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On the Cretaceous Genus *Podoseris* Duncan, 1869 (Scleractinia; Albian; England)

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2 Plates

Albian
England
Hunstanton Red Chalk
Taxonomy
Morphology
Scleractinia

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Die kretazische Gattung *Podoseris* Duncan, 1869 (Scleractinia; Albium; England)

Zusammenfassung

Die Gattung *Podoseris* Duncan wird auf der Grundlage des Studiums von Typus- und Originalmaterial, welches von der Typuslokalität stammt, revidiert. Im Gegensatz zu der bislang traditionell vertretenen Auffassung, dass diese Gattung eine solitäre Form repräsentiert, zeigen jüngste Untersuchungen an Exemplaren von der Typuslokalität, dass die Typusart dieser Gattung, P. *mammiliformis* Duncan in späten Ontogeniestadien reptoide und subplocoide bis subfasciculate Kolonien bilden kann. Die Gattung *Podoseris* besitzt haplaraeide Septen- und Wandstrukturen. Bezüglich ihrer sowohl solitären als auch kolonialen morphologischen Korallumstypen weisen die Exemplare Ähnlichkeiten zu Gattungen, wie z.B. *Rhizangia* Milne Edwards & Haime und *Brachyphyllia* Reuss auf.

Abstract

The scleractinian genus *Podoseris* Duncan is revised on the basis of the study of type and original material from the type locality. In contrast to traditional interpretations, according to which this genus is considered a solitary form, the study of topotypes from the type locality of the type species of the genus *P. mammiliformis* Duncan shows that it has the capability to form colonial reptoid and subplocoid to subfasciculate clumps in later stages of ontogeny. The genus *Podoseris* is characterized by septal and thecal structures which are similar to the kinds seen in the haplaraeids. Regarding morphological features of its solitary and colonial stages, this genus corresponds to, e.g. *Rhizangia* Milne Edwards & Haime, and *Brachyphyllia* Reuss.

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Introduction

The genus *Podoseris* DUNCAN, 1869, represents a poorly known taxon which has been considered endemic to its type locality, the Hunstanton Red Chalk (middle to late Albian) of Norfolk, England. Since it was first described by DUNCAN (1869, p. 25, Pl. 9, Figs. 2–15), the genus *Podoseris* has been briefly mentioned by many authors, but without a description or illustration. Until the first photographic documentation was given in 2002 (BARON-SZABO, 2002, Pl. 73, Fig. 4), this genus had been illustrated three times in works by DUNCAN (1869, Pl. 9, Figs. 2–15; 1889, Pl. 5, Figs. 1–14) and TOMES (1885, Pl. 14, Figs. 7–9). In a recently carried out revision, further photographic material of this genus was provided (LÖSER, 2012). Up to now, the genus *Podoseris* was considered to form only solitary corralla. However, in stating "…*while in three instances only have I seen the corallites connected by the calcified stolon*…", TOMES (1885, p. 550) was the first to imply that this genus could also form colonies.

The purpose of this paper is to illustrate unpublished material belonging to the genus *Podoseris* from the type locality that was found in the Duncan (= Wiltshire), Tomes, and H. le Strange collections deposited in the Natural History Museum London, as well as to establish the taxonomic position of the genus, to document its various growth forms and to compare them to taxonomically unrelated groups.

Material

The material used in this work includes specimens from:

NHM Natural History Museum London, UK.

SMNS State Museum of Natural History Stuttgart, Germany (Staatliches Museum für Naturkunde, Stuttgart, Deutschland).

Note that specimens marked with * represent material from the type locality of *Podoseris* (middle to late Albian, Hunstanton Red Chalk, Hunstanton, Norfolk, England):

**Podoseris mammiliformis* DUNCAN, 1869, NHM R.25089 (marked as holotype).

**Podoseris mammiliformis* DUNCAN, 1869, NHM R.6459 (topotype, Tomes collection, original material of TOMES, 1885, p. 550, Pl. 14, Fig. 7).

**Podoseris mammiliformis* DUNCAN, 1869, NHM R.6460 (topotype, Tomes collection, original material of TOMES, 1885, Pl. 14, Fig. 8).

**Podoseris mammiliformis* DUNCAN, 1869, NHM R.42034 (topotype, H. le Strange collection).

**Podoseris elongata* DUNCAN, 1869, NHM R.25091 (topotype [?holotype]; this specimen might correspond to the one figured in DUNCAN [1889, p. 26, Pl. 5, Figs. 14–16]. Based on its collection number, it most likely belongs to the type series by Duncan and could, therefore, be the holotype).

**Podoseris jessoni* DUNCAN, 1889, NHM R.25087 (marked as holotype).

**Podoseris anomala* DUNCAN, 1889, NHM R.25086 (marked as holotype).

Haplaraea elegans MILASCHEWITSCH, 1876, SMNS 21874 (syntype, figured in MILASCHEWITSCH, 1876, p. 229, Pl. 51, Fig. 2), Late Jurassic, Nattheimer Schichten, Germany. This taxon represents the type species of the genus *Haplaraea* and, therefore, embodies the nominatform of the haplaraeid-group. This specimen is presented on Pl. 1, Figs. 1–4.

Systematic Paleontology

Order Scleractinia BOURNE, 1900

Suborder Fungiina VERRILL, 1865

Family Haplaraeidae VAUGHAN & WELLS, 1943

Diagnosis: Solitary and colonial. Colony formation by intra- and extratentacular budding. Corallite wall synapticulothecal, poorly defined or absent, costate, usually epithecate, porous. Septa exsert, composed of one fan system of compound trabeculae, with vertical axis of divergence, irregularly porous and thick. Dissepiments thin. Columella absent or parietal or feebly developed.

Remarks: DUNCAN (1884) described the family Podoseriidae (= Podoserioida DUNCAN, 1884, p. 153) which is, however, a *nomen oblitum*.

Subfamily Haplaraeinae VAUGHAN & WELLS, 1943

Diagnosis: Solitary and colonial. Polyps rather large, with a wide base of attachment. Trabeculae thick. Synapticulae numerous. Columella parietal. Dissepiments thin, large.

Genus *Podoseris* DUNCAN, 1869

Pl. 1, Figs. 5–8; Pl. 2, Figs. 1–6

Type species: *Podoseris mammiliformis* DUNCAN, 1869, middle to late Albian of England (Hunstanton Cliff near Hunstanton, Norfolk).

Diagnosis: Solitary, forms cupolate, tympanoid to cylindrical with a corallite diameter to around 15 mm (in specimens corresponding to the species *mammiliformis*). Colonial forms arranged in reptoid (as in, e.g. *Rhizangia*) or subplocoid-subfasciculate, sometimes encrusting clumps (as in, e.g. *Brachyphyllia*), connected by a lamellar coenosteum that appears unstructured and dense, or ?vesicular. Solitary stage probably with a corallite height to 5 mm, or, as a result of re-juvenation of the solitary stage, much higher (at least to 40 mm). Budding intracalicinal-marginal and extracalicinal. Costosepta generally compact with a small number of mainly axially occurring pores. Anastomosis present. Sep-

tal thickness ranges between 65 and around 600 µm. Septal flanks covered with granules varying in size and shape (e.g. rounded, pointed, flat, long and hook-like); laterally (conical to hook-like) and distally (rather regular teeth) ornamentations are similar to the kinds seen in the genus *Haplaraea*. Endothecal dissepiments vesicular, thin, irregularly disposed. Columella parietal. Synapticulae present. Wall parasynapticulothecal, porous.

Cretaceous species of Podoseris

From the Cretaceous (middle to late Albian of England; Hunstanton Cliff near Hunstanton, Norfolk), DUNCAN (1869, 1889) described seven species: *P. mammiliformis* DUNCAN, 1869; *P. affinis* DUNCAN, 1889; *P. anomala* DUNCAN, 1889; *P. brevis* DUNCAN, 1889; *P. dubia* DUNCAN, 1889; *P. elongata* DUNCAN, 1869; *P. jessoni* DUNCAN, 1889.

Due to their great re-juvenating potential, individual specimens of the species of this genus show remarkable morphological plasticity, resulting in ever changing corallite diameters and septal numbers throughout their ontogeny. Therefore, a clear specific distinction of the species described is problematic. LÖSER (2012) considered all the species from the type locality synonymous, by which, however, he combines species with larger corallites having a smaller number of septa with those with smaller corallites that have a larger number of septa. Based on these characters, the English species can be grouped in two categories:

***P. mammiliformis* DUNCAN, 1869, p. 25, Pl. 9, Figs. 2–5** (= *P. affinis* DUNCAN, 1889; *P. anomala* DUNCAN, 1889; *P. brevis* DUNCAN, 1889; *P. dubia* DUNCAN, 1889):

In corallites with diameters of 6–7 mm, there are usually 4 complete cycles of septa in 6 irregular systems (= 48 septa); in corallites with diameters of around 10 mm, there are around 80 septa; and in corallites that have a diameter of 12 mm and larger, there are at least 5 complete cycles of septa in 6 irregular systems (96 or 96 + s6 septa).

***P. elongata* DUNCAN, 1869, p. 24, Pl. 9, Figs. 16–17** (= *P. jessoni* DUNCAN, 1889):

In corallites with diameters of up to 13 mm, there are septa arranged in 4 complete and some of the beginning 5th cycle in 6 irregular systems (= in a corallite with a diameter of 9 mm, usually 50–60 septa are present; in corallites ranging between 11.5 and 13 mm in diameter, there are around 80 septa in 6 irregular systems).

Taxonomic affinities of Podoseris

In forming a cupolate corallum and having compact costosepta; synapticulae; a parietal-papillose columella; (sparse) endothecal dissepiments; synapticulothecal wall; and septal ornamentations which resemble the kinds seen in *Podoseris*, the material described as *Actinoseris* ? *alloiteaui* by BEAUVAIS & ZLATARSKI (1966), from the Barremian (?or Aptian) of Bulgaria appears to be related to the genus *Podoseris*.

Morphology of Podoseris

Recently, LÖSER (2012: p. 9) carried out a revision of the genus *Podoseris* DUNCAN, in which he stated that, "*the genus can be confounded with the very early stages of any colonial corals* […]. *From the type locality of the type species of Podoseris mammiliformis, no other corals are known, so that it can be excluded that Podoseris represents just early stages of colonial corals*." However, this is a fallacy as it cannot be concluded that the maximum size of a species found in one locality, especially with conditions unfavorable for coral growth, represents the maximum size reached by the very same species in other localities. Investigation by e.g. BARON-SZABO (1997, 2003) and SANDERS & BARON-SZABO (2008) on Upper Cretaceous corals from the Gosau Group clearly showed that in areas unfavorable for coral growth the size reached by corals of all taxa were significantly smaller than the size of the very same taxa in other areas favorable for coral growth (also compare SANDERS & BARON-SZABO, 2005). Colonial corals with an extended solitary stage would remain solitary. Moreover, species forming various types of solitary conical coralla before becoming colonial have been repeatedly documented: In the type material of the Upper Cretaceous taxon *Rhabdopsammia lanquinei* ALLOITEAU, 1952, the corallum occurs in the solitary stage up to the corallum height of around 25 mm (ALLOITEAU, 1957; CAIRNS, 2001; BARON-SZABO, 2002, Pl. 56, Fig. 3). Closely corresponding observations have been reported for species of other Cretaceous and Tertiary genera like, e.g. *Brachyphyllia* REUSS, 1854 (in *B. felixi* BARON-SZABO, 2000, Pl. 11, Fig. 5), *Syzygophyllia* (SANDERS & BARON-SZABO, 2007), and *Sideroseris* WELLS, the latter of which stays in the solitary stage until the corallum has reached a height of around 10 mm (BARON-SZABO et al., 2004; BARON-SZABO, 2008, p. 158–159, Text-Fig. 31). A good example is *Sideroseris*, a taxon which was reported from the type locality (Eocene of Barbados) by a single solitary corallum, but was later observed solely occurring with a colonial-branching polyp integration in the Palaeocene of southern France (ALLOITEAU & TESSIER, 1958; see BARON-SZABO, 2008, p. 158–159), and was additionally documented in both solitary and colonial stages from the Paleocene of Argentina (BARON-SZABO et al., 2004, and unpublished data) and the Eocene of Mexico (FROST & LANGENHEIM, 1974, p. 212–214, Pl. 69, Figs. 1–9). In light of this evidence, the conclusions by LÖSER (2012) can only be considered implausible.

In addition, Löser's statement that only solitary corals are known from the type locality of *Podoseris mammiliformis* (Hunstanton, Norfork, Red Chalk) is incorrect. There are several colonial specimens in the Tomes and H. le Strange collections from the type locality Hunstanton, Norfolk (verification of locality data of the material by Jill DARRELL, British Museum London, pers. comm. March 8th, 2013), which, based on their skeletal features, show colonial polyp integration (see Pl. 1, Fig. 8 and Pl. 2, Figs. 1, 4–6) as well as very close affinities to *Podoseris mammiliformis*. In *Podoseris* coralla can remain in the solitary stage to at least 40 mm in height as can be seen in Fig. 4 of Pl. 2. The solitary stage consists of a series of re-juvenation processes. The colonial stage can therefore be assumed to possibly also occur at a much smaller corallum height of around 5 mm (measurement taken from corallum of latest re-juvenation cycle). Moreover, in some specimens from the type locality of the type species of the genus *Podoseris*, corallites are arranged in encrusting colonies having reptoid or subplocoid polyp integration, which was previously pointed out by TOMES (1885). The original specimens of TOMES (1885) are figured on Pl. 1, Fig. 8 and Pl. 2, Fig. 1.

Taxonomic considerations

The taxonomic position of the genus *Podoseris* has long been discussed. Originally, DUNCAN (1869) placed it in the family Fungiidae DANA, 1846. Later, TOMES (1885) synonymized *Podoseris* with the genus *Rhizangia* MILNE EDWARDS & HAIME, 1848. VAUGHAN & WELLS (1943) and WELLS (1956) questionably grouped *Podoseris* with the family Astrangiidae VERRILL, 1869, which was later interpreted to be a junior synonym of the family Rhizangiidae D'ORBIGNY, 1851 (see WELLS, 1956, p. F.410). BARON-SZABO (2002) grouped this genus with the family Haplaraeidae VAUGHAN & WELLS, 1943. On the basis of the alleged presence of pennulae, LÖSER (2012) grouped *Podoseris* with the family Synastreidae ALLOITEAU, 1952. Pennulae are cup- or hook-shaped extensions which stand off the septal flanks and are positioned in an alternating fashion with regard to the ones of neighboring septa. In addition, in cross view these cup- or hook-shaped extensions are positioned in a way by which they stand off with the septal trabeculae as central points (GILL, 1967, 1982; and pers. comm. Bernard LATHUILIÈRE, 2013). In *Podoseris*, however, lateral extensions often stand in one plane (non-alternating) and, instead of forming processes expanding from the trabeculae center, they are occasionally formed by what appears to be diverging trabeculae, which, to some extent, are comparable to the kinds seen in e.g. forms assigned to *Columnocoenia* (see MORYCOWA, 1971). MORYCOWA & RONIEWICZ (1995) described for some members of the family Synastreidae structures, which they referred to as decomposed pennulae. But those features as well show the basic pennulae formation as the decomposing effects are observed on the pennulae edge. Therefore, the genus *Podoseris* is excluded from the family Synastreidae ALLOITEAU, 1952, and kept with the family Haplaraeidae VAUGHAN & WELLS, 1943.

Lithology and Paleoenvironment of the type locality (Hunstanton Red Chalk)

The Hunstanton Formation is generally characterized by rubbly to massive chalks with marl bands; typically pink to brick-red (due to disseminated hematite), locally grey due to secondary alteration of the iron minerals. Its lower part is commonly weakly sandy (HOPSON et al., 2008: p. 55). Paleoecologically, this formation was formed in a shallow marine, low-energy environment with alternating periods of sedimentation and non-deposition, during which iron-oxide hardgrounds developed (OWEN, 1995). These environmental features are comparable to some coral-bearing sites of the Gosau Group characterized by soft-bottom, low-energy environments, e.g. the deposits of the Tyrolean Brandenberg, Hochmoos and Grabenbach layers of the greater Salzburg area, and other sites. These layers are often dominated by forms of the solitary cupolate genus *Cunnolites* or very small-sized colonial specimens (BARON-SZABO, 1997, 2003; SANDERS & BARON-SZABO, 2008).

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Plate 1

Figs. 1–4: *Haplaraea elegans* MILASCHEWITSCH, 1876, syntype, SMNS 21874, Late Jurassic of Germany (Nattheim).

Fig. 1: Upper surface, lateral view of corallum.

Fig. 2: Upper surface, cross view of corallum.

Fig. 3: Close-up of Fig. 2, showing septa with lateral granules varying in size and shape. The more regularly developed granules show some resemblance to carinae.

Fig. 4: Close-up of Fig. 1, showing lateral development that closely corresponds to the kinds seen in *Podoseris* (compare with Fig. 7).

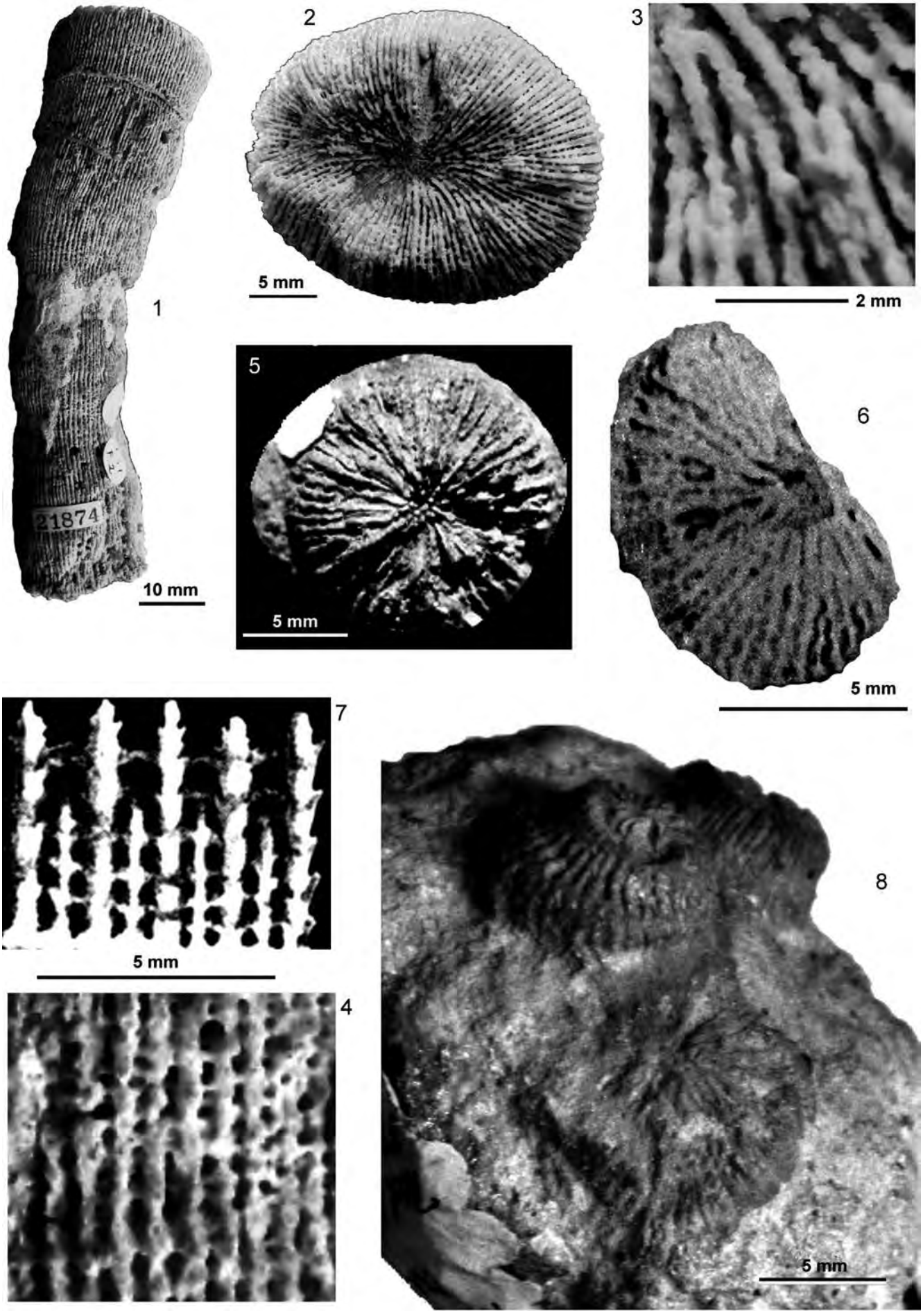
Figs. 5, 7, 8: *Podoseris mammiliformis* DUNCAN, 1869, middle to late Albian, Hunstanton Red Chalk, Hunstanton, Norfolk, England.

Fig. 5: Cross view of holotype, NHM R.25089.

Fig. 7: Sketch of lateral view, showing developments that closely correspond to the kinds seen in the type material of *Haplaraea elegans* MILASCHEWITSCH (compare with Fig. 4). Sketch corresponds to the original of DUNCAN (1869, Pl. 9, Fig. 17). Dimensions estimated based on information provided by DUNCAN (1869).

Fig. 8: Polyps of *Podoseris mammiliformis* DUNCAN, 1869, arranged in an encrusting subplocoid-reptoid polyp integration. Specimen represents the original of TOMES (1885, p. 550, Pl. 14, Fig. 7), NHM R.6459.

Fig. 6: *Podoseris elongata* DUNCAN, 1869, NHM R.25091 (topotype [?holotype]. Thin section of cross view, slightly oblique.


1
21874
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2
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4
8
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Plate 2

Figs. 1, 4–6: *Podoseris mammiliformis* DUNCAN, 1869.

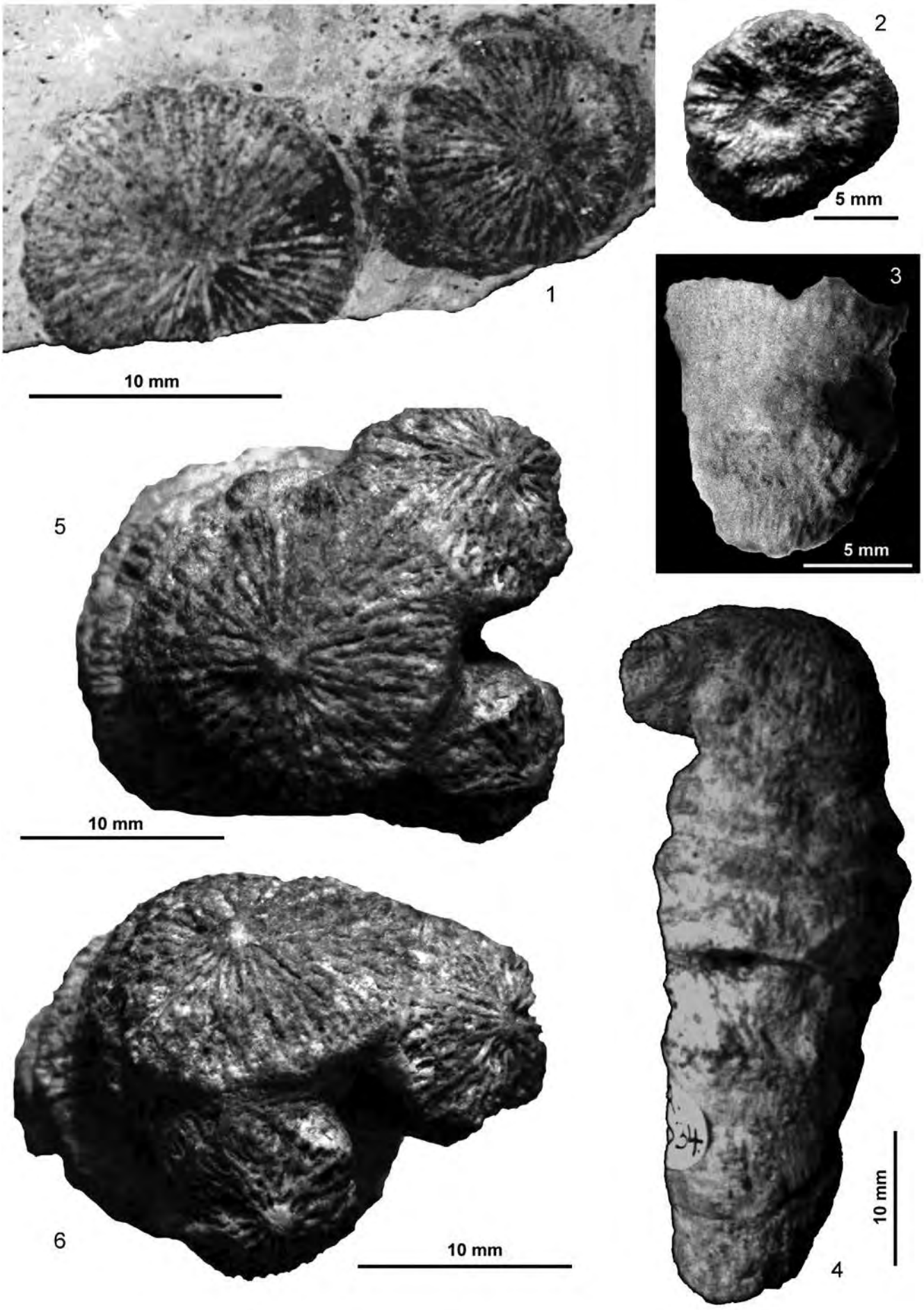
Fig. 1: Corallites arranged in reptoid polyp integration. Specimen represents the original of TOMES (1885, p. 550, Pl. 14, Fig. 7), NHM R.6459.

Fig. 4: Upper surface, longitudinal view, showing a corallite in a series of re-juvenation stages before forming a small subplocoid colony by intracalicinal budding. Specimen NHM R.42034 of the H. le Strange collection.

Figs. 5, 6: Same as Fig. 4, showing upper surface of colony, cross view in different angles.

Fig. 2: *Podoseris jessoni* DUNCAN, 1889, NHM R.25087 (holotype), middle to late Albian, Hunstanton Red Chalk, Hunstanton, Norfolk, England. Upper surface, cross view of corallite.

Fig. 3: *Podoseris anomala* DUNCAN, 1889, NHM R.25086 (holotype), middle to late Albian, Hunstanton Red Chalk, Hunstanton, Norfolk, England. Upper surface, lateral view of corallite, showing re-juvenation.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