Cirripedes (Crustacea, Thoracica) from the Eocene (Lutetian–Bartonian) of the United Kingdom, France and Romania

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Received 25 January 2022, revised version accepted 6 May 2022

New material of cirripedes from the Lutetian of Campbon and Le Bois-Gouët (Loire-Atlantique, France), the Bartonian of Florești (Transylvania, Romania) and the Priabonian of the Isle of Wight (UK) provides novel insights into the taxonomy and distribution of the group during this period. The UK material of *Aporolepas reflexa* (J. de C. Sowerby, 1829) permits the first reconstruction of the capitular morphology of the genus. *Aporolepas angulata* var. *crepidula* Withers, 1953 is raised to species level on the basis of material from Campbon, and *Aporolepas* sp. from Romania constitutes the first record of the genus from eastern Europe. Possible records of a surviving Mesozoic cretiscalpellid and a virgoscalpelline (scalpellid) from Florești, are based on single plates and need further material for confirmation. Abundant Lutetian and Bartonian balanomorphs from Campbon and Romania, respectively, are referred to *Vectibalanus erisma* (J. de C. Sowerby, 1846), a species previously recorded only from the Hampshire Basin (UK). *Archaeobalanus semicanaliculatus* Menesini, 1971, from the Bartonian of the Paris Basin (France), is a probable junior synonym of *V. erisma*. Species of the genera *Aporolepas* Withers, 1953 and *Vectibalanus* Gale, 2020 are found along the Gulf and Atlantic seaboards of the USA, in northern and western France and the southern UK, and extend east to Romania. They were able to tolerate low salinities and their ranges extended from fully marine environments into brackish waters.

KEY WORDS: Palaeogene, Mesozoic survivors, barnacles, Europe

Introduction

The Eocene was a critical period in the history of cirripede evolution, because it marked the commencement of diversification and widespread abundance of the superfamily Balanoidea Leach, 1817 (Chan *et al*., 2021, fig. 9) and the first appearance of balanoids which possessed tubiferous parietes (Gale, 2021) and were subsequently able to dominate many shallow-marine habitats globally (Stanley & Newman, 1980). Barnacles are locally common fossils in Eocene marine and brackish sedimentary rocks in northern France and southern England (United Kingdom). Their occurrences were reviewed by Withers (1953), who monographed all the pedunculate taxa (Pollicipedomorpha, Calanticomorpha, Scalpellomorpha and Brachylepadomorpha, in current terminology). Subsequently, Gale (2021) redescribed the Balanomorpha from southern England and Manche (northern France) and reviewed Menesini's (1971) records from the Paris Basin.

Rather few Eocene cirripedes have been recorded from the Mediterranean region (Gale *et al*., 2021), including three scalpellomorph species from the Lutetian of Torino (Withers, 1953) and three verrucomorphs from the Priabonian of northern Italy (Carriol & Dieni, 2005). Additionally, Menesini (1984) recorded '*Balanus*' *stellaris* Brocchi, 1814 from the middle Eocene of Hérault (southern France). Records from eastern Europe rely upon brief descriptions, mostly without illustrations, by Kolosváry (1947, 1956, 1961, 1962). These include *Balanus hantkeni* Kolosváry, 1947, *B. phineus* Kolosváry, 1956 and *B. vialovi* Kolosváry, 1961 from Hungary, as well as a record of *B. unguiformis* (J. de C. Sowerby, 1846) from Bulgaria (Kolosváry, 1962). Ross (1965) was not able to confirm the validity of these records, as all were based on isolated wall plates which are of limited taxonomic value.

It was therefore of considerable interest when one of us (NF) was able to recover abundant cirripede valves from the Bartonian of Florești (central Romania); these were sent to ASG for identification in 2021. At approximately the same time, ST collected numerous cirripedes from the Lutetian of Campbon, on the southern part of the Armorican Massif in western France. Additionally, ASG found a lens containing abundant valves of the enigmatic genus *Aporolepas* Withers, 1953 in the Priabonian of Whitecliff Bay (Isle of Wight, southern England) which permitted reconstruction of capitular morphology. The results of these discoveries are documented in the present paper.

Geographical and stratigraphical settings

Material from Florești, central Romania

Specimens described originate from middle Eocene deposits that crop out on the left bank of the River Someșul Mic, at Florești Dam, on the outskirts of the locality with the same name. Florești is located in the north-western part of the Transylvanian Basin, 7 km west of the city of Cluj-Napoca. The Transylvanian Basin is situated in the central part of Romania, bordered by the Apuseni Mountains to the west, by the Eastern Carpathians to the north and east and the Southern Carpathians to the south (Fig. 1A). The basin has a 10-km-thick fill of Upper Cretaceous to Pliocene strata (Huismans *et al*., 1997), composed of four tectonostratigraphical megasequences: a latest Cretaceous one, a Palaeogene one, an early Miocene megasequence and a middle–late Miocene megasequence (Krézsek & Bally, 2006). The barnacle-bearing deposits studied are part of the Palaeogene megasequence (more exactly: pre-Palaeocene to pre-early Miocene) and belong to the Călata Group (Lutetian–Priabonian). In the area situated west of Cluj-Napoca, this lithostratigraphical unit includes three formations, viz. the Căpuș Formation, the Mortănușa Formation and the Viștea Limestone. The Mortănușa Formation (Bombiță & Moisescu, 1968) consists of three sub-units; the Inucu Member, the Văleni Limestone and the Ciuleni Member. In marginal positions the Mortănușa Formation is replaced by the clastic Stejerea Formation (Fig. 1B) (Popescu, 1984). For the present study, the Ciuleni Member has been of interest because this yielded the cirripede material described below.

The Ciuleni Member is represented by grey to greenish-grey sands and clays with a weakly developed laminated structure, reaching a total thickness of at least 45 m (Rusu, 1995; up to 80 m according to Popescu, 1984). These levels are interpreted to have been laid down in low-energy, muddy, offshore marine shelves; the occurrence of some high-energy laminations indicates possible storm layers (Codrea & Hosu, 2001).

The main portion of the Ciuleni Member is dated as middle to late Bartonian (NP17 Biozone), while the uppermost part includes the base of the Priabonian (NP18 Biozone) (Rusu, 1987; Rusu *et al*., 2004). A zonal marker level of the ostreid bivalve *Cubitostrea orientalis* (Dillwynn, 1817) is indicative of the limit between the Bartonian and Priabonian stages within this unit (Rusu, 1987; Rusu *et al*., 2004).

The macrofauna recorded previously from this unit comprises sorted accumulations of oysters and small pectinids, while the microfauna consists of benthic foraminifera belonging to the *Pararotalia subnimemis* local Zone and ostracods assigned to *Leguminocythereis striatopunctata* and *Quatrocythere leghiensis* local Zone (Popescu, 1978; Rusu, 1995). This assemblage indicates a normal marine palaeoenvironment with episodes of low salinity due to occasional increase of freshwater input (Rusu, 1995). A similar conclusion was drawn from a recent integrated analysis of the lower part of the Ciuleni Member (Trif *et al*., 2020).

The section of the Ciuleni Member exposed at the Florești dam outcrop (Fig. 1B) is approximately 15 m thick and consists of weakly laminated grey sandy clay with occasional thin macrofossil accumulations. Most of the cirripede specimens were collected from within these accumulations.

Material from Campbon and Le Bois-Gouët, Loire-Atlantique (France)

Outliers of Eocene deposits rest unconformably on a metamorphic basement across the southern part of the Armorican Massif in Loire-Atlantique (Fig. 2A). These include the Campbon and Saffre basins, both of which are infilled with fossiliferous sedimentary rocks which have been dated as Bartonian (Durand, 1960; Lebrun *et al*., 2014). However, the molluscs suggest a late Lutetian age (ST, pers. obs.).

Temporary excavations (Fig. 2B) along the edge of the orchard of Chateau de Coislin, 3.5 km north-north-east of Campbon (co-ordinates 47°26’29.2”N, 1°57’06.2”W) exposed several metres of dark brown, shelly, gritty sandy silt. This has yielded an abundant fauna of batillariid and potamidid gastropods, with other species indicating a mixture of material from brackish, marginal-marine and fully marine habitats. Shelly lenticles at one level produced abundant valves of a balanomorph barnacle. Nannofossil data suggest a Lutetian age and a neritic habitat (Dr J.R. Young, pers. comm., March 2021). A limited amount of material was collected from residues obtained from shelly sands at Le Bois-Gouët, in the Saffre Basin, a well-known locality (Lebrun *et al*., 2014).

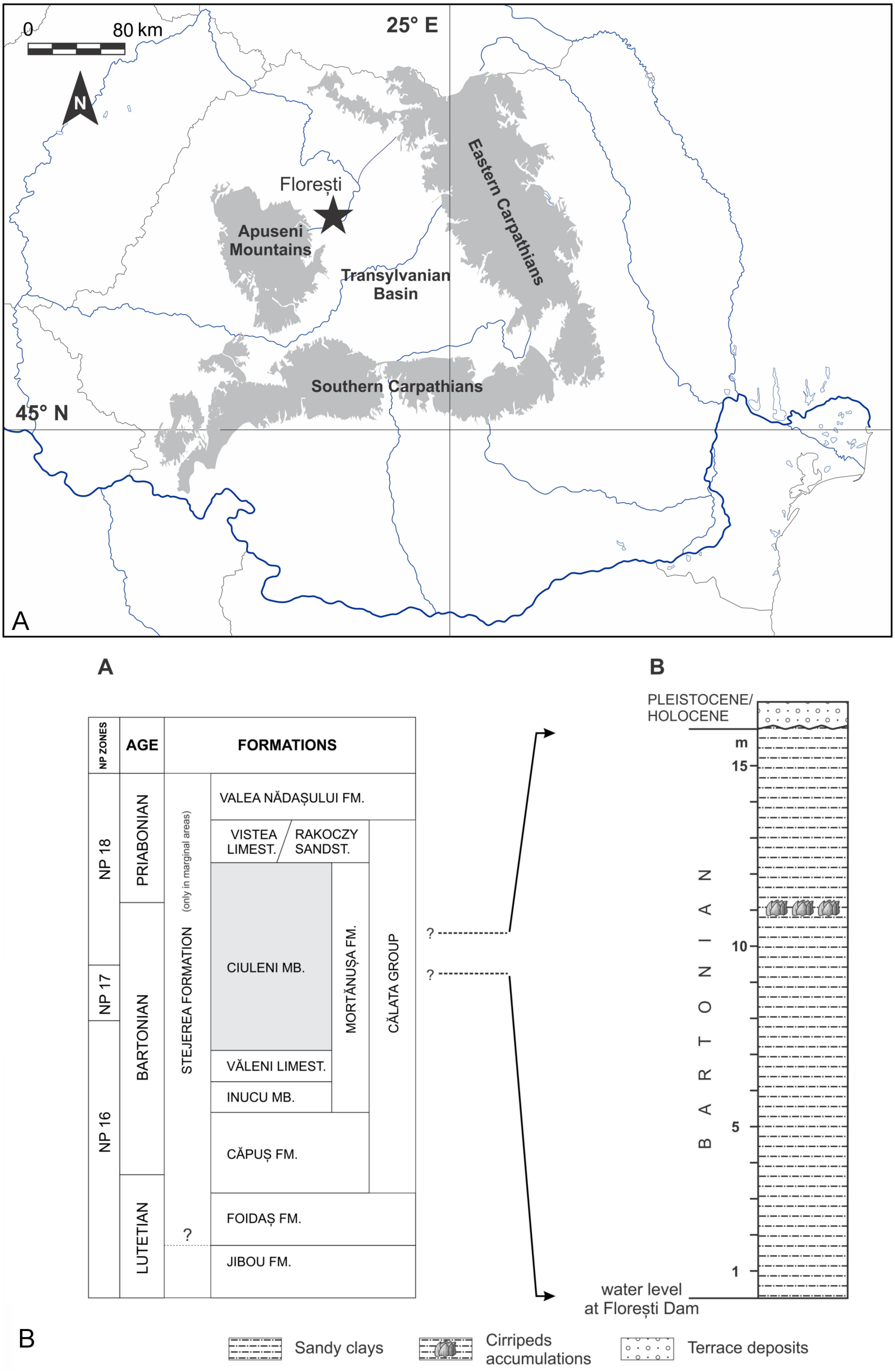
Material from the Isle of Wight, United Kingdom

The Eocene succession in the Hampshire Basin and Isle of Wight (Fig. 2A) was reviewed by White (1921) and King (2016). Samples of sandy clay containing abundant cirripedes were collected from the upper part of the Bembridge Oyster Bed, near the base of the Gurnard Member of the Bouldnor Formation (Gale, 2021) in Whitecliff Bay. This level yields a brackish molluscan fauna and associated ostracod assemblages suggest a salinity in the range of 9-25 ppt (Keene, 1977). This level is assigned a late Priabonian age, falling within magnetozone c15n (King, 2016).

Overview

The distribution of cirripedes at Le Bois-Gouët and Campbon (Loire-Atlantique, France) and Florești (Ro-

Figure 1. A. Position of Florești in central Romania (Transylvanian Basin); **B**. Lithostratigraphical units (left) recognised in the north-west of the Transylvanian Basin (Gilău depositional area) and log (right) of the section outcropping at Florești Dam (after Popescu, 1984; Rusu *et al*., 2004).


0
80 km
N
25° E
Florești
Apuseni Mountains
Transylvanian Basin
Eastern Carpathians
Southern Carpathians
45° N
A
A
NP ZONES
AGE
FORMATIONS
NP 18
NP 17
NP 16
PRIABONIAN
BARTONIAN
LUTETIAN
STEJEREA FORMATION (only in marginal areas)
VALEA NĂDAȘULUI FM.
VISTEA LIMEST.
RAKOCZY SANDST.
CIULENI MB.
VĂLENI LIMEST.
INUCU MB.
MORTĂNUȘA FM.
CĂLATA GROUP
CĂPUȘ FM.
FOIDAȘ FM.
JIBOU FM.
?
B
PLEISTOCENE/ HOLOCENE
m
15
10
5
1
B A R T O N I A N
water level at Florești Dam
B
Sandy clays
Cirripeds accumulations
Terrace deposits

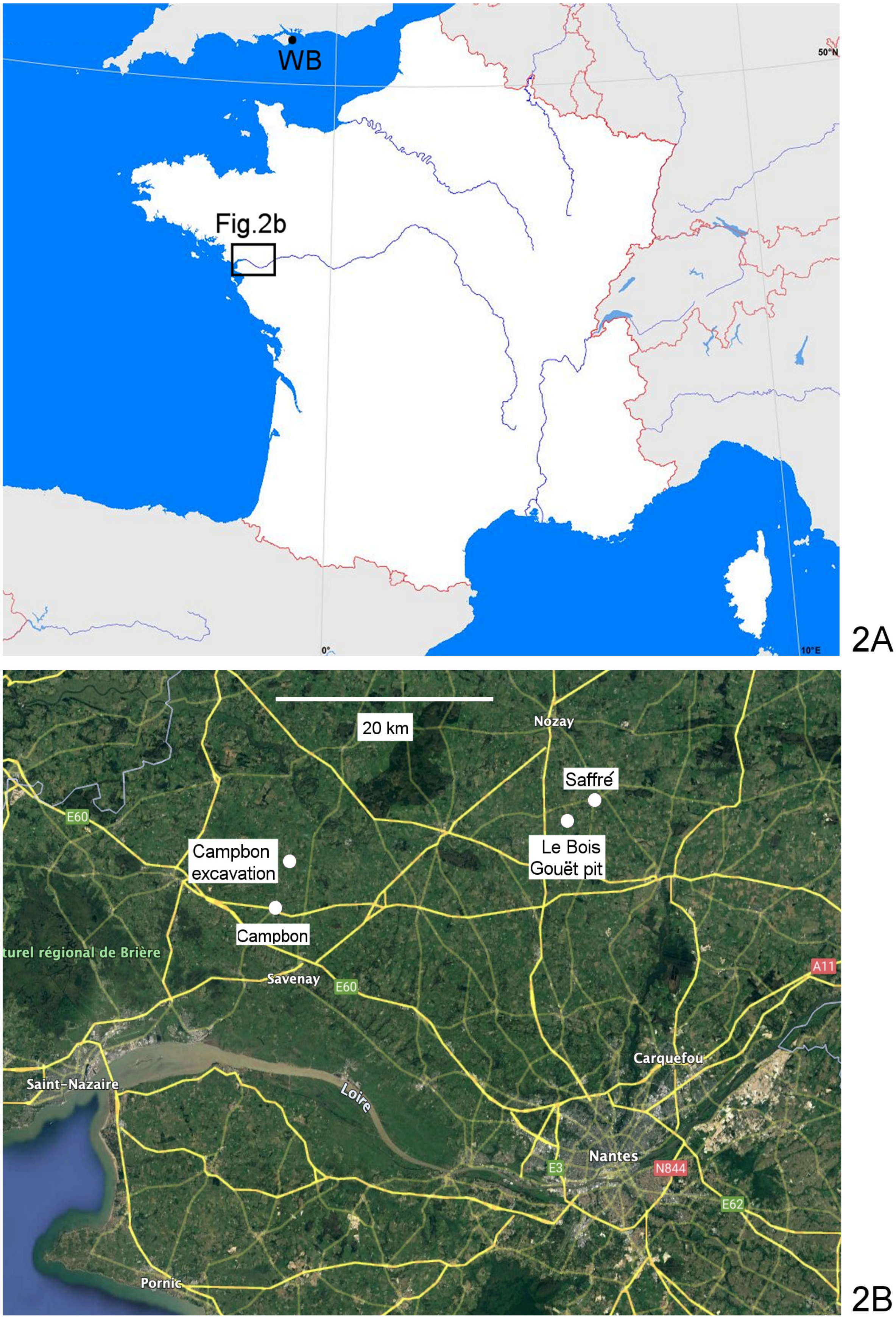


Figure 2. A. Map of southern England (United Kingdom) and France to show position of Whitecliff Bay (WB) and of Figure 2B. **B.** Google Earth view of the region around Nantes (Loire-Atlantique) to show the position of localities near Campbon and Le Bois-Gouët.

Locality	*Aporolepas crepidula*	*Aporolepas* sp.	*Scalpellum fischeri* forma *costatum*	*Scalpellum* sp. nov.	?*Virgiscalpellum* sp.	?Cretiscalpellidae	*Vectibalalanus erisma*
Le Bois-Gouët	10		3				
Campbon	35				1		3,125
Florești		1		7		1	150

Table 1. Occurrences of cirripedes, and numbers of specimens available, at the localities studied.

mania), on the basis of currently available material, is shown in Table 1.

The occurrence of *Vectibalanus* in the Lutetian of Campbon (Loire-Atlantique, 42–44 myr) constitutes the oldest known occurrence of balanids in which the parietes contain tubes. The genus is positioned at the base of a major radiation, commencing in the Oligocene and subsequently leading to diverse forms with complex parietal and radial structure (Gale, 2021). *Vectibalanus* spread widely during the later Eocene, with its geographical range extending from the Gulf Coast of the USA, east through northwest Europe and into southeast Europe (Romania; Fig. 3) and being represented by two successive species, *V. erisma* (J. de C. Sowerby, 1846) (Lutetian–Bartonian) and *V. unguiformis* (Priabonian–Rupelian). *Vectibalanus* is the dominant balanid genus to the north of Tethys during the Eocene, and the few contemporary Tethyan records (southern France, Italy) known to date are of '*Balanus' stellaris* (Menesini, 1984). Balanids described from the Eocene of Bulgaria and Hungary (Kolosváry 1947, 1956, 1961) are in need of further investigation (Ross & Newman, 1967), because they are based on shell plates which are not diagnostic at the generic level.

This begs the question why balanids should suddenly appear in local abundance in the Lutetian of northwest Europe, when they are absent from all older Palaeogene sedimentary rocks? Stanley & Newman (1980) argued that the evolution of tubiferous wall structure in balanids was the key adaptive breakthrough to their success, because this permitted more rapid growth and greater resistance to predatory drilling by gastropods. Remarkably few of the valves of *Vectibalanus* contain gastropod drill holes; in the assemblage from the Priabonian of Colwell Bay (Isle of Wight), a single drill hole was found in a collection of 522 plates (0.12%). In the Lutetian Campbon assemblage, only four plates were bored (0.19%), and none in the Bartonian Florești sample (Table 2). Bivalves and gastropods in the first two of these assemblages commonly show evidence of predation by gastropods. In contrast, Klompmaker *et al.* (2015) found a mean value of 3% for

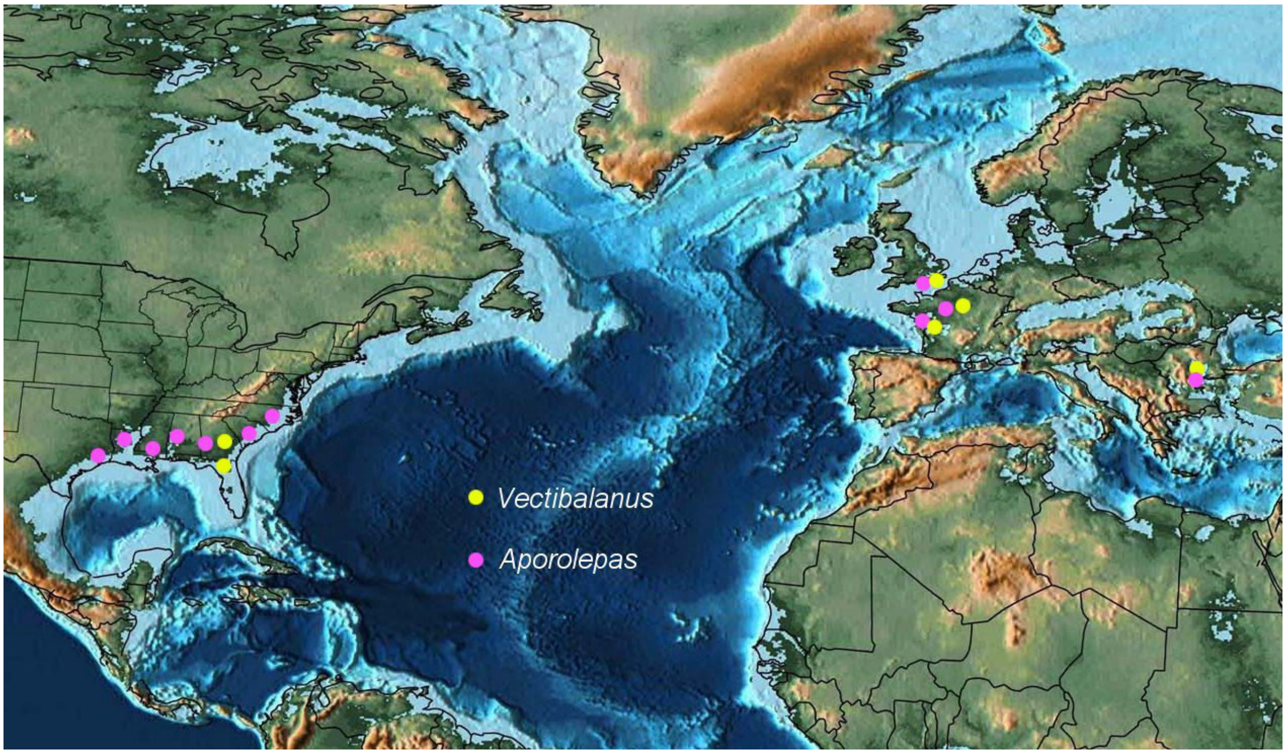


Figure 3. Map of the northern Atlantic Ocean during the middle Eocene, with occurrences of *Vectibalanus* and *Aporolepas* in the south-eastern US and north-west Europe plotted; map provided by Dr Chris Scotese.

Sample	**Number of valves**	**Number of opercular valves bored**	**Number of wall plates bored**	**Percentage**
Campbon	3,525	0	4	0.12
Colwell Bay	522	0	1	0.19
Florești	115	0	0	0.0

Table 2. Distribution of predatory boreholes of carnivorous gastropods in *Vectibalanus erisma*.

borings in Cainozoic balanomorph plates. Additionally, there were no borings in opercular plates at all, whereas these were relatively common in the data supplied by Klompmaker *et al.* (2015). The low level of predation is surprising given the abundance and diversity of muricid and naticid gastropods at Campbon and Colwell Bay.

It is possible that the tubiferous wall prevented significant predation on *Vectibalanus* by drilling gastropods, but this is largely untestable. Alternatively, muricids simply may not have selected these cirripedes as a food source or preyed on them without drilling.

Vectibalanus and *Aporolepas* occur most abundantly in brackish palaeoenvironments with salinities of 10-30 ppt, although they are present, but rarely abundant, in fully marine facies (Gale, 2021). *Aporolepas* apparently did not survive the Priabonian extinctions associated with terminal events, but *Vectibalanus* continued into the Rupelian. Younger records of the genus have not (yet) been confirmed.

Repositories of specimens

NHMUK Natural History Museum, London, UK.

Systematic palaeontology (ASG)

Order Calanticomorpha Chan, Dreyer, Gale, Glenner, Ewers Saucedo, Pérez-Losada, Kolbasov, Crandall & Høeg, 2021

Diagnosis – Capitulum with three to five pairs of larger lateral plates; subrostrum and subcarina usually present; smaller laterals variably developed, often absent.

Family Calanticidae Zevina, 1978

Diagnosis – Number of plates highly variable (Jones & Hosie, 2009); usually with three pairs of larger laterals (rostrolatus, upper latus and carinolatus), often with subrostrum and subcarina; inframedian latus probably absent.

Genus *Aporolepas* Withers, 1953

Diagnosis – Calanticids in which the kite-shaped scutum possesses a basitergal angle of 90°; surface of scutum adjacent to occludent margin depressed; all plates show conspicuous colour banding; carinae lack intraparietes.

Type species – *Scalpellum recurvatum* Bertrand, 1891, by original designation.

Included species – In addition to the type species, *A. angulata* Withers, 1953, *A. crepidula* Withers, 1953, *Zeugmatolepas americana* Withers, 1936, *A. rhombica* Withers, 1953, *Pollicipes reflexus* J. de C. Sowerby, 1829 and *A. howei* Cheetham, 1963.

Remarks – *Aporolepas* is a somewhat enigmatic genus of pedunculate thoracican, which occurs in the middle Eocene (Lutetian–Priabonian) and lower Oligocene (Rupelian) of the US Gulf states (Texas to North Carolina), in the Anglo-Paris Basin (UK, France) and in the Loire-Atlantique region of France. It is known exclusively from disarticulated plates and is most abundant in strata laid down in settings with restricted salinity (10-30 ppt), although it also occurs in fully marine deposits.

In his description of the genus, Withers (1953, p. 126) considered that it possessed, “at least 21 valves”, including “at least 8 pairs of lower latera”, and for this reason suggested that the genus lay close to the Cretaceous *Zeugmatolepas* Withers, 1913, although he included *Aporolepas* in the family Scalpellidae Pilsbry, 1907, then a very broad concept. In his description of *A. recurvata* (Bertrand, 1891), Withers separated and figured five distinct types of lower latera but did not identify which of these might be *Aporolepas* (Greek *aporos*, meaning a puzzle, or matter of doubt, with reference to the identity and arrangement of the lower latera). Chan *et al.* (2021) have recently assigned this genus to the Zeugmatolepadidae.

The discovery of abundant (>1,000), exceptionally preserved valves of *A. reflexa* (J. de C. Sowerby, 1829) in residues from the Priabonian Bembridge Oyster Bed in Whitecliff Bay (Isle of Wight) has now permitted a reassessment of the morphology of the genus. The material from Whitecliff Bay includes hundreds of lateral plates, which can be identified as falling into a number of discrete categories, as follows:

Upper latera (Fig. 4; Pl. 1, figs 4, 7): 4-5-sided valves, height slightly exceeding width; interior surface (Pl. 1, fig. 4b) flat, with weakly bevelled apical margins. The planar interior surface is typical of upper latera, which are positioned such that they weakly overlap both scutum and tergum. The longest (dorsal) margin weakly imbricates the tergum (Fig. 4), and the ventral apical margin rests on the scutum. Withers (1953, pl. 5, figs 8, 9) had correctly identified similar, but more elongated, plates of *A. recurvata* as upper latera;

Lower latera; although Withers (1953) was uncertain about correct placement of these, all are characterised in calanticids and scalpellids by a slightly inflexed apex and a straight basal margin (Gale, 2015). Comparison with calanticid genera permits identification of individual types, as follows:

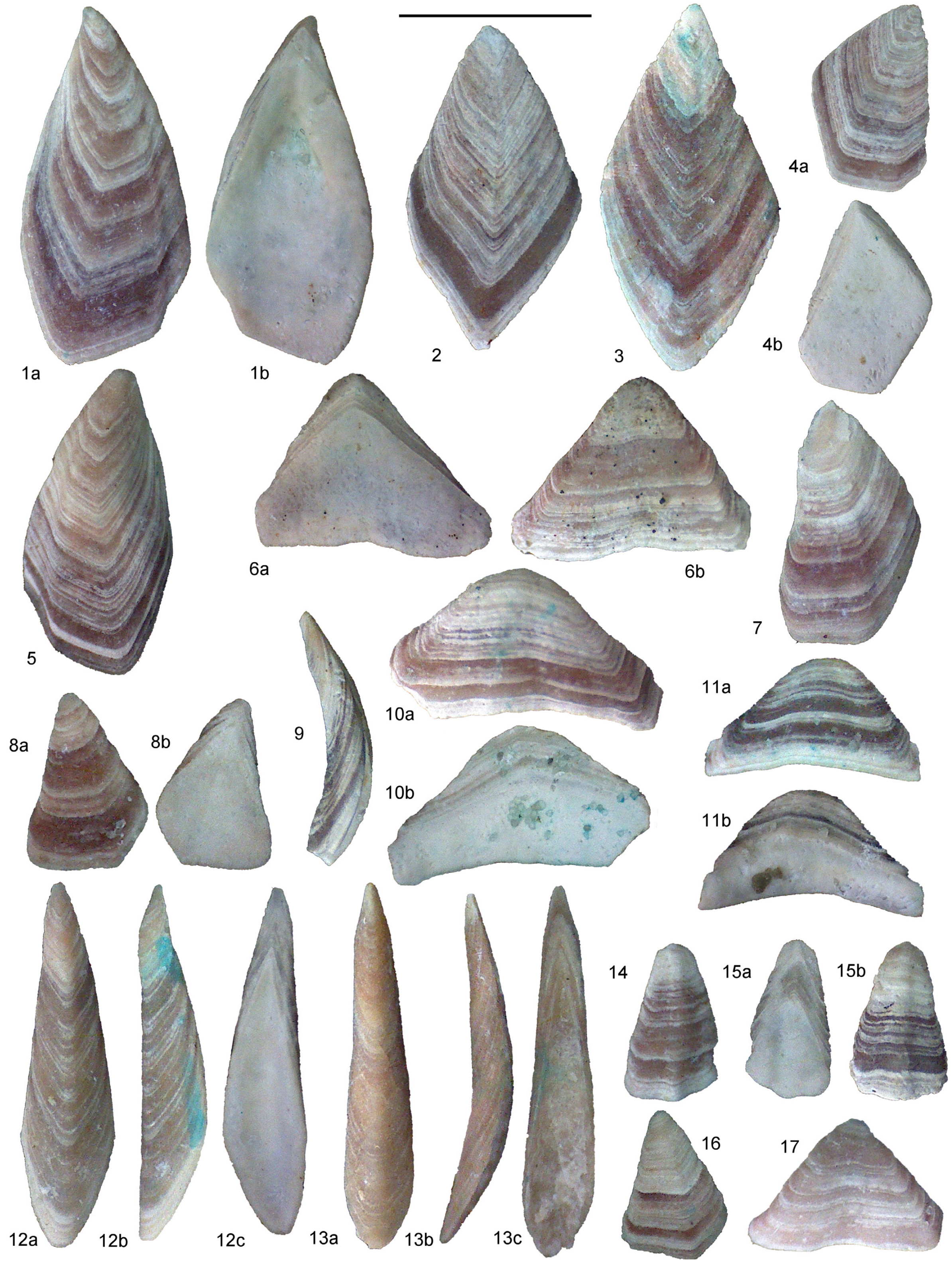


Plate 1. *Aporolepas reflexa* (J. de C. Sowerby, 1829) from the upper Eocene (Priabonian) Bembridge Oyster Bed in the Gurnard Member (Bouldnor Formation) of Whitecliff Bay, Isle of Wight (United Kingdom): 1, 5. scuta, in external and internal views, respectively (NHMUK IC 1927, 1931); 2, 3. terga, in external view (NHMUK IC 1928, 1929); 4, 7. upper latera, in external (4a, 7) and internal (4b) views (NHMUK IC 1930, 1933); 6, 17. inframedian latera, in external (6b, 17) and internal (6a) views (NHMUK IC 1932, 1943); 10, 11. carinolatera, in external and internal views, respectively (NHMUK IC 1936, 1937); 8, 16. rostrolatera, in external (8a, 16) and internal (8b) views (NHMUK IC 1934, 1942); 9. subcarina, in lateral view (NHMUK IC 1935); 12, 13. carinae in dorsal, lateral and interior views, respectively (NHMUK IC 1938, 1939)); 14, 15. rostra, in ventral (14, 15b) and internal (15a) views (NHMUK IC 1941,1942). Scale bar 5 mm.

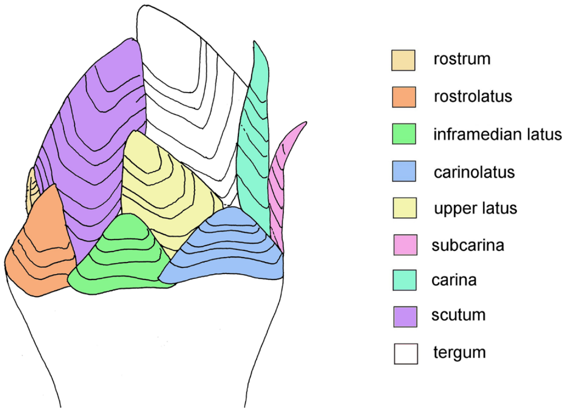


Figure 4. Reconstruction of *Aporolepas reflexa* (J. de C. Sowerby, 1829), based on material from Whitecliff Bay (Isle of Wight) Illustrated in Plate 1.

Rostrolatera (Pl. 1, figs 8, 16): isosceles triangle, convex, breadth 1.5 x height;
Inframedian latera (Pl. 1, figs 6, 17): isosceles triangular outline, flat, nearly symmetrical, long basal margin, centrally slightly concave;
Carinolatera (Pl. 1, figs 10, 11): quadrangular, height slightly greater than maximum breadth, apex acute.

In summary, the lower latera of *A. reflexa* include only four types that are identifiable as the inframedian latus, rostrolatus, carinolatus and subcarina, and in addition to the paired scuta, terga and upper latera, plus carina and rostrum, this gives a total number of valves of 15 (Fig. 4). The number of plates, in addition to the morphology of the lower latera, suggest placement of the genus in the Calanticidae. The absence of peduncular plates in the fine residue suggests that the peduncle was entirely organic, as in lepadids.
However, other species of *Aporolepas*, including the type species, *A. recurvata*, have a significantly greater number of valves, some of which do not match those of *A. reflexa* illustrated here (Pl. 1). The illustrations of lateral valves of *A. howei* (see Cheetham, 1963, pl. 46, figs 1-8; Zullo & Kite, 1985, pl. 1) and those of *A. recurvata* and *A. angulata* (see Withers, 1953, pls 58) show very close similarities, and these species evidently had numerous lateral plates of distinctive types, some named types 1, 2 and 4, by Cheetham (1963). The diversity of the lateral plates of *A. howei*, which include subcarinae and subrostra, has been confirmed by Ray Perreault (pers. comm., March 2021), who also noted that *A. howei* possessed numerous, spinose, peduncular plates. It is thus evident that *Aporolepas* includes distinctive species groups characterised by differences in the number and development of lateral and peduncular plates, which may subsequently be separated as discrete genera.

Aporolepas crepidula Withers, 1953

Plate 3, figs 1-12, 15; Plate 4, figs 1-3, 5-7

1953 *Aporolepas angulata* var. *crepidula* Withers, p. 125, pl. 8, figs 8-17.

Diagnosis – *Aporolepas* in which the apical part of the carina forms a hollow, spur-like dorsal protuberance.

Type – The carina figured by Withers (1953, pl. 8, fig. 10) is the holotype (NHMUK In.39373) from the Lutetian at Le Bois-Gouët (Loire-Atlantique, France).

Material – Ten carinae and numerous scuta, terga and rostra (NHMUK 1950-1960) from the Lutetian of Campbon (France). A single upper latus and a lower latus of type 2 (Withers 1953 p. 125) from the same locality.

Description – Height of carina four times breadth, tapering evenly from base to apex in dorsal view, bearing poorly defined, round-topped central ridge. In lateral view, apical portion forming hollow, spur-like lateral projection, apical margin of which being convex, lower margin concave (Pl. 3, figs 4, 6, 10; Pl. 4, fig. 3). Scutum kite shaped, basitergal angle slightly acute; depressed region subparallel with occludent margin poorly defined, broad (Pl. 3, figs 1, 3; Pl. 4, fig. 1). Tergum (Pl. 3, fig. 5; Pl. 4, fig. 2) rhombic, slightly asymmetrical, short upper carinal margin, long lower carinal margin. Occludent and scutal margins of equal length; basally broadening, poorly defined apicobasal ridge present. One tergum (Pl. 3, fig. 5) preserving colour, with four symmetrically placed, dark, apicobasally expanding bands. Rostra (Pl. 3, figs 8, 9) oval to subtriangular, height four times breadth, rounded apicobasal ridge present, interior face weakly concave. Upper latus (Pl. 3 Fig. 12) subrectangular, height 2X breadth, upper ventral margin strongly sloping. An oval, worn lower latus (Pl. 3 Fig. 15) has strong light:dark banding and is comparable in shape with the lower latus type 2 of *Aporolepas angulata* figured by Withers (1953, pl. 7 figs 15, 16).

Remarks – This form, known only from the Lutetian strata at Le Bois-Gouët and Campbon (Loire-Atlantique, France), is here elevated to species rank, on account of the distinctive dorsal process on the carina, and the robust, elongated rostra. The species is distinguished from its congeners particularly by the unique shape of the carina.

Aporolepas sp.

Plate 2, fig. 1

Material – A single scutum from the Bartonian of Florești, Romania (NHMUK IC 1944).

Description – Scutum robust, occludent margin straight, basal margin rounded. Tergal margin straight, short, rounded contact with lateral margin. External surface gently convex, lacking apicobasal ridge. Large, deep scutal adductor pit. Basal part of valve incomplete.

Remarks – This scutum differs from all other described species in the very long, straight occludent margin, the short, straight tergal margin, the rounded lateral margin and the absence of an apicobasal ridge.

Family Scalpellidae Pilsbry, 1907
Subfamily ?Virgiscalpellinae Gale, 2020

Diagnosis – Scalpellids in which the carinal and scutal umbones are sub-apical to sub-central, and in which the interior apical regions of the terga and scuta bear tubercles.

Genus ?*Virgiscalpellum* Withers, 1935

Diagnosis – Virgiscalpellinae which possess a full complement of lateral plates, including paired carinolatera, inframedian latera, upper latera and rostrolatera.

Type species – *Scalpellum beisseli* Bosquet & Müller, *in* Bosquet, 1857, by original designation.

?*Virgiscalpellum* sp.
Plate 4, fig. 4

Material – A single incomplete carina (NHMUK 1967) from the Lutetian of Campbon (Loire-Atlantique, France).

Description – Incomplete carina with umbo in approximately central position, upper portion angled to basal part at 130°. Cross-section of carina V-shaped, tectum narrow, poorly defined. Parietes and intraparietes not distinguished, lateral surfaces of carina finely striate, striae extending from umbo to tergal and basal margins.

Remarks – If this specimen were from Upper Cretaceous strata, it would without doubt be referred to *Virgiscalpellum* on account of the complete lack of separation of the parietes and intraparietes, the narrow, poorly defined tectum and the fine ribbing radiating from the umbo. It compares with the carina illustrated as *V. beisseli* from the Campanian of Wiltshire, United Kingdom (Withers, 1935, pl. 37, fig. 5), but has finer ribbing. The certain range of *Virgiscalpellum* extends from the Aptian to the Maastrichtian; the genus is presumed to have disappeared at the K/Pg boundary (Gale, 2020). It is homoeomorphic with *Scalpellum* in the central position of the carinal umbo and the shape of the upper and inframedian latera and the rostrum, but the latter differs importantly from *Virgiscalpellum* in the shape of the scutum, the rostrolatus and the carinolatus. In the carina of species of *Scalpellum*, the tectum, parietes and intraparietes are consistently sharply defined (see Withers, 1953, pls 38–54). However, we have only a single carina and certain identification must await the discovery of additional material.

Subfamily Scalpellinae Pilsbry, 1907
Genus *Scalpellum* Leach, 1817

Type species – *Lepas scalpellum* Linnaeus, 1767, by the subsequent designation of Leach (1825).

Diagnosis – Derived scalpellines in which the carinal and scutal umbones are subapical, the carinolatus has a horn-like projection, often recurved, extending beyond the carinal margin; the inframedian latus is rectangular to slightly trapezoidal, with a low umbo, and the upper latus is rhomboidal with a subapical umbo; the rostrum is rectangular, pyramidal, with a large subumbonal surface.

***Scalpellum fischeri* forma *costatum* Withers, 1953**
Plate 3, Figs 13, 14

1953 *Scalpellum fischeri* var. *costatum* Withers, p. 257, pl. 39, figs 6-8.

Diagnosis – '*A Scalpellum* like *S. fischeri* but with the carina having the intraparietes more strongly ribbed. Upper latus with the umbo central, and the whole outer surface coarsely ribbed. Infra-median latus with the umbo near the base, and the outer surface with numerous ribs' (Withers, 1953, p. 257).

Type – The holotype is an upper latus (NHMUK In. 39605), from the Lutetian of Le Bois-Gouët (Loire-Atlantique, France).

Material – Three latera: an upper latus (NHMUK IC 1961) and two inframedian latera (NHMUK IC 1962, 1963) from the Lutetian of Le Bois-Gouët.

Remarks – The newly collected material does not provide information further to that supplied by Withers (1953).

***Scalpellum* sp. nov.**
Plate 2, figs 2-6

Material – One scutum, two terga and two carinae (NHMUK IC 1945-1949) from the Bartonian of Floreşti, Romania.

Description – Scutum (Pl. 2, fig. 4) asymmetrically rhomboidal; basal and upper occludent margins short, lower occludent and tergal margins elongated. Rostral (40°) and basitergal (130°) angles rounded. Umbo subapical in position; external face smooth, bearing a weak depression parallel to tergal margin. Apex broken off. Terga (Pl. 2, figs 3, 5) flat, crescentic, length twice breadth, apical and basal angles acute, carinal margin straight, occludent margin short. Shallow groove running from apex to upper part of scutal margin. Carinae (Pl. 2, figs 2, 6) incurved, laterally compressed; tectum sharply defined, weakly convex, bearing commarginal growth lines. Umbo apical to subapical, intraparietes triangular, deep, poorly demarcated from parietes.

Remarks – The scutum appears to have the apex and upper part of the occludent margin broken off, and lacks the erect, acuminate apical process which is conjoined at right angles to a ridge by a flat or concave sheet at the apex of the tergal margin in scuta of *Scalpellum*. The conspicuously inset tergal surface is distinctive, and the scutum cannot be readily identified with any species illustrated by Withers (1953, pls 38-54). The poorly preserved carinae and terga can only be assigned to *Scalpellum* sp. The scutum evidently represents a new species, description of which must await discovery of further material.

Family Cretiscalpellidae Buckeridge, 1983

?*Cretiscalpellum* sp.

Plate 4, Fig. 10

Material – A single rostrum (NHMUK IC 1973) from the Bartonian of Florești, Romania.

Description – Rostrum low, triangular, breadth greater than height, strongly concavo-convex. Basal margin concave centrally, laterally convex, surface smooth.

Remarks – The low, triangular form of this rostrum, which is thin and concavo-convex, is similar in shape and form to that of mid- and Late Cretaceous Cretiscalpellidae (Withers, 1935; Gale, 2015, fig. 4D, F) and different to those of scalpellids (Gale, 2015, figs 11, 12). However, this is the first possible post-Cretaceous record of the family, and certain identification awaits the discovery of more material.

Order Balanomorpha Pilsbry, 1916

Remarks – Balanomorph barnacles were first illustrated from the Eocene of the Hampshire Basin (southern England) by J. de C. Sowerby (1846), under the names of *Balanus unguiformis* and *B. erisma*. Darwin (1854) described the material in detail and decided that *B. erisma* was a ribbed variety of *B. unguiformis*. Gale (2021) recorded abundant new material from the Bartonian to Rupelian of the Hampshire Basin, separated *erisma* and *unguiformis,* placed both in a new genus, *Vectibalanus*, and added a third species from the Bartonian with smooth wall plates, *V. mortoni*.

Balanomorph records from the Paris Basin (France) have a complicated history. De Alessandri (1907, pl. 9, fig. 30) recorded and illustrated *Balanus bisulcatus* Darwin, 1854 from the Bartonian and Stampian (now Rupelian) of Le Ruel, Marines and Pierrefitte near Paris. However, this is a Pliocene species, now referred to *Actinobalanus* Moroni, 1967 (Zullo & Perreault, 1989) recorded from the UK, France and Belgium, and most unlikely to occur in the Eocene. De Alessandri (1907) also recorded *B. unguiformis* from the Eocene of Etampes (France), without figures. Subsequently, Carriol (1982, p. 7) repeated De Alessandri's records of *B. bisulcatus* from the Eocene and Oligocene of the Paris Basin and indicated occurrences of *B. unguiformis* with question marks (Carriol, 1982, table 1), stating that the occurrences were probable but unconfirmed.

Menesini (1971) described a collection of balanomorphs from the upper Eocene and Oligocene of the Paris Basin and assigned the majority of specimens to *Archaeobalanus semicanaliculatus* Menesini, 1971 (type material from the Bartonian) and *Balanus* (*Hesperibalanus*) *parahesperius* Menesini, 1971 (type material from the Rupelian). She did not cite or discuss *Balanus unguiformis*, even though the type material came from localities of similar age (less than 300 km distant from the Paris Basin) and the taxa are morphologically similar. Gale (2021) retained *Archaeobalanus* as a separate genus, and placed *B.* (*H.*) *parahesperius* in *Kathpalmeria* Ross, 1965, a genus first described from the Eocene of Georgia, Alabama and Florida (see also Zullo & Kite, 1985).

The subsequent discovery by one of us (ST) of abundant balanomorphs in the Lutetian of Campbon (Loire-Atlantique, France) and by another (NT) in the Bartonian of central Romania has now permitted a revision of the taxonomy of various Eocene species, leading to the following conclusions:

It is evident that there is considerable variation within single assemblages in the degree of costation of the wall plates of species referred to *Vectibalanus*, such that the presence/absence of ribbing does not permit discrimination of species or subspecies. Thus, the Bartonian *V. mortoni* becomes a synonym of *V. erisma*;

Morphology of the terga (Fig. 5) permits consistent discrimination of an older (Lutetian–Bartonian) species, here identified as *V. erisma,* and the younger (Priabonian-Rupelian) *V. unguiformis*.

However, this information does not throw much light on the problem of the relationships, and possible synonomy, of J. de C. Sowerby's (1846) Eocene-Oligocene species from the Hampshire Basin, and Menesini's (1971) taxa from strata of the same age in the adjacent Paris Basin. In terms of parietal structure, *V. erisma* and *Archaeobalanus semicanaliculatus* appear to be identical, but the lack of opercular plates in the type material of the latter species does not allow certain identification. Here, *A. semicanaliculatus* is provisionally treated as a junior synonym of *V. erisma*. Opercular plates are known for *Kathpalmeria parahesperius* (see Menesini, 1971, pl. 1, figs 2-5); the terga differ significantly from those of the contemporaneous *V. unguiformis* from the UK in the shape of the tergal spur, and lack of an overfolded spur furrow, and the parietal plates appear to completely lack pores (Menesini, 1971, pls 3, 4). The taxon is provisionally left in *Kathpalmeria*.

Genus *Vectibalanus* Gale, 2020

Diagnosis – Scutum with striated apical callus, lacking adductor ridge, lateral depressor pit shallow; tergum with prominent spur, separated from base of scutal margin by V-shaped notch; spur furrow well demarcated; parietes with simple longitudinal pores and inner lamina; radii with coarsely denticulate sutural edges. Basis solid, with radiating ridges.

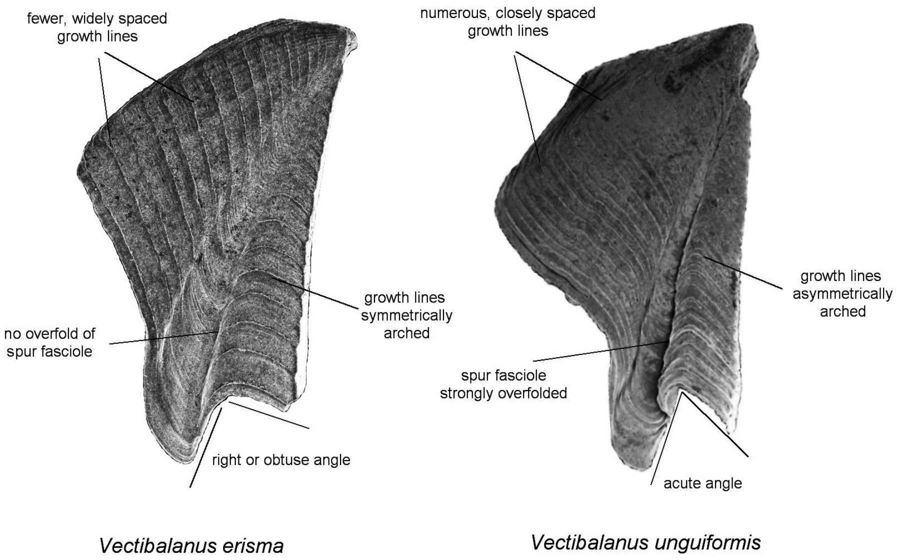


Figure 5. Comparison between terga of *Vectibalanus erisma* (J. de C. Sowerby, 1846) and *V. unguiformis* (J. de C. Sowerby, 1846) as a basis for differential diagnosis.

Type species – *Balanus unguiformis* J. de C. Sowerby, 1846, by original designation.

Included species – Additional to type species, *V. erisma* (J. de C. Sowerby, 1846).

Remarks – In the present revision, *V. mortoni* Gale, 2020 is treated as a synonym of *V. erisma*, and *Archaeobalanus semicanaliculatus* Menesini, 1971 from the Bartonian of the Paris Basin is a probable synonym as well. Thus, material of *Vectibalanus* can be placed in an older species, *V. erisma* (Lutetian-Bartonian, UK, France, Romania) and a younger one, *V. unguiformis* (Priabonian-Rupelian, UK).

Vectibalanus erisma (J. de C. Sowerby, 1846)

Fig. 5A; Plate 4, figs 8, 9, 11, 12; Plate 5, figs 1-10; Plate 6, figs 1, 5-8; Pl. 7, figs 1-11

*1846	*Balanus erisma* J. de C. Sowerby, pl. 648, fig. 2.
1854	*Balanus unguiformis* var. *erisma* J. de C. Sowerby – Darwin, p. 40, pl. 2, fig. 4b.
1971	*Archaeobalanus semicanaliculatus* Menesini, p. 28, pl. 2, figs 1-6; pl. 5 figs 6-8, pl. 6; pl. 7, figs 1-4.
2021	*Vectibalanus erisma* (J. de C. Sowerby) – Gale, p.18, pl. 3, figs 7-10; pl. 5, figs 4-13; pl. 7, figs 1-7.
2021	*Vectibalanus mortoni* Gale, p. 19, pl. 7, figs 8-16; pl. 8, figs 1-4, 11, 12.

Diagnosis – *Vectibalanus* in which the spur furrow of the tergum is shallow and is not overlain by a recumbent fold of the scutal surface; right or slightly obtuse angle between the tergal spur and scutal margin of the tergum.

Types – The remains of a specimen (pyrite decay has broken the material up), originally attached to a gastropod shell (*Ampullina* sp.) and illustrated on the left of J. de C. Sowerby's plate 648, figure 2 is lectotype (NHMUK In. 17027); it was refigured by Gale (2021, pl. 1, figs 4, 5) and came from the Bartonian (Barton Clay Formation) at Barton, Hampshire. The two smaller individuals on the right of the same figure are paratypes, also attached to a shell of *Ampullina* sp., from the same locality (NHMUK In. 17028).

Material – Several thousand isolated parietal plates and opercular valves from the Lutetian of Campbon (Loire-Atlantique; NHMUK IC 1974-1992), plus a single articulated wall and approximately 125 isolated valves from the Bartonian of Florești (Romania; NHMUK IC 1995-2003).

Remarks – Discovery of abundant material from the Lutetian (Campbon) and Bartonian (Florești) permits a fuller understanding of the morphology of this species, particularly of the opercular plates, which are poorly known from UK material (Gale, 2021). The ribbing of the parietal plates is highly variable within an assemblage, ranging from specimens which are completely smooth (*e.g.*, Pl. 5, figs 3, 7; Pl. 7, fig. 6) through to individuals which bear strong, evenly spaced ribs (*e.g.*, Pl. 5, fig. 5; Pl. 7, figs 1, 2, 4, 5). In the Campbon material, a preponderance of the wall plates are smooth (>80%), whereas in the one from Florești over 70% are strongly ribbed.

Both the Campbon and Florești assemblages contain numerous, well-preserved opercular plates (Pl. 6 figs 6, 8; Pl. 7, figs 7-11). The terga are distinctive in that the spur furrow is shallow and is not overfolded by a ridge on the scutal surface of the valve, and the notch created between the tergal spur and the scutal margin has right-angled or slightly obtuse margins (Fig. 5A). Additionally, the growth lines on the scutal surface of the tergum are symmetrically arched and widely spaced. These features provide consistent criteria with which to separate *V. erisma* and *V. unguiformis* (Fig. 5; Pl. 6, figs 2-4, 9).

Occurrence – *Vectibalanus erisma* is locally abundant in the Lutetian and Bartonian of the United Kingdom, France and Romania.

Conclusions

The capitular morphology of the enigmatic genus *Aporolepas* is reconstructed for the first time on the basis of numerous isolated valves of *A. reflexa* from the Bembridge Oyster Bed (Priabonian) of the Isle of Wight (UK). This species has 15 capitular plates and is provisionally transferred to the Calanticidae, from the Zeugmatolepadidae. *Aporolepas angulata* var. c*repidula* Withers, 1953 is redescribed on the basis of new material from the Lutetian of Campbon (Loire-Atlantique, France) and elevated to species rank. An undescribed species of *Aporolepas* is recognised from the Bartonian of Florești (Romania), constituting the first record of the genus from eastern Europe. A single carina from Campbon is provisionally referred to the scalpellid genus *Virgiscalpellum*, and if correct, is the first post-Cretaceous record of the genus. *Scalpellum* sp. nov. is recorded from the Bartonian of Florești (Romania).
The balanomorph species *Vectibalanus erisma*, first described from the Bartonian of the Hampshire Basin (UK), is recorded as occurring abundantly in the Lutetian of Campbon (France) and the Bartonian of Florești (Romania). *Vectibalanus mortoni* and *Archaeobalanus semicanaliculatus* are identified as junior synonyms of *V. erisma*. A distinctive middle-late Eocene fauna, dominated by *Aporolepas* and *Vectibalanus,* extends from the Gulf coast of the USA, through northwest Europe to Romania in eastern Europe, and both genera were able to live in brackish water palaeoenvironments with salinities of 9-30 ppt. Assemblages of *Vectibalanus* are very rarely bored by predatory gastropods which is unusual for Cainozoic balanomorphs.

Acknowledgements

NT wishes to thank Viorel Arghiuș for reporting the fossiliferous potential of the Florești outcrop and Ms Anca Jeler for her help with the logistics of transporting the material studied. The samples in which the Campbon valves were recovered were kindly provided by Malcolm Symonds and Olivier Gain. Thanks are also addressed to Alexandru Solomon for discussion on the geological settings, and to the journal reviewers, Ray T. Perreault and John W.M. Jagt for pertinent comments on an earlier version of the typescript.

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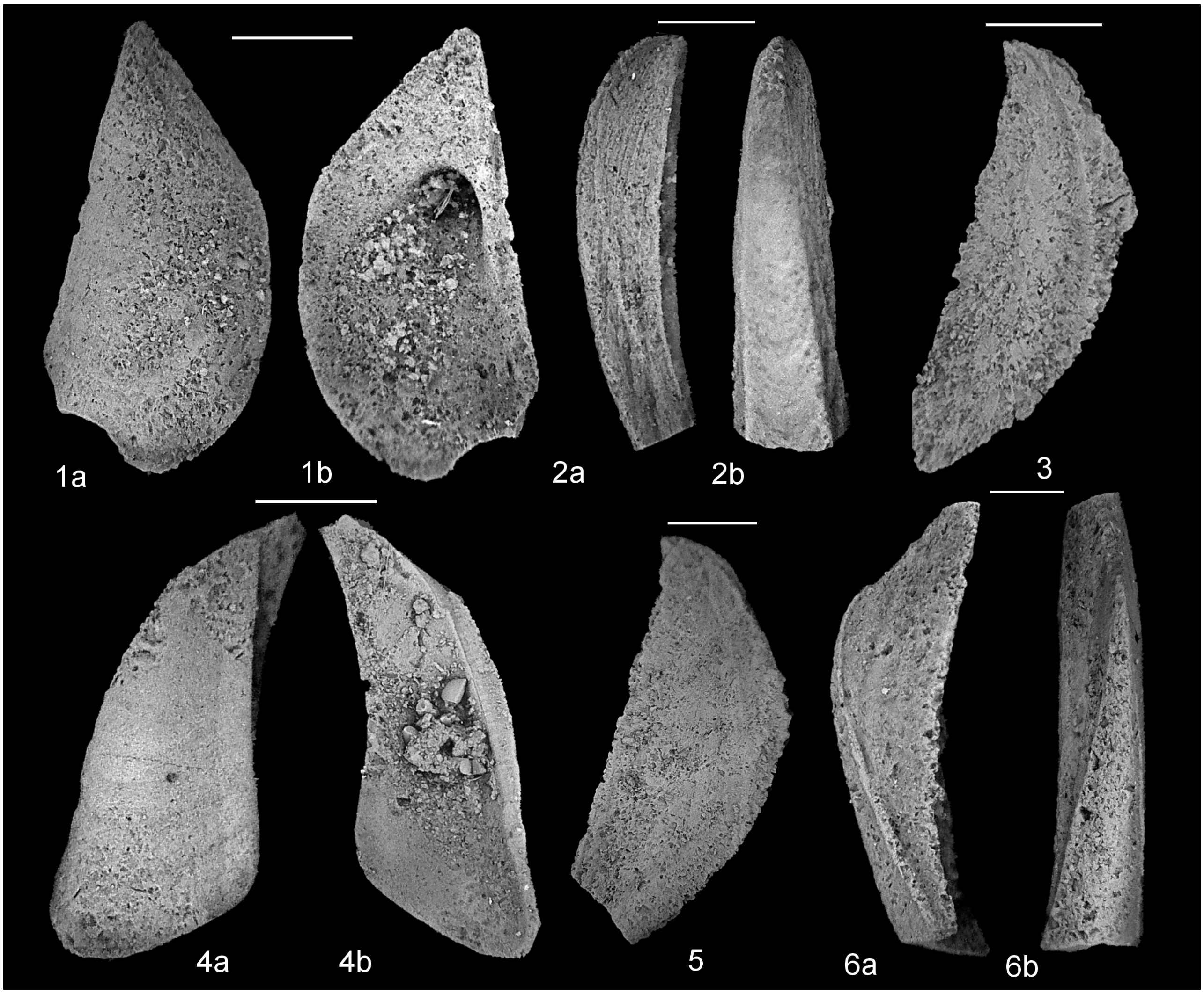

Plate 2. *Aporolepas* sp.: 1. scutum, in external and internal views, respectively (NHMUK IC 1944). *Scalpellum* sp. nov.: 2, 6. carinae, in lateral and dorsal views, respectively NHMUK IC 1945, 1949); 3, 5. terga, in external view (NHMUK IC 1946, 1948); 4. scutum, in external and internal views, respectively (NHMUK IC 1947). Provenance: Bartonian (NP17 Biozone), Ciuleni Member (Mortănușa Formation), left bank of the River Someșul Mic, Florești Dam, Florești (Romania). Scale bars equal 5 mm (1, 5) and 2 mm (2-4, 6).

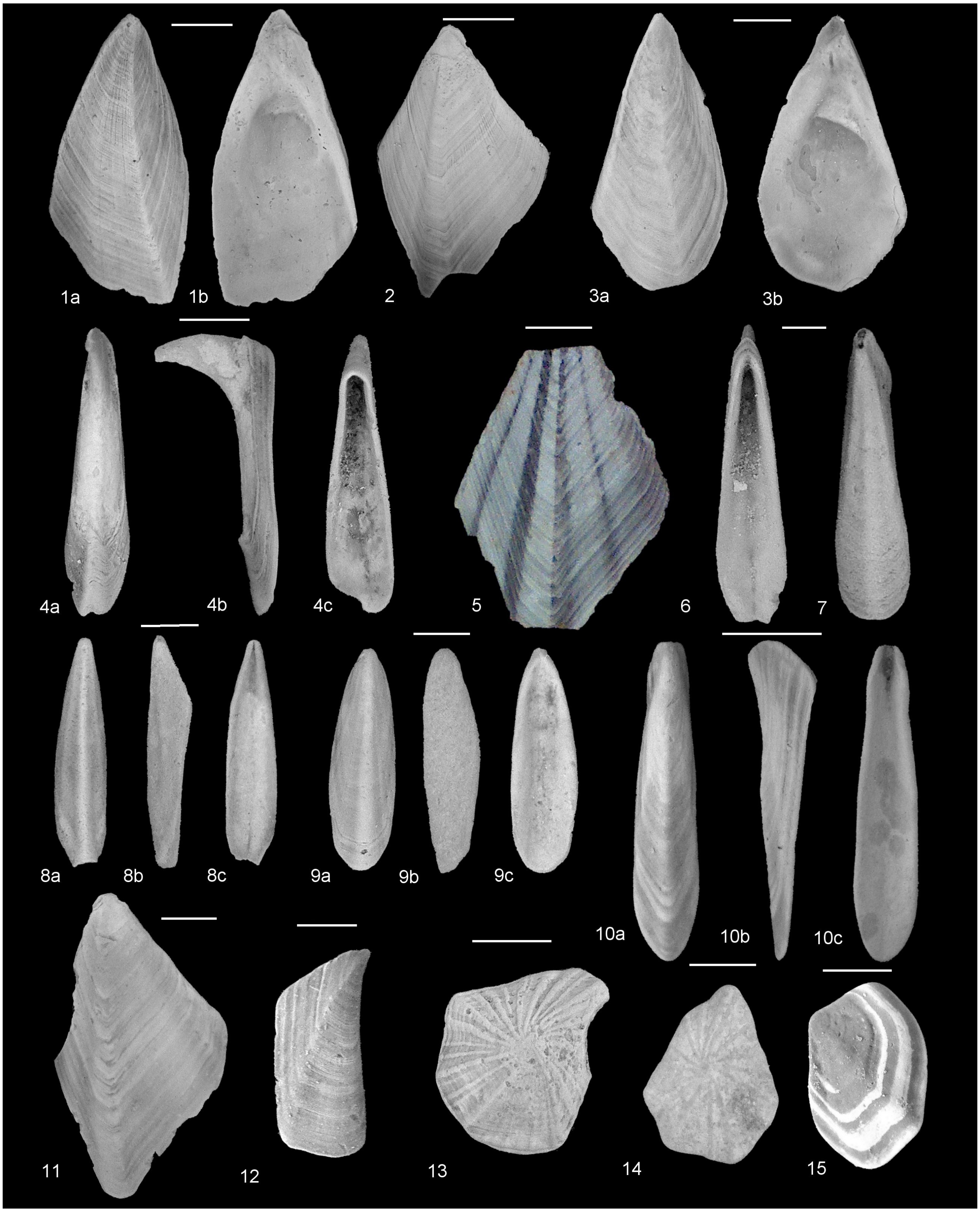

Plate 3. *Aporolepas crepidula* Withers, 1953: 1, 3. scuta, in external and internal views, respectively (NHMUK IC 1950, 1952); 2, 5, 11. terga, in external view; the one in Fig. 5 retains the original colour pattern (NHMUK IC 1951, 1954, 1959); 4, 6, 7, 10. carinae, in dorsal, lateral and internal views (4, 10) (NHMUK IC 1953, 1958), in internal view (6) (NHMUK IC 1955) and in dorsal view (7) (NHMUK IC 1956); 8, 9. rostra, in ventral, lateral and internal views, respectively (NHMUK IC 1957); 12. upper latus, in external view (NHMUK IC 1960). 15, lower latus of "type 2" of Withers 1953, p. 125 (NHMUK IC 1963). *Scalpellum fischeri* forma *costatum* Withers, 1953: 13. inframedian latus (NHMUK IC 1961); 14, upper latus (NHMUK IC 1962). Provenance: Lutetian of Bois-Gouët (Loire-Atlantique, France) (10, 13, 14); all others from the Lutetian of Campbon (Loire-Atlantique, France). Scale bars equal 5 mm (1-4, 10) and 3 mm (5-9, 11-15).

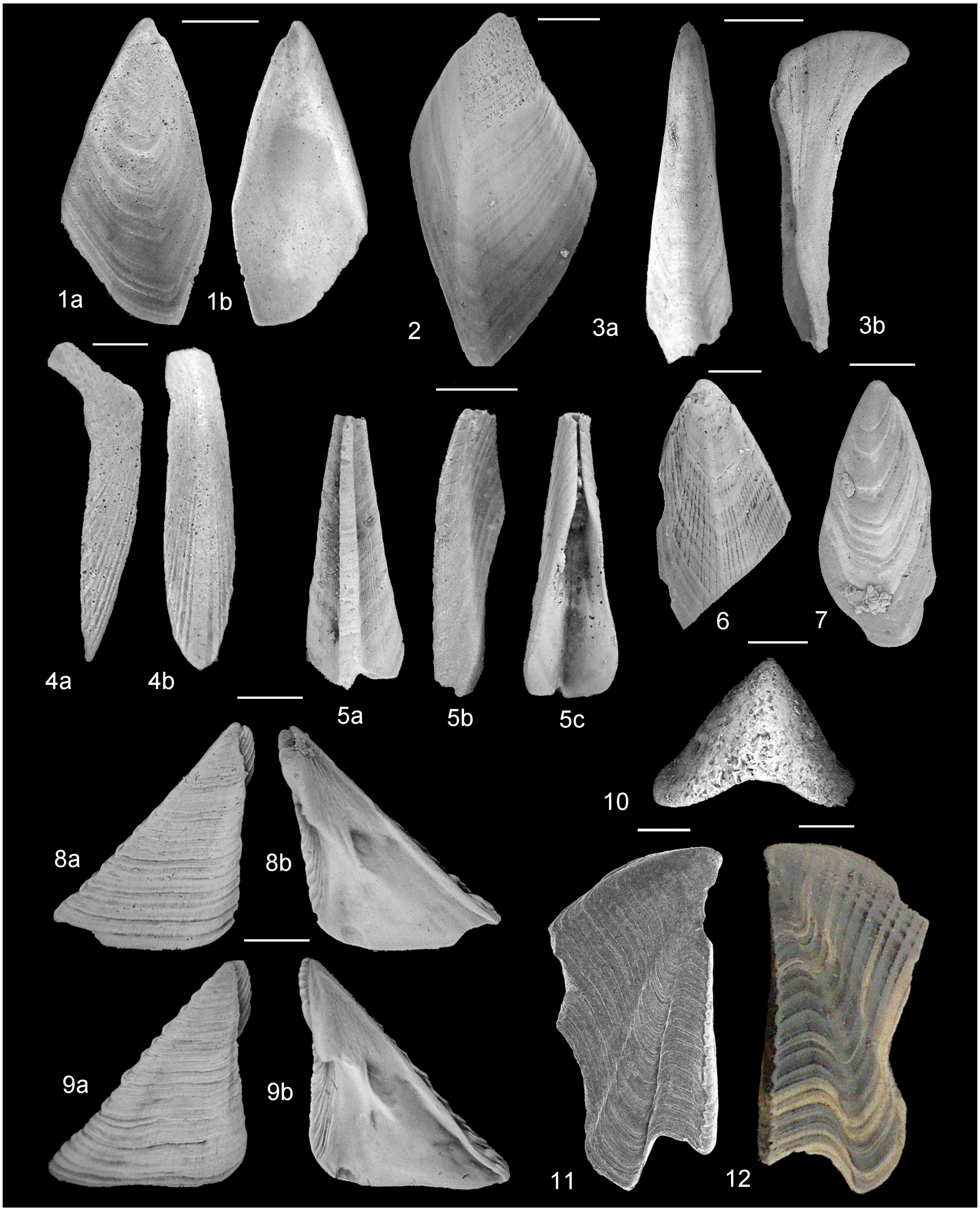

Plate 4. *Aporolepas crepidula* Withers, 1953: 1. scutum, in external and internal views, respectively (NHMUK IC 1964); 2. tergum, in external view (NHMUK IC 1965); 3. carina, in external and lateral views, respectively (NHMUK IC 1966); 5. small carina in dorsal (5a), lateral (5b) and ventral (5c) views. (NHMUK IC 1967a); 6. external view of scutum (NHMUK IC 1967b); 7. small scutum, in external view (NHMUK IC 1970). ?*Virgiscalpellum* sp.: 4. carina, in lateral and dorsal views, respectively (NHMUK IC 1967). *Vectibalanus erisma* (J. de C. Sowerby, 1846): 8, 9. scuta, in external and internal views, respectively (NHMUK IC 1971, 1972); 11, 12. terga, in external view (NHMUK IC 1974, 1975). ?Cretiscalpellidae: 10. rostrum, in ventral view (NHMUK IC 1973). Provenance: Bartonian (NP17 Biozone), Ciuleni Member (Mortănușa Formation), left bank of River Someșul Mic, Florești Dam, Florești (Romania) (Fig. 10); all other specimens from the Lutetian of Campbon (Loire-Atlantique, France). Scale bars equal 5 mm (1, 3), 3 mm (4-7) and 1 mm (8-12).

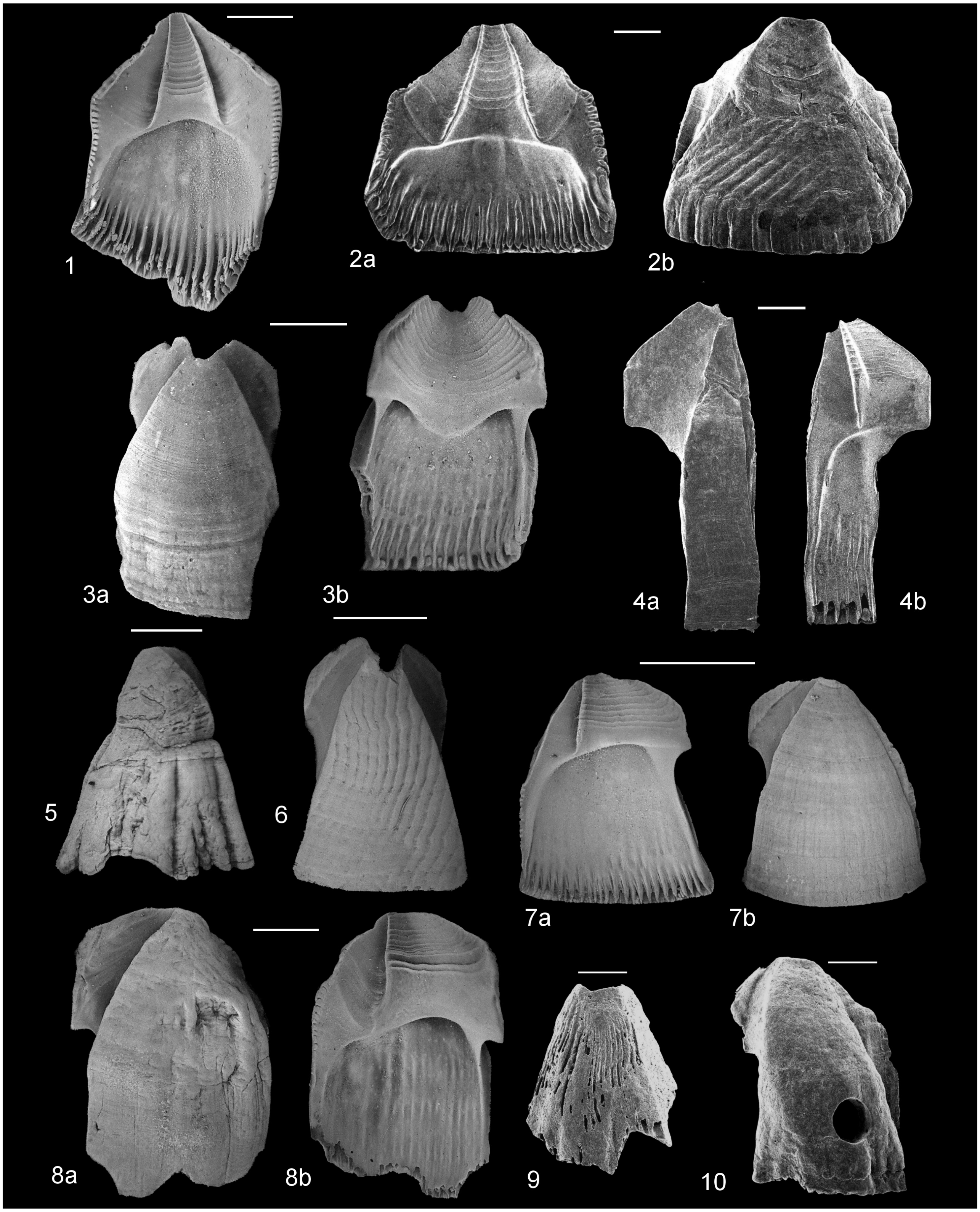

Plate 5. *Vectibalanus erisma* (J. de C. Sowerby, 1846), compartments: 1, 2. rostral plates, comprising fused rostrum and rostro-marginals, in internal view (1, NHMUK IC 1976) and in internal (2a) and external (2b) views of specimen with xenomorphic markings (NHMUK IC 1977); 3, 5, 6, carinae: 3. smooth carina in external and internal views, respectively (NHMUK IC 1978); 5. carina with strong irregular ribbing (NHMUK IC 1984); 6. external view of carina with xenomorphic markings (NHMUK IC 1985); 4. carinomarginal, in external (a) and internal (b) views, respectively (NHMUK IC 1979); 7, 8. marginals, in external (7b, 8a) and internal (7a, 8b) views, respectively (NHMUK IC 1986, 1987); 9. apical portion of worn plate, to show longitudinal pores (NHMUK IC 1988); 10. marginal plate with gastropod boring (ichnotaxon *Oichnus simplex* Bromley, 1981; NHMUK IC 1989). Provenance: Lutetian, Campbon (Loire-Atlantique, France). All scale bars equal 1 mm.

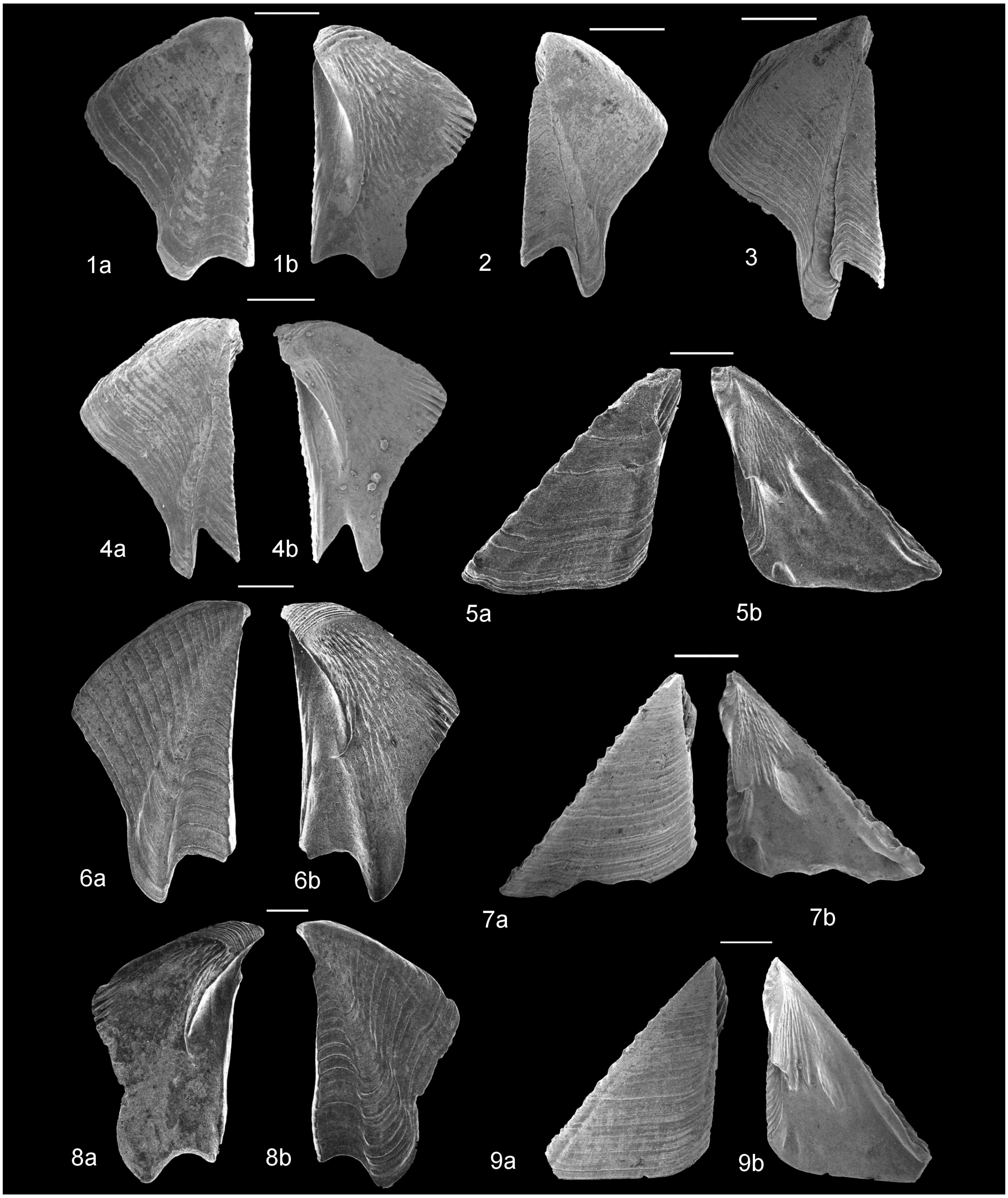

Plate 6. Opercular plates of *Vectibalanus* spp.: 1, 5-8. *Vectibalanus erisma* (J. de C. Sowerby, 1846); 1. holotype of *V. mortoni* Gale, 2021 (the original of Gale, 2021, pl. 8, fig. 1), in external and internal views, respectively (NHMUK IC 1913); 5. scutum, in external and internal views, respectively (NHMUK IC 1990); 7. paratype scutum of *V. mortoni* Gale, 2021 (the original of Gale, 2021, pl. 8, figs 11, 12), in external and internal views, respectively (NHMUK IC1915); 6, 8. terga, in external and internal views, respectively (NHMUK IC 1991, 1992). 2-4, 9. *Vectibalanus unguiformis* (J. de C. Sowerby, 1846); 2, 3. terga, in external views; 2 is the original of Gale (2021, pl. 8, fig. 7; NHMUK IC 1918), 3 is the original of Gale (2021, text-fig. 12A, B; NHMUK IC 1921); 4. tergum, in external and internal views; the original of Gale (2021, pl. 8, figs 5, 6; NHMUK IC 1917); 9. scutum, in external and internal views, the original of Gale (2021, pl. 8, figs 9, 10; NHMUK IC1920). Provenance: middle Barton Clay (Bartonian), Barton, Hampshire (UK) (1, 7); upper Venus Bed, Colwell Bay Member, Headon Hill Formation (Priabonian), Whitecliff Bay, Isle of Wight, UK (2-4, 9); Lutetian, Campbon (Loire-Atlantique, France) (5, 6, 8). Scale bars equal 3 mm (1-3, 9) and 1 mm (4).

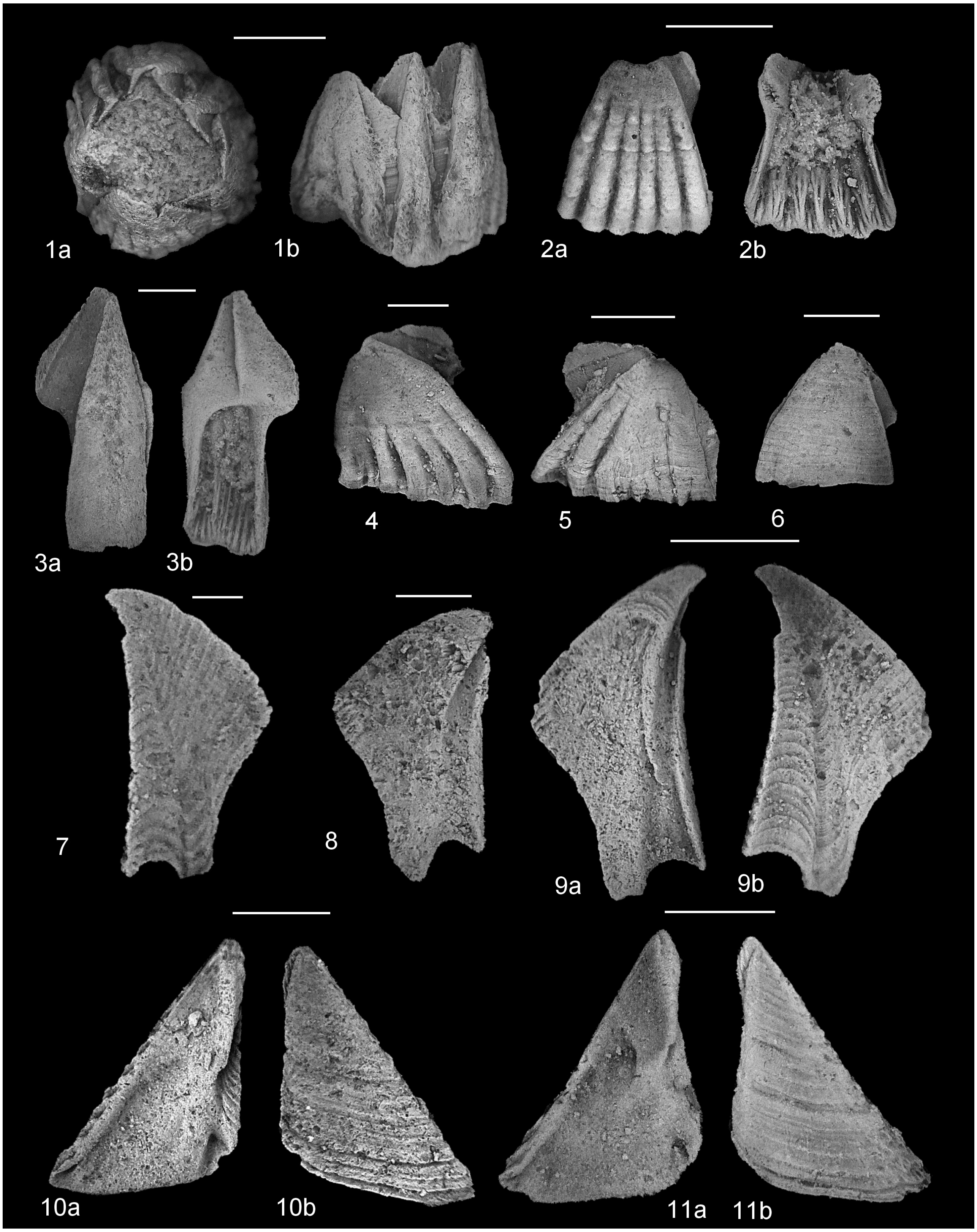

Plate 7. *Vectibalanus erisma* (J. de C. Sowerby, 1846): 1. complete shell in apical and lateral views, respectively (NHMUK IC 1993); 2. strongly ribbed carina in external and internal views, respectively (NHMUK IC 1994); 3. carinomarginal, in external and internal views, respectively (NHMUK IC 1995); 4, 5. ribbed marginal plates, in external view (NHMUK IC 1996, 1997); 6. marginal plate with smooth exterior (NHMUK IC 1998); 7-9. terga: 7. small tergum, in external view (NHMUK IC 1999); 8. internal view (NHMUK IC 2000); 9. large tergum, in internal and external views, respectively (NHMUK IC 2001); 10, 11. scuta, in external and internal views, respectively (NHMUK IC 2002, 2003), Provenance: Bartonian (NP17 Biozone), Ciuleni Member, left bank of River Someșul Mic, Florești Dam, Florești (Romania). Scale bars equal 5 mm (1), 2 mm (2-11) and 1 mm (7).