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Eco-taphonomy of mass-aggregated giant balanids *Concavus* (*Concavus*) *concavus* (DARWIN, 1854) from the Lower Pliocene (Zanclean) of Rafina near Pikermi (Attica, Greece)

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ABSTRACT:

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The large- to giant-sized balanids, mass-aggregated in a tempestite of the Lower Pliocene (Zanclean) section at Rafina near Pikermi, Greece, represent a single species, *Concavus* (*Concavus*) *concavus* (DARWIN, 1854) [*non* BRONN, 1831], the taxonomy of which is revised. The peculiarly shaped forms '*raphanoides*' and '*scutorum*' are ecophenotypes of this species; the same applies to the '*tulipiformis*' specimens reported previously from this section. Discussed are dynamic events controlling the life and death conditions in the nearshore (offshore) environment of Rafina, where the giant specimens of *Concavus* (*Concavus*) *concavus* (DARWIN, 1854) flourished through several successive generations. As opportunistic species they adopted the *r*-selection reproduction strategy in order to dominate over other biota. The intermittent action of high-energy agents was responsible for the production of balanid-shell hash that involved taphonomic feedback. This enabled further colonization of the biotope and the growth of multiphased (bouquet-like and pyramidal) clusters. The demise of the monospecific balanid communities is ascribed to a heavy storm which stirred-up the whole balanid-bearing sequence, to produce a proximal tempestite. This final burial and subsequent depositional lull in the Rafina environment was favoured by a temporary deepening of the whole Lower Pliocene (Zanclean) basin beyond the bathymetric range in which the balanid population could survive.

Key words: Eco-taphonomy, Cirripedes, Balanids, *Concavus*, Pliocene (Zanclean), Greece.

INTRODUCTION

The ecology of fossil acorn barnacles, the balanids, is as yet very poorly known; except for the creusioid barnacles, close relatives of the balanids, which live commensally in solitary or colonial corals. The acorn barnacles, commonly occurring in some Palaeogene and Neogene sequences of many countries, have been subjected to detailed ecologic and taphonomic analysis quite sporadically, and only when larger samples were available from one location (see STRAUCH 1968, DONOVAN 1988, 1989; and early contributions by BEETS 1945, BÁLDI 1959). In this context, the present authors became fascinated by the succession displayed by the cliff exposures at Rafina near the classic Pikermi GeoSite in Attica, some 27 kms NE of Athens in Greece (see Text-fig. 1) during their first visit in 1989. In these exposures, the balanids that occur throughout the fine-clastic sequence of Pliocene age, appear to be the main rock-building component of one sandy layer, less than one metre thick. This layer is replete with thousands of large-sized balanid crowns (up to about 10 cm high), or their clusters, and extends conspicuously along the cliff (see Text-figs 2-3 and Pl. 1).

The ubiquity of balanid specimens in the Rafina section has allowed us to undertake an analysis of their ecologic features and the taphonomic pathways through which they became mass-aggregated in one layer (Bed No. 9 in Text-fig. 3), interpreted as a tempestite. The whole Rafina Cliff section is the subject of a separate report (Dermitzakis & *al.*, *in preparation*), which includes the history of investigation, description of lithology and sedimentary features, faunal content, and environmental conclusions (cf. also Guernet & Sauvage 1970, Symeonidis & Marcopoulou-Diacantoni 1977, Georgiades-Dikeoulia & *al.* 1979).

The Pliocene age of the balanid-bearing Rafina section was recognized by Mitzopoulou (1948) on the basis of the malacofauna, and by Christodoulou (1961) on foraminifera. The succession belongs to the Astian facies, that is the Lower Pliocene Zanclean Stage (5.33-3.60 my) in the presently used standard international geochronologic scale (see Gradstein & *al.* 2004).

TERMINOLOGY OF BALANID SHELLS

To describe the mode of occurrence and morphology of the studied balanids, and to avoid any confusion when using both English and Latin nouns, the particular terms are used as follows (see Text-fig. 4).

Fig. 1. Location of the Lower Pliocene (Zanclean) balanid-bearing sequence at Rafina near Pikermi, in Attica, Greece

The balanid **shell** consists of the **basal plate**, or basis (**B** in Pls 3-8), and the **crown**. The crown is composed of six **compartments**, or compartmental plates (in Latin: parietes): a **rostrum** (plural: rostra) anteriorly (**R** in Pls 3-8), paired broad **laterals** and narrow **carinolaterals (L** and **CL** in Pls 3-8), and a **carina** (plural: carinae) posteriorly (**C** in Pls 3-8). The crown, and hence the entire shell, is closed by four opercular valves: paired terga (singular: **tergum**) and paired scuta (singular: **scutum**); the adjectives being *tergal*, and *scutal*, respectively.

The isolated compartments are recognizable from their interlocking appendages: the alae (singular: **ala**) which underlie the radii (singular: **radius**) of the adjacent compartment (see **a** and **r** in Text-fig. 4). Of the compartmental plates located at the anterior and posterior ends of the crown respectively, the rostrum has only two radii, whereas the carina bears only two alae.

The variably-sized debris of shattered balanid shells is termed the **hash**, of which one supplied from compartmental plates is the **parietal hash**.

THE BALANID-BEARING TEMPESTITE

The balanid-bearing tempestite exposed at Rafina Cliff (Bed No. 9a-9b in Text-fig. 3) is characterized by a compound structure acquired during sedimentation and, most likely, slightly modified by diagenetic events. Its thicker lower part, a proximal tempestite (9a in Text-fig. 3), includes more or less bulbous to thick-lenticular bodies (1.0-1.5 m wide and up to 0.5 m high) replete with balanids, but embedded in sand almost devoid of balanids. Some of these bulbous parts are cemented more firmly with calcite than others, the sand remaining nearly loose.

The thinner upper part, a distal tempestite (9b in Text-fig. 3) that grades upwards from the proximal one, is finely and irregularly stratified. It bears balanid hash that diminishes in size upwards, a few small-sized shells and relatively common opercular valves, mostly the scuta.

The bulbous-to-lenticular bodies in the main part of the tempestite may be interpreted either as synsedimentary forms deposited by highly agitated waters (eddies ?), or as diagenetic structures resulted from the sinking ('load-casting') of the balanid-bearing load into the less coherent sand upon which the storm supply was blanketed (cf. a similar case in Dżułyński & Kubicz 1975, figs 4-5).

Within the Rafina sequence, the tempestite with mass-aggregated balanids appeared during the sedimentation of a renewed high-stand pulse (see Der-

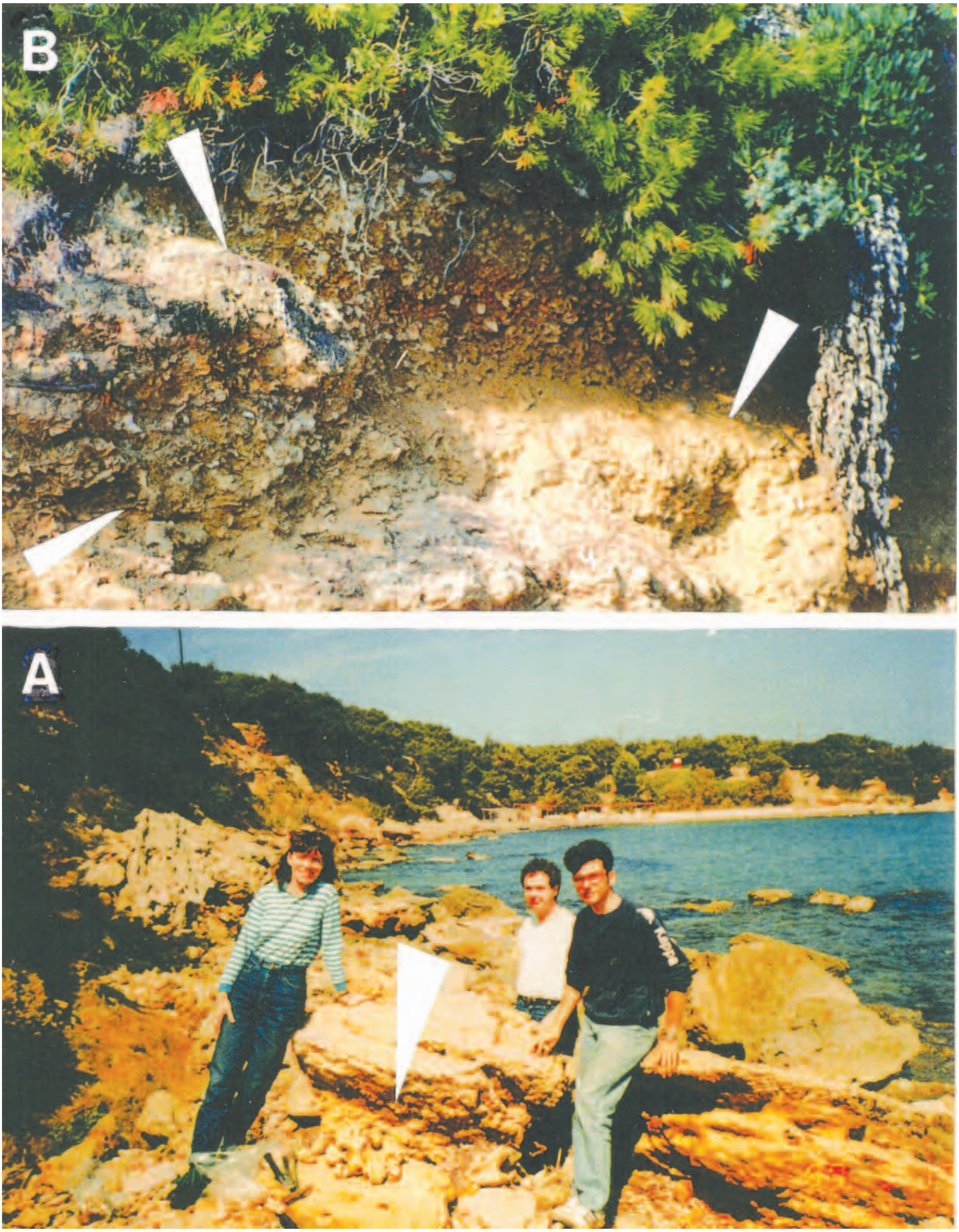


Fig. 2. The balanid-bearing Lower Pliocene (Zanclean) sequence exposed along shores of the Rafina Bay, Attica, Greece. A – General landscape of the Rafina Bay, along the shores of which the sequence studied is exposed; photo taken at the best accessible section (see Text-fig. 3), to show a cliff-derived block (*arrowed*) with mass-aggregated giant balanids *Concavus* (*Concavus*) *concavus* (Darwin, 1854). B – Detail of the Rafina Cliff exposing sandy layers replete with giant balanids *Concavus* (*Concavus*) *concavus* (Darwin, 1854) in Beds No. 7, 8 and 9a (see Text-fig. 3; arrowed are more resistant parts of sand); the cliff is densely draped with hanging shoots of the Hottentot Fig, *Carpobrotus edulis* (Linnaeus)

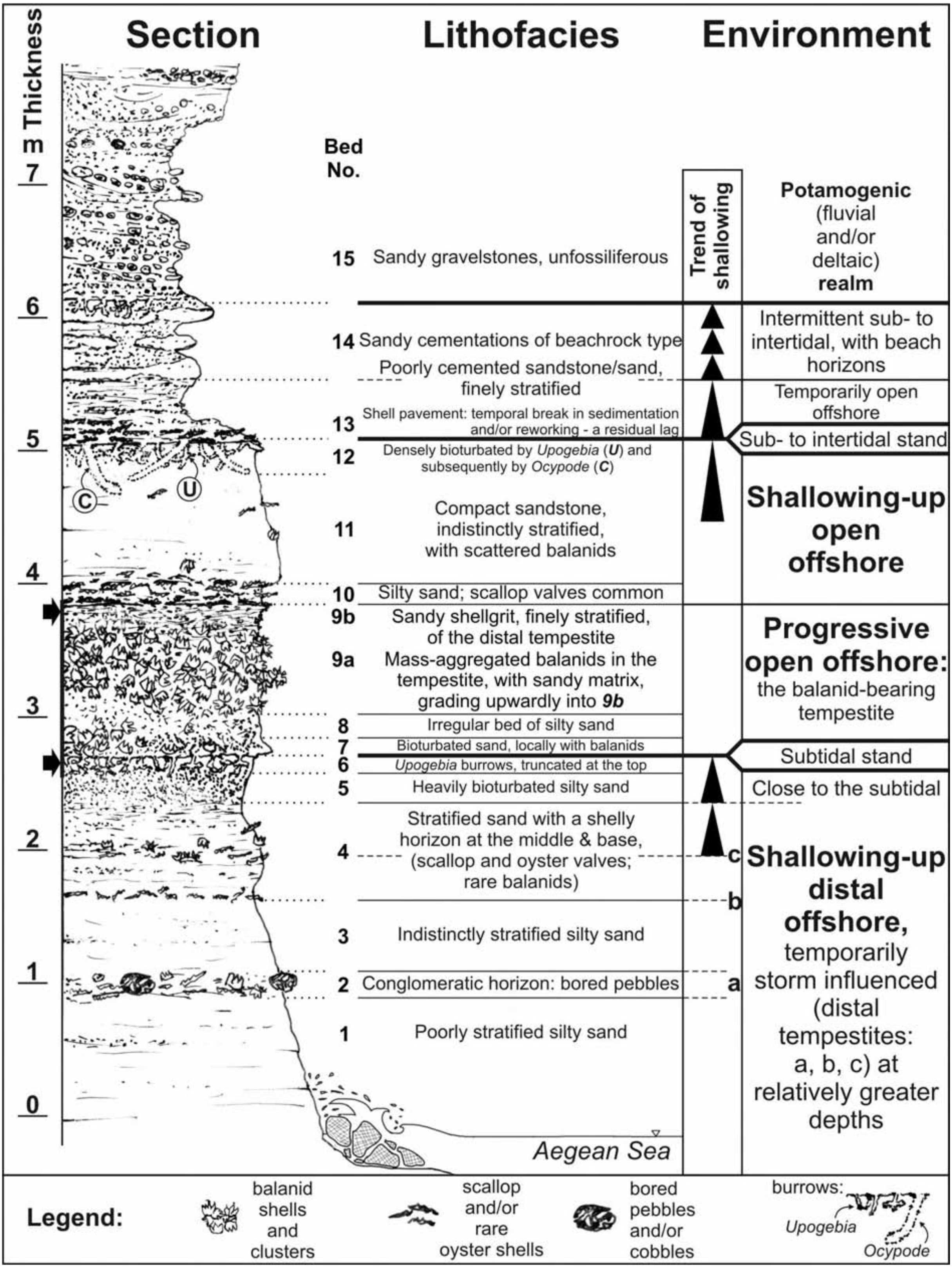
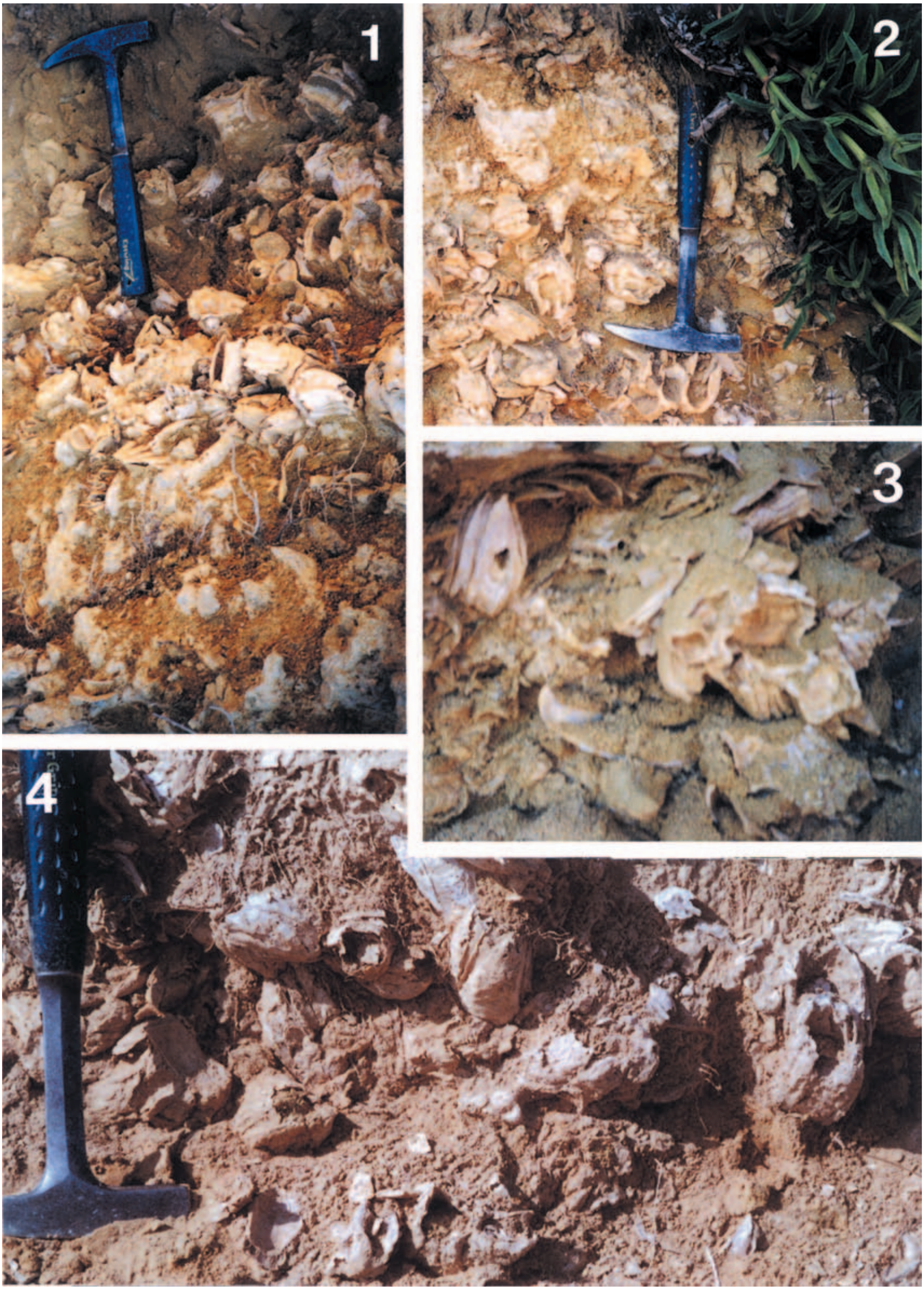


Fig. 3. Lower Pliocene (Zanclean) sequence exposed at Rafina Cliff (see Text-fig. 2B), to show the different lithofacies and their environmental interpretation



Mass-aggregated balanids *Concavus* (*Concavus*) *concavus* (Darwin, 1854) in the Lower Pliocene (Zanclean) tempestite (Bed No. 9a; see Text-fig. 3) at Rafina Cliff, Greece. **1** – Middle part of Bed No. 9a, to show the haphazard structure of the balanid-bearing tempestite. **2** – Upper part of Bed No. 9a, grading upwards into the finely stratified Bed No. 9b, as exposed after removal of dense draperies of hanging shoots of the Hottentot Fig, *Carpobrotus edulis* (Linnaeus). **3** – Detail of Bed No. 9a, to show a larger balanid cluster (centre) and isolated shells projecting from the sandy matrix. **4** – Another detail of Bed No. 9a, to show balanid shells, their clusters and parietal hash, after winnowing of loose sandy matrix

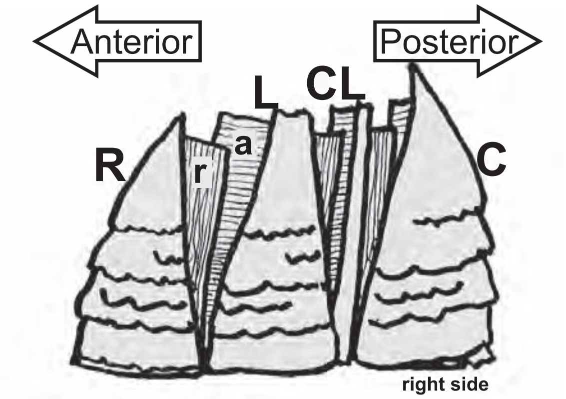


Fig. 4. Nomenclature of shell elements in balanids, as used in the present paper; lettered symbols, the same as in Plates 3-8, are explained in the text; the balanid crown is shown viewed from the right, to show how the compartments interlock by their appendages

MITZAKIS & *al., in preparation*) which progressed after a short-term sedimentary break, the scouring of the bottom, and truncation of upogebiid burrows (see top of Bed No. 6 in Text-fig. 3).

GENERAL ACCOUNT OF THE BALANID MATERIAL

The balanid material from the tempestite is represented by single or clustered specimens, all devoid of opercular valves. No specimen is preserved in life position, all having been uprooted, transported and/or reworked.

Within the single or clustered specimens, the crowns predominate (with the adherent basal plate). The majority of these look quite fresh, devoid of any encrusters, and not having been damaged to any extent, but some specimens are worn by physical abrasion or (see below) bio-eroded by rock-borers. The larger fragments composing the parietal hash belong to carinae, laterals and rostra, while the slender and fragile carinolaterals are much underrepresented. The isolated opercular valves are numerically less common than the crowns, and the massive scuta dominate over fragile terga, the delicate spur of which is usually broken off.

All the collected specimens are bleached, not bearing any traces of primary coloration. No specimens are sand-armoured (pitted by sand grains), a feature recorded in some other cases of balanids (BÁLDI 1959, DONOVAN 1988) and other invertebrates contained in a sandy matrix that underwent pressure-solution processes (see RADWAŃSKI 1965, p. 205; RADWAŃSKI & WYSOCKA 2004).

There are countless numbers of balanid specimens in the exposure. During fieldwork in the years 1989-2005, several hundreds up to a thousand of the best preserved crowns and their clusters were investigated, as well as numerous isolated compartmental plates and opercular valves.

All of the material collected, including the figured specimens (see Pls 2-11), is kept in Eco-taphonomic Collection of the Department of Palaeontology, University of Warsaw.

Rock-borers in balanid shells

Some of the collected specimens, either isolated or those of one generation within chain-like clusters (see generations 1 and 2; Pl. 9, Figs 1a-1b), are damaged, to a variable extent, by such ordinary rock-borers (see RADWAŃSKI 1969, 1970) as the sponges *Cliona celata* GRANT, 1826, and *Cliona vastifica* HANCOCK, 1849, the common polychaete *Polydora ciliata* (JOHNSTON, 1838) and rare *Polydora hoplura* (CLAPARÈDE, 1869), as well as by the bivalve *Gastrochaena* sp., the species assignment of which would most likely be *Gastrochaena dubia* (PENNANT, 1777). These rock-borers, e.g. *Gastrochaena* (see Pl. 3, Fig. 8), also damaged other shell material, prior to its colonization by balanids, as well as pebbles and/or cobbles in the lower part of the Rafina section (Bed No. 2; see Text-fig. 3). Concerning the balanids themselves, there is no evidence whether the rock-borers were boring into the shells of living individuals, or into their dead shells.

THE MASS-AGGREGATED BALANID SPECIES

For the taxonomy of balanids, it is the opercular valves, particularly the terga (see NEWMAN 1982, ZULLO 1992) that are diagnostically decisive and which, in the material studied (see Pl. 2, Figs 1-8), constitute the basis for the identification of the mass-aggregated species. This species has been referred to previously as "*Balanus concavus* BRONN, 1831", but is herein referred to as *Concavus* (*Concavus*) *concavus* (DARWIN, 1854) [*non* BRONN, 1831] (see taxonomic discussion below).

To this species are ascribed all the mass-aggregated crowns, which display a great variety of overall shapes and detailed morphologies, as well as their parietal hash; the identity of the smallest-sized specimens may, however, remain open to discussion (see below). All the material studied is treated as conspecific, representing a single species, *Concavus* (*Concavus*) *concavus* (DARWIN, 1854).

A former record of the species "*Balanus tulipiformis* Ellis, 1758" in Attica generally (Boenzi 1947: Mitzopoulou's specimens in collection) and in the Rafina section in particular (Mitzopoulou 1948, Marcopoulou-Diacantoni & *al.* 1998), cannot be substantiated. Moreover, of ten balanid species distinguished by Marcopoulou-Diacantoni & *al.* (1998) in their study of Rafina cirripedes, only the species *concavus* of Darwin (1854) is determinable from the opercular valves illustrated therein (six specimens of scuta: Marcopoulou-Diacantoni & *al.* 1998, pl. 1, fig. 5), the other specimens being presumably conspecific.

The idea, stated repeatedly by all subsequent Greek authors, that "*Balanus tulipiformis*" occurs at Rafina, was originally introduced by Boenzi (1947) who suggested that the elongated crowns (tubular to almost cylindrical) devoid of opercular valves should be referred to this taxon. The two specimens (one isolated, and one clustered) figured by Boenzi (1947, pl. 1, fig. 1 and pl. 2) are nearly identical with those presented in this study (comp. Pl. 6, Fig. 4 and Pl. 10, Fig. 2, respectively), and should certainly be assigned to *Concavus* (*Concavus*) *concavus* (Darwin, 1854). Such tubular to almost cylindrical empty crowns, with the width of the apertures equal to that of the crown, have often been referred to as *tulipiformis* in the Italian literature (see Menesini 1966, p. 108, pl. 25, figs 2-6; and earlier, Seguenza 1874-76, pl. 1, figs 1, 1a, 1b, and pl. 9, fig. 2; De Alessandri 1895, pl. 2, fig. 5a; 1906, pl. 16, figs 1-2). Moreover, exactly the same morphology is displayed by two empty crowns from Rafina, classified as *tulipiformis* by Marcopoulou-Diacantoni & *al.* (1998, pl. 1, figs 9-10). It should be noted that a common misinterpretation of the species *concavus* as *tulipiformis* was already evident to Darwin (1854a, p. 238; and 1854b, p. 19).

At Rafina, the mass occurrence of specimens and their free or clustered growth allow a study of the integrated eco-taphonomy of one single, well defined balanid species, *Concavus* (*Concavus*) *concavus* (Darwin, 1854). The Rafina case differs from those recognized in other eco-taphonomic studies of fossil balanids in which (see Beets 1945, Báldi 1961, Strauch 1968, Donovan 1988, Collins 1989) mostly the encrusters of shell (live or dead) or gravel material were documented.

THE '*BALANUS CONCAVUS* GROUP'

The species *Balanus concavus* and its allies have long intrigued cirripedologists, both with regard to their taxonomy, as well as their stratigraphic range and geographic distribution (see Darwin 1854a, p. 235; De Alessandri 1895, p. 284, and 1906, p. 296; Yamaguchi 1982, pp. 282-283). The variability of the crown morphology and the sculptural details of opercular valves, noted previously by Darwin (1854a) and Pilsbry (1916), have resulted in the '*Balanus concavus* Group' containing as many as 16 nominal taxa at the species/subspecies level, as listed by Newman & Ross (1976, pp. 60-61). Most or all of them have subsequently been revised by Newman (1982), who referred them to a new genus, *Concavus*, subdivided into three subgenera; the species *concavus* was selected as type of the genus and of the nominate subgenus *Concavus* Newman, 1982. From this and subsequent revisions, surveyed soon after by Yamaguchi (1982) and Zullo (1992), it is evident that the systematics of the genus *Concavus* Newman, as diagnosed by Newman (1982), rely solely on the terga, and partially also on the scuta, as stated by Zullo (1992).

Consequently, any taxonomic recognition/revision of the numerous former records of empty crowns classified as *concavus* from the Oligocene, Miocene, or Pliocene of Europe and elsewhere, remains a vain hope, unless opercular valves are reported. In this context it is ridiculous to attempt to establish, based only on empty crowns, balanid species different from those based upon isolated scuta, as in the case of the balanids from the Miocene Moniwa Formation of Japan treated by Hatai & *al*. (1976).

The Recent species of the genus *Concavus*, have previously been known from the eastern Pacific, that is, from the shores of the tropical/subtropical zone of the Americas (see Newman 1979, fig. 8). When an assessment of some subsequently studied species is undertaken (see Newman 1982, Yamaguchi 1982, Zullo 1992), it is evident that the distribution of *Concavus* is generally confined to the Indo-Pacific Province. An Indo-Pacific provenance of the genus is thus also postulated in the Palaeogene(?) to Neogene of Europe, including the region of Greece. Its occurrence in the Caribbean at that time (see Newman 1979, fig. 8) is thought to have resulted when the Central American oceanic seaway was still open.

The nominate subgenus *Concavus* Newman, 1982, ranges from the Early Neogene to Early Pleistocene (see Darwin 1854b, Newman 1982, Zullo 1992). It is absent from the Recent fauna.

AUTHORSHIP OF THE SPECIES *CONCAVUS*

Following Darwin (1854a, b), the species '*Balanus concavus*' has always been ascribed to Bronn (1831, *Italiens Tertiär-Gebilde*...), without any comments (see

SEGUENZA 1873-76; PILSBRY 1916; DAVADIE 1963; MENESINI 1965; NEWMAN & ROSS 1976; NEWMAN 1979, 1982; ZULLO 1992). However, when checking the list of fossils (no figures!) catalogued by BRONN (1831), it is clear that his item No. 729 of *Balanus*, captioned as "*concavus* BRN. n. 262" (see BRONN 1831, p. 127) is not provided with the designation "n.sp." (as in the case of the other species), but is identified with the '*Balaniten*' types figured by KNORR (see Text-fig. 5A). The illustrations of KNORR (1769, pl. K.I., figs 6 and 7; see Text-fig. 5C herein) show two different specimens, the second of which (KNORR's fig. 7) is a deeply abraded barnacle (?balanid) crown, and the first one (KNORR's fig. 6) is strictly uninterpretable. The structure (position) of its alae and radii (see Text-fig. 5C) suggests either an 8-compartmental barnacle, or drawing errors; in any case, it is not a *Balanus*! As concerns the species name *concavus*, BRONN himself in his subsequent works (BRONN 1853-56, p. 605) dates it back to 1827, when item "n. 262" was first catalogued (BRONN 1827, p. 544: "*Balanus concavus* nob. B.").

The first illustration labelled "*Balanus concavus* BR." was presented by BRONN (1838, pl. 36, fig. 12; and then repeatedly 1853-56, Atlas 1850-1856). It shows (Text-fig. 5B herein) a *Balanus*, the opercular valves of which are, however, very distinct from those documented by DARWIN (1854a, b) and subsequent authors as *concavus*, as well as from those collected at Rafina (Pl. 2, Figs 1-8) and identified with the latter. Consequently, the authorship of the species name *concavus* should be ascribed to DARWIN (1854a) who first provided the illustration of the two actual fossil specimens of opercular valves (see DARWIN 1854a, pl. 4, figs 4d and 4e; = DARWIN 1854b, pl. 1, figs 4g and 4o: the first from the Pliocene Coralline Crag of England, the second from the Neogene of northern Italy).

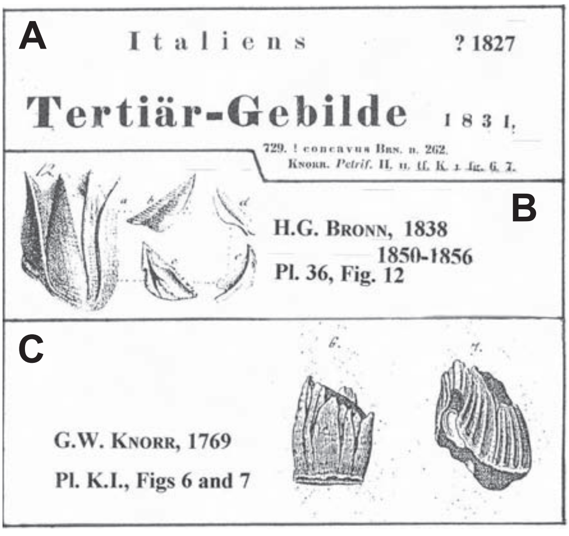


Fig. 5. Facsimiles of original data referred to as '*Balanus concavus* BRONN'. **A** – From BRONN's *Italiens Tertiär-Gebilde...* (1831, by some authors referenced as 1827); **B** – From BRONN's *Lethaea geognostica...* (1838, pl. 36, fig. 12a-e; and subsequent editions up to 1853-1856); **C** – From KNORR's *Die Naturgeschichte...* (1769, pl. K.I., figs 6-7)

SYSTEMATIC ACCOUNT

Subclass Cirripedia BURMEISTER, 1834
Order Thoracica DARWIN, 1854a
Suborder Balanomorpha PILSBRY, 1916
Superfamily Balanoidea LEACH, 1817
Family Balanidae LEACH, 1817
Subfamily Concavinae ZULLO, 1992
Genus *Concavus* NEWMAN, 1982
Subgenus *Concavus* NEWMAN, 1982

Concavus (*Concavus*) *concavus* (DARWIN, 1854a)
[*non* BRONN, 1831]
(Plates 2-11)

1854a. *Balanus concavus*; C. DARWIN, p. 235, pl. 4, figs 4d, 4e [only].
1854b. *Balanus concavus*; C. DARWIN, p. 17, pl. 1, figs 4g, 4o [only].
1895. *Balanus concavus* BRONN; G. DE ALESSANDRI, p. 282, pl. 2, figs 10b-10e [only].
1906. *Balanus concavus* BRONN; G. DE ALESSANDRI, p. 295, pl. 17, figs 2-4 [only].
1952. *Balanus* (*Balanus*) *concavus* BRONN *scutorum* (SEGUENZA); M.A. MORONI RUGGIERI, p. 67, pl. 1, figs 5-6; pl. 2, figs 9-12 [see Remarks hereafter].
1952. *Balanus* (*Balanus*) *concavus* BRONN *raphanoides* n.subsp.; M.A. MORONI RUGGIERI, p. 71, fig. 1 [see Remarks hereafter].
1965. *Balanus concavus* BRONN; E. MENESINI, p. 110, pl. 29, figs 4-5; pl. 34, figs 7-8; pl. 35, figs 1-2.
1982. *Concavus* (*Concavus*) *concavus* (BRONN, 1831); W.A. NEWMAN, p. 28, fig 1c.
1983. *Balanus concavus concavus* BRONN; T. YAMAGUCHI, p. 283.
1992. *Concavus concavus* (BRONN, 1831); V.A. ZULLO, p. 5, figs 3.1-3.8.
1998. *Balanus concavus* BRONN; [plus attached] *Balanus curvicostatus* [sic!] MEN.; A. MARCOPOULOU-DIACANTONI & *al*., p. 75, pl. 1, fig. 3 [only].

REMARKS: Only opercular valves are included in this synonymy, as empty crowns are inadequate for taxonomic identification. However, two taxa established by MORONI RUGGIERI (1952) represent ecotypes [not subspecies, as treated by NEWMAN & ROSS (1976, p. 61)] which occur in the material studied and are discussed below. In this context, we are aware of the fact that the isolated crowns presented in the literature as *concavus*, to which some of the specimens studied are compared, may represent other species of the '*Balanus concavus* Group', that is, any member of the genus *Concavus* sensu NEWMAN (1982) and ZULLO (1992).

OVERALL MORPHOLOGY: Regardless of whether they grow freely or clustered, the basic morphological features of the balanids studied remain constant. The outer surface of the crown compartments, devoid of any longitudinal ribs, is almost smooth in some freely growing specimens, in which only very indistinct longitudinal lamination (striation) may be detected (best discernible: Pl. 5, Fig. 1a' on the rostrum; and Pl. 7, Fig. 1). The majority of specimens, however, have their crowns sculptured by the more or less pronounced **growth bands** ('prominent ridges' of DARWIN 1854a) resulting from a break in continuous accretion of the growthlines. These growth bands, bounding the sets of minute growthlines ('growth striae' of BOURGET 1981), show an almost constant number of seven or eight bands per specimen (Pl. 5, Figs 1-2). To follow the classic interpretation of DARWIN (1854a), the growth bands result from successive moulting stages of the balanids; their time frequency (annual, or semiannual) cannot, however, be recognized in the fossil state (BOURGET 1981). In the specimens studied, the growth bands may be regularly continuous (Pl. 7, Fig. 1), but usually they are more or less ragged, with their lower margin not firmly adhered to the crown, which thereby acquires a pagoda-like shape (Pl. 5, Figs 1-2; Pl. 6, Fig. 1; Pl. 11, Fig. 2.4). It should be noted that the growth bands, so characteristic of the outer surface, are not transmitted onto the sheath, where only the growthlines are discernable (Pl. 9, Fig. 3; arrowed).

In specimens growing upon a small-sized hard particle (commonly, the balanid hash), thick (up to 10-12 mm!) **parietal lobes** (cf. STRAUCH 1968) develop, which almost completely embrace the basal plate and the substrate (Pl. 3, Fig. 5). When developed by all the compartments, these lobes often become confluent, and produce a kind of sole to the crown that takes over the function of the basal plate (Pl. 3, Fig. 6). In specimens growing upon the parietal hash, a parietal lobe may appear on one compartment only, and then it acquires a heel-like shape (Pl. 4, Fig. 4).

The general shape of the specimens studied ranges from very low, flattened horizontally (Pl. 4, Fig. 1), through diverse conical ones, to tubular with a narrow conical orifice (Pl. 6, Figs 1-2), and cylindrical, with a broad orifice equal in width to that of the crown (Pl. 6, Fig. 4; Pl. 9, Fig. 4; Pl. 10, Fig. 2.2). In conical forms, the apical angle varies, and is responsible for the width of the orifice, which ranges from very narrow (Pl. 4, Fig. 4) to more or less widely open, and finally to that typical of cylindrical specimens.

The alae and radii are widely developed in low, flat-shaped specimens, thereby enlarging the circumference (that is, the space) of their shells (see Pl. 4, Fig. 1).

The attitude of the specimens studied is generally straight vertical, but many specimens deviate into more or less arch- or horn-shaped forms, distinguished herein as 'scaphoid' (Pl. 6, Figs 1-3 and Pl. 7, Fig. 2). Both in these, as well as in the conical or cylindrical specimens, a more or less strongly convex part of the crown may attain an extremely large size, up to 130 mm in length. The extreme convexity may develop along any one of the crown compartments: the carina (Pl. 6. Figs 1 and 3), the lateral (Pl. 4, Fig. 3; Pl. 5, Fig. 2; Pl. 6, Fig. 2), as well as the rostrum (Pl. 4, Fig. 5b and Pl. 6, Fig. 4).

The morphology of the basal plate and its size relative to that of the crown, as well as the other features dependent on either a free or clustered lifestyle of the specimen, are presented in the autecological analysis in the following chapter.

In contrast to the crowns, the opercular valves (both terga and scuta) do not display any morphological variability (see Pl. 2, Figs 1-8), except for a few much thicker and robust valves, usually with densely spaced growthlines at their margin, which are interpreted as belonging to gerontic animals (Pl. 2, Fig. 4a-4b).

DISCUSSION: The broad variety of shapes displayed by the shells studied ranges from almost flat, through variably conical, to cylindrical. Although the extremes differ distinctly from one another, there is a full range of intermediate forms. The variable morphology is thought to have been controlled by environmental conditions (access to the substrate, ambient water agitation) and by the resulting lifestyle of particular specimens (solitary, or clustered).

Consequently, all the morphotypes discussed above are regarded as ecophenotypes of a single species, *C.* (*C.*) *concavus*. This concerns not only cylindrical specimens, classified at Rafina formerly as "*Balanus tulipiformis* (ELLIS, 1758)", but also '*raphanoides*' and '*scutorum*' (see below), treated as separate taxa of species or subspecies rank (SEGUENZA 1874-76; MORONI RUGGIERI 1952; NEWMAN & ROSS 1976, p. 61). Apart from the overall shapes, some detailed features of the shells studied are also of ecophenotypic nature, primarily the size of the orifice, which is sometimes regarded (see YAMAGUCHI 1982) as taxonomically important.

To summarize the above discussion, a single balanid species is thought to have lived in the Rafina environment, instead of two, as listed originally by MITZOPOULOU (1948), or even ten as distinguished by MARCOPOULOU-DIACANTONI & *al*. (1998).

Concerning the biology of the species studied, the growth bands, ascribed herein to a biological stress during moulting, may remain open for further consideration. This is due to the fact that in present-day balanids, as reported by BOURGET (1981, pp. 480 and 485), the moulting may leave no record on the outer shell surface and, on the other hand, the growth bands may be induced not by a biological stress, but by a physical one of various kind (photic conditions, feeding, temperature, air exposition at low tides, or other circumstances of life).

AUTECOLOGY

The growth of single *versus* clustered specimens

At Rafina, *C.* (*C.*) *concavus* grew either singly (freely) or in more or less bulky clusters, dependent on local bottom conditions. Within the clusters, two types may be distinguished:

(*i*) **Bouquet-like clusters**, occurring rarely, consisting of numerous specimens growing upon, or around, any substratal object, usually a damaged balanid crown of an older generation (see Pls 8-9);

(*ii*) **Pyramidal clusters**, occurring commonly, often chain-like, consisting of specimens of several generations (usually 4 or 5; see Pls 10-11), the last of which is represented by minute-sized specimens (? spat, or phenotypic dwarfs; see below).

Single specimens

The single specimens were growing primarily on the parietal hash to which they firmly adhered with their basal plate (Pl. 4, Figs 4-5), which is always xenomorphic. Some specimens were growing on fragmented calcitic valves, e.g. of oysters and scallops, to which they remained attached (Pl. 3, Figs 4 and 7-8; Pl. 7, Fig. 1). Only very few specimens display on their basal plate the xenomorphic cast of the aragonitic shell of other molluscs, e.g. the bivalves *Cardium* (Pl. 7, Fig. 2) and *Anomia* (Pl. 5, Fig. 1), or the gastropod *Xenophora* (Pl. 3, Fig. 3). Several specimens bear a basal plate that is quite smooth, lacking any xenomorphic imprint. These are semitubular in shape, suggesting that they embraced an elongated soft substrate that was not otherwise preservable as a fossil (? algal fronds, see DONOVAN 1988).

Bouquet-like clusters

In bouquet-like clusters, almost all the specimens are xenomorphic, having their shape adapted to the coevally, or almost coevally, grown neighbouring specimens (see Pls 8-9). The basal plate has then elongated into a cup-, or even tube-like form, the size (length) of which usually exceeds that of all compartments, that is of the whole crown (Pl. 9, fig. 4), to attain the extreme length (depth) of 12-13 centimetres.

Specimens of *C.* (*C.*) *concavus* with a similarly elongated basal plate (83 mm long/deep) from the Pliocene of Italy were distinguished as a separate subspecies *raphanoides* by MORONI-RUGGIERI (1952, p. 71 and fig. 1). In the Rafina balanids, it is evident that the *raphanoides*-type specimens are merely an ecotype of the species *C.* (*C.*) *concavus* resulting from cramped growth conditions, and are actually quite common in many clusters (see Pl. 9, Figs 1-4). A cylindrical and/or pipe-like (tubular) shape of the shell appears in various balanid species, especially in those growing under cramped conditions (see DARWIN 1854a, PILSBRY 1916, STRAUCH 1968, NEWMAN & ROSS 1976).

In the Rafina clusters, the tubular basal plates are always hollow, not having been filled with any of the cellular (cystose) structure that is typical of some large-sized balanid species with tubularly developed shells (see DARWIN 1854a, pl. 4, fig. 2a = NEWMAN & LADD 1974, fig. 1f; = NEWMAN & ROSS 1976, fig. 10C; = BOUCOT 1990, fig. 3f; moreover, PILSBRY 1916, pl. 28, figs 3-4 and pl. 29, fig. 1). ZULLO (1964) already interpreted this structure as eco-phenotypic, related presumably to a high sedimentation rate with which the growing balanid had kept pace.

Such strong elongation of basal plates is also met in other balanids, for instance in some creusioids growing coevally (and commensally) in coral colonies (see BAŁUK & RADWAŃSKI 1967; ROSS & NEWMAN 1973; NEWMAN & LADD 1974; BOUCOT 1990, figs 4-5).

Pyramidal clusters

In pyramidal clusters (see Pls 10-11), the specimens were growing either with the same geotropic orientation, to form trunk-like pairs and longer chains (Pl. 11, Fig. 1), or at random upon already clustered older specimens (Pl. 11, Fig. 2). Except for the last generation, the tiered specimens are of a similar size, and have thus been regarded as adults. Their state of preservation may, however, be variable: some are bio-eroded by sponges (Pl. 10, Fig. 1; Pl. 11, Figs 1-2), or abraded, either more distinctly than the preceding generation or than the subsequent one. Consequently, it is thought that the successive balanid generations in such clusters are represented by fully-grown (adult) specimens which died of senility. Nevertheless, some were exposed for a more or less long time to post-mortal bio-erosion and/or physical abrasion, and were damaged prior to overgrowth by the next generation. This indicates that settlements of successive generations within pyramidal clusters were separated by time breaks of variable duration, similar to these recognized by SEILACHER (1985) in present-day balanid clusters of the intertidal zone at Jeram in Malaysia. During periods of non-deposition, the bottom paved with the balanid hash was shaped into temporary residual lags, upon which the new generation of balanids could flourish when quiet water conditions returned.

The last generation, composed of small-sized specimens, appears on abraded clusters of emptied shells, the inner side of which has also been inhabited (see Pl. 10, Fig. 2.3; arrowed).

The giant size

A significant feature of the *Concavus* (*Concavus*) *concavus* (DARWIN, 1854) specimens from Rafina is their remarkable size, both the average and extreme sizes exceeding those reported in this species previously.

The largest of the collected specimens, which was growing singly (see Pl. 5, Fig. 2), is 80 mm high, measured at right-angles to the basal plate, and 96 mm along the rostral curvature, at a diameter of 75 mm. The specimens growing in clusters, with elongated, cup- or tube-like shells, attain a total height (basal plate + crown) of 100-115 mm (see Pl. 6, Fig. 4). The horn-shaped specimens reach as much as 135 mm, measured along their carinal curvature (see Pl. 6, Fig. 3). The average height of large-sized specimens is estimated as 60-80 mm, at diameters ranging from 60 to 75 mm. The largest scuta attain 35-38 mm along the occludent margin, and the largest terga 30-35 mm along the spur.

Similarly sized specimens of *C.* (*C.*) *concavus* appear in many Italian locations, either of definitely Pliocene (Zanclean) age, or most probably of that age. They were noted from Sicily by SEGUENZA (1874-76, pl. 10, fig. 1: '*un gigantesco esemplare*' about 88 mm high). DE ALESSANDRI (1906, p. 296) classified such specimens as '*esemplare grande*' 100 mm high, at a diameter of 55 mm, and contrasted with '*esemplare medio*' 55 mm high, at a diameter of 50 mm; the scuta and terga being 23 and 21.5 mm, respectively. Three large specimens illustrated by D'ALESSANDRO & *al*. (1979, pl. 18, fig. 5) are each about 80 mm high. A large tergum from Torino, described by DARWIN (1854b, p. 20, pl. 1, fig. 4o), is about 33 mm in length, measured along the spur.

A similarly large size in other European balanids of Neogene age is attained only in specimens determined as "*Balanus tintinnabulum* LINNAEUS, 1767" by D'ALESSANDRO & *al*. (1979, pl. 18, fig. 12).

Of the present-day balanids, giant size has long been known in a species endemic to the coasts of Chile and Peru, *Balanus psittacus* (MOLINA, 1782), as reported by DARWIN (1854a, p. 207: 9 in. ≅ 228 mm high), PILSBRY (1916, p. 77: 200 mm high), NILSSON-CANTELL (1957, p. 207), and MENESINI (1967, p. 47: 240 mm high), albeit the giant specimens occur there only in some locations, while in others they are much smaller, e.g. 35-45 mm high (PILSBRY 1916, p. 76; see also MENESINI 1967, p. 55). [MENESINI herself has suggested that the giant forms should be distinguished as a separate subspecies, *chilensis*.] PILSBRY (1916, p. 76) reported that the lengthened basal plate was about half of the total shell height/length (compare Pl. 9, Figs 2-4 herein); this feature is, however, not recognizable in the enclosed photos, taken in outer views (PILSBRY 1916, pl. 18, fig. 1; see also MENESINI 1967, pls 1-2).

The large-to-giant size of the Rafina balanids, displayed by innumerable specimens (see Pl. 1), suggests that this may have been an immanent feature of the species *C.* (*C.*) *concavus* which did not appear before the Early Pliocene (Zanclean). All older occurrences, after the Oligocene(?) – Early Miocene (see e.g. DAVADIE 1963; MENESINI 1965, 1966; NEWMAN & ROSS 1976; NEWMAN 1979), are characterized by a distinctly smaller size, and most probably represent a different, ancestral species, as postulated by ZULLO (1992, p. 5).

On the other hand, DARWIN (1854a, p. 238; and 1854b, p. 19) drew attention early on to the fact that Neogene specimens were much larger in size – sometimes slightly exceeding 2 inches (~50 mm) in basal diameter, and three inches (~76 mm) in height – than the present-day ones which attained not more than 1.2 inches (~30 mm) in diameter.

Pseudomorphic sculpture

Some crowns of the studied specimens of *Concavus* (*Concavus*) *concavus* (DARWIN, 1854) are more or less distinctly sculptured by a reproduced (duplicated) positive shape of the substrate. Such transmitted sculpture, long known in some modern and ancient balanids (see

Darwin 1854a; Seguenza 1874-76; De Alessandri 1895, 1906; Pilsbry 1916; Gregg 1948), and called mimetic (see De Alessandri 1895, p. 241 and 1906; Bieda 1931, p. 210), originates from the growth of balanid parietes overlapping widely the basal plate and thus contacting directly and tightly the sculptured substrate. As having nothing in common with the mimesis in other animals (see Bałuk & Radwański 1967, p. 488 and references therein), the discussed paradigm in balanids should be classified with a separate name, and is referred to the **pseudomorphy** or **pseudomorphic sculpture**, to follow a suggestion once proposed by Saint-Seine (1951).

The pseudomorphic sculpture, thoroughly studied in balanids both present-day (Gregg 1948) and fossil (Strauch 1968), is best recognizable in specimens growing upon thick-ribbed scallop valves, as illustrated by De Alessandri (1895, fig. 1; and 1906, pl. 16, fig. 25; reproduced in Text-fig. 6A herein) for *C. concavus* from the Pliocene of Italy. Of other substrates, the pseudomorphic sculpture in balanids is known to duplicate echinoid test-tubercles (De Alessandri 1895, fig. 2; reproduced in Text-fig. 6B herein), gastropods and small bivalves (Strauch 1968, figs 29-31), bryozoan colonies (Strauch 1968, fig. 33), all of Palaeogene and/or Neogene age, as well as the groove-and-ridge pattern of gramophone records (!) in the case of present-day specimens reared in sea water by Gregg (1948, pl. 2, figs 6-8).

At Rafina, the pseudomorphic sculpture is acquired by balanids growing upon ribbed shells of bivalves (see Pl. 7, Figs 1-2) and also on isolated balanid scuta (see Pl. 7, Fig. 3). In some specimens, the parietal hash upon which they were growing is duplicated in the form of numeous irregularities in the balanid crowns (see Pl. 4, Fig. 4).

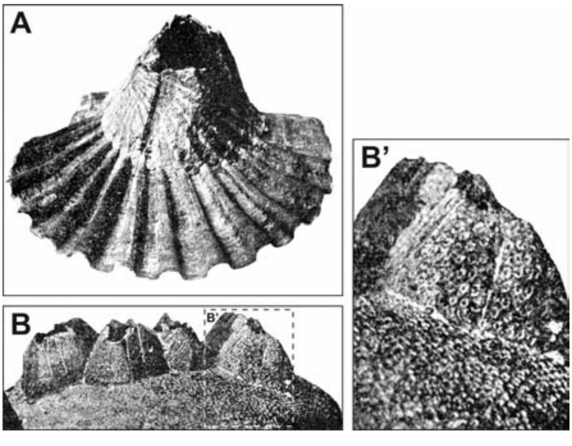


Fig. 6. Spectacular examples of pseudomorphic sculpture in balanids from the Neogene of Italy (adapted from De Alessandri 1895). **A** – '*Balanus concavus*' upon a scallop valve (see De Alessandri 1895, p. 241, fig. 1); **B** – '*Balanus mylensis*' upon an echinoid, *Echinolampas* (see De Alessandri 1895, p. 242, fig. 2); **B'** – Close-up, to highlight the duplication of the echinoid tubercles all over the balanid crown

It is both noteworthy and intriguing that pseudomorphism in ancient balanids is documented (see De Alessandri 1895, 1906; Gregg 1948, fig. 9; Riba-Viñas & Martinell 1986, fig. 3G) almost exclusively in *C.* (*C.*) *concavus*.

Babies, dwarfs, or a separate species?

In the Rafina section, apart from balanids of average and giant size, classified as *Concavus* (*Concavus*) *concavus* (Darwin, 1854), there quite frequently occur tiny specimens of two types, the ecological interpretation and taxonomic assignment of which remain unclear.

The **first type** is represented by specimens sparsely distributed over the larger-sized ones, especially those of the pyramidal clusters, from which they differ distinctly in size (see Pl. 11). All are oriented at random in relation to the attitude of the host specimens. They are regarded, until their opercular valves are found, as spat of the subsequent *C.* (*C.*) *concavus* generation which did not achieve adulthood because of rapid burial of the clusters. It is also possible, however, that they developed during deterioration of the environmental conditions, such as e.g. a rapid(?) drop in salinity due to an immense influx of rainwater, prolonged exposure to the air at extreme ebbs or other low-water stands, or drowning at a high-water stand. In the latter cases, the tiny specimens under discussion should be treated as phenotypic dwarfs of *Concavus* (*Concavus*) *concavus* (Darwin, 1854).

The **second type** appears exclusively, either singly or in groups of a few specimens, in the apical part of opercular valves (particularly scuta, see Pl. 4, Figs 2a-2b; rarely terga) of *C.* (*C.*) *concavus*. All tend to grow in proximity to the occludent margin, along which they are flattened distinctly (Pl. 4, Fig. 2a, arrowed). Moreover, their carina is usually oriented towards the scutal apex. The overall sculpture of such specimens varies to a considerable extent, having been transmitted by the substratal valve (see Pl. 7, Fig. 3), in the same way as in the case of the large-sized specimens.

Such specimens from Rafina have already been figured by Marcopoulou-Diacantoni & *al.* (1998, pl. 1, fig. 3) under the name "*Balanus curvi***c***os***ta***tus* [sic!] Men.". This assignment is evidently erroneous, since the species established by Menesini (1968) as "*Balanus curvirostratus*", regardless of its doubtful distinction from *Balanus balanus* (Linnaeus), comprises specimens that are almost one order larger in size, and bear differently sculptured opercular valves. As may be ascertained from the illustrations (MENESINI 1968, fig. 2 and pl. 1), this species is very variable in morphology, the extremely strong rostral curvature being not a constant feature, but a phenotypic variable.

Nevertheless, tiny specimens growing at the scutal apex of *Concavus* (*Concavus*) *concavus* (DARWIN, 1854) similar to, if not identical with, those of Rafina, were earlier reported from the Pliocene (Zanclean) of Sicily by SEGUENZA (1874-76, pl. 9, fig. 5; pl. 10, fig. 7), who distinguished them as a separate species, "*Balanus scutorum* SEGUENZA, 1872" [manuscript date]. This was discussed in detail by MORONI RUGGIERI (1952), who reported other Pliocene occurrences in Italy, and regarded *scutorum* as a phenotype of subspecies rank in the species *concavus*. MENESINI (1965, pp. 110 and 113, pl. 29, figs 4-5) has consequently synonymized both species. A flattening of the crown at the scutal occludent margin was noted not only by SEGUENZA (1874-76, pl. 10, fig. 7), and MORONI RUGGIERI 1952, pl. 1, figs 5-6), who observed the pseudomorphic sculpture (especially of the rostrum; see MORONI RUGGIERI 1952, p. 70), but also by MENESINI (1965, pl. 29, fig. 5) in specimens of Plio-Pleistocene (Calabrian) age. A similarly flattened, tiny specimen, located at the scutal apex, has subsequently been figured by ZULLO (1992, fig. 3.1) from the Pliocene (Zanclean) of Tuscany, Italy.

The fact that the occurrence of the specimens under discussion is always confined to the scutal apex of *C.* (*C.*) *concavus* may suggest highly selective, host-specific behaviour indicative of a separate species that lived preferentially on, or even in a commensal relationship to, the scutum-bearing host.

Regardless of their taxonomic status, the dwarf-sized specimens may be interpreted as stenomorphic ecotypes, having their growth limited by the space accessible at the scutal apex. The flattening of the crown along the occludent margin of the host scutum clearly indicates growth when the opercular valves were functioning, that is while the *C.* (*C.*) *concavus* host was still alive. The orientation of the carina towards the scutal/tergal apex has allowed such specimens to keep their cirral net facing the food-bearing water flow induced by the host balanid (cf. CRISP & STUBBINGS 1957). If this is so, the lodgement and mode of life of these specimens are comparable to those of the commensal polychaete described below

The commensal polychaete

At Rafina, one of the rock-borers of stony/skeletal materials also bored in shells of live specimens of *Concavus* (*Concavus*) *concavus* (DARWIN, 1854). This is the polychaete *Polydora ciliata* (JOHNSTON, 1838), an extant, cosmopolitan species, widely distributed along European shores of the Atlantic, and in the Mediterranean. Although the species was formerly reported to bore exclusively in empty shells and shore rocks or stones (see RADWAŃSKI 1969, 1970), it was KORRINGA (1951) who first noted its boring activity in shells of living individuals of the oyster *Ostrea edulis* (LINNAEUS, 1758), of which it is a commensal, but commonly also a harmful 'shell parasite'.

The commensal nature of the polychaete *Polydora ciliata* (JOHNSTON, 1838) in the geological past was first recognized in the Middle Miocene (Badenian) gastropod species, classified previously as *Columbella curta* (DUJARDIN, 1835), and reclassified by BAŁUK (1995, p. 234) as *Pyrena* (*Alia*) *polonica* (PUSCH, 1837). In specimens illustrated by RADWAŃSKI (1969, pl. 37, fig. 3) and BAŁUK & RADWAŃSKI (1977, p. 106 and pl. 4, figs 1-2), a single *Polydora ciliata* (JONHSTON 1838) always appears to have bored along the adapical channel of the gastropod shell, that is along the course of the water streams induced by the inhalant current from which the gastropod (and simultaneously the commensal polychaete) received its food supply.

In Rafina specimens (see Pl. 7, Figs 4-7), borings of *Polydora ciliata* (JOHNSTON, 1838) are lodged exclusively in the apical part of balanid scuta, and the boring openings are always oriented towards the scutal apex, that is the region where the water is inhaled and expelled by the cirri of the balanid when its opercular valves are in action. All the specimens collected (Pl. 7, Figs 4-7) are thus interpreted to represent the polychaete *Polydora ciliata* (JOHNSTON, 1838) boring in shells of living specimens *C.* (*C.*) *concavus*, with which they had a commensal relationship, receiving their food supply from the water flow induced by the cirri, and thus having been not harmful to the balanid host.

LIFE HABITAT AND TAPHONOMY

The structure of particular beds in the Rafina sequence (see DERMITZAKIS & *al.*, *in preparation*), primarily the tempestite features of some intervals and their content (rock-borers, burrows), provides basic information on the environmental conditions under which the balanids lived and became buried; in general, these were open offshore conditions of sublittoral depths, relatively distant from the shore.

The ubiquitous colonization of diverse bottom material by *C.* (*C.*) *concavus* in the Rafina sequence indicates that it was an opportunistic species, using the *r*-selection reproduction strategy in order to dominate the available ecospace over a long period. Its spat flourished profusely upon any hard substrate, mostly shells of dead balanids, and the hash of their shattered crowns. Successive accumulations of balanid debris produced a shell grit or pavement upon which the subsequent balanid generations could flourish (*taphonomic feedback* of KIDWELL & JABLONSKI 1983; *taphonomic pathway of autogenic mode* of KIDWELL 1986). In monospecific balanid communities whose elements are mass-aggregated, the hash particles were often the dominant type of substrate, and these significantly influenced the shape of the balanids growing on it. More stable bottom conditions resulted in balanid growth in clusters of the bouquet shape. An unstable substrate, and/or its temporary damage, most likely by storm agitation, resulted in the growth of pyramidal clusters.

As is apparent from the preservation state and orientation of specimens in pyramidal clusters, at least four or five generations of balanids survived temporary damage, following which their communities became reestablished. Such features as intensive boring by sponges (*Cliona* sp.) of the second generation in the pyramidal clusters (see Pls 10-11), and the appearance of the last generation consisting exclusively of the smallest-sized specimens, may indicate the contemporaneity of these clusters. But, this does not indicate whether or not the other four- or five-generation clusters are coeval. The singly growing specimens may be ascribed to any one of the successive generations. Of such specimens, the horn-shaped ('scaphoid', see Pl. 6, Figs 1-3) ones are interpreted as growing in a geotropic (? phototropic, see CRISP & STUBBINGS 1957) way when their substrate became more or less permanently unstable during strong agitation of the water.

The continuous alternation of physical conditions, favouring either the growth of the balanid communities, or their damage, resulted in the production and spreading of a profuse balanid hash upon which the spat of the subsequent communities was able to develop. This interaction is here termed a *perpetual taphonomic feedback*.

Although the balanid accumulation is taphonomically filtered, the ubiquity of parietal hash adhered to the basal plates of the balanids, and the paucity of casts of aragonite-shelled biota (e.g., the gastropod *Xenophora*, the bivalves *Cardium* and *Anomia*), suggest that the accumulation largely reflects the long-term balanid-dominated biotope. The very few casts of soft bodies (? algal fronds, ? twigs of terrestrial plants) do not contradict this scenerio.

Moreover, it is also suggested that the life conditions of these communities were optimal for the successful growth and longevity of the many specimens that were able to attain a giant size. The eco-space of the *C.* (*C.*) *concavus* studied may easily be compared to that of the present-day giant specimens of *Balanus psittacus* (MOLINA, 1782) from the coasts of Chile, where they occupy the lowest part of the tidal zone (see NILSSON-CANTELL 1957, pp. 19-20), growing in smaller groups, or in clusters (see NILSSON-CANTELL 1957, figs 1-2; also collection specimens *in* MENESINI 1967, pls 1-2).

Under such conditions, changing intermittently from those enabling the profuse growth of balanids at quiet periods (that is, at *taphonomic lull*), to those causing damage of the balanid biotopes and/or their sand overburden (that is, at *taphonomic noise*), balanid habitats have spread over a wide range of bottom areas, ranging from the intertidal zone (like in present-day Jeram beaches in Malaysia; see SEILACHER 1985) to shallow subtidal.

The final stage in colonization of the Rafina balanid biotopes is recorded by the last generation settled upon the pyramidal clusters. The minute balanids, scattered at random (cf. CRISP & STUBBINGS 1957) all over the clusters, including the shell interiors, indicate that the clusters of dead or even still living balanids were uprooted, and presumably covered with sand to such an extent that only their parts projecting above the sediment surface could be inhabited. Further growth of this generation could, in the other way discussed above, have been hampered by a change in environmental conditions (deterioration, or destruction).

The demise of the profusely grown balanid communities of Rafina is thought to have been a catastrophic event, caused by a violent storm that acted as a mortal agent. The balanids were then torn out of their biotopes, stirred up with a large amount of sand, and transported, the heavy crowns and clusters being then mass-aggregated in a proximal tempestite (Bed No. 9a), and the selected opercular valves, mostly scuta, in the overlying distal tempestite (Bed No. 9b). The lightest parts of the shells, the terga, if they survived transport, were presumably swept out beyond the area where the section formed. The lack of any cross- or flaser bedding, typical of present-day shallowest subtidal and/or intertidal settings, suggests storm deposition under thin, but stable water masses covering the vast Rafina offshore area. It should be noted that the catastrophic pathway which the Rafina balanids have undergone, to be mass-aggregated in a tempestite, and to form a unique Fossillagerstätte, is apparently similar to those that affected offshore echinoids in the Miocene of Poland and the Ukraine (see RADWAŃSKI & WYSOCKA 2001, 2004).

The rocky shores, from where the rock-boring polychaetes and bivalves propagated, and the limestone pebbles or cobbles riddled by rock-boring bivalves present in the lower part of the sequence (see DERMITZAKIS & *al.*, *in preparation*), were seemingly distant from Rafina. It is probable that these were similar in morphology and rock-borer activity to those of other regions of the Lower Pliocene (Zanclean) transgression in the Mediterranean (see SCHWARZHANS 1986), for instance in the Lower Nile Valley in Egypt (see SAID 1981, AIGNER 1983), or in the French and Spanish gulfs and rias (see MARTINELL & DOMÈNECH 1995, DE GIBERT & MARTINELL 1998, DE GIBERT & *al*. 1998)

FINAL REMARKS

The availability of hundreds of well preserved specimens enables recognition of the extensive variability in morphology of one balanid species, *Concavus* (*Concavus*) *concavus* (DARWIN, 1854). It has become apparent that neither the overall shapes of the crowns (basal plates and parietes) nor their morphology can be regarded as taxonomically important. The sculpture, if present, is commonly controlled by the shape of the substrate, having been duplicated by the crowns, or their component parts. Some peculiar shapes of the shell ('raphanoides', 'scaphoid' and possibly also 'scutorum') are nothing other than phenotypic variants, that is, ecotypes of *C.* (*C.*) *concavus*. Only the opercular valves (terga and scuta) are exclusively diagnostic for this species, having not been influenced by the pseudomorphic and/or xenomorphic growth of shells in the clusters under cramped conditions.

The giant size achieved by specimens of *C.* (*C.*) *concavus* at Rafina, and known in many populations of predominantly Early Pliocene (Zanclean) age in other regions of the Mediterranean (see SEGUENZA 1874-76, DARWIN 1854a, b, DE ALESSANDRI 1906, D'ALESSANDRO & *al*. 1979), is thought to have been resultant from phylogenetic trends rather than ecological factors controlled by environmental conditions.

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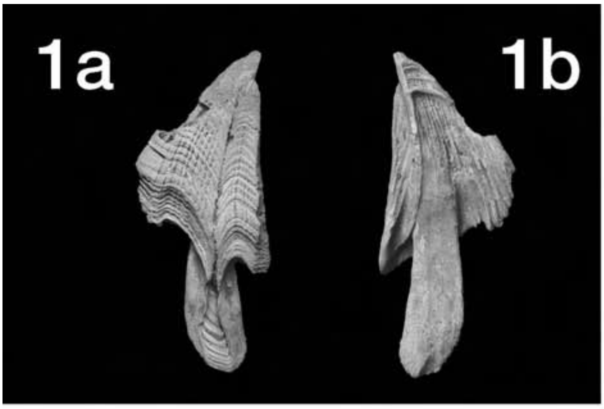
PLATE 2

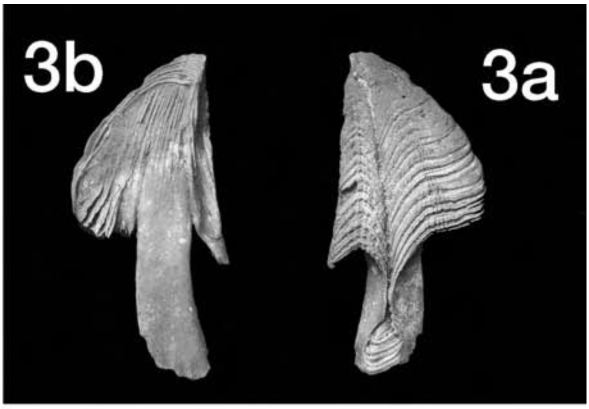
Concavus (*Concavus*) *concavus* (DARWIN, 1854) – Opercular valves of adult specimens, shown in outer (**a**) and inner (**b**) views; all × 1.5

1-4 – Four terga (1 and 2 – left terga, 3 and 4 – right terga); in one of them (Figs 2a-2b) the tip of the spur is broken; the specimen presented in Figs 4a-4b belonged to a gerontic individual

5-8 – Four scuta (5 and 6 – left scuta, 7 and 8 – right scuta); one of them (Figs 8a-8b) displays a broadly extended basal margin


1a
1b


2a
2b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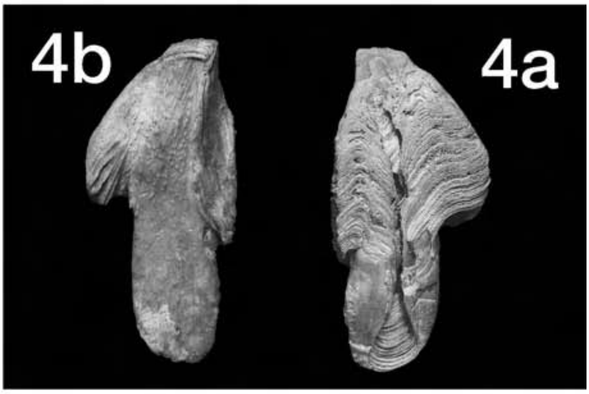
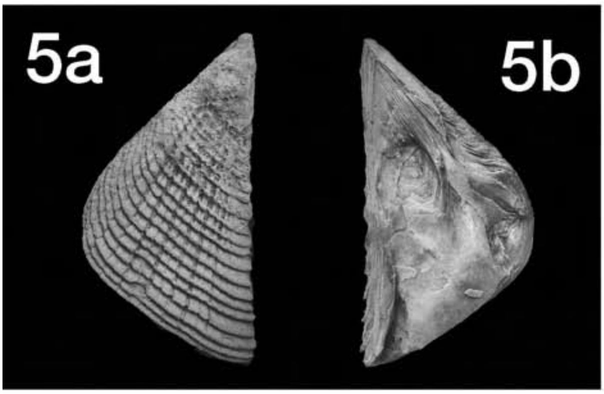
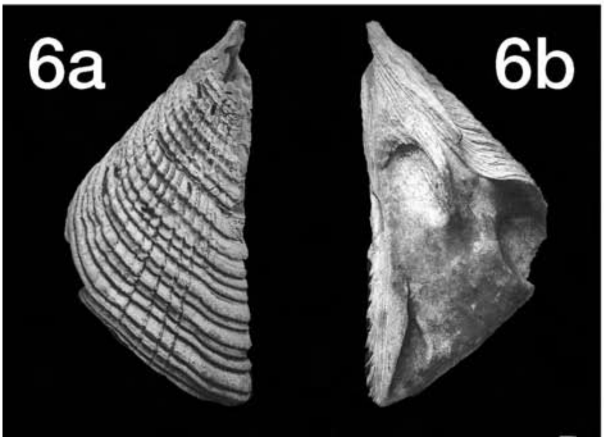

4b
4a


5a
5b


6a
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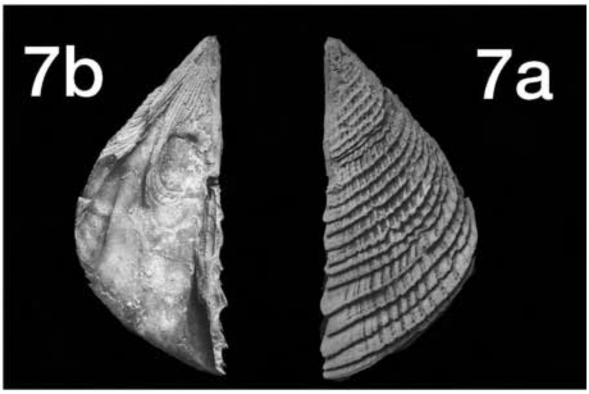
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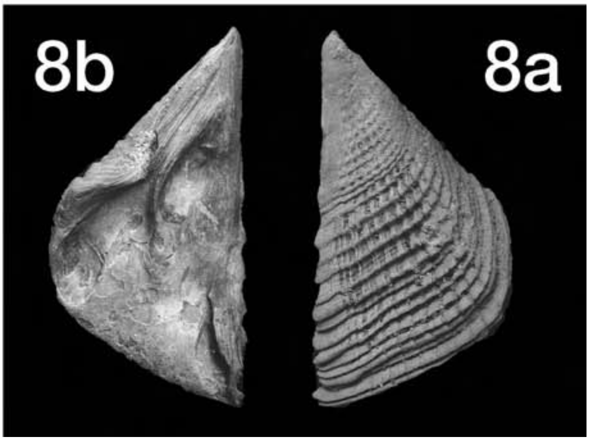

8b
8a

PLATE 3

Concavus (*Concavus*) *concavus* (Darwin, 1854) – Basal plates and crowns adapted to variably shaped substrate

1 – Inner view of a bowl-shaped basal plate extending deeply amidst the simultaneously growing neighbours; nat. size

2 – Outer view of a bowl-shaped basal plate, strongly extended at its centre into a cone seated deeply amidst the simultaneously growing neighbours and the balanid hash inbetween: consequently, the basal plate acquired a much corrugated shape; nat. size

3 – Outer (bottom) view of a xenomorphic basal plate shaped by its adjustment to the lower (apertural) side of the shell of the gastropod *Xenophora* sp.; note the pagoda-like overlap of this xenomorphic basal plate by the balanid crown; nat. size

4 – Scallop left valve (seen from its inner side; adductor muscle scar and pallial line are visible) overlapped all over its margin by the balanid crown; nat. size

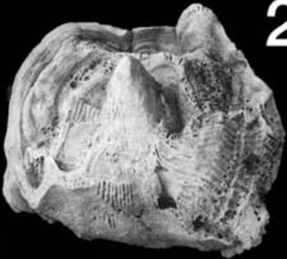
5 – Parietal lobes extending onto a shell fragment (lateral compartment, heavily bored by the sponge *Cliona* sp., arrowed), to which the basal plate adheres; nat. size

6 – Parietal lobes developed around a very small basal plate, the substrate of which has not been preserved; parietal lobes of *CL* and *L* are conjoined; nat. size

7 – Two specimens growing simultaneously (oblique bottom view) at an acute angle on a scallop valve; note the balanid compartmental plates overlapping the scallop valve; nat. size

8 – Specimen growing upon a scallop left valve fragment (oblique bottom view); note the carina (*C*) overlapping the broken valve fragment bored by minute clionid sponges (marked *S*) and the bivalve *Gastrochaena* sp. (marked *G*); note also the very narrow, lath-shaped carinolateral compartment (*CL*); nat. size

2



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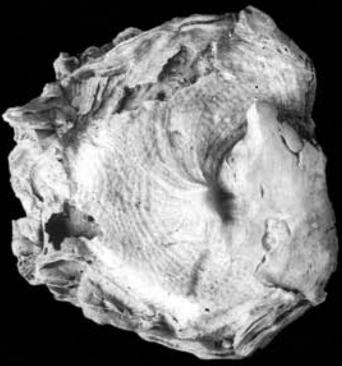

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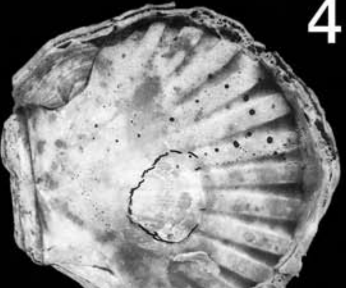
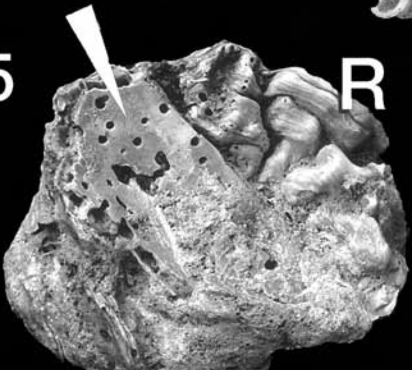


1

5



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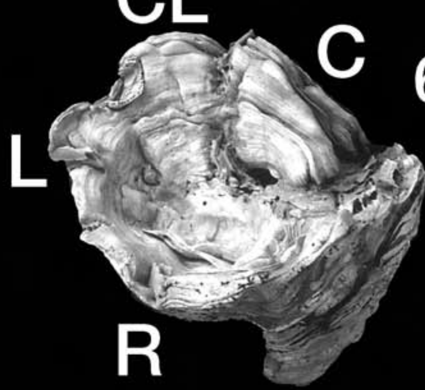

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8

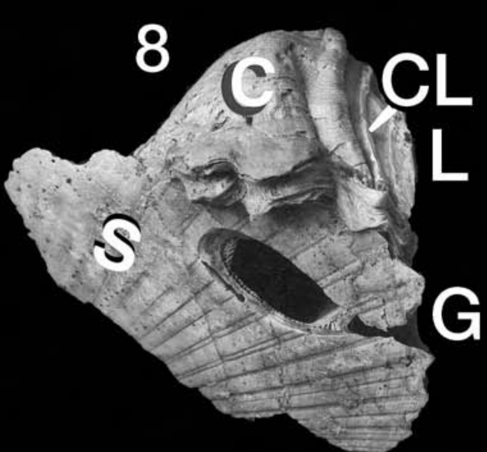


PLATE 4

Shape diversity of shells in *Concavus* (*Concavus*) *concavus* (DARWIN, 1854)

1 – Two, very broad, almost flat specimens with distinctly developed alae and radii on all compartments; nat. size

2a-2b – Minute specimen growing at the scutal apex of an adult shell (2a – upper view, 2b – occludent-side view); × 1.5

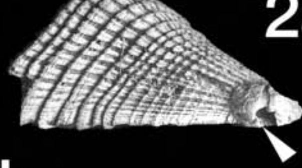
3 – Large specimen growing upon an isolated lateral compartment of an earlier balanid generation; the lateral compartment (*L*) extends strongly downward, completely embracing the substrate plate, and resulting in a bud-like crown morphology; nat. size

4 – Large, cone-shaped specimen growing upon, and adjusting its shape to, parietal hash of loose coquina type (oblique-bottom view); the crown irregularities result from the pseudomorphic growth upon hash particles, the left carinolateral compartment (*CL*) forms a heel-like parietal lobe; nat. size

5a-5b – Large, broad, but stumpy specimen growing upon parietal hash (5a – right-side view; 5b – left-side view); note the ragged growthlines and bands; nat. size

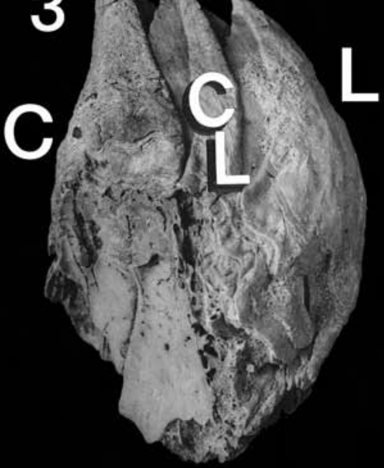
1

2a

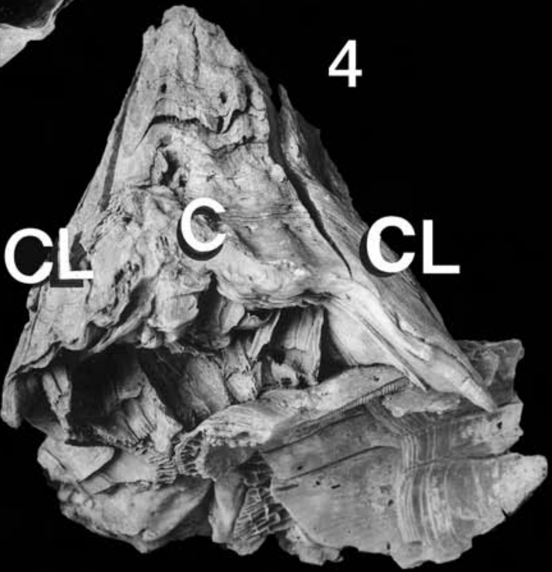


2b

3



4



5a

5b

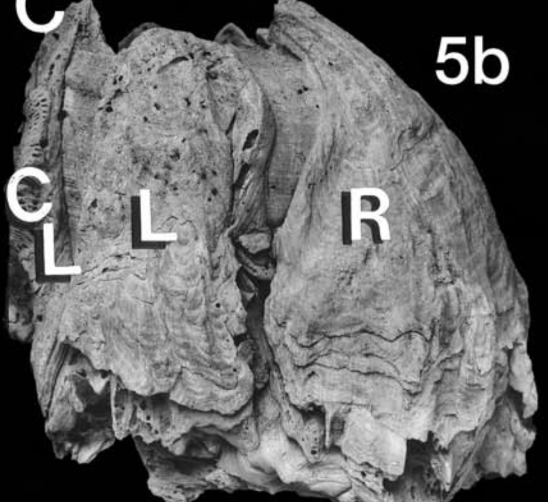


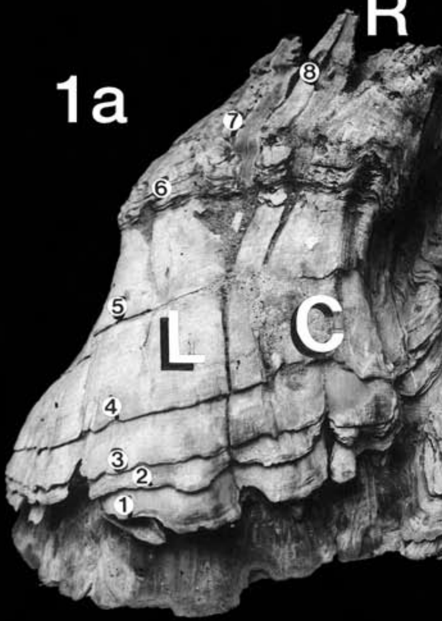
PLATE 5

Shell banding in *Concavus* (*Concavus*) *concavus* (DARWIN, 1854)

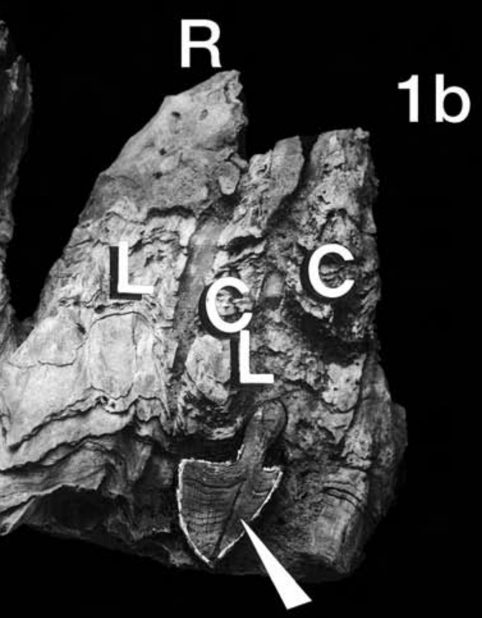
1a,a'-1b – Two specimens growing simultaneously, and parallel to each other, upon a valve of the bivalve *Anomia* sp., displaying the best pagoda-like pattern of growth bands, bounded into 8 sets (*numbered*) corresponding to successive ecdyses; to one of the specimens (see Fig. 1b) an isolated tergum is adhered (*arrowed*); **1a'** – Front view of one of these specimens (see Fig. 1a), to show the pagoda-like pattern of growth bands on the rostrum; note that the band numbered *2* overlaps the first one (numbered *1* in Fig. 1a); nat. size

2 – The largest of the specimens collected, displaying a pagoda-like pattern of growth bands, bounded into 7 sets (*numbered*); nat. size

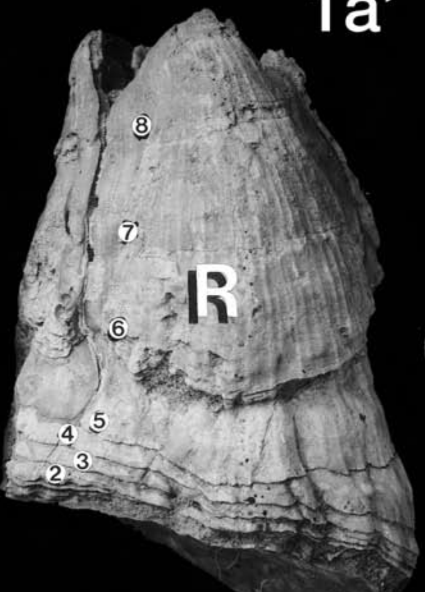
1a



1b



1a'



2

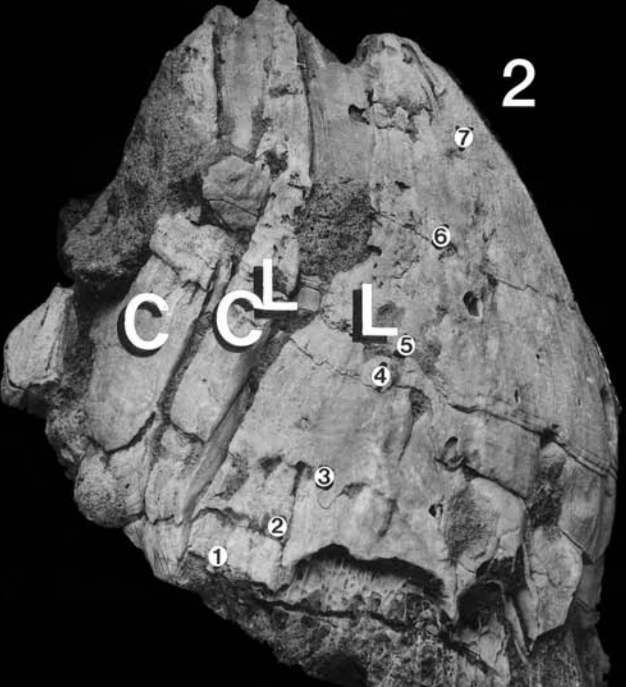


PLATE 6

Singly growing horn-shaped (‘scaphoid’) and tubular specimens of *Concavus* (*Concavus*) *concavus* (DARWIN, 1854)

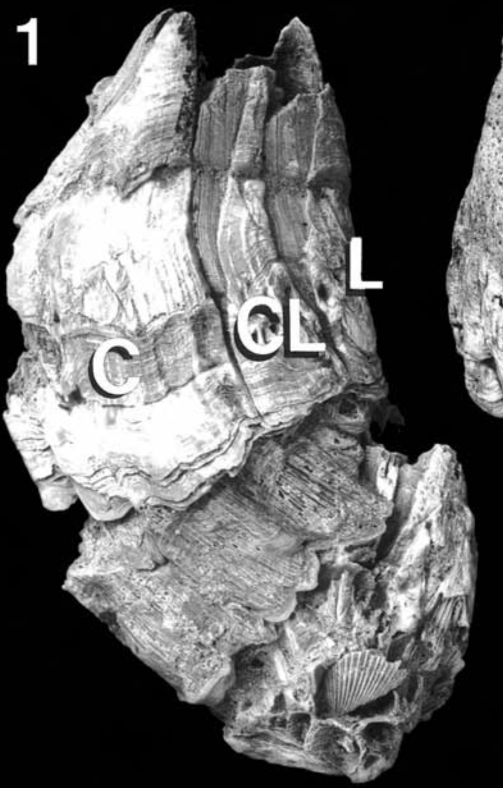
1 – Horn-shaped (‘scaphoid’) specimen, growing upon shell hash, with a strongly convex carina (*C*), and a pagoda-like pattern of growth bands; nat. size

2 – Horn-shaped (‘scaphoid’) specimen, with strongly convex lateral compartment (*L*); nat. size

3 – Horn-shaped (‘scaphoid’) specimen, with extremely elongated (130 mm), convex carina (*C*); nat. size

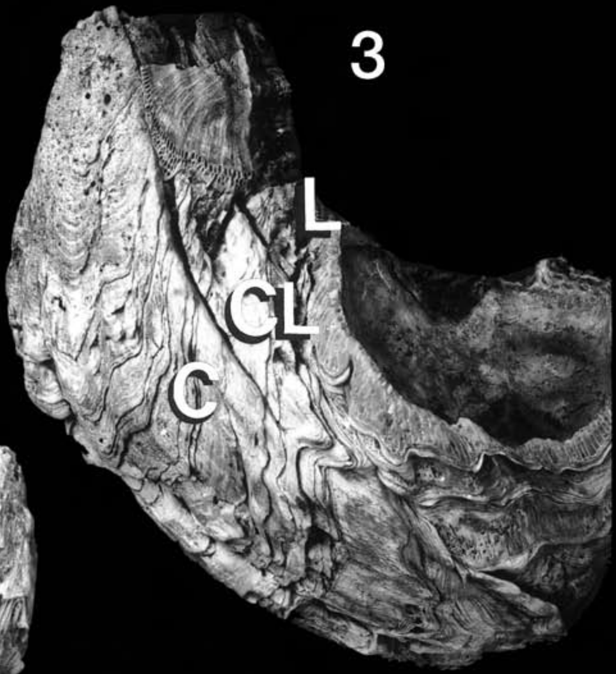
4 – Tubular specimen, almost straight, with widely developed alae and radii, and a broad aperture equal to the diameter of the crown; note the extremely elongated lateral compartment (*L*, 105 mm long) and rostrum (*R*); nat. size

1



2

3



4

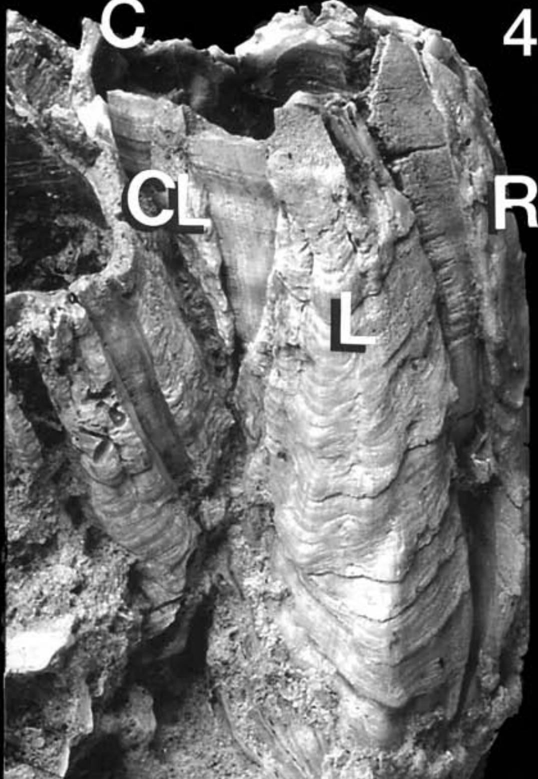


PLATE 7

Pseudomorphic sculpture of the shell, and a commensal polychaete of *Concavus* (*Concavus*) *concavus* (DARWIN, 1854)

1 – Two specimens growing simultaneously, oriented at right angles to, and adherent on, the left valve of a scallop; the rostra (*R*) of both specimens acquired pseudomorphic sculpture of the scallop ribs (*arrowed*); delicate longitudinal striation is also discernible; nat. size

2a-2b – Xenomorphic basal plate (*B*, bottom view) growing upon a shell of the bivalve *Cardium* sp. (Fig. 2a), the ribs of which are duplicated on the lateral compartment (*L*), and less distinctly on the rostrum (*R*); the horn-shaped (‘scaphoid’) specimen is bored by the sponge *Cliona* sp.; nat. size

3 – Small-sized specimen growing upon the outer side of an isolated scutum, the reticulate sculpture of which is transmitted all over the crown; × 1.5

4-7 – Four scuta, bored at their apex by the polychaete *Polydora ciliata* (JOHNSTON, 1838), which lived in a commensal relationship to the scuta owners; × 1.5. In one specimen (Fig. 5), the boring has been exposed mechanically, to show the greatly elongated, *U*-shaped course (*arrowed*)

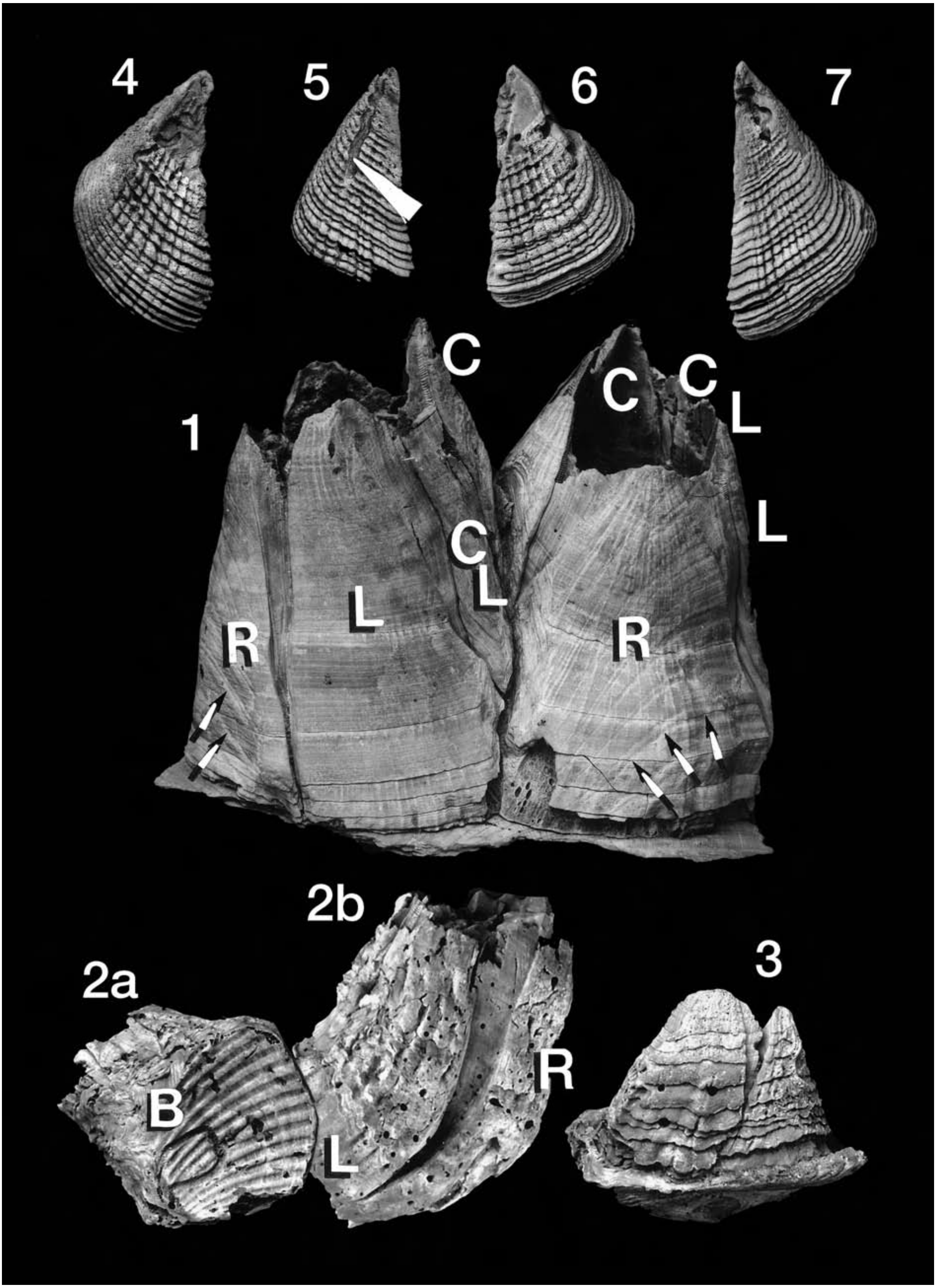

4
5
6
7
C
1
C
C
L
L
C
L
L
R
R
2b
2a
3
B
R
L

PLATE 8

Bouquet-like clusters of *Concavus* (*Concavus*) *concavus* (DARWIN, 1854)

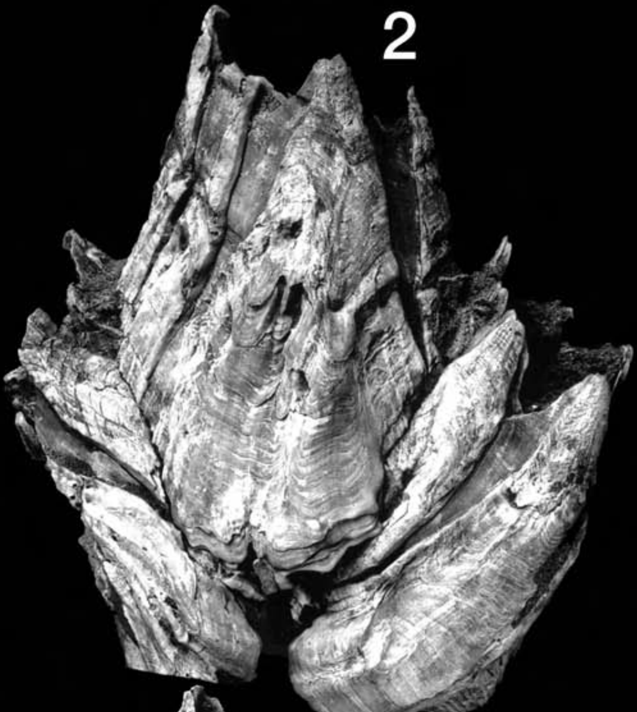
1 – Group of three juvenile specimens growing simultaneously upon an isolated lateral compartment of the former balanid generation, to form an initial bouquet-like cluster; nat. size

2 – Larger cluster, composed of shells of two generations; nat. size

3 – Larger cluster, composed of elongated crowns of three generations, the first of which was developing upon a piece of the crown densely bored by the sponge *Cliona* sp. (*arrowed*); nat. size

1

2



3

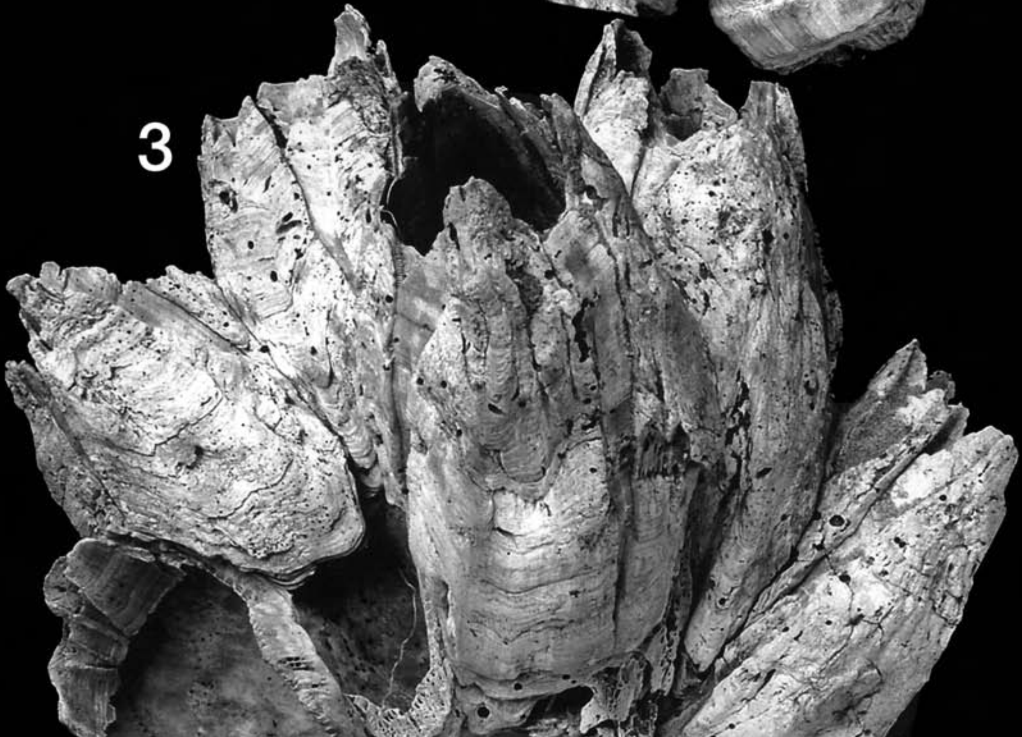


PLATE 9

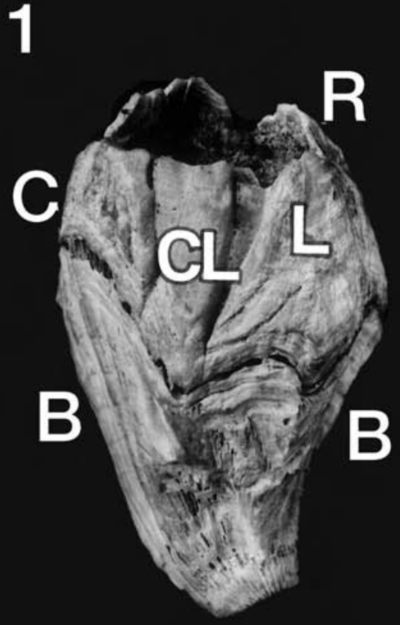
Xenomorphic growth under cramped conditions in bouquet-like clusters of *Concavus* (*Concavus*) *concavus* (Darwin, 1854)

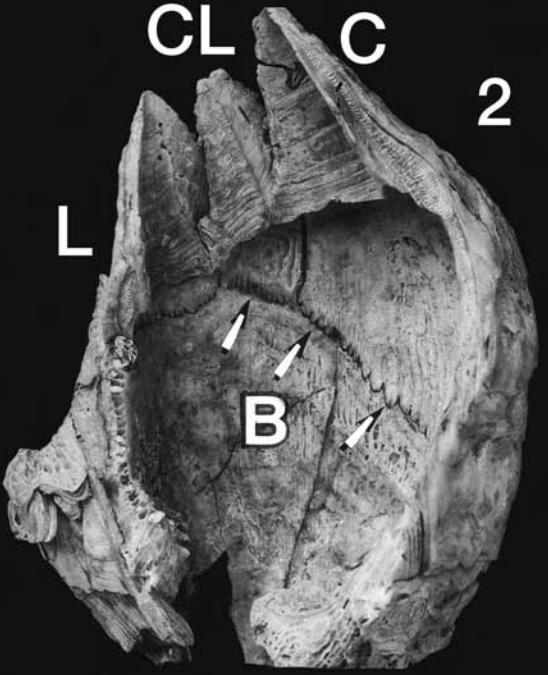
1 – Complete juvenile shell, composed of the bowl-shaped basal plate (*B*) and a relatively smaller crown, thereby acquiring a '*raphanoides*' shape; × 4

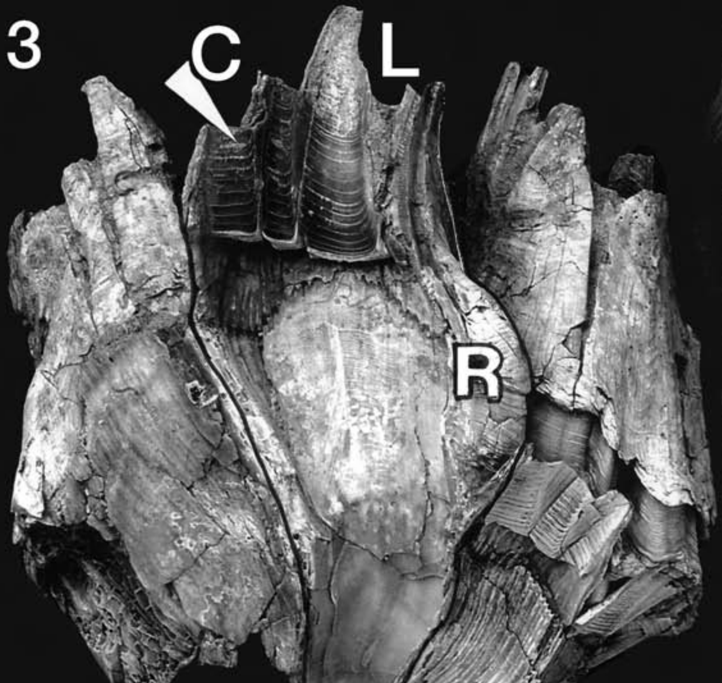
2 – Large specimen sectioned, to show its interior: the bowl-shaped basal plate (*B*) takes over half the space and the crown thus acquires the character of a cap (its lower margin is arrowed); nat. size

3 – Bouquet-like cluster of large specimens, sectioned to show the highly elongated '*raphanoides*' shape of basal plates; in the central specimen (outlined), growthlines on the sheath (arrowed at the carina, *C*), and the strongly inflated rostrum (*R*) are clearly visible; nat. size

4 – One of the clustered specimens, sectioned to show its bowl-shaped basal plate (*B*) extending deeply down amidst the simultaneously growing neighbours, and the crown filling the space – more pronouncedly at the lateral compartment (*L*, whose lower margin is arrowed) and strongly reduced at the carina and carinolateral (*C* and *CL*); nat. size


1
R
C
CL
L
B
B


CL
C
2
L
B


3
C
L
R

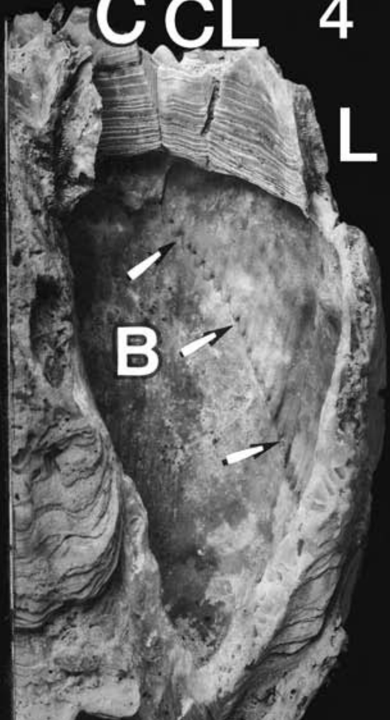

C
CL
4
L
B

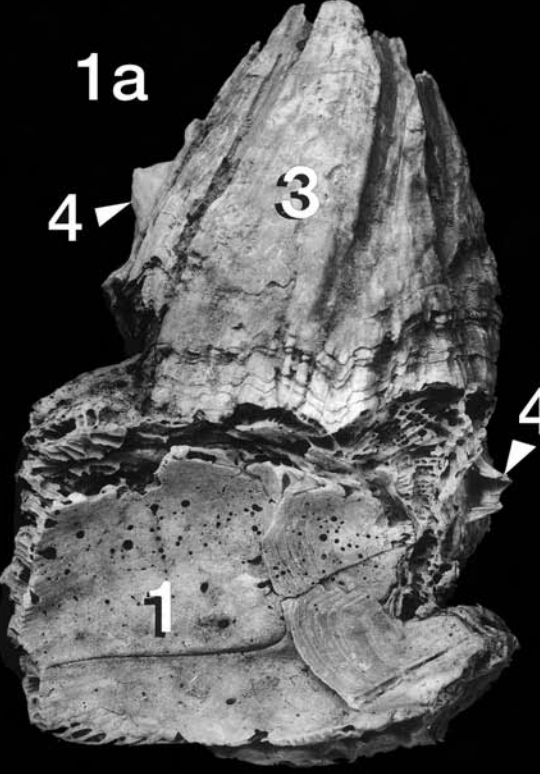
PLATE 10

Four/five staged pyramidal clusters of *Concavus* (*Concavus*) *concavus* (Darwin, 1854)

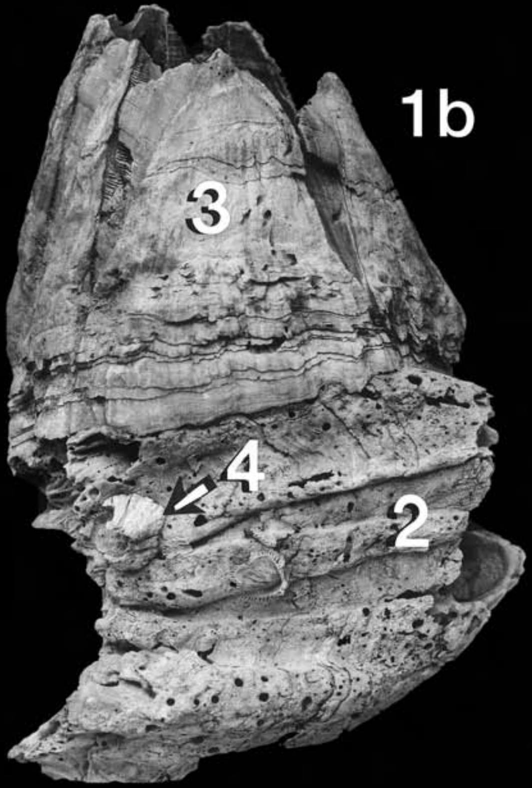
1a-1b – Cluster viewed from two opposite sides, to show four generations of balanids: the first of which (numbered *1*) supplied a balanid hash (a piece of conjoined lateral and carinolateral compartments, bored by the sponge *Cliona* sp.); the second (numbered *2*), seen on the opposite side of the specimen, is densely bored by the sponge *Cliona* sp.; the third (numbered *3*) adjusts its shape to the two former ones, and is not bored by sponges; the fourth (numbered *4*), dispersed sparsely all over the cluster, is composed of tiny specimens; nat. size

2 – Larger cluster, to show a perpetual feedback effect in five generations of balanids: the first generation (numbered *1*) was a cluster of small-sized individuals; the successors (numbered *2-4*) were large-sized specimens; the fifth generation (numbered *5*) was composed of tiny specimens, some of which (one is arrowed) were growing inside the empty shell of a former generation; nat. size

1a



1b



2

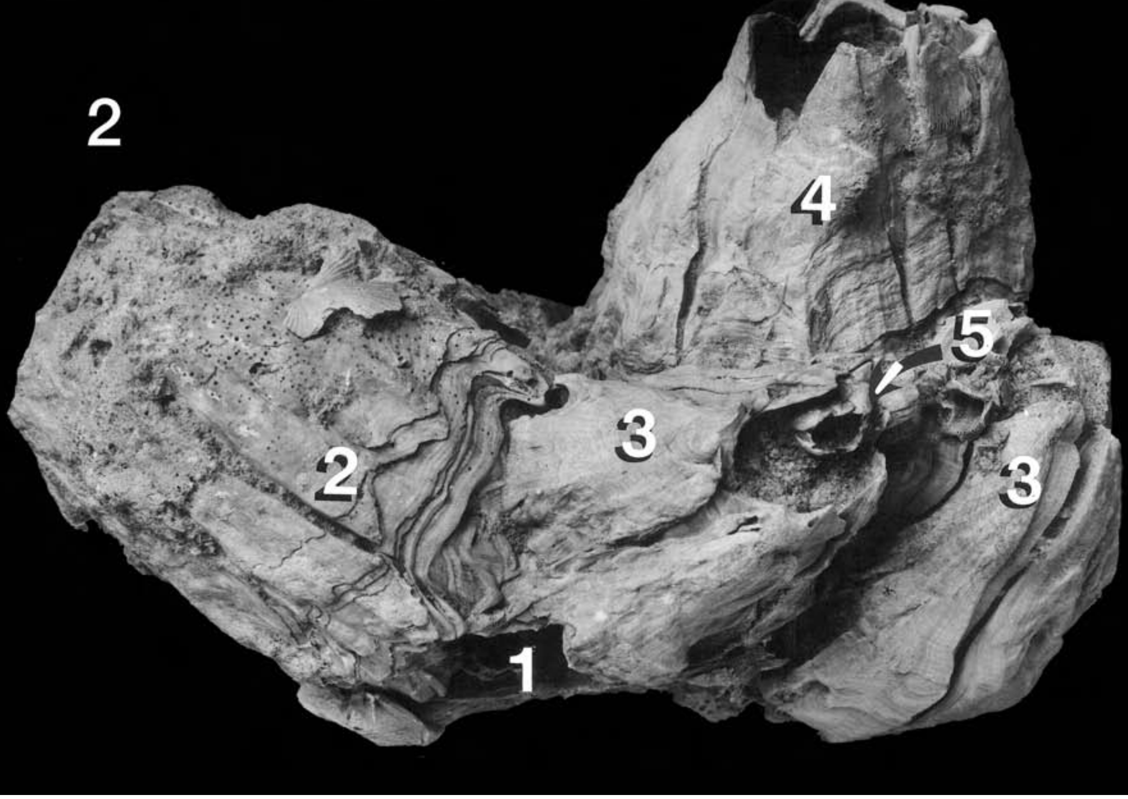
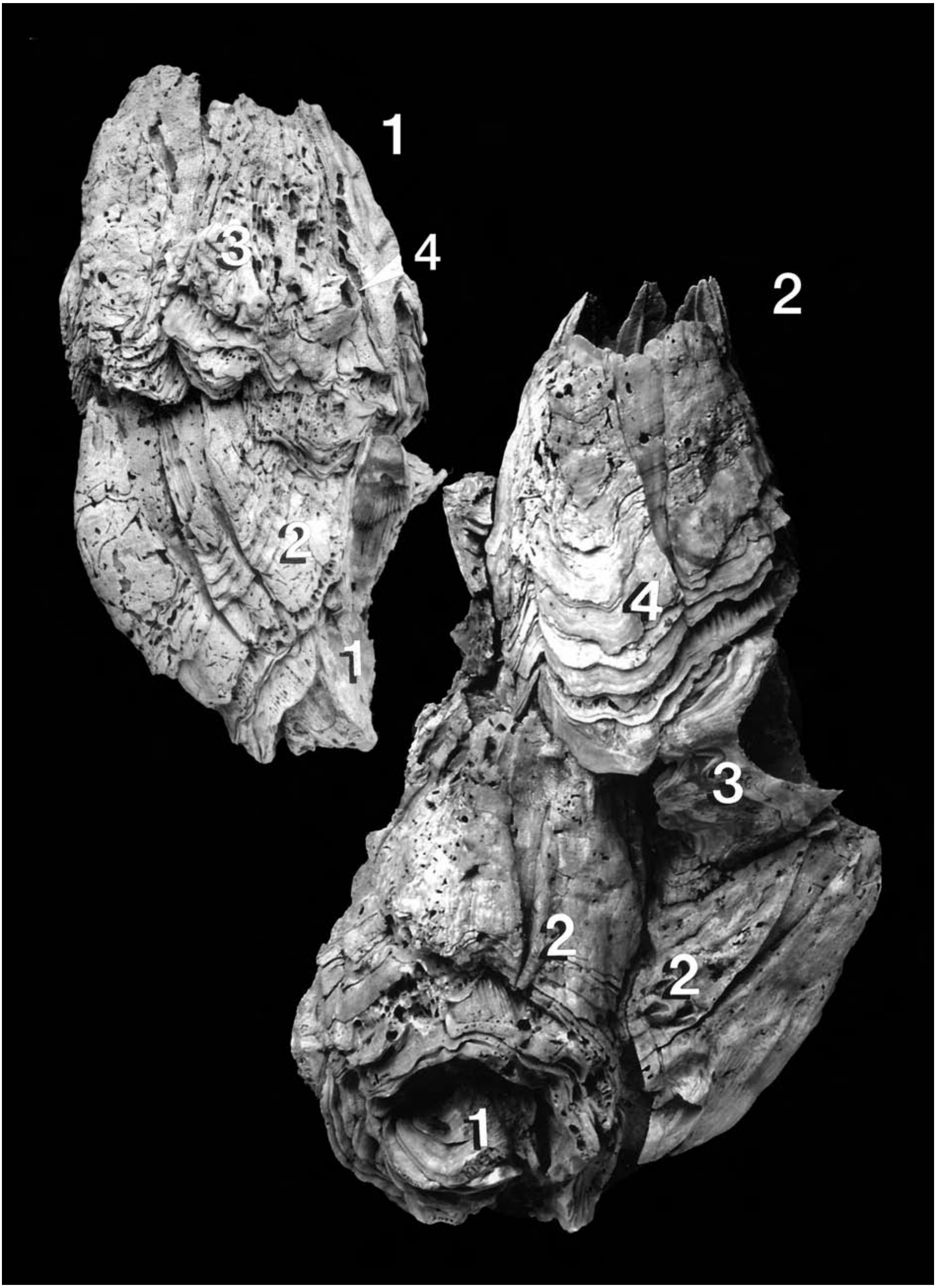


PLATE 11

Four-staged pyramidal clusters of *Concavus* (*Concavus*) *concavus* (DARWIN, 1854)

1 – Cluster of four generations, the second of which is bored by the sponge *Cliona* sp., and the last composed of tiny specimens; nat. size

2 – Cluster of four generations, the second of which is bored by the sponge *Cliona* sp., and the fourth, attaining a large size, shows eight pronounced growth bands of a pagoda-like appearance; nat. size


1
3
4
2
1
2
4
3
2
2
1