence. Palaeocene to Recent.

Remarks. Note that genus Isopora Studer, 1878 was removed from Acropora by elevation from subgeneric to generic status by Wallace et al. (2007).

***rudis* species group**

Diagnosis. Radial corallites rounded tubular, evenly sized; coenosteum throughout includes elaborated spinules; colonies with simple, irregular branching.

Acropora salentina sp. nov.
(Fig. 3)

Material. Holotype: IPUM 28316: Zinzulusa Cave, Castro Limestone, Castro, Apulia, southern Italy, F. R. Bosellini Collection. Paratype: IPUM 28319, details as for holotype.

Etymology. Named for the type locality, on the Salento Peninsula, Apulia, southern Italy (see Bosellini & Russo 1992; Bosellini 2006).

Diagnosis. General colony form unknown at present, the two specimens in the type series suggesting indeterminate growth with irregular branching. Radial corallites all same size, not touching, tubular with round openings, projecting outwards from branches; coenosteum dense reticulate to reticulo-costate both on and between radials.

Description. Holotype IPUM 28316: fragment from branch tip, 40 mm long; base diameter 15 mm, tip diameter 12 mm, branching simple hispidose with four branchlets visible. Axial corallites present on these as well as on main branch tip, but some are deeply eroded and septa cannot be seen: outer diameters 1.2–1.9 mm, inner diameter 0.8–1.3 mm. Radial corallites < 10 per branchlet, appressed tubular with wide, round to oval openings, lower wall thickened and extended to a point; septa appear to have been lost from corallites or are very small. Coenosteum reticulate on and between radial corallites.

Paratype IPUM 28319: fragment 52 mm long and forking at the tip, plus three incipient branchlets, fragment is fractured vertically, exposing central axial corallites of the main branches.

Occurrence. Oligocene, Chattian. Italy.

Remarks. Although this species is described from only two fragments, their morphological characteristics are sufficiently different from described fossil *Acropora* to

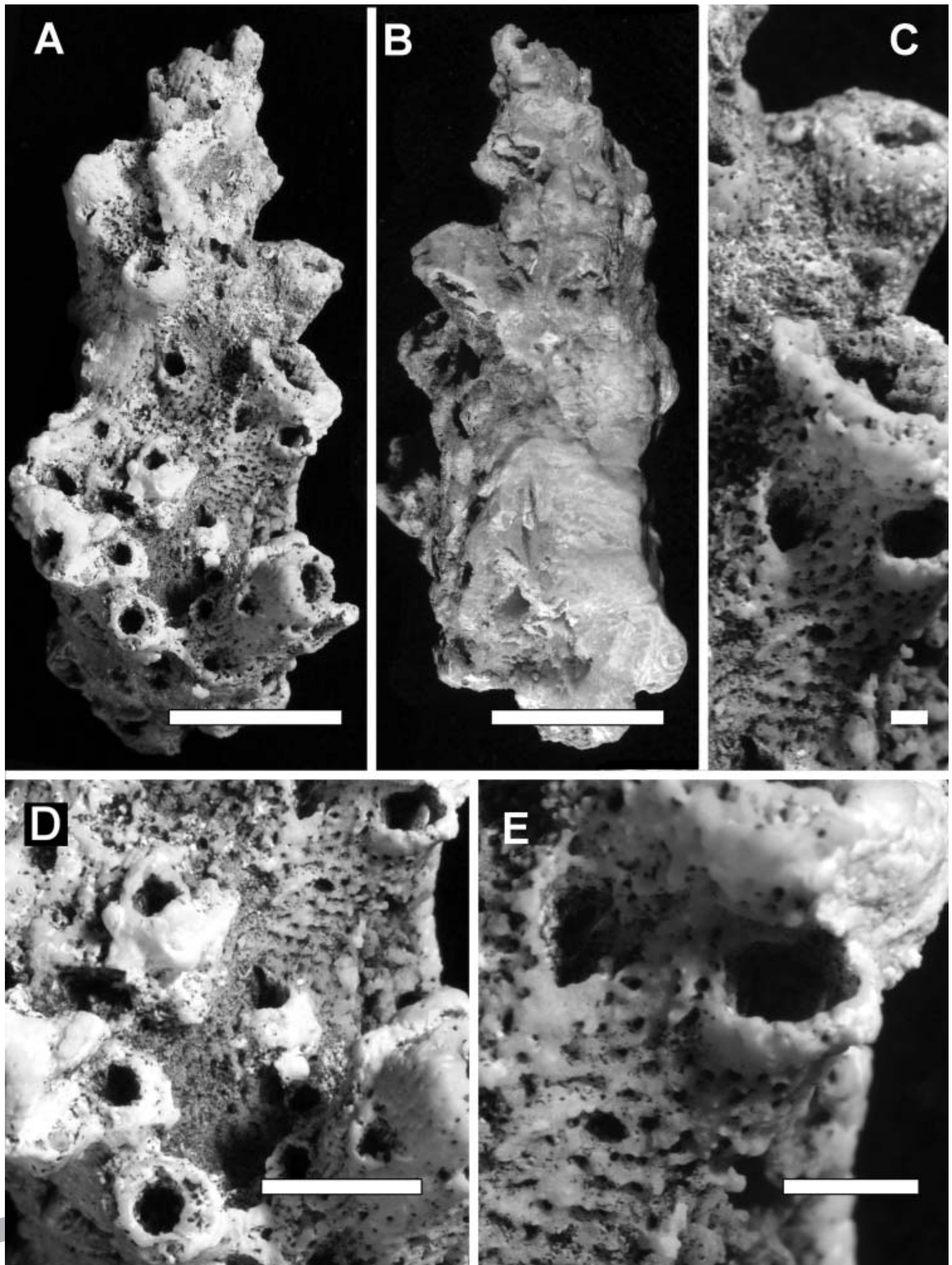

Figure 3. *Acropora salentina* sp. nov., Oligocene, Chattian, Castro, Italy; holotype IPUM 28316; **A, B,** whole specimen from both sides; **C,** detail showing two branchlets with axial and radial corallites; **D,** detail of branch showing tubular radial corallites with round openings, not touching, projecting outwards from branches; **E,** detail of dense reticulate to reticulo-costate coenosteum on and between radial corallites. Scale bars A, B, 10 mm; C, E, 1 mm; D, 5 mm.

indicate a previously undescribed species. In relation to modern species and species groups (Wallace 1999), *A. salentina* is most similar to *A. austera* in the *rudis* species group, because of its coenosteal structure, irregular hispidose growth form and large corallites. The modern species *A. austera* is widespread in the Indo-Pacific (Wallace *et al.* 2012), but all other species in the group are restricted to the Indian Ocean or Red Sea. This group was indicated as the basal group of *Acropora* in the morphological phylogeny of Wallace (1999). *Acropora salentina* sp. nov. is the earliest nominated member of this lineage found to date.

Other literature. Bosellini & Russo (1992); Bosellini (2006) (stratigraphical and palaeoenvironmental setting of the type locality).

***humilis* species group**

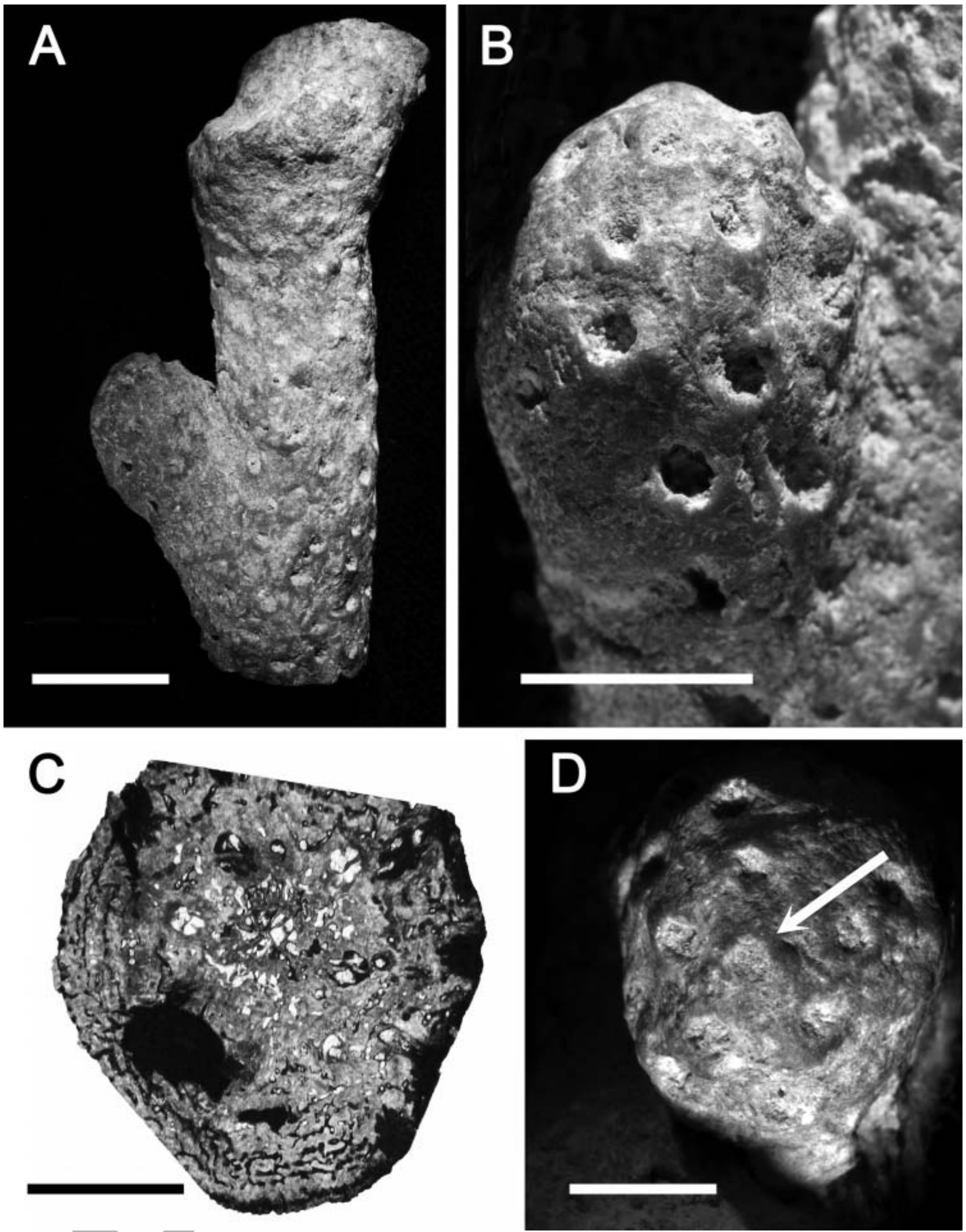

Figure 4. *Acropora slovenica* sp. nov., Oligocene, Rupelian, Dol (Gornji Grad), Slovenia. **A, B, D,** holotype IPUM 28287; **A,** entire specimen; **B,** detail showing short sturdy branch, axial corallite and radial corallites appressed tubular, all the same size and not touching, evenly distributed on branch and reticulo-costate coenosteum between radial corallites; **D,** branch tip showing axial corallite (arrow) surrounded by radial corallites. **C,** paratype IPUM 28289, transverse section through branch showing axial surrounded by radial corallites. Scale bars: A, 10 mm; B, D, C, 5 mm.

Diagnosis. Radial corallites short, thickened tubular with dimidiate openings, evenly sized or in two sizes; coenosteum throughout reticulate with laterally flattened irregular spinules, sometimes reticulo-costate; colonies corymbose or digitate.

Acropora slovenica sp. nov. (Fig. 4)

Material. Holotype: IPUM 28287, Gornji Grad, Slovenia, J. Nebelsick Collection. Paratypes: IPUM 28288, IPUM 28289, details as for holotype.

Etymology. Named for the country of the type locality.

Diagnosis. Caespito-corymbose or arborescent colony with terete branches, up to 13 mm in diameter, with the major contribution to branch diameter coming from the axial corallite. Radial corallites all the same size and not touching, evenly distributed on branch, appressed tubular with round opening and possibly a lip. Axial corallites 0.8 mm inner diameter and 1.2–1.5 mm outer diameter. Coenosteum reticulo-costate between radial corallites, costate or reticulo-costate on radial corallites.

Description. Holotype IPUM 28287: overall length of specimen 47 mm. Fragment of branch, with a complete branch 14 mm long given off towards its base and an indication of another branch towards its upper end. Branches terete, with most of the diameter provided by the axial corallite; branch diameter 12 mm; diameter of tip of short branch 7 mm. One axial corallite visible, at tip of short branch: outer diameter 1.44 mm, inner diameter 0.87 mm, septa not visible; radial corallites evenly distributed on branch, all one size, appressed tubular with round opening and strong indications of a lip on some corallites. Coenosteum: some indications of a reticulo-costate structure between corallites; coenosteum on radial corallites difficult to determine because of absence of wall.

Paratypes. IPUM 28288: overall length of specimen 39 mm. Fragment of branch, forked into two towards tip; branch diameter 7–13 mm. One axial corallite visible, outer diameter 1.25 mm, inner diameter 0.84 mm. Radial corallites scattered on branch, mostly not touching, appressed tubular with round opening, possibly with a lip; coenosteum as for holotype. IPUM 28289: fragment of branch without side branches, maximum branch diameter 13.5 mm (part of this specimen used for thin section). Radial corallite and coenosteal characters as for holotype.

Occurrence. Oligocene, Rupelian. Slovenia.

Remarks. This distinctive species does not appear to have been reported previously. In comparison with modern *Acropora* species, it bears some resemblance in structure and dimensions to the modern Indo-Pacific species *Acropora samoensis* (Brook, 1891), which has similar branch dimensions and axial-dominated terete branches with radial corallites not touching (Wolstenholme *et al.* 2003; Wallace *et al.* 2012) and is placed in the humilis species group (Wallace 1999). The structure of the branches in the type series suggests a sub-branching corymbose colony shape similar to that of *A. samoensis* (see Wallace *et al.* 2012, fig. 86). It appears to be the third oldest species in the *A. humilis* group, following the Eocene species *A. deformis* (Michelin, 1840), from the Bartonian of France, and *A. britannica* Wallace (2008) from the late Priabonian of England.

Other literature. Nebelsick *et al.* (2000); Silvestri *et al.* (2011) (stratigraphical and palaeoenvironmental setting of the type locality).

cervicornis species group

Diagnosis. Radial corallites approximately tubo-nariform, evenly sized; coenosteum reticulate between radial corallites, costate on radial corallites, with laterally flattened spinules more or less in lines (costae); colony shape various.

Acropora haidingeri (Reuss, 1864) (Figs 5, 6)

1864 *Dendracis haidingeri* Reuss: 27, pl. 8, figs 2–5.

Type locality. Krznar Section, Gornji Grad, Slovenia.

Material. Topotypes: IPUM 28318 (3 specimens), IPUM 28317 (3 specimens), IPUM 28291 (1 specimen), Gornji Grad, Slovenia, J. Nebelsick Collection. Additional material: IPUM 28326 (one specimen), Gornji Grad, Slovenia, J. Nebelsick Collection; IPUM 28290 (4 specimens), IPUM 28292 (4 specimens), IPUM 28323 (43 specimens), IPUM 28324 (one specimen), IPUM 28325 (5 specimens), Cascine, Piedmont, Italy, F. R. Bosellini Collection; IPUM 28293, San Luca, Vicenza, Italy, T. Pfister Collection; MTQ G65021, Eocene, Jaca, Atares, Spain, collected by G. Álvarez Pérez c.2005.

Diagnosis. Colony arborescent, branches reaching at least 72 mm without branching, 6 to 10 mm in diameter and tapering. Axial corallite slender at tip but the major contributor to branch diameter. Radial corallites all same size, tubular appressed and mostly not touching. Coenosteum on radials costate, between radials reticulo-costate.

Description. IPUM 28318 (3 specimens) (Fig. 5A–C); Fig. 5A is the best-preserved specimen, showing some complete radial corallites. Branches 42, 50 and 72 mm long respectively, each a portion of a longer branch; Fig. 5A is a branch tip, indicating that the branches taper; diameters 10, 9.5 and 9 mm, respectively. Fig. 5B is forked, 11 mm from the top of the specimen, forming two equal branches. Axial corallite of A degraded and cannot be measured, although the branch tip diameter is 2.3 mm. Radial corallites mostly not touching, evenly distributed, appressed tubular with round openings; primary septa all present up to R, secondary septa some visible. Coenosteum radial corallites costate, between radials reticulo-costate. IPUM 28317 (3 specimens): fragments of branches, lengths 23, 42 and 52 mm, each a portion of a longer branch, without a tip; diameters 7, 6 and 10 mm respectively. Radial corallites mostly not touching, evenly distributed, appressed tubular with round openings; septa not apparent. Coenosteum on radial corallites costate between radials reticulo-costate.

Occurrence. Eocene: Bartonian, Spain; Priabonian, Germany. Oligocene: Rupelian, Slovenia, Italy, France, Spain; Chattian, Italy, France.

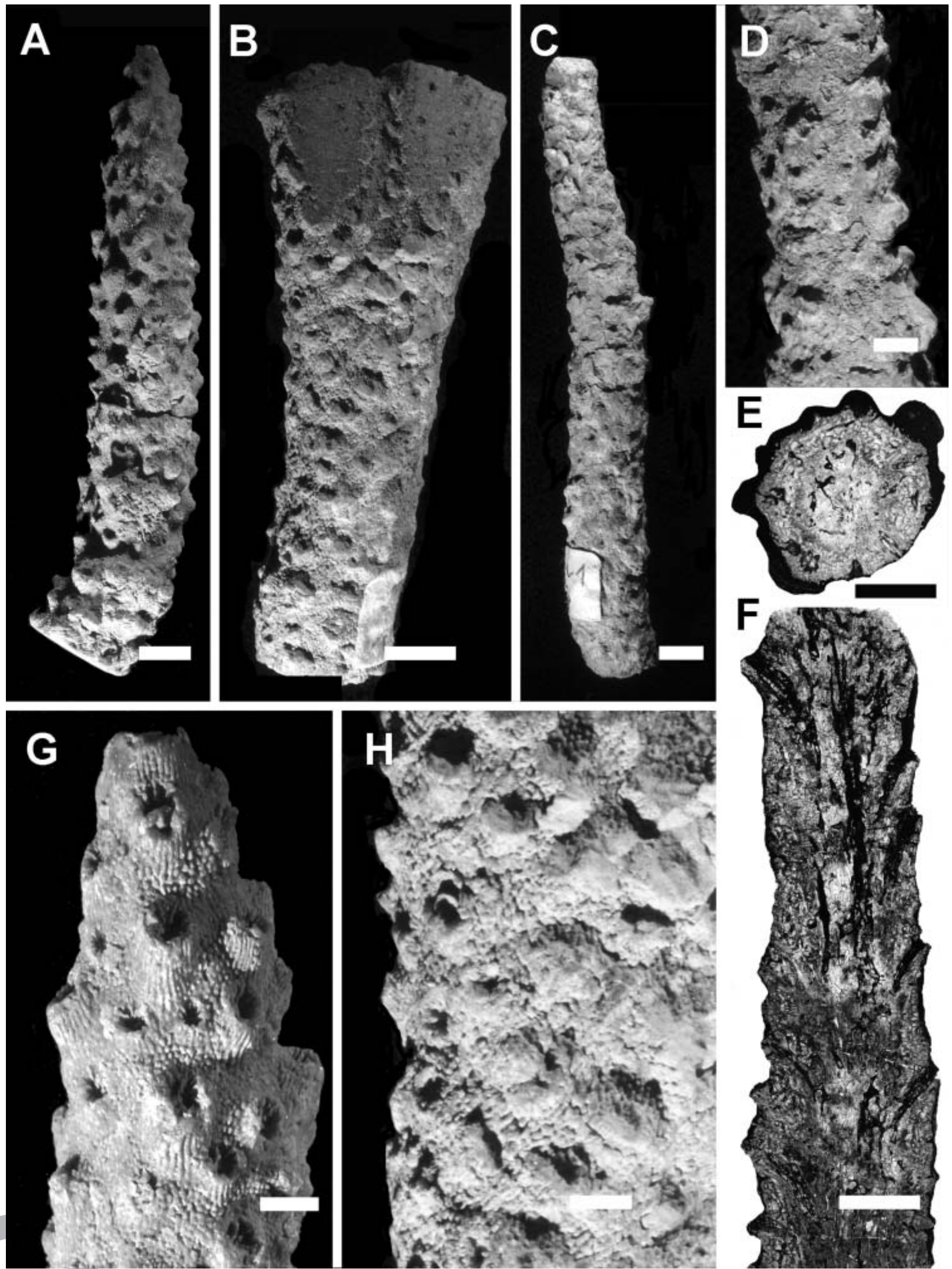

Figure 5. *Acropora haidingeri* (Reuss, 1864), Oligocene, Rupelian, Dol (Gornji Grad), Slovenia; **A, G,** IPUM 28318a; **B, H,** IPUM 28318b; **C, D,** IPUM 28318c; **E, F,** IPUM 28317. **A–C,** whole specimen; **G,** detail of branch showing axial corallite, radial corallites all same size, tubular appressed and mostly not touching and coenosteum costate on radials, reticulo-costate between radials; **D, H,** detail of branch showing radial corallites and coenosteum; **E,** transverse thin section through branch; **F,** longitudinal thin section through branch. Scale bars A–C, 5 mm; D, G, H, 2 mm; E, F, 5 mm.

Remarks. The specimens from Slovenia (Fig. 5) are collected from the type locality and have well-preserved radial corallites and coenosteum, which match very clearly the description by Reuss (1864) and other authors as well as the type series (seen from photographs). The Italian specimens, on the other hand, were very weathered and the form of the radial corallites could not be determined from external examination. We resolved this issue by comparing longitudinal and transverse sections from the Slovenian and Italian specimens, which showed strong similarity in size and spatial arrangement of the radial corallites (see Figs 5E, F, 6D, G). This concurs with the opinion of Pfister (1980b) that specimens from Italy and Slovenia represent the same species.

From the descriptions, *Acropora pachymorpha* Chevalier, 1956 and *A. pseudolavandulina* Chevalier, 1956 may

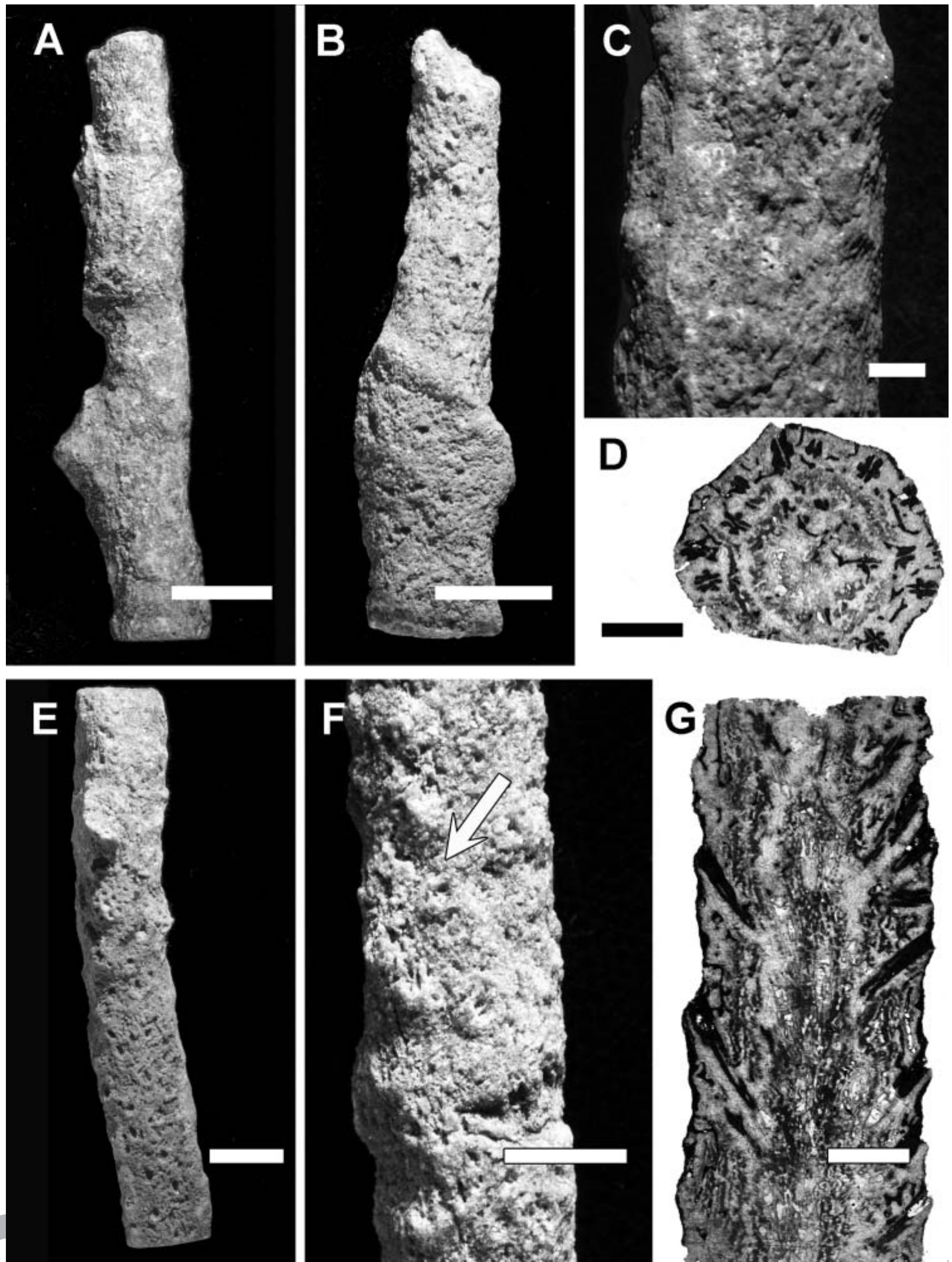

Figure 6. *Acropora haidingeri* (Reuss, 1864), Oligocene, Upper Rupelian–Lower Chattian, Cascine, Italy; **A,** IPUM 28290a; **B, C,** IPUM 28290b; **E, F,** IPUM 28290c; Oligocene, Rupelian, San Luca, Italy; **D, G,** IPUM 28293. **A, B, E,** whole specimen; **C, F,** detail of branch showing weathered radial corallites and coenosteum (arrow on F); **D,** transverse thin section through branch; **G,** longitudinal thin section through branch. Scale bars A, B, 10 mm; C, 2 mm; E, F, 5 mm; F, 1 mm; D, G, 5 mm.

be synonyms of this species. The Slovenian specimens were compared to samples of modern species and the greatest similarity was found with *A. cervicornis*, hence we have placed this species in the *cervicornis* group. This group is also represented by the Eocene species *A. alvarezi* Wallace, 2008 from France.

Other literature. Chevalier (1956, p. 375, pl. 1, fig. a–c); Pfister (1980a, fig. 13, 1980b, pp. 56–57, pl. 1, fig. 8); Álvarez Pérez *et al.* (1989); Ramos-Guerrero *et al.* (1989); Darga (1992, p. 70, pl. 12, figs 5, 6); Cahuzac & Chaix (1994, 1996).

robusta species group

Diagnosis. Radial corallites dimorphic, one form long tubular with dimidiate opening, the other submersed; coenosteum reticulate between radial corallites, costate on radial corallites; colonies subarborescent. Q7

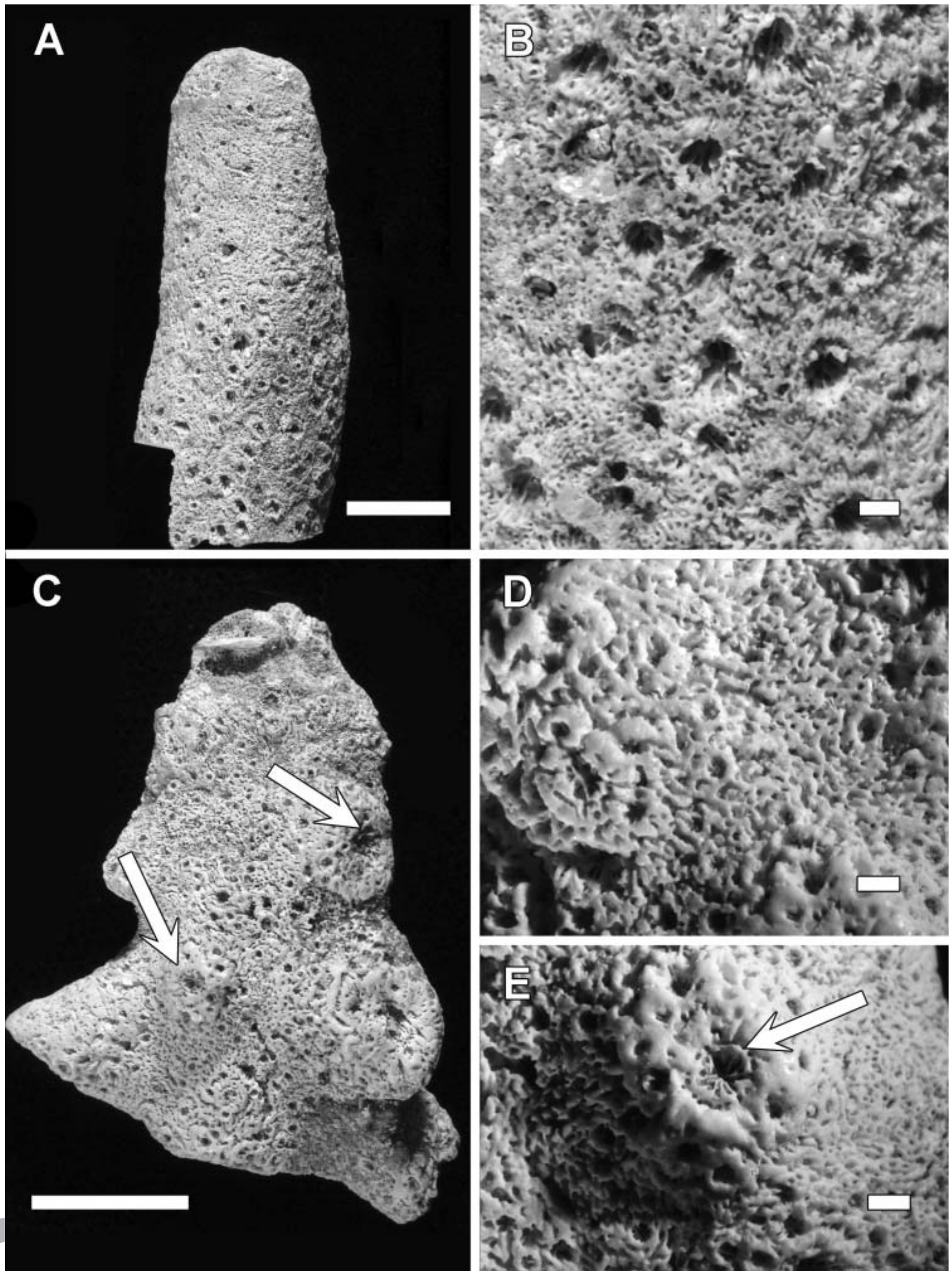

Figure 7. *Acropora anglica* (Duncan, 1866). **A, B,** IPUM 28295, Miocene, Aquitanian, Carrière Vives, France; **C−E,** IPUM 28294, Oligocene, Chattian, Abesse, France. **A, C,** whole specimen; arrows on C indicate branchlet (upper) and incipient branchlet (lower); this branch shows the broad, tapering branch, with the major contribution to branch diameter coming from the axial corallite; **B,** detail showing radial corallites in two distinct sizes and reticulate coenosteum between radials; **D, E,** detail showing radial corallites, coenosteum and incipient branchlet (arrow on E). Scale bars A, C, 10 mm; B, D, E, 1 mm.

Acropora anglica (Duncan, 1866)
(Fig. 7)

1866 *Madrepora anglica* Duncan: 51, pl. 8, figs 1−7.

Type locality. Brockenhurst, England.

Material. IPUM 28295 Carrière Vives, Aquitaine, France, collected by F. R. Bosellini and G. Silvestri; IPUM 28294 Abesse, Aquitaine, France, collected by F. R. Bosellini and G. Silvestri; NHMUK 49583 (two fragments), Eocene, Middle Headon Beds, Brockenhurst, Hampshire, England; NHMUK R2339, Eocene, Brockenhurst, Hampshire, England.

Diagnosis. Colony sturdy, probably subarborescent, branches tapering, up to 20 mm in diameter, with the

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major contribution to branch diameter coming from the axial corallite; radial corallites in two distinct sizes, appressed tubular, some touching; coenosteum costate on radials, reticulate between radials.

Description. IPUM 28295: one fragment of a branch tip 43 mm long and tapering from 20 mm at base to 11.5 mm at tip. Axial corallite can be seen at tip, its inner diameter 1.2 mm. Radial corallites two sizes discernable, all are very worn but some show a small amount of wall. Coenosteum costate on radial corallite walls, reticulate between radials. IPUM 28294: one fragment, of a flattened branch tip 44 mm long with seven broken or short branchlets coming off; main branch 12 mm wide at base and partly eroded at tip, one surface bears at least two incipient branches consisting of an axial corallite surrounded by radial corallites, and numerous radial corallites, the other surface has no corallites or branches. Three of the branches (branchlets) are almost complete to the tip. Axial corallite can be seen at the tip, outer diameter 3 mm, inner diameter 1.6 mm. Radial corallites two sizes discernable. Radial corallites and coenosteum as for previous specimen.

Occurrence. Eocene: late Priabonian, England. Oligocene: Chattian, France. Miocene: Aquitanian, France.

Remarks. This species has only previously been recorded from the late Priabonian of Brockenhurst, England. Its presence in the Aquitanian, along the western coast of France, up to 13.47 myr after the end of this period, indicates that this species persisted in the 'northern Tethys' region of Europe for at least 10 myr. As pointed out by Duncan (1866), this species shows close similarities to *A. crassa* (= *A. abrotanoides*), a modern species in the *A. robusta* group (Wallace 2008). Although the two specimens are well preserved and give a good indication of two aspects of branching, it is still possible that two species rather than one are represented, one having a simpler branching pattern similar to that of modern *A. robusta*, and the other branching in a similar manner to the modern *A. abrotanoides*. Note that '*A. abrotanoides*' reported from the Torino area by Michellotti (1838, pl. 6, fig. 7) is not this species, but was recognized as *A. lavandulina* by Michelin (1840).

Other literature. Wallace (2008, pp. 323–324, fig. 7).

aspera species group

Diagnosis. Radial corallites labellate, upper wall absent, lower wall developed into a flaring lip; coenosteum open reticulate with few, simple spinules between radial corallites, costate on radial corallites; colonies corymbose or arborescent.

Acropora wilsonae Wallace, 2008
(Fig. 8)

2008 *Acropora wilsonae* Wallace: 324, fig. 8.

Type locality. Paris Basin, France.

Material. Holotype: NHMUK R54847, Eocene, Paris, France. Other material: NHMUK R54842, Middle Eocene, France; NHMUK R2209c, Eocene (Middle Gervillei) Sables Moyens, Auvers, France; NHMUK R45677, R45678, Eocene, Auvers-sur-Oise, France; NHMUK R52065, Eocene, Upper Calcaire Grossier, Chambors, France, A. G. Davis Collection, 1957. IPUM 28296 (3 specimens), 28297 (1 specimen), 28298 (2 specimens), Carrière Vives, Aquitaine, France, collected by F. R. Bosellini and G. Silvestri; IPUM 28299 (3 specimens), Abesse, Aquitaine, France, collected by F. R. Bosellini and G. Silvestri.

Diagnosis. Colony arborescent, with branches given off singly or in groups; branches tapering to terete, diameters up to 20 mm; radial corallites two sizes or mixed sizes, probably lipped; coenosteum costate to reticulo-costate on radial corallite walls, reticulate between radials.

Description. IPUM 28296: three specimens, overall lengths 34, 50 and 60 mm. These indicate arborescent branching: one specimen gives off a branch, which is broken off at the base and another has an incipient branch. One branch (illustrated in Fig. 8A) tapers almost to a complete tip and also has a small incipient branch; branch diameters 4–12 mm; radial corallites two sizes, mostly not touching. Openings round, apparently with lip. Coenosteum on radial corallites costate; interradial coenosteum reticulate. IPUM 28297: fragment of branch, 41 mm long and 8 mm diameter at base, apparently arborescent, with three branches present at tip; not possible to tell whether terete or not, but from appearance, probably terete. Other branch diameters 6.5–8.0 mm. Radial corallites two sizes or mixed, mostly not touching, tubular appressed with round openings; a rounded lip can be seen in some protected corallites between branches. Coenosteum on radial corallite walls reticulo-costate, between radials reticulo-costate. IPUM 28298: two branch fragments, one giving off a single broken branch overall lengths both 49 mm; diameters 8–10 mm. Radial corallites two sizes or mixed, most not touching; walls abraded. Coenosteum on radial corallite walls reticulo-costate, between radials reticulo-costate or reticulate. IPUM 28299: three branch fragments, on with indications of two branch bases coming off close together; fragment lengths 27, 37, 37 mm; diameters 6–9 mm. Radial corallites two sizes or mixed, mostly not touching. One specimen has well-developed rounded lips on radial corallites. Coenosteum on radial corallite walls costate, between radials reticulate.

Occurrence. Eocene: Lutetian to Bartonian, France. Oligocene: Chattian, France. Miocene: Aquitanian, France.

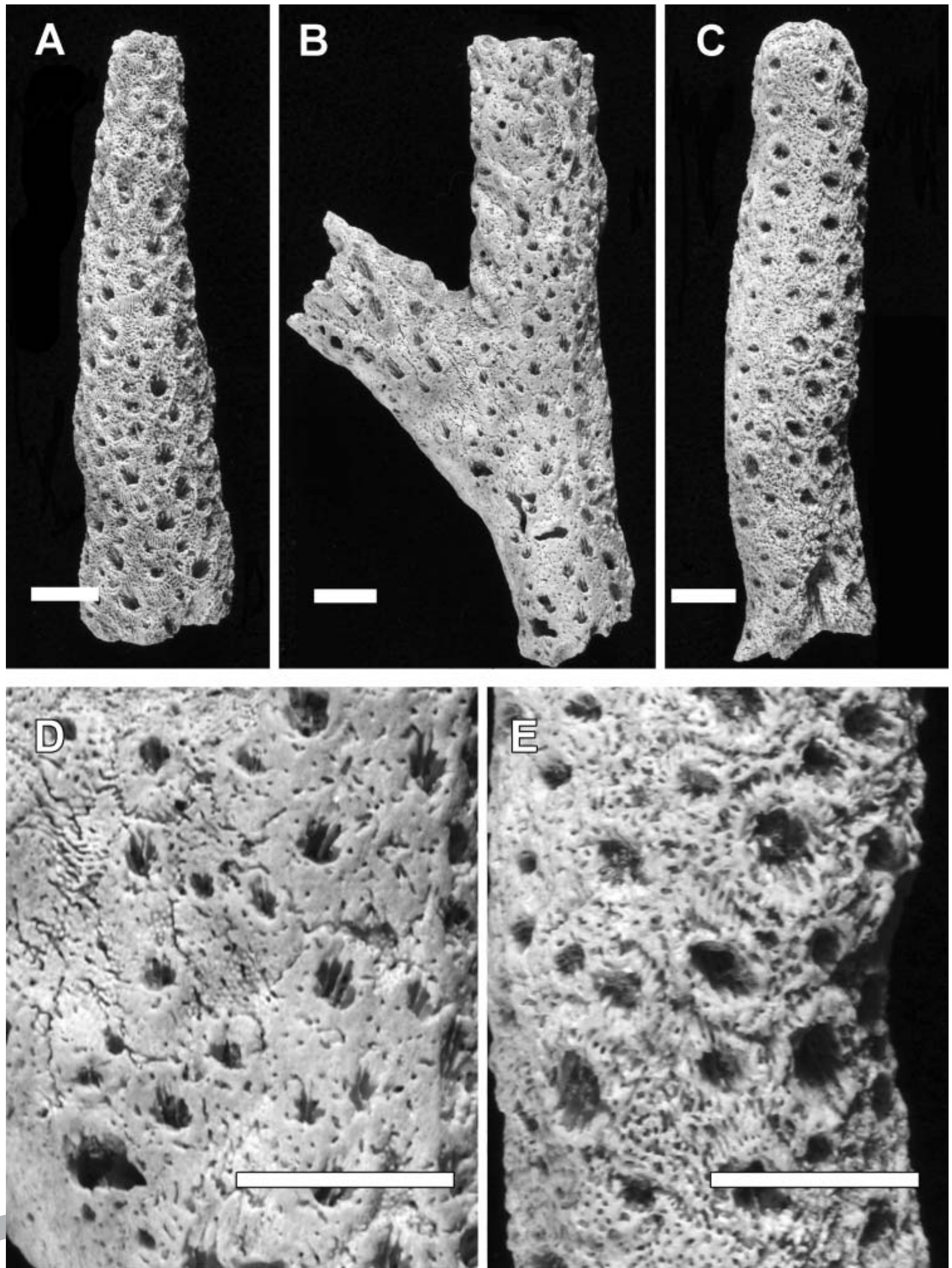

Figure 8. *Acropora wilsonae* Wallace, 2008, Miocene, Aquitanian, Carrière Vives, France. **A,** IPUM 28296a; **B, D,** IPUM 28298a; **C, E,** IPUM 28298b. **A–C,** whole specimen; **D, E,** detail showing lipped radial corallites in two sizes or mixed sizes and coenosteum reticulo-costate on radial corallites, reticulate between radials. Scale bars 5 mm.

Remarks. With its apparently compact arborescent growth form, mixture of large and small radial corallites, and round radial corallite openings (suggesting the previous presence of a lip), as well as the branch dimensions, this species is most reminiscent of *Acropora pulchra*, of the *A. aspera* modern species group (from Wallace 2008).

florida species group

Diagnosis. Radial corallites appressed tubular with thickened, lip-like lower wall and round openings, evenly sized; coenosteum between radial corallites reticulate and simple, with very little spinule development, on radial corallites costate or reticulo-costate; colonies based on hispidose branching.

Acropora piedmontensis sp. nov.
(Fig. 9)

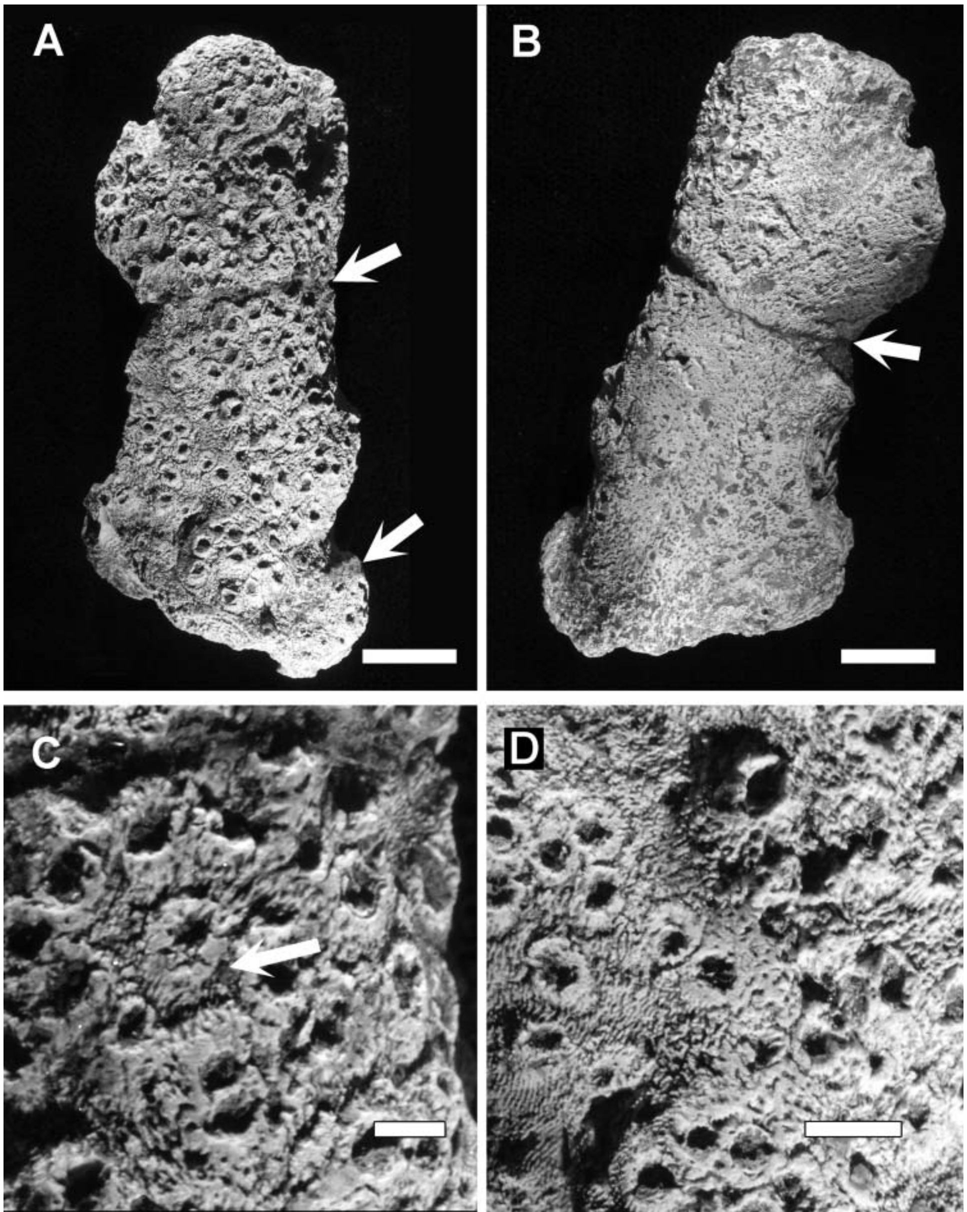

Figure 9. *Acropora piedmontensis* sp. nov.; holotype IPUM 28303a, Miocene, Burdigalian, Valle Ceppi, Torino Hills, Italy. **A, B,** whole specimen from both sides; top arrows indicate break in specimen, other arrow on A indicates incipient branchlet; **C, D,** detail of branch showing radial corallites in mixed sizes, rounded tubular with round openings and coenosteum costate on radial corallite walls, reticulate between; arrow on C indicates incipient branchlet, with central axial corallite surrounded by radial corallites. Scale bars A, B, 10 mm; C, D, 2 mm.

Type locality. Valle Ceppi, Torino Hills, Piedmont region of Italy.

Material. Holotype: IPUM 28303A; paratypes: IPUM 28303B, 28303C, Valle Ceppi, Torino Hills, Italy, Bugnano Collection. Other material: IPUM 28301 (3 fragments), Valle Ceppi, Torino Hills, Italy; IPUM 28305 (6 specimens), Valle Ceppi, Torino Hills, Italy, Bugnano Collection. Other material not examined: IPUM 28302 (4 specimens), Valle Ceppi, Torino Hills, Italy, Rocca Collection; IPUM 28304 (1 specimen), Valle Vergnana, Torino Hills, Italy.

Etymology. Named for the type locality, the Piedmont region of Italy.

Diagnosis. Colony simple hispidose, with secondary branchlets up to 11 mm diameter given off regularly from a broader branch up to 17 mm in diameter; radial corallites mixed sizes, rounded tubular with round openings;

coenosteum costate on radial corallite walls, reticulate between radials.

Description. Holotype IPUM 28303A: overall length of specimen 68 mm, fragment of a main branch (with a glued join) diameter 30 mm, giving off two other branches 13 and 17 mm in diameter, indicated only by their bases (see Fig. 9B); three other short branchlets (consisting of a central axial corallite surrounded by radial corallites) can be seen, up to 10 mm in diameter (see Fig. 9A) and there are indications of further short branchlets, indicating a simple hispidose branching pattern. Axial corallites inner diameters 1.18–1.41 mm; outer diameters 1.41–1.63 mm; radial corallites mixed sizes, short tubular with round openings, mostly not touching: inner diameters 1.03–1.75 mm; outer diameters 1.48–2.16 mm. Coenosteum costate on walls, intercorallite areas reticulate.

Paratypes: IPUM 28303B is a branch fragment, overall length 45 mm; showing some branchlets; branch diameter 43 mm at base and 13 mm at top. IPUM 28303C is an eroded branchlet, overall length 42 mm; branch diameter 16 mm at base and 11 mm at top. Both show corallite and coenosteal characters similar to those of the holotype.

Other material: IPUM 28301: three fragments of branches, all quite worn, overall length (A) 35 mm, (B) 30 mm (C) 25 mm; diameters at base (A) 13, (B) 12, (C) 8 mm; at tip (A) 15, (B) 14 and (C) 8 mm; simple hispidose, incipient branchlets present in (C) and possibly in (A); radial corallites rounded tubular, evenly but widely spaced; coenosteum on and between radial corallites reticulo-costate. IPUM 28305: six fragments all without secondary branching, lengths 16–35 mm; diameters at base 7–12 mm; diameters at top 5–12 mm, radials mixed sizes, mostly not touching, tubular, round openings; coenosteum costate on radials, reticulo-costate between radials. In all the above specimens, axial corallite contributes the main part of diameter.

Occurrence. Burdigalian, Italy. Only found to date from two valleys (Ceppi and Vergnana) in the Torino Hills.

Remarks. The holotype and two paratypes were all collected at the same time and in the same lot: thus they may be from the same colony, but there is no way of determining this. The diameters of branches here include some of the widest seen in any European fossil *Acropora*. This species is interpreted as being a member of the *florida* species group, based on the 'simple hispidose' form, where short branchlets occur around a main branch.

Other literature. None.

Acropora bartonensis Wallace, 2008
(Fig. 10)

2008 *Acropora bartonensis* Wallace: 326, fig. 10.

Type locality. Barton Beds, Hampshire, England.

Material. Holotype: NHMUK R19125, Eocene, Barton Beds, Barton, Hampshire, collected and presented by H. E. Walton, 1916. Other material: NHMUK R14571, Barton, Hampshire, England; NHMUK R54915, Upper Eocene, Barton Beds, Barton Cliffs, Barton, Hampshire, J. C. Daniels Collection, presented 1980; NHMUK R28205, Barton Cliffs, Barton, Hampshire, England, collected and presented by E. St. J. Barton, 1980. IPUM 28306 (1 specimen) and IPUM 28307 (1 specimen), Carrière Vives, Aquitaine, France, F. R. Bosellini collection; IPUM 28308, (1 specimen), Valle Ceppi, Torino Hills, Italy.

Diagnosis. Colony simple hispidose, secondary branchlets up to 8 mm long and 7 mm diameter given off regularly from a broader branch up to 9 mm in diameter; radial corallites one size or mixed, rounded appressed tubular with round openings; coenosteum costate on radial corallite walls, broken costate to reticulate between radials.

Description. IPUM 28306: fragment of branch, 41 mm long, 9 mm diameter at base, with short, rounded branchlets (up to 8 mm long) coming off along its length. At least six branchlets are intact with terminal axial corallite opening; diameters of branchlets 5.0–7.0 mm. Radial corallites one size, not touching, rounded appressed tubular with round openings. Coenosteum: radial corallite walls costate, interradial coenosteum reticulate. IPUM 28307: fragment of branch, 44 mm long and 7 mm diameter at base, with at least three branchlets present, two branchlets are complete with an axial corallite. Axial corallites outer diameter 2.32–3.27 mm, inner diameter 1.03–1.9 mm; radial corallites mixed sizes, mostly not touching, some tubular appressed with round openings, others apparently tubular exert with round openings. Coenosteum: on radial corallite walls costate, clearly visible in three corallites; interradial coenosteum reticulo-costate. IPUM 28308: fragment of main branch, 35 mm long, with three broken branches coming off towards top and one basal. This sample has few radial corallites and branchlets so is only provisionally placed in *A. bartonensis*.

Occurrence. Eocene: Bartonian, England. Miocene: Aquitanian, France, ?Burdigalian, Italy.

Remarks. This species was considered most likely to be associated with the *florida* group by Wallace (2008) because of the branchlets regularly distributed along a main branch. The Aquitaine specimens compare well with the holotype of *A. bartonensis* but the degree of weathering of the Torino Hills specimen (Fig. 10C) makes it difficult to be certain of its identification.

***hyacinthus* species group**

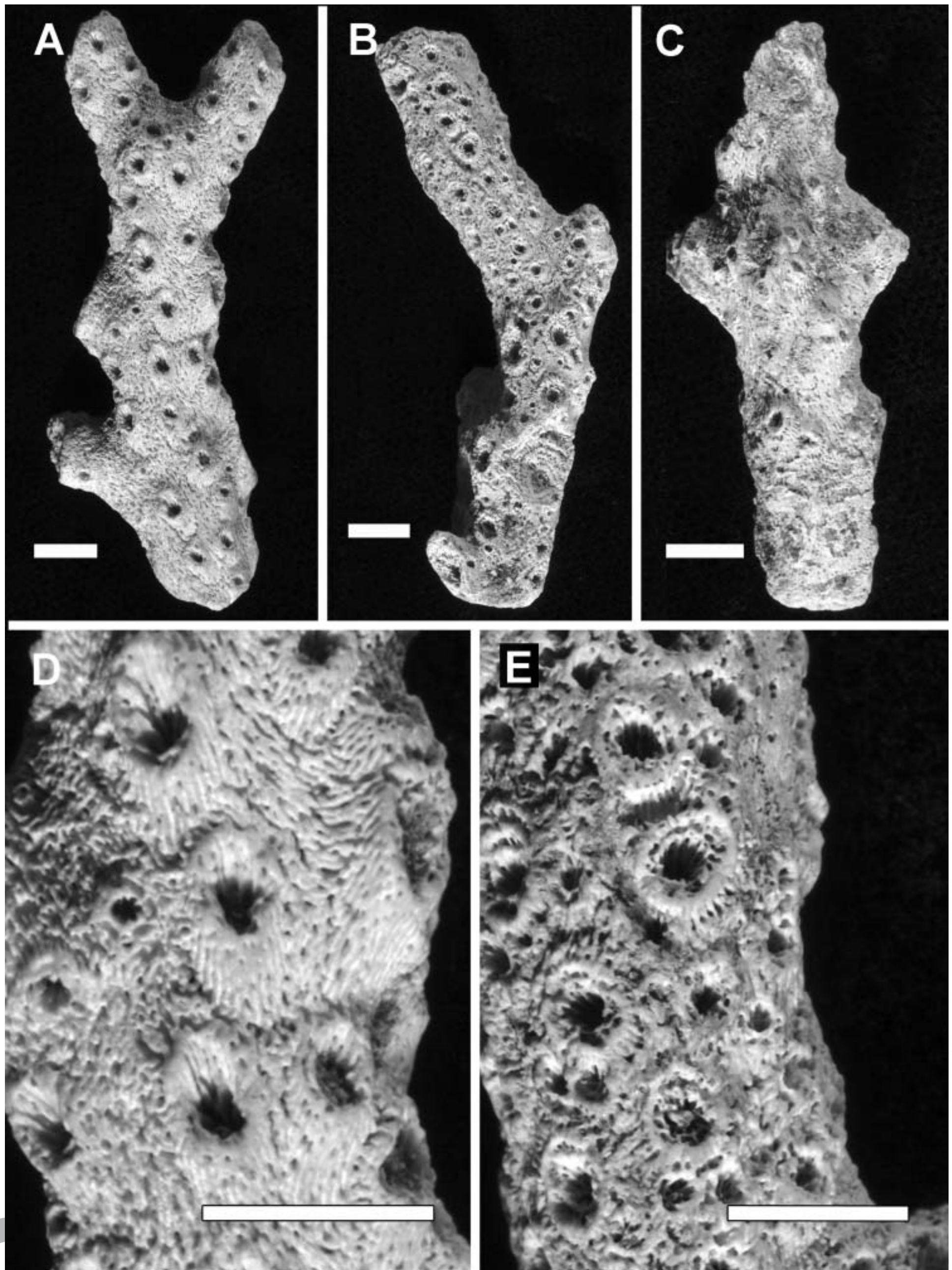

Figure 10. *Acropora bartonensis* Wallace, 2008. **A, D,** IPUM 28306, Miocene, Aquitanian, Carrière Vives, France; **B, E,** IPUM 28307, Miocene, Aquitanian, Carrière Vives, France; **C,** IPUM 28308, Miocene, Burdigalian, Torino Hills, Italy. **A–C,** whole specimen showing simple hispidose branching into secondary branchlets; **D, E,** detail of specimen showing radial corallites rounded appressed tubular with round openings, in two sizes or mixed sizes and coenosteum costate on radials, reticulate between radials. Scale bars 5 mm.

Diagnosis. Radial corallites labellate, upper wall absent, lower wall developed into a rectangular lip, evenly sized; coenosteum between radial corallites reticulate with simple spinules, costate on radial corallites; colonies table or plate form, with central to side attachment.

Acropora proteacea Wallace, 2008
(Fig. 11)

2008 *Acropora proteacea* Wallace: 327, fig. 11.

Type locality. Auvers, Sables Moyens (France).

Material. Holotype: NHMUK R18265, Eocene, Lower Bartonian, Auvers, Sables Moyens, France, R. F. Tomes Collection, presented 1905. Other material: NHMUK R45679, Eocene, Auvers-sur-Oise, France, collected and presented by L. J. Pitt, 1964. IPUM 28309 (in 2 pieces),

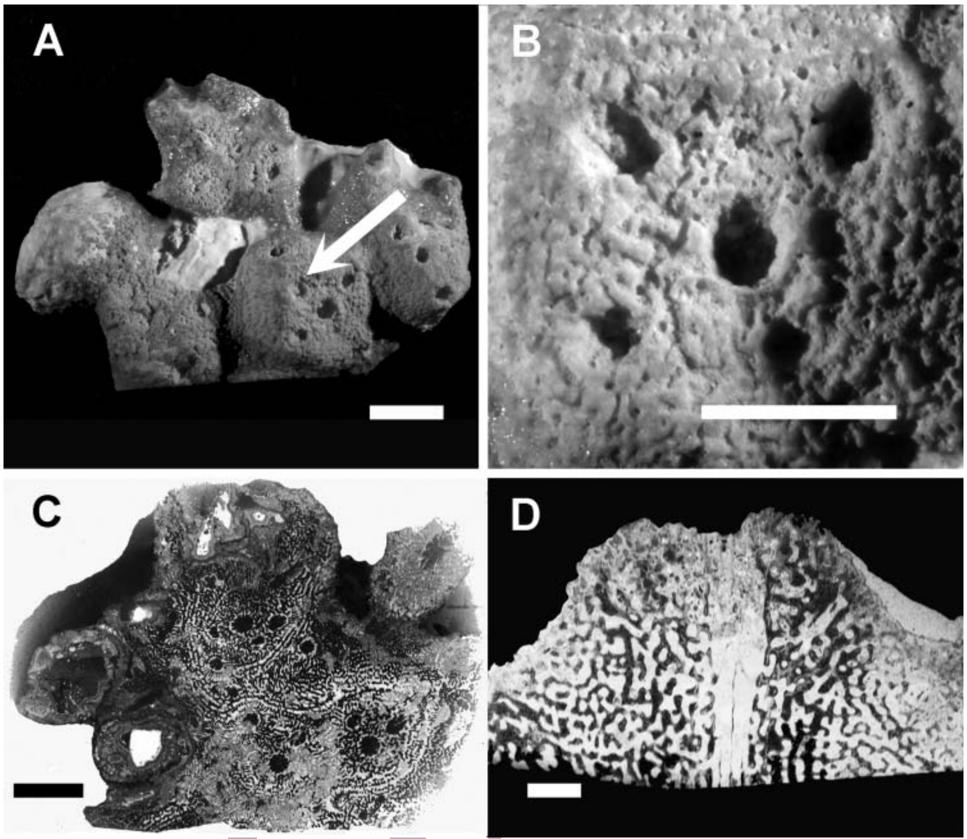

Figure 11. *Acropora proteacea* Wallace, 2008, IPUM 28309, Oligocene, Chattian, Castro, Italy. **A,** whole specimen (cut from larger piece), arrow indicates branchlet in B; **B,** detail of branchlets, showing central axial corallite surrounded by radial corallites; **C,** transverse section through corallum, showing branchlets in TS, including a central axial surrounded by radial corallites; **D,** longitudinal section through branchlet, showing central axial corallite and detail of reticulate coenosteal structure. Scale bars A, B, C, 5 mm; D, 1 mm.

Zinzulusa Cave, Castro, Apulia, Italy, collected by F. R. Bosellini.

Diagnosis. Colony probably tabular; vertical, regular terete branchlets up to 7 mm long, 3.5 mm in diameter, arising from horizontal branches; radial corallites one size, lipped; coenosteum costate on radial corallite walls, reticulate between radials.

Description. IPUM 28309: overall diameter of corallum 35 mm. Five very short branchlets, diameters 9−14 mm, arising from a basal region, indicative of digitate corymbose or tabular growth form. Axial corallites outer diameter 1.06−1.60 mm, inner diameter 0.76−1.03 mm; septa two complete cycles, primary septa reach centre of corallite. Radial corallites all one size, arranged around the axial corallites, not touching, with round openings and thicker lower lip. Coenosteum costate on lip, reticulate between radial corallites.

Occurrence. Oligocene, Chattian. Italy.

Remarks. In identifying this specimen a comparison was made with the holotype of *A. astreoites* (von Gümbel, 1861), which has its type location in the Oligocene (Rupelian) of Bavaria, Germany. The growth form of the two samples is similar; however, the branchlets of the Italian specimen have four radial corallites arranged around the central axial corallites, as seen also in the holotype of *A. proteacea*, whereas the holotype of *A. astreoites* has a large number of radial corallites surrounding the axial (see Reis 1889). It is possible that specimens interpreted as *A. proteacea* (including the holotype) are not fully developed or otherwise are deviations from the type of *A. astreoites*. If this were found to be the case, *A. proteacea* would become a (junior) synonym of *A. astreoites*.

Other literature. von Gümbel (1861, p. 665); Reis (1889, p. 100, pl. 1, fig. 3 for descriptions of *A. astreoites* (von Gümbel, 1861)).

latistella species group

Diagnosis. Radial corallites appressed tubular with round openings, evenly sized; coenosteum throughout reticulate with well-spaced, simple spinules; colonies corymbose, with slender branches.

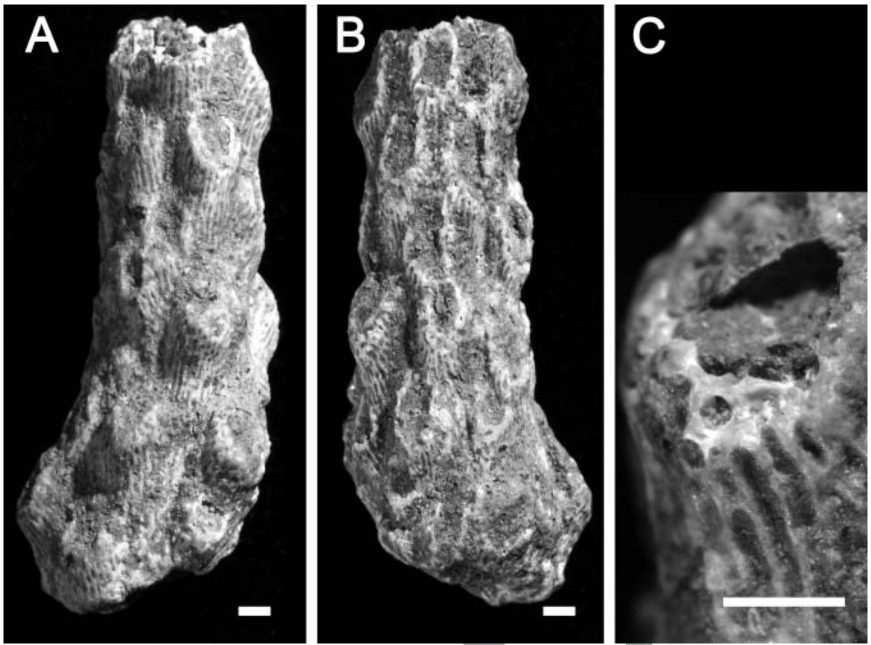

Figure 12. *Acropora lavandulina* (Michelin, 1840), IPUM 28312, Miocene, Burdigalian, Valle Ceppi, Torino Hills, Italy. **A, B,** whole specimen from both sides, showing radial corallites all same size, not touching, tubular with round openings; **C,** detail of radial corallite, showing costate coenosteum. Scale bars A, B, 5 mm; C, 1 mm.

Acropora lavandulina (Michelin, 1840) (Fig. 12)

1840 *Madrepora lavandulina* Michelin: 67, pl. 14, fig. 2a, b.

Type locality. Torino Hills, Piedmont, Italy.

Material. IPUM 28312 (2 specimens), 28310 (2 specimens), 28313 (1 specimen), Valle Ceppi, Torino Hills, Italy, Bugnano Collection; IPUM 28321 (1 specimen), 28322 (1 specimen), Valle Ceppi, Torino Hills, Italy. NHMUK R54844, Middle Eocene, France. MPUR 2876 (2 specimens), Upper Rupelian–Lower Chattian, Sassello, Italy, Michelotti Collection.

Diagnosis. Colony possibly corymbose, with tapering branchlets, around 45–50 mm long and 7 mm diameter; radial corallites all same size, not touching, tubular with round openings; coenosteum costate on radials, reticulate to broken costate between radials (from Wallace 2008).

Description. IPUM 28312: two small branch fragments, one used for thin sections, dimensions of other given here. Overall length of specimen 18 mm. Specimen consists of one branch without an axial tip; branch diameter 6 mm at base, 4 mm at tip. Radial corallites well preserved, tubular, slightly overlapping on branch, partly appressed with round opening (slightly worn). Coenosteum on radial corallite walls costate, interradial areas mostly not visible. IPUM 28310: two fragments, lengths 20 and 25 mm, basal diameters 7 and 2 mm respectively (second branch worn at base), tip diameters 10 and 7.5 mm; incipient branch forming towards tip of fist branch. On both fragments, radial corallites are all same size, tubular, appressed, with round openings and overlapping. First fragment has a broken branch base. IPUM 28313: fragment of a branch, length, 22 mm, diameter 6.5 mm at base, 4 mm at tip. Radial corallites quite worn, all similar size touching, appressed tubular with round openings. Coenosteum worn and not discernable. IPUM 28321: fragment of branch, length 24 mm; diameter 4.5 mm at base, 6.5 mm at tip, one surface worn or without radial corallites. Radial corallites all same size, apparently worn down from a tubular shape. Coenosteum probably costate on radials, reticulo-costate between radials. IPUM 28322: fragment of branch, length 20.5 mm; diameter 6.5 mm at base, 6 mm at tip, quite worn. Radial corallites as for previous specimen, coenosteum worn, but apparently reticulo-costate throughout.

Occurrence. Eocene: France, Spain (G. Álvarez Pérez pers. comm.). Oligocene: Chattian, France; Upper Rupelian–Lower Chattian, Italy. Miocene: Aquitanian, Portugal; Burdigalian, Italy, France.

Remarks. Although the material available was very limited, it did show consistency with the Eocene specimen described in Wallace (2008, fig. 12), which was seen to be most similar in branch and corallite characters to the modern species *A. aculeus* of the *latistella* species group. Unfortunately, no specimens have been found that indicate that this species is corymbose, as are the members of that group: however all branches found to date, and

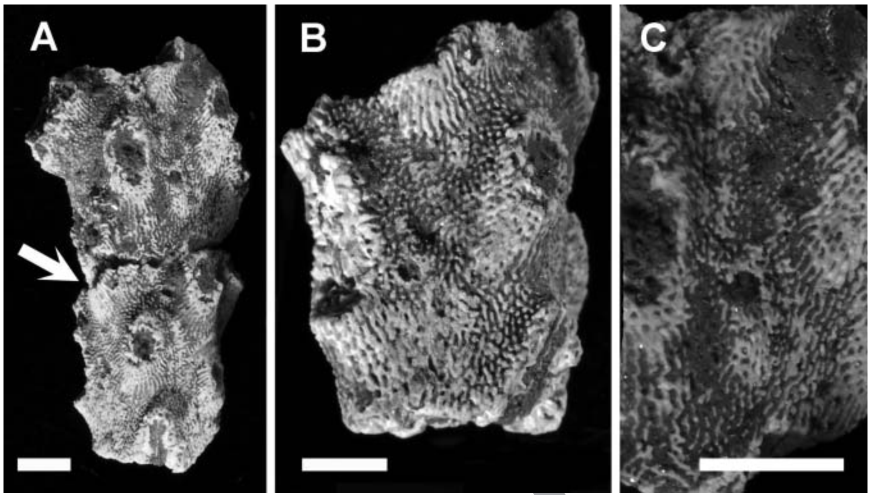

Figure 13. *Acropora macrocalyx* sp. nov., holotype IPUM 28320, Miocene, Burdigalian, Torino Hills, Italy. **A,** entire holotype, the two fragments placed together in life position; **B,** upper fragment, showing detail of large and small radial corallites and coenosteum which is dense reticulo-costate on and between radials; C, detail of lower fragment, showing small radial corallites between large ones. Scale bars 2 mm.

particularly that of Michelin's type (illustration repeated in Wallace 2008) are consistent with short branchlets such as those seen in corymbose colonies.

Q15 **Other literature.** Michelin (1840) cited Michelotti (1838, p. 185, pl. 6, fig. 7) as recording this species as *A. abrotanoides*; Felix (1884, p. 447, pl. 5, figs 2, 3); Chevalier (1962, p. 500); Chevalier (1963); Antunes & Chevalier (1971); Cahuzac & Chaix (1996); Wallace (2008, p. 327, fig. 12).

horrida species group?

Diagnosis. Radial corallites simple tubular with round openings, evenly sized; coenosteum throughout with simple to moderately elaborated spinules, with parts of coenosteum fused and arborescent to hispidose.

Acropora macrocalyx sp. nov.
(Fig. 13)

Material. Holotype: IPUM 28320 Valle Vergnana, Torino Hills, Italy, Rocca Collection.

Etymology. Named for the long corallites, from the Greek *macros* long and *kalyx* cup.

Diagnosis. Colony form probably arborescent with vertical branches, reaching at least 13.5 mm diameter; radial corallites all same size, not touching, tubular with round corallites, appressed at base then projecting outwards from the branch; coenosteum dense reticulo-costate on and between radials.

Description. Holotype IPUM 28320: two contiguous fragments of branch, total length 25 mm, fragments 13.5 and 11 mm; branch width 7–9 mm. One incipient branchlet can be seen at the top of the upper fragment (Fig. 13B). No tip to branch, but axial corallite can be seen in the axis of the fragments. Large radial corallites all same size, not touching, tubular with round opening, partially appressed, then extending outwards from branch; some very small radial corallites present in the coenosteum between corallites. Coenosteum on and between radial corallites reticulo-costate.

Occurrence. Miocene, Burdigalian. Italy.

Remarks. Although represented by only the holotype, this species appears significantly different from those previously recognized and illustrated in the literature. The long tube-like corallites are reminiscent of those seen in the type of the extant species *A. abrolhosensis* Veron, 1985 (see Wallace *et al.* 2012, fig. 1), and hence the species is attributed to the *horrida* group. Q16

Discussion

The specimens of *Acropora* described here are grouped into 10 separate forms whose characters are consistent with separate species. Six existing fossil species are identified amongst these: *Acropora haidingeri*, *A. anglica*, *A. wilsonae*, *A. bartonensis*, *A. proteacea* and *A. lavandulina*. The remaining material is interpreted as representing four new species: *A. salentina* sp. nov., *A. piedmontensis* sp. nov. and *A. macrocalyx* sp. nov. from Italy, and *A. slovenica* sp. nov. from Slovenia (Table 2). The

Table 2. Species of *Acropora*, described or revised in this paper, showing type localities and their stratigraphical age. Strings of localities are from descriptions not providing discreet holotype location. New species names are in bold.

Acropora species	Type locality	Eocene representatives (Wallace 2008 or CR)	Oligocene–Miocene representatives (this paper)
A. salentina **sp. nov.**	Castro (Lecce), Italy	None	Chattian, Italy
A. slovenica **sp. nov.**	Gornji Grad, Slovenia	None	Rupelian, Slovenia
A. haidingeri	Gornji Grad, Slovenia	Spain (CR)	Rupelian: Slovenia, Italy, Spain, France Chattian: Italy, France
A. anglica	Brockenhurst, England	Late Priabonian, England	Chattian, France Aquitanian, France
A. wilsonae	Paris, France	Lutetian to Bartonian, France	Chattian, France Aquitanian, France
A. piedmontensis **sp. nov.**	Torino Hills, Italy	None	Burdigalian, Italy
A. bartonensis	Barton Beds, Hampshire, England	Bartonian, England	Aquitanian, France Burdigalian, Italy
A. proteacea	Auvers, Sables Moyens (France)	Bartonian, France	Chattian, Italy
A. lavandulina	Bordeaux and Dax, France	Eocene, France	Chattian: France Aquitanian: Portugal Burdigalian, Italy, France
A. macrocalyx **sp. nov.**	Vergnana, Torino Hills, Italy	None	Burdigalian, Italy

Abbreviation: CR = collection record.

number of specimens available for each species ranged from only a single specimen for *A. macrocalyx* sp. nov., to numerous specimens for *A. haidingeri*; however in the latter case it could not always be determined how many colonies were represented by the numerous branches.

Our results indicate that the EOT in the western Tethys did not impact greatly on *Acropora* diversity, given that six of the 10 species detected in the Oligocene, Miocene or both periods have their first occurrence in the Eocene (Wallace 2008). Two species previously known only from the Eocene of England (*A. anglica* and *A. bartonensis*), apparently expanded geographically into the eastern Atlantic sub-region following the end of the Eocene (Table 2). Alternatively, material of the species missing from Eocene locations in mainland Europe may await discovery, but either way these species had both a large range and considerable longevity. Three French species from the Late Eocene (*A. wilsonae*, *A. proteacea* and *A. lavandulina*) as well as *A. haidingeri*, for which there is also a collection record from the Eocene of Spain (see below), complete the six species with Eocene origins and thus great longevities (Table 2).

Modern species of *Acropora* have been arranged in species groups, based on their position in a phylogeny based on macro- and microskeletal characters of living species (Wallace 1999) and modified to admit newly described species (Wallace *et al.* 2012 and other publications) and fossil species (Wallace 2008). When the fossil species in this paper are aligned against the species group to which they show the greatest similarity (Table 3), nine species groups are represented, including seven previously found amongst Eocene *Acropora* from England and France (Wallace 2008) and two not previously found in pre-Holocene material. There does, however, appear to have been some speciation and apparent replacement within species groups following the EOT, with our study adding two new species from the Oligocene. We document the origin of *A. slovenica* sp. nov., which possibly replaced the English Eocene species *A. britannica*, not recorded in our study but belonging to the same species group (*humilis* group). We interpret *A. salentina* sp. nov. as representing a species group not previously recorded in the fossil record, but thought (Wallace 1999) to be basal to the genus (the *rudis* group: see species description below). Q17 From the Miocene, two new species, *A. piedmontensis* and *A. macrocalyx* were both found in the Piedmont area. The first species is interpreted as being a member of the *florida* species group, also represented in the Eocene, so this may represent species turnover, possibly from *A. roemeri* from Brockenhurst, England. *Acropora macrocalyx*, represented only by the holotype, may represent the first recorded occurrence of the *A. horrida* group, based on available morphological evidence. Although the *horrida* group is placed in the final clade of species groups in Figure 2, there is a suggestion from molecular work that this species group may have origins towards the base of *Acropora* phylogeny (Richards *et al.* 2013).

Based on their skeletal features (Table 3) and the most similar modern species in each case (indicated in the relevant descriptions in the systematic palaeontology section), the species identified are interpreted as representing seven extant species groups previously documented from the Eocene of Europe (*humilis*, *cervicornis*, *robusta*, *aspera*, *florida*, *hyacinthus* and *latistella* groups), as well

Table 3. Summary of main skeletal characteristics of *Acropora* species described in this paper from European Oligocene /Miocene deposits, together with the species group to which each species is attributed. Question marks denote uncertainty. Characters are described in Wallace (1999, 2008) and Wallace *et al.* (2012): note that the 'branch diameter component' character indicates relative contributions of axial versus radial corallites to the diameter of the branch. New species names are in bold.

Acropora species	Colony form and branch type	Branch diameter component	Radial corallites	Coenosteum on radials	Coenosteum between radials	Putative species group
A. salentina sp. nov.	Indeterminate with irregular branching	50 /50	One size, some touching, appressed tubular	Reticulo-costate	Reticulo-costate	*rudis*
A. slovenica sp. nov.	Caespito-corymbose or arborescent	Axial dominated	One size, not touching, appressed tubular	Costate or reticulo-costate	Reticulo-costate	*humilis*
A. haidingeri	Arborescent	50 /50	One size, mostly not touching, appressed tubular	Costate	Reticulate	*cervicornis*
A. anglica	Sturdy sub-arborescent, branches tapering	Axial dominated	Two distinct sizes, some touching, appressed tubular	Costate	Reticulate	*robusta*
A. wilsonae	Arborescent?, branches terete	50 /50	Two distinct sizes, not touching, probably lipped	Costate	Reticulate	*aspera*
A. piedmontensis sp. nov.	Simple hispidose, branchlets short and rounded	Axial dominated	Two sizes, most not touching, rounded appressed tubular, round openings	Costate	Reticulate	*florida*
A. bartonensis	Simple hispidose, branchlets short and rounded	50 /50	One size or graded, not touching, rounded tubular, round openings	Costate	Broken costate or reticulate	*florida*
A. proteacea	Tabular, branchlets terete	Radial dominated	One size, touching, lipped	Costate	Reticulate	*hyacinthus*
A. lavandulina	Corymbose? branches tapering	Radial dominated	One size, not touching, tubular appressed, round openings	Costate	Reticulate to broken costate	*latistella*
A. macrocalyx sp. nov.	Unknown, probably arborescent	50 /50	One size, not touching, tubular round openings	Reticulo-costate	Reticulo-costate	*?horrida*

as first records for two further extant groups (*rudis* and putative *horrida* groups) (Fig. 2). This complements previous findings of Eocene diversification of *Acropora* into the beginnings of up to 10 of the 20 recognized modern species groups (Wallace & Rosen 2006; Wallace 2008).

From our findings three main patterns that apparently characterized *Acropora* evolution during the Oligo-Miocene can be highlighted: (1) persistence of Eocene species and lineages; (2) turnover of species within lineages continuing on from the Eocene; and (3) origination of new species and lineages, probably associated with changes in configuration of the western Tethys Sea. Although the material available for the study was limited, it does indicate great longevity for the six species with Eocene origins, e.g. *Acropora anglica* is recorded from late Priabonian to Aquitanian, *A. bartonensis* from Bartonian to Aquitanian and *A. wilsonae* from Lutetian to Aquitanian (Table 2), giving them longevities of up to 17, 20 and 28 million years respectively.

The new descriptions and records provide evidence that *Acropora* not only diversified rapidly into the beginnings of modern species groups after its first appearance in the fossil record, but maintained and added to this species-group level diversity into the Miocene. This information is relevant to 'molecular clock' interpretations in molecular analyses of modern material and to the evolution of Indo-Pacific *Acropora* (Chen *et al.* 2009). These results indicate the potential of the *Acropora* fossil record to play a part in the resolution of the biogeographical and evolutionary history of modern coral reef diversity, particularly when the European systematic record is combined with new information from the Caribbean (Wallace 2012) and Indo-Pacific (Santadomingo *et al.* 2012).

Of the locations studied in this work, the Late Oligocene Castro Limestone (Zinzulusa Cave) is represented by only three specimens; however, these include a new species, *A. salentina*, and a new palaeogeographical record for another species, *A. proteacea*. This suggests that further exploration of the *Acropora* fauna from this site (Bosellini & Russo 1992; Bosellini 2006) and others in the Eastern Mediterranean such as Greece (Schuster 2002) would expand our understanding of the development of reef-edge Mediterranean communities and provide a more complete record of the scale of diversification achieved by *Acropora* during its period of evolution in Europe.

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