Acorn barnacles (Crustacea, Thoracica, Balanomorpha) from the Eocene and Oligocene of the Isle of Wight and Hampshire (United Kingdom) and Manche, northern France

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ABSTRACT:

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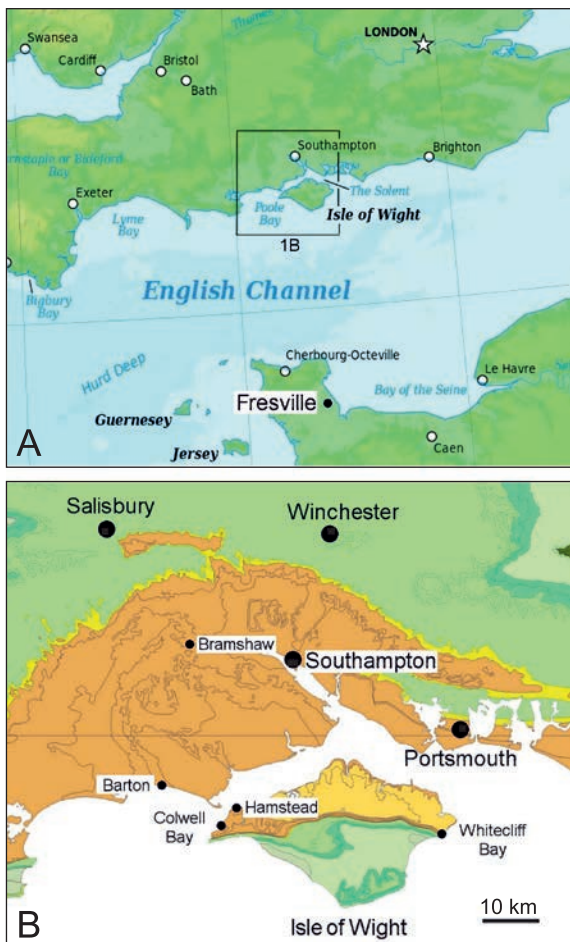
Balanomorph cirripedes from the Eocene–Oligocene of the Hampshire Basin (United Kingdom) and the Middle Eocene of the Cotentin Peninsula, Manche (France) are described. A new genus, *Vectibalanus*, is founded, with the type species *Balanus unguiformis* J. de C. Sowerby, 1846; assigned to this are also *Balanus erisma* J. de C. Sowerby, 1846 and *Vectibalanus mortoni* sp. nov. In addition, a new species of *Lophobalanus* Zullo, 1984, *L. fresvillensis* sp. nov., is described. This is the first record of that genus from outside the eastern USA and the oldest species known to date. Cladistic analysis of 24 morphological characters suggests that *Vectibalanus unguiformis* is sister taxon to a group comprising the most derived balanomorph taxa, and thus represents an important transition in the evolution of the group, with the initiation of development of a complex parietal wall structure. *Vectibalanus unguiformis* was evidently adapted to low salinity habitats (10–30 ppt), and is the oldest known brackish water barnacle. The other species (*V. erisma*, *V. mortoni* sp. nov.) occupied more clearly marine environments (>30 ppt). Balanomorph barnacles appeared simultaneously in the Priabonian (Upper Eocene) of the Gulf and Atlantic seaboards of the USA and northwest Europe, which probably represents a northerly migration from Tethys.

Key words: Acorn barnacles; Paleogene; Northwest Europe; New taxa.

INTRODUCTION

In 1846, James de Carle Sowerby illustrated fossil balanomorph barnacles in the *Mineral Conchology of Great Britain*, giving specimens the names *Balanus unguiformis* and *Balanus erisma* on plate 648, figure 1, but without any explanation or description. Charles Darwin (1854a) discovered that the original material came from the Eocene of the Hampshire Basin (United Kingdom) and described the species in some detail, deciding that *B. erisma* was a variety of *B. unguiformis*, and that Sowerby's material probably included a further, undescribed species. Although balanomorph material from the Eocene of the Hampshire Basin is common at some stratigraphical levels and localities (e.g., Forbes 1856; White 1921; Withers 1953; Stinton 1971), Darwin (1854a) remains the last publication actually figuring specimens. The UK species has been referred to in various publications dealing with Eocene balanomorphs (e.g., Ross 1965; Zullo 1966; Ross and Newman 1967) and *B.* aff. *unguiformis* has been

Text-fig. 1. A – Map of the English Channel to show the position of Text-fig. 1B, and the location of Fresville on the Contentin Peninsula (France). B – Geological map of part of the Hampshire Basin to show important localities and major cities. Highcliffe is 2.7 km west of Barton. Shades of yellow/brown = Paleogene; shades of green = Cretaceous.

recorded from the Eocene of Alabama (Ross and Newman 1967). Several other species and genera of balanomorphs have been described from the Eocene of the Gulf and Atlantic coastal plains of the USA (Zullo and Kite 1985), including *Kathpalmeria geor-giana* Ross, 1965 and *Hesperibalanus huddlestuni* Zullo and Kite, 1985.

Menesini (1971) described new balanomorphs from the Eocene and Oligocene of the Paris Basin (France), under the names of *Balanus (Archaeobalanus) semi-canaliculatus* and *B. (Hesperibalanus) parahesperius*. The first-named was described as having very irregu-larly developed parietal tubes, a derived feature in bal-anomorphs. However, she did not compare these spe-cies with *B. unguiformis* from contemporaneous rocks
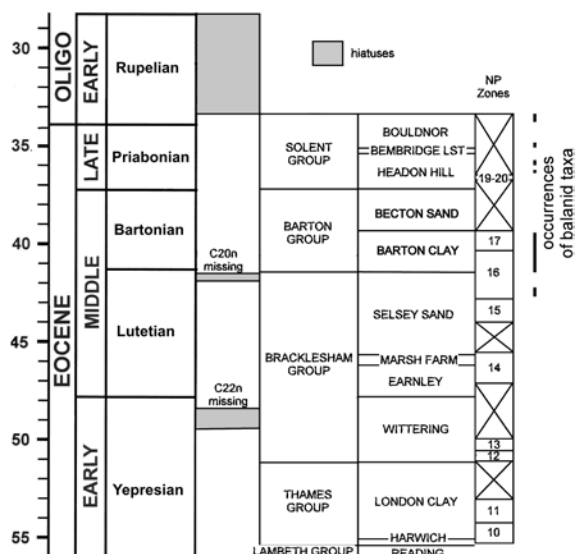
in the adjacent Hampshire Basin. The stratigraphical details and occurrences of the Paris Basin records were summarised by Plaziat and Cavelier (1973).

Balanomorph (acorn) barnacles are one of the great evolutionary success stories of the thoracican cirripedes, having lost the peduncle and evolved a rigid, firmly articulated (sometimes fused) wall of four to eight plates, surrounding an orifice within which the four opercular plates (paired terga and scuta) fit precisely, attached to the shell by a strong membrane (Darwin 1854a, b; Newman and Ross 1976; Anderson 1994; Southward 2008). Opening the median slit of the operculum permits extension of the cirri (modified limbs) for feeding, copulation, release of eggs and closure, by means of specialised musculature, provides protection and considerable resistance to desiccation. Balanomorphs have suc-cessfully colonised the intertidal to subtidal environ-ments of all the world's oceans through the Cenozoic, and extended into the deep sea. The balanomorphs originated during the Late Cretaceous (Gale and Sørensen 2015) and underwent a major radiation in the Paleocene, the details of which are not well under-stood, and only two taxa are known from this period (Buckeridge 1983). Balanomorphs were moderately diverse and widely distributed during the Eocene, but the precise relationships of many taxa with mod-ern forms are contentious (e.g., Zullo 1966; Zullo and Kite 1985). Molecular studies of balanomorphs (Pérez-Losada *et al.* 2014; Chan *et al.* 2017) provide a convincing phylogeny, which requires calibration by fossil species.

The present study was stimulated by new ma-terial from the Eocene of the Isle of Wight and the Hampshire coast (Text-fig. 1) collected by Alan Morton, Adrian Smith and the author. Alan Morton has found numerous very well-preserved specimens of articulated balanomorphs, and the author exten-sively sampled and processed all horizons from which material has been recorded. Stephen Tracey pro-vided a unique specimen from the Lutetian (Middle Eocene) of Cotentin, Manche (France).

STRATIGRAPHY AND LOCALITIES

The stratigraphy of the Eocene and Oligocene of the Hampshire Basin has recently been extensively reviewed and revised (King 2016) and correlated to the international Geological Time Scale (Speijer *et al.* 2020). This correlation is based largely upon a combination of magnetostratigraphy and nannofossil evidence (Text-fig. 2).

Text-fig. 2. Stratigraphy of the Paleogene (Eocene–Oligocene) succession in the Hampshire Basin (modified from King 2016) and the levels of occurrence of balanomorph (balanid) taxa. The leftmost column gives ages in Ma. Oligo stands for Oligocene; NP stands for nannoplankton.

The oldest balanomorph material from the Hampshire Basin comes from the 'Brook Bed' in the Selsey Sand Formation (Bracklesham Group), at Bramshaw in inland Hampshire, which has been dated as earliest NP16 (King 2016, p. 412). The overlying Barton Clay Formation (Barton Group) has yielded important cirripede material on the Hampshire coast between Barton (Barton on Sea) and the nearby Highcliffe (Text-fig. 1), with records extending through the Naish Member (equivalent to Beds A1–3 of the older classification) and overlying Highcliffe Member (beds B–E) shown by King (2016). The boundary between zones NP16 and NP17 falls within the lower part of the Naish Member (King 2016).
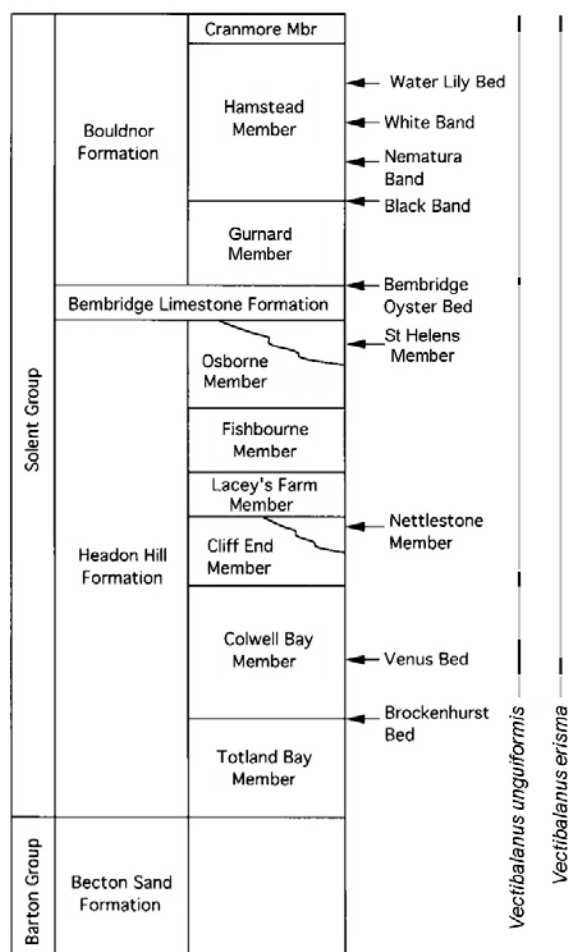
The Solent Group of the Isle of Wight (Text-fig. 3) has yielded abundant balanomorph material from specific levels within the Headon Hill Formation and the base of the Gurnard Member of the Bouldnor Formation. The succession is well exposed in Whitecliff Bay (Gale *et al.* 2006; Text-figs 1 and 4 here), where the upper part of the Venus Bed (Colwell Bay Member) contains numerous articulated balanomorphs attached to the apertural regions of the gastropod *Ptychopotamides vagus* (Solander in Brander, 1766). The Bembridge Oyster Bed, at the base of the Gurnard Member, yields abundant valves and some articulated individuals. The Venus Bed in Colwell Bay, in the west of the Isle of Wight (Text-fig. 1), has

been a rich source of cirripedes since the 19th century. Balanomorphs also occur in the highest unit of the Solent Group preserved, the Cranmore Member of the Bouldnor Formation, on Hamstead Cliff in the west of the Isle of Wight (Text-fig. 3), which represents a brackish-marine transgression of early Rupelian age (King 2016).
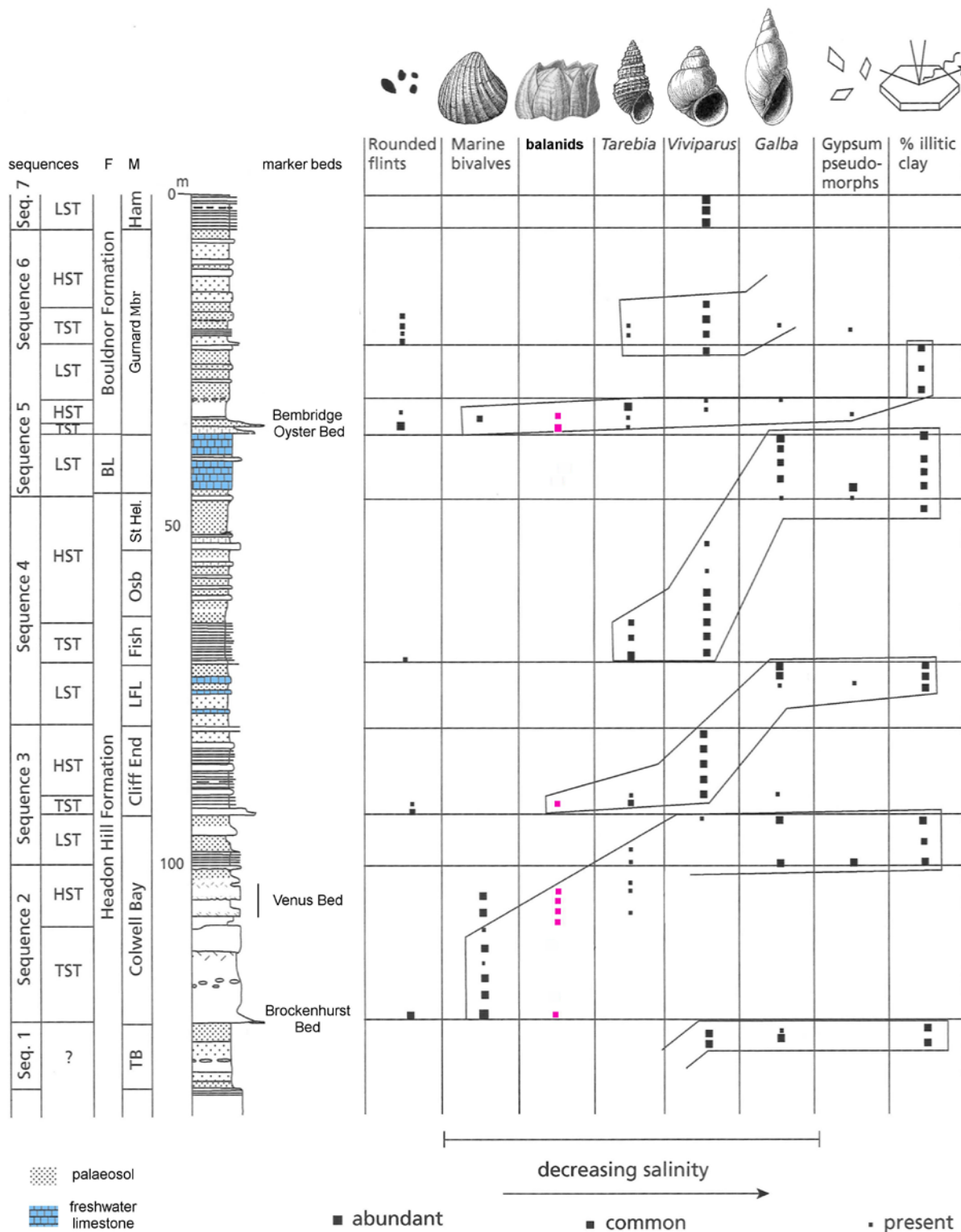
An outlier of Faluns de Hautteville-Bocage (Lutetian, Middle Eocene), at Fresville, on the Cotentin Peninsula (Manche, France; see Dugué *et al.* 2012) has yielded a single, very well-preserved balanomorph shell.
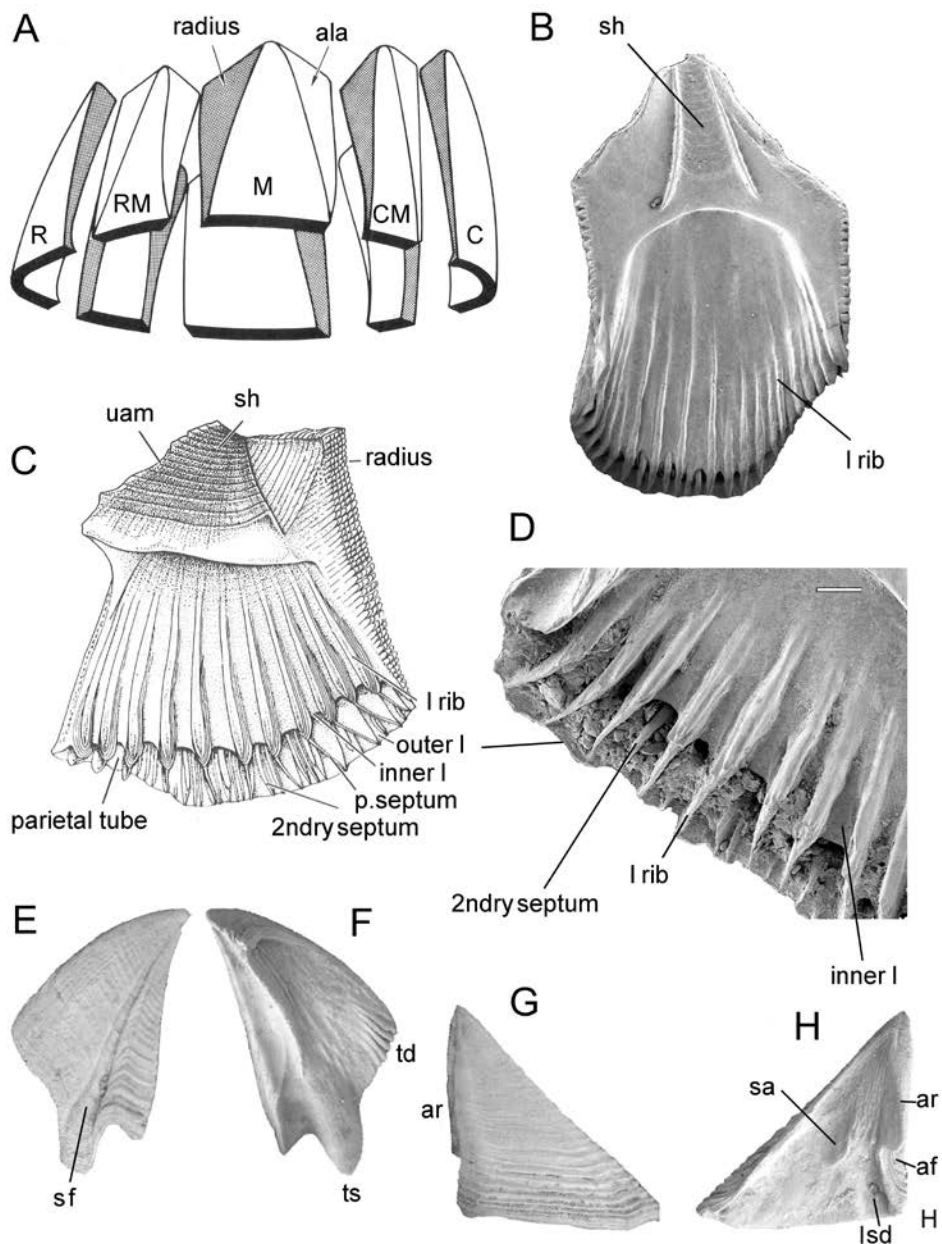
METHODS

All specimens retrieved were collected by surface picking, or manual disaggregation of samples. Valves, including abundant opercular plates, were

Text-fig. 3. Stratigraphy of the Solent Group on the Isle of Wight (modified after Gale *et al.* 2006, fig. 2), and the occurrence of balanomorph taxa.

Text-fig. 4. Stratigraphical succession through the Solent Group (Priabonian) in Whitecliff Bay, Isle of Wight (see Text-fig. 1) to show the distribution of balanomorphs in relation to lithostratigraphy, sequence stratigraphy and salinity. Abbreviations; F, Formations; M, Members; TB, Totland Bay Member; LFL, Laceys Farm Limestone; Fish, Fishbourne Member; Osb, Osborne Member; St Hel., St Helens Member; BL, Bembridge Limestone Member; Ham., Hamstead Member; TST, transgressive system tract; LST, lowstand system tract; HST, highstand system tract (modified after Gale *et al.* 2006, fig. 4).

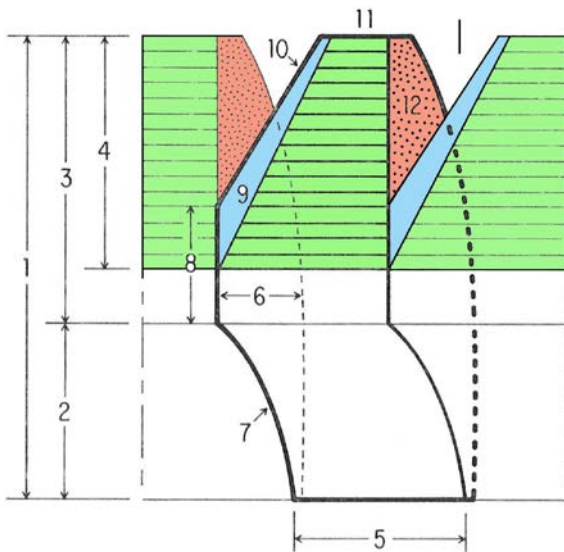Text-fig. 5. Nomenclature of balanomorph plates. A – overall construction of 8-plated balanomorph; R, rostrum; RM, rostromarginal; M, marginal; CM, carinomarginal; C, carina. B – internal view of rostral plate in *Vectibalanus unguiformis* (J. de C. Sowerby, 1846) formed by fusion of R and RM, to show sheath (sh) and longitudinal internal ribbing (l rib). C – interior view of marginal of *Amphibalanus amphitrite* (Darwin, 1854) (after Newman *et al.* 1969, fig. 105.1). Abbreviations: sh, sheath; p. septum, primary septum; inner l., inner layer; outer l., outer layer; sam, superior alar margin (see also Text-fig. 6). D – detail of base of *Vectibalanus* gen. nov. marginal plate to show contact with basis. E, F – external (E) and internal (F) views of tergum of *Vectibalanus unguiformis* to show spur fasciole (sf), tergal depressor attachment (td) and tergal spur (ts). G, H – external (G) and internal (H) views of scutum of *Vectibalanus unguiformis* to show articular furrow (af), articular ridge (ar), scutal adductor scar (sa) and lateral scutal depressor scar (lsd).

obtained by washing moderately large samples (10–20 kg), screening and picking the + 0.5 mm fraction under a binocular microscope. The specimens were photographed using a dinolite USB microscope, or if small, imaged in a SEM. Valves were thin sectioned for study of the wall structure.

Text-fig. 6. Construction and nomenclature of balanomorph wall plating. A, B – carinomarginal, external and internal views. C, D – marginal. E, F – rostral plate, fused rostromarginal+ rostrum. G, H – carina. I – partly dissociated interior view to show plate articulations. A–H – *Chirona hameri* (Ascanius, 1767); I – *Solidobalanus fallax* (Broch, 1927). Abbreviations: aas – alar articular surface; iaa – internal alar articulation; r – radius; rp – rostral plate; M – marginal plate; CM – carinomarginal plate.

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Text-fig. 7. Nomenclature of compartments in balanomorphs. 1 – total height; 2 – height below sheath; 3 – height of entire sheath; 4 – height of sheath with growth lines created by recession of opercular membrane; 5 – width of basal margin; 6 – width of ala; 7 – inferior alar margin; 8 – alar angle; 9 – welting; 10 – superior alar margin; 11 – apex; 12 – portion of wall overlapping adjacent plate, without radii, the radii being the exterior counterpart of the welting (modified after Newman and Ross 1971, fig. 70).

BALANOMORPH NOMENCLATURE

Nomenclature for balanomorph cirripede plate morphology is largely derived from Charles Darwin's classic studies (Darwin 1854a, b). The plates making up the wall are called compartments, and each is divided into a central parietes and lateral processes which either overlap the adjacent plates, called radii, or are overlapped, called alae (Text-figs 5A, C, 6, 7). The lateral compartments were re-named as marginals, because the original homology with lateral plates of pedunculated cirripedes was proved to be incorrect (Gale and Sørensen 2015). Thus, in a 6-plated form, the wall is made up of a carina, a rostrum and paired marginals, rostromarginals and carinomarginals (Text-fig. 5A). In most derived balanomorphs (4- and 6-plated), the rostrum and rostromarginal have fused to form a rostral plate (Text-fig. 6E, H). Details of compartment nomenclature are provided in Text-fig. 7. The parietes may have a single outer layer (monolamellar), or possess an inner layer with the development of parietal tubes between the two (Text-fig. 5C, D). The opercular plates comprise paired scuta and terga which fit within the diamond-shaped orifice, and articulate with the smooth
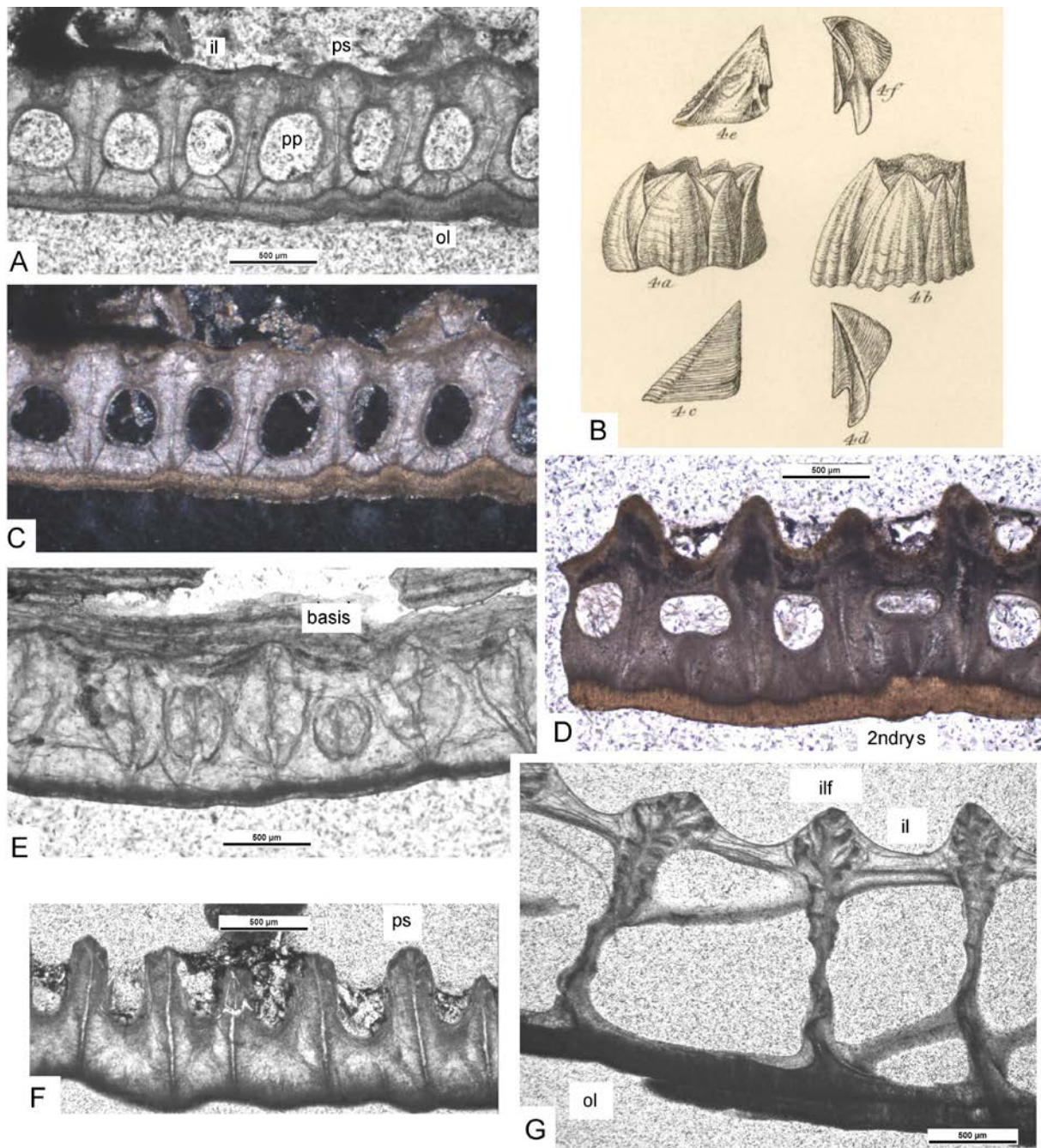
inner rim which is called a sheath (Text-figs 5, 6). Nomenclature for opercular plates (Text-fig. 5E–H) is taken from Zullo (1992), who distinguished between a spur furrow, in which the borders of the furrow are overfolded, and a shallow spur fasciole in which they are not.

WALL STRUCTURE

Wall structure in balanomorphs has been studied quite extensively (De Alessandri 1895; Cornwall 1962; Davadie 1963; Newman *et al.* 1969; Newman and Ross 1976), and has informed classification of the group, as there is a consensus that more complex structures (e.g., pores in parietes and basis, pores in radii, interlaminate figures) are indicative of more derived states.

Charles Darwin (1854a, p. 30) noted that in *Balanus unguiformis*, "The species, as yet the oldest one known, presents to the systematist a most unfortunate peculiarity, in the parietes being almost as often as not permeated by small pores." This was discussed by Kolosváry (1956) and Newman and Ross (1967), who argued that the parietal pores in this species were not homologous with those in "true *Balanus*." Davadie (1963) illustrated the transverse section of a wall of *B. unguiformis* (his pl. 40, fig. 5) in which he identified pores, and also remarked that these were not always present.

The complex parietal structure of balanids is related to the development of articular structures between the basis and base of the wall, where interlocking longitudinal (in the wall) and radiating (in the basis) septa develop. These may also display branch-like lateral denticles. The septa, set at right angles to the outer wall of the parietes, are formed of a narrow central sheet of calcite, called the longitudinal rib (Newman *et al.* 1969, fig. 105/2), on either side of which fine calcite crystals develop, the c-axes of which are parallel with the parietal wall. Denticles are formed as lateral processes from the central rib, from which obliquely oriented calcite crystals grow. In transverse sections of the wall of derived balanids, the septa appear as tree-like structures called interlaminate figures, which have been used in taxonomy (Davadie 1963; Newman *et al.* 1969). As the barnacle grows, the septa become incorporated into the parietal wall structure, and may become conjoined by a sheet of calcite called an inner lamina, such that the grooves between the septa become longitudinal pores. Transverse or oblique partitions can develop within the pores, or they may be partially or completely infilled with calcite.

Text-fig. 8. Structure of balanomorph parietal wall. **A, C–E** – transverse sections of parietes of *Vectibalanus unguiformis* (J. de C. Sowerby,1846), from the upper Venus Bed, Whitecliff Bay, Isle of Wight (lower Priabonian). A, C – section of lower wall of marginal plate; A – plane polarised light; C – crossed nicols; note inner and outer laminae (il, ol), parietal tubes (pt) and primary septum (ps); D – section of parietes to show secondary septa (2ndry septa); E – transverse section of parietes with basis attached; the hoof-shaped regions are secondarily infilled parietal tubes (pp). **B** – Darwin's illustration of *Balanus unguiformis* J. de C. Sowerby, 1846 (from Darwin 1854b, pl. 2, fig. 4a–f). **F** – transverse section of parietes of *Chirona hameri* (Ascanius, 1767) to show primary septum (ps). **G** – transverse section of parietes of *Balanus crenatus* Bruguière, 1789, to show tall interlaminate figures (ilf), transverse septum (ts), inner and outer layers (il, ol).

The basic wall structure solid-walled balanids is shown here in *Chirona* (Text-fig. 8F), in which simple septa are developed. In the derived *Balanus crenatus* Bruguière, 1789 (Text-fig. 8G) the septa are

tall and have complex interlaminate structure, reflecting the extensive developments of denticles at the basis-parietal boundary and transverse septa are developed. In neither of these taxa is the outer lamina sharply demarcated from the septa.

The parietal structure of *Archaeobalanus semicanaliculatus* was illustrated by a series of transverse thin sections (Menesini 1971, pl. 5, figs 6–8; pl. 6, figs 1–8; pl. 7, figs 1–4). Pores are only locally developed and very variable in size. This condition appears to be unique.

The arborescent septal structure found in derived balanids is a consequence of the growth of complex, highly structured denticles at the basal contact. Although the septa are denticulate in some specimens of *V. unguiformis*, these do not have a comparable internal structure (Text-fig. 8A, C–E). The sharply demarcated peripheral wall found in *V. unguiformis* (and in *A. semicanaliculatus*) appears to be crystallographically and chemically different from inner layers and does not appear to have any parallel in other balanids; this needs further investigation. The presence of secondary calcite infilling the pores of some specimens of *V. unguiformis* (e.g., Text-fig. 8E) might explain why Darwin (1854a) and Ross and Newman (1967) observed pores in some specimens but not in others.

PHYLOGENY

The relationships of *Vectibalanus* gen. nov. (see below) to other Balanomorpha was investigated using cladistic analysis of 24 morphological characters (Tables 1, 2), a list modified from Pitombo (2004), who only studied more derived taxa generally ascribed to the Balanidae. A pachylasmatid and two bathylasmatids were used as outgroups in the present study, and unconstrained heuristic analysis, optimised to Deltran was applied. This generated a consensus tree (Text-fig. 9) which is stratigraphically calibrated using known fossil occurrences of genera (Chan *et al.* in press). The molecular analyses of Pérez-Losada *et al.* (2014) and Chan *et al.* (2017) did not recover a discrete basal Archaeobalanidae or a more derived Balanidae (as in the classification of Newman and Ross 1976).

The present tree shows strong support for a monophyletic Balanoidea (Bremer 4, bootstrap 90), paralleling the molecular trees of Pérez-Losada *et al.* (2014) and Chan *et al.* (2017). It shows *Chirona* as basal to the Balanoidea, and, successively, *Hesperibalanus*, *Solidobalanus* and *Vectibalanus* gen. nov. as sister

No.	Character
1	basis membranous (0); basis calcified, solid (1); basis with radial tubes (2)
2	basis without multilayering (0); with multilatering, vesicular (1)
3	inner surface of parietes smooth (0); with longitudinal ribs (1)
4	parietes solid (0); parietes tubiferous (1)
5	parietal inner lamina absent (0); inner lamina present (1)
6	septa absent in parietal wall (0); present (1)
7	septal edges smooth (0); with short processes (1); with lateral denticles (2)
8	transverse septa in parietal tubes absent (0); present (1)
9	radii absent (0); present (1)
10	sutural edges of radii smooth (0); with transverse teeth or septa (1)
11	teeth of sutural edge smooth (0); with denticles (1)
12	height of teeth or septa of the sutural edge of the radii low (0); tall (1)
13	specialised alar articulation surfaces present (0); present (1)
14	alar welting absent (0); present (1)
15	longitudinal abutment on inner face of radii absent (0); present (1)
16	radii solid (0); radii tubiferous (1)
17	lateral margin of sheath not extending over ala (0); extending over ala (1)
18	basal margin of sheath continuous with inner lamina (0); not continuous (1)
19	scutal lateral depressor ridge absent (0); present (1)
20	scutal adductor scar without ridge (0); with ridge (1)
21	basal extension to articular ridge absent (0); present (1)
22	tergal spur absent (0); present, short (1); present, long (2)
23	tergal fasciole absent (0); present (1)
24	scutal callous absent (0); present (1)

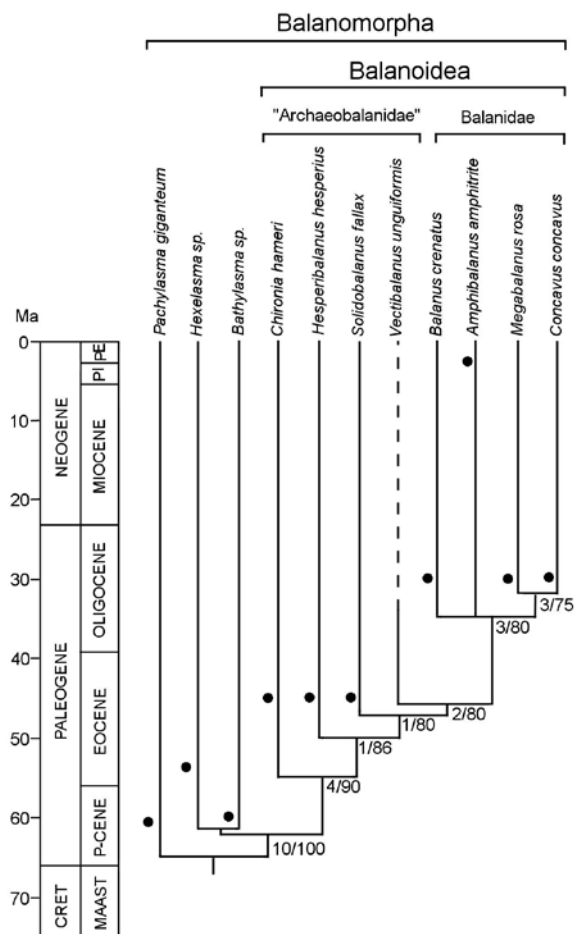Table 1. Characters used in cladistic analysis of balanomorphs.

groups to the Balanidae, effectively constituting a paraphyletic 'Archaeobalanidae'. It also provides strong support for a monophyletic Balanidae (*sensu* Pitombo 2004) as a crown group, incorporating highly derived taxa such as *Balanus*, *Concavus*, *Megabalanus* and *Amphibalanus*, which have been placed in eponymous subfamilies (Pitombo 2004). It also suggests that *Concavus* and *Megabalanus* are more closely related to each other than to *Balanus* and *Amphibalanus*, in agreement with the analysis of Pitombo (2004, figs 9–11).

The tree (Text-fig. 9) shows considerable agreement between stratigraphical first occurrences and topology. Thus, the basal balanomorphs Pachylasmatoidea and Bathylasmatidae first appear in the Paleocene (Buckeridge 1983), with the first, basal, Balanoidea appearing in the Eocene. The more

Character	Pachylasma giganteum (Philippi, 1836)	Hexelasma foratum Jones, 2000	Bathylasma hirsutum (Hoek, 1883)	Chirona hameri (Ascanius, 1767)	Solidobalanus fallax (Broch, 1927)	Hesperibalanus hesperius (Pilsbry, 1916)	Balanus crenatus Bruguière, 1789	Perforatus perforatus (Bruguière, 1789)	Amphibalanus amphitrite (Darwin, 1854)	Megabalanus rosa Pilsbry, 1916	Vectibalanus unguiformis (J. de C. Sowerby, 1846)
1	0	0	0	1	1	1	2	2	2	2	1
2	0	0	0	0	0	0	0	1	0	1	0
3	0	0	0	1	1	1	1	1	1	1	1
4	0	0	0	0	0	0	1	1	1	1	1
5	0	0	0	0	0	0	1	1	1	1	1
6	0	0	0	1	1	1	1	1	1	1	1
7	0	0	0	0	1	0	2	2	2	2	1
8	0	0	0	0	0	0	1	1	1	0	0
9	0	0	0	0	1	1	1	1	1	1	1
10	0	0	0	0	0	1	0	1	0	1	0
11	0	0	0	0	0	0	1	1	1	1	0
12	0	0	0	0	0	0	0	1	0	1	0
13	0	0	0	1	1	1	1	1	1	1	1
14	0	1	1	1	1	1	1	1	1	1	1
15	0	0	0	0	0	0	0	1	0	1	0
16	0	0	0	0	0	0	0	0	0	1	0
17	0	0	0	0	0	0	0	1	0	1	0
18	0	0	0	1	1	1	1	1	1	1	1
19	0	0	0	0	0	0	0	1	0	0	0
20	0	0	0	0	0	1	1	1	1	1	1
21	0	0	0	0	0	1	1	1	1	1	1
22	0	1	1	1	1	1	1	2	2	2	1
23	0	0	0	1	0	0	1	1	1	1	1
24	0	0	0	0	0	1	0	0	0	0	1

Table 2. Matrix of character states for balanomorphs. For character see Table 1.

Text-fig. 9. Cladistic analysis of selected Balanomorpha, stratigraphically calibrated, to show possible phylogenetic position of *Vectibalanus* gen. nov. Consensus tree from heuristic analysis of 24 morphological characters (Tables 1, 2), optimised to Deltran. The analysis places *Vectibalanus* gen. nov. as sister taxon to the Balanidae (*sensu* Pitombo 2004), which form a strongly supported group, appearing in the Oligocene. The Balanoidea first appear in the Eocene. Note that living species have been used in the analysis, but the extension into the fossil record is based upon first occurrences of extinct species of the same genera, marked by dots. The overall distribution of first occurrences is broadly congruent with the phylogeny, except for the late appearance of *Amphibalanus*. Cret – Cretaceous; Maast – Maastrichtian; P-cene – Paleocene; Pl – Pliocene; PE – Pleistocene.

derived Balanidae first occur in the Oligocene. Although data are limited to the taxa studied, it can perhaps be used to provide some better calibration to the molecular trees of Pérez-Losada *et al.* (2014) and Chan *et al.* (2017). Perez-Losada *et al.* (2014, fig. 2) produced a Bayesian chronogram of balanomorph phylogeny which implied that the Balanomorpha originated around 110 Ma (i.e., during the Albian, late Early Cretaceous), and that all major groups had evolved by the end of the Cretaceous (66 Ma). Derived Balanoidea (i.e., Balanidae *sensu* Pitombo

2004) had a divergence time at around 60 Ma for clades including *Concavus* and *Megabalanus*. These estimates appear to be improbably early.

It can be argued from the evidence presented here that the initial radiation of the Balanomorpha (minus the Cretaceous Pachydiademoidea Chan *et al.*, in press) took place shortly after the K–Pg extinction (i.e., Paleocene occurrences of Pachylasmatidae and

Bathylasmatidae), followed by a radiation of basal Balanoidea in the Eocene. The major radiation of derived Balanoidea took place early in the Oligocene, and continues through to the present day. Most of the morphological evolution involved modifications of the parietal structure and their articulations (Pitombo 2004).

PALAEOECOLOGY

Vectibalanus gen. nov. occurs in a considerable range of palaeoenvironmental settings within the mid-Eocene to Lower Oligocene strata of the Hampshire Basin. Its more sporadic occurrences in the Lutetian and Bartonian (Selsey and Barton formations) are in fully marine, shallow-water settings in association with diverse gastropod and bivalve faunas (King 2016). In the overlying Solent Group (Priabonian–Rupelian) *Vectibalanus* gen. nov. occurs in a wider diversity of settings. The Solent Group formed in an estuarine coastal plain, bordering the proto-Solent River (Murray and Wright 1974; Keen 1977; Gale *et al.* 2006), and it represents a wide range of palaeoenvironments, from fully marine (Text-fig. 4: Brockenhurst Bed) through brackish estuarine, to moving freshwater (fluviatile), ephemeral lakes (lacustrine) and emergent surfaces (palaeosols). The succession includes a number of transgressive-regressive cycles (sequences) which commence with a marine-brackish transgression, passing through fluviatile, lacustrine and finally emergent facies. The cirripede *V. unguiformis* occurs exclusively within the transgressive to highstand parts of the cycles, and is abundant only in brackish estuarine facies (Text-fig. 4). Keen (1977) used ostracods to identify palaeosalinities in the Solent Group, and the records of balanomorphs all fall within his assemblages IV (9–16.5 ppt) and V (16.5–35 ppt). Most of the specimens come from levels with palaeosalinities in the range of 10–30 ppt, and the species is absent in the single level of fully marine salinity (Brockenhurst Bed). It therefore appears that *V. unguiformis* was adapted to living in lower salinities, perhaps similar to the living *Amphibalanus improvisus* (Darwin, 1854), which prefers salinities beneath 20 ppt (Southward 2008). *Vectibalanus unguiformis* is therefore the oldest known barnacle which was adapted to brackish environments. Sundall *et al.* (2019) argued that tolerance to low salinities evolved independently a number of times in the sessile barnacle clade.

The main levels of balanomorph occurrence are in the Venus Bed (Colwell Bay Member), in the lower part of which valves are abundant in residues, and articulated specimens can be found. In the upper part of the Venus Bed at Whitecliff Bay, representatives of *Vectibalanus* gen. nov. are abundant, attached to the apertural region of the gastropod *Ptychopotamides vagus*, either singly (Pl. 2, Figs 2, 3) or more rarely in clusters (Pl. 2, Fig. 4). It is likely that the shells were occupied by hermit crabs (Paguridae) and that the cirripedes were commensals, with larvae preferentially selecting sites close to the aperture of this one species.

Vectibalanus gen. nov. also occurs abundantly in the Bembridge Oyster Bed, a brackish-marine horizon (approximately 20 ppt; Keen 1977) at the base of the Gurnard Member (Text-fig. 4), where it is associated with the zeugmatolepadid cirripede *Aprololepas reflexa* Withers, 1953. Most specimens of *Vectibalanus* gen. nov. were attached to oyster shells, but more occasionally to gastropods. *Vectibalanus* gen. nov. also occurs, albeit less commonly, in the brackish Cranmore Member of the Bouldnor Formation at Hamstead Cliff (Text-figs 1, 2). Balanomorphs appeared suddenly in shallow-marine sediments of the Selsey Formation (Lutetian), but are entirely absent from very similar facies in the underlying formations of the Bracklesham Group and from the deeper marine London Clay.

A remarkable feature of the material of *Vectibalanus* gen. nov. is the almost complete absence of borings made by predatory gastropods, common in fossil balanomorphs back into the Eocene (Klompmaker *et al.* 2015). Only a single, incomplete boring has been found in the examination of over 500 valves of *V. unguiformis* from the Headon Hill and Bouldnor formations on the Isle of Wight, in spite of the presence of common (up to 7 species) of muricid gastropods (website: *A Collection of Eocene and Oligocene Fossils*, compiled by Alan Morton), the most likely predator (Klompmaker *et al.* 2015). Bivalves and gastropods in the same assemblages as the barnacles commonly display borings made by predatory gastropods.

Institutional abbreviations

NHMUK, Natural History Museum, London, UK.
USNM, United States National Museum, Washington DC, USA.
IGPUP, Istituto di Geologia e Paleontologia dell'Università di Pisa, Italy.
UCMP, University of California Museum of Paleontology, Berkeley, CA, USA.

SYSTEMATIC PALAEONTOLOGY

Order Balanomorpha Pilsbry, 1916
Superfamily Balanoidea Leach, 1817

REMARKS: Derived balanomorphs have traditionally been divided into a more basal Archaeobalanidae, characterised by relatively simple parietal structure (rarely tubiferous, with solid radii) and a more derived Balanidae, in which the wall structure is more complex and the radii are commonly tubiferous (Newman and Ross 1976). On the basis of recent molecular studies, there is no consistent separation of the Archaeobalanidae and Balanidae in the genera studied (Pérez-Losada *et al.* 2014; Chan *et al.* 2017), and it appears that the families represent grades rather than clades; neither appears to be a truly monophyletic entity. The distribution of characters in the various genera of Eocene balanomorphs described from the eastern USA and northwest Europe is given in Text-fig. 10.

Genus *Archaeobalanus* Menesini, 1971

TYPE SPECIES: *Balanus* (*Archaeobalanus*) *semicanaliculatus* Menesini, 1971, by original designation.

DIAGNOSIS: Low, conical form, parietes solid, externally with coarse buttresses; radii narrow, coarsely denticulate; margins of sheath separated from radii by deep groove; interior of compartments below sheath deeply concave, concavity overhung by margins of plates. Parietes with locally developed parietal pores of variable sizes. Operculars unknown.

REMARKS: The material described by Menesini (1971) from the Bartonian and Rupelian of the Paris Basin is a distinctive form, distinguished by the very coarsely denticulate radii (e.g., Menesini 1971, pl. 2, fig. 5), the deep grooves between the sheath and the radii on the rostral plate (Menesini 1971, pl. 2, fig. 2) and the sheath and radius on the marginal plate (Menesini 1971, pl. 2, fig. 4). The interiors of the compartments beneath the sheath are overhung by their margins (e.g., Menesini 1971, pl. 2, figs 2, 5). *Archaeobalanus* can be distinguished from *Kathpalmeria* Ross, 1965, which is similar in overall construction, by the variable development of parietal pores of different sizes in the parietes, which are monolamellar in the latter genus (Zullo and Kite 1985). In *Vectibalanus* gen. nov. the parietal pores are pervasively developed and of equal size and extend to the apices of the compartments.

Archaeobalanus semicanaliculatus (Menesini, 1971)

*1971. *Balanus* (*Archaeobalanus*) *semicanaliculatus* Menesini, p. 28, pl. 2, figs 1–6; pl. 5, figs 6–8; pl. 6; pl. 7, figs 1–4.

DIAGNOSIS: As for genus.

TYPES: The shell figured by Menesini (1971, pl. 2, fig. 1) is here selected as lectotype. It should be in the collections of the Istituto di Geologia e Paleontologia

Character	*Kathpalmeria*	*Hesperibalanus*	*Archaeobalanus*	*Vectibalanus*	*Solidobalanus*	*Lophobalanus*
parietal structure	solid	solid	small irregular pores	large regular pores	solid	solid
parietal ribbing	strong, external sulci form internal buttresses	variable	strong, no internal buttresses	variable	externally weak, fine ribs internally	smooth to plicate
radii	absent or narrow	broad	narrow	narrow	broad	narrow
sutural margins of radii	smooth	denticulate	coarsely denticulate	coarsely denticulate	coarsely denticulate	smooth
basis	thick, solid	thin, solid	thin, solid	radially ribbed	thick, solid	thick, solid
scutal callous	absent	present, smooth or ribbed	–	strong, ribbed	absent	absent
scutal adductor ridge	absent	present	–	present, short	absent	present, short
scutal lateral depressor pit	large	weak	–	large	small, deep	small
tergal spur	narrow, rounded tip	narrow, short	–	long, subacuminate	short, round tip	short
spur fasciole	shallow	shallow	–	deeply impressed	shallow	shallow
tergal interior	rugose	rugose	–	strongly rugose	smooth	smooth

Text-fig. 10. Character distribution in selected living and fossil balanomorphs.

dell'Università di Pisa, but is presumably unregistered. It came from the 'Marinesian' (Upper Eocene, Bartonian) of Chars, near Paris (France).

REMARKS: The opercular plates of this species are unknown. The material requires new investigation in the light of more recent discoveries.

Genus *Kathpalmeria* Ross, 1965

TYPE SPECIES: *Kathpalmeria georgiana* Ross, 1965, by original designation.

OTHER INCLUDED SPECIES: *Balanus* (*Hesperibalanus*) *parahesperius* Menesini, 1971.

DIAGNOSIS: Wall composed of six moderately thick, markedly costate, monolamellar compartments; sulci between external ribs forming internal buttresses; radii very narrow; interior of scutum without rugosities or scutal adductor ridge; tergal spur narrow, moderately long, spur furrow not depressed (emended from Zullo and Kite 1985, p. 11).

REMARKS: Zullo and Kite (1985) provided a detailed description of extensive material of *K. georgiana* from the Upper Eocene (Priabonian, NP19/20) of Georgia (USA), including the opercular valves. The morphology of both the compartments and opercular valves of *K. georgiana* is similar to that of *Balanus* (*Hesperibalanus*) *parahesperius* in many features, including:

The shape of the tergum, with an acuminate, moderately elongated spur and very shallow spur furrow (compare Zullo and Kite 1985, fig. 2A–D, G with Menesini 1971, pl. 1, figs 4, 5).

The interior of the scuta lack a striated callus and adductor ridge and have deeply impressed adductor and lateral depressor scars (Zullo and Kite 1985, fig. 2I, K, F).

The compartments are monolamellar, strongly costate and the external sulci between the external ribs form internal buttresses (Menesini 1971, pl. 1, figs 6b, 7b).

For these reasons, *Balanus* (*Hesperibalanus*) *parahesperius* is here reassigned to the genus *Kathpalmeria*.

Kathpalmeria parahesperia (Menesini, 1971)

*1971. *Balanus* (*Hesperibalanus*) *parahesperius* Menesini, p. 22, pl. 1, figs 1–10.

DIAGNOSIS: *Kathpalmeria* in which the scutal margin of the tergum is weakly concave and the tergal spur has a bluntly rounded termination. External ribs do not extend to the apices of the compartments.

TYPES: The tergum figured by Menesini (1971, pl. 1, fig. 4) is here selected as lectotype. It should be in the collections of the Istituto di Geologia e Paleontologia dell'Università di Pisa, but is presumably unregistered. It was from the lower 'Sables de Fontainbleu', Lower Oligocene (Rupelian) of Champlan, near Paris (France).

REMARKS: Comparison of the illustrations in Zullo and Kite (1985) and Menesini (1971) suggests minor differences in tergal shape between *K. parahesperia* (tergal spur with blunter termination, narrower gap between tergal spur and base of tergal margin, scutal margin less deeply concave) and *K. georgiana*. In *K. parahesperia*, the external ribbing on the compartments does not extend to the apex, whereas it appears to do so in *K. georgiana* (Zullo and Kite 1985, fig. 3a).

Genus *Lophobalanus* Zullo, 1984

DIAGNOSIS: Shell wall of six, smooth to plicate, compartmental plates; parietes, radiiand basis solid; radii narrow with smooth sutural edges; interior of scutum and tergum without rugosities; true scutal adductor ridge present; no callus between scutal adductor and articular ridges; scutal depressor muscle pit small, distinct, without crests; tergal spur furrow flush with plate surface or slightly depressed (after Zullo 1984).

TYPE SPECIES: *Balanus kellumi* Zullo and Baum, 1979, by original designation.

OTHER INCLUDED SPECIES: *Lophobalanus baumi* Zullo, 1984 and *L. fresvillensis* sp. nov.

REMARKS: *Lophobalanus* has been recorded from the Lower Oligocene to Lower Miocene of Mississippi, North Carolina and South Carolina (Zullo 1984). In the discussion of the genus, Zullo (1984, p. 1317) noted that it was distinguished largely upon the basis of the well-developed scutal adductor ridge, but also by "narrow radii with smooth sutural edges which do not articulate with the parietes of adjacent compartmental plates".

Lophobalanus fresvillensis sp. nov.
(Pl. 3, Figs 1–5)

DIAGNOSIS: *Lophobalanus* in which the tall, sub-conical shell has smooth parietes and a small, toothed orifice.

TYPE: A single, very well-preserved shell (NHMUK IC 1875) from the Middle Eocene (Lutetian) Faluns de Hautteville-Bocage at Fresville (Manche, France), collected by Mr Steve Tracey.

DESCRIPTION: Shell conical, as tall as broad, sides slightly concave, parietes solid. Orifice small, pyriform, toothed. Parietes smooth, with fine growth lines, irregularly and discontinuously folded towards basal margin. Radii very narrow, with strongly declined summits, contacting parietes of adjacent plate over short distance. Sheath low, interior of parietes with well-developed longitudinal ribs. Basis calcareous, solid.

REMARKS: This species is referred to *Lophobalanus* with some uncertainty in the absence of opercular plates. The narrow radii, solid parietes and limited contact between the radii and adjacent parietal margin all agree with Zullo's (1984) diagnosis and discussion. It differs from *L. kellumi* and *L. baumi* in the smooth parietes (*vs* ribbed in *L. kellumi* and *L. baumi*). *Lophobalanus fresvillensis* sp. nov. differs from *Zullobalanus* Buckeridge, 1989 (see also Winkelmann *et al.* 2010) in the narrower radii and smaller orifice.

Genus *Vectibalanus* gen. nov.

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 deep; parietes with simple, evenly sized pores and inner lamina; radii with coarsely denticulate sutural edges. Basis solid, with radiating ridges.

TYPE SPECIES: *Balanus unguiformis* J. de C. Sowerby, 1846.

DERIVATION OF NAME: After Vectis, the Roman name for the Isle of Wight, United Kingdom, where the genus is abundant at several levels in the Upper Eocene and Lower Oligocene.

OTHER INCLUDED SPECIES: *Balanus erisma* J. de C. Sowerby, 1846 and *V. mortoni* sp. nov.

DISCUSSION: There has been considerable discussion on the generic placement of *B. unguiformis*. Davadie (1963) placed the species in *Chirona*, on the basis of the interlaminate figures. Zullo (1966) suggested that it showed features of both *Hesperibalanus* (broad radii, apical callus on scutum) and *Chirona* (long narrow form of tergal spur, crenulate sutural edges of radii), but that it probably belonged to an undescribed genus. Ross and Newman (1967) assigned Alabama specimens to *Balanus* (*Hesperibalanus*) aff. *unguiformis*. Subsequently, Newman and Ross (1976) placed *B. unguiformis* in *Chirona* (*Chirona*), and later Zullo (1984, p. 1336) assigned it to *Archaeobalanus*, stating "As discussed previously, at least one archaeobalanid, *Archaeobalanus unguiformis* (Darwin, 1854) from the English Eocene, may have either a solid monolamellar or tubiferous bilamellar wall."

The scuta of *V. unguiformis* (Pl. 8, Figs 9, 10, 13, 14) possess a finely striated apical callus, a short articular ridge and a shallow but clear lateral scutal depressor pit. These features compare well those in Recent *Hesperibalanus hesperius* (Pilsbry, 1916) (see Text-fig. 11C, D) and Late Eocene *Solidobalanus cornwalli* (Zullo, 1966) (see Text-fig. 11L, M) and *Kathpalmeria georgiana*. The terga of *V. unguiformis* (Text-fig. 11R, S), however, differ from those of *S. cornwalli* (Text-fig. 11J, K) in possessing a longer tergal spur separated from the base of the scutal margin by a V-shaped notch, and a deep tergal spur furrow (see also Text-fig. 12A, B). There is closer comparison with *Chirona hameri* (Ascanius, 1767) (see Text-fig. 11F, I) in the development of the tergal spur and the deep spur furrow, but there are significant differences in the shapes of the terga between the two taxa. In conclusion, the opercular plates of *V. unguiformis* show a mosaic of features of different extant genera.

The compartments of *V. unguiformis* differ significantly from those of species of *Hesperibalanus*, *Chirona*, *Solidobalanus* and *Armatobalanus* in their ubiquitous possession of evenly sized parietal pores and an inner lamina (Text-fig. 8A, C–E).
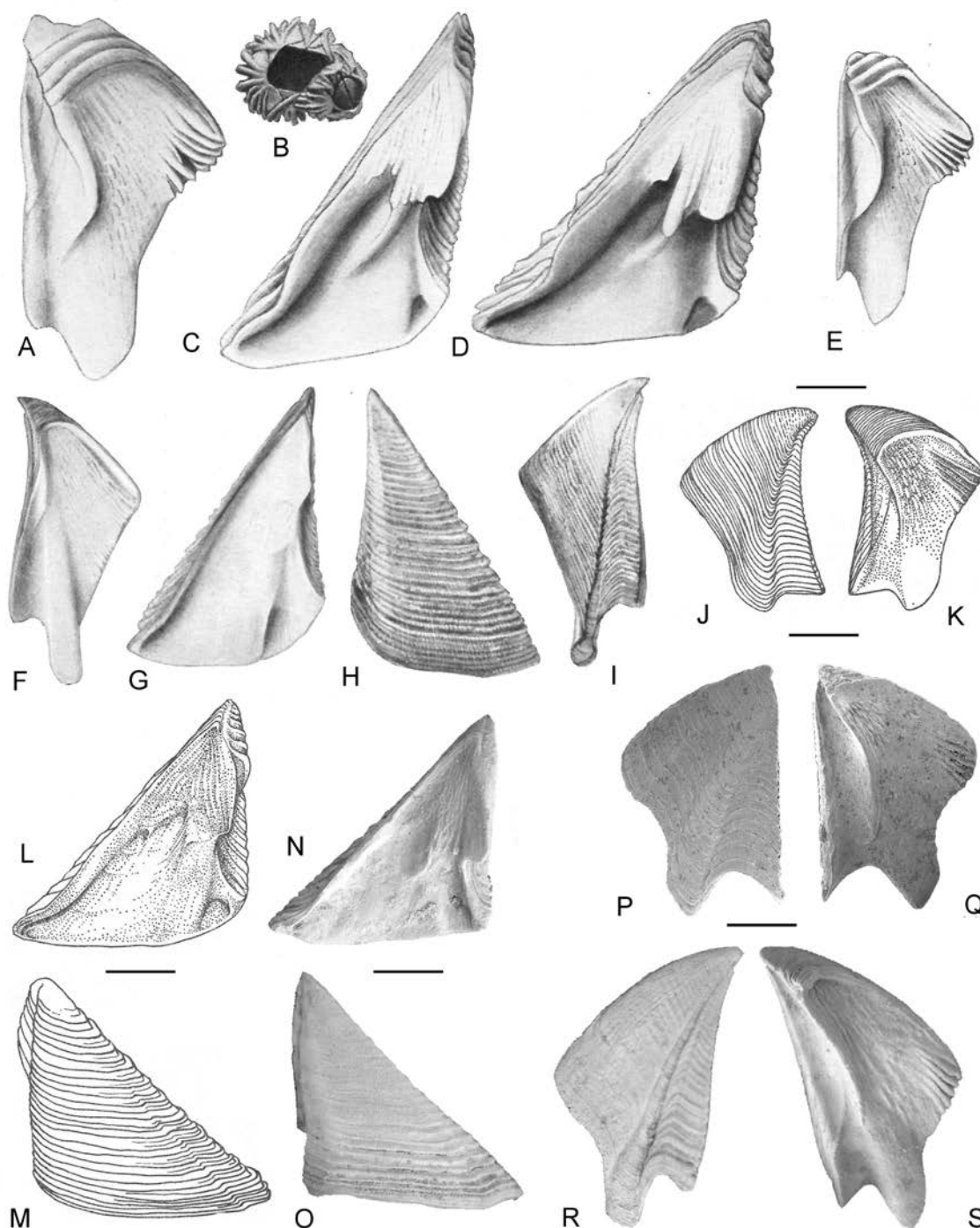
Archaeobalanus semicanaliculatus (see above) has irregularly developed parietal pores of variable size, which are not present throughout the parietes (e.g., Menesini 1971, pl. 5, figs 6–8). It therefore seems prudent to follow Zullo's original suggestion (Zullo 1966) and to place the species in a new genus.

Vectibalanus unguiformis (J. de C. Sowerby, 1846)
(Text-fig. 8A, C–E; Pl. 2, Figs 1–12; Pl. 4, Figs 1–11; Pl. 6, Figs 1–9; Pl. 8, Figs 5–10, 13, 14)

*1846. *Balanus ungiformis* J. de C. Sowerby, pl. 648, fig. 1.

Text-fig. 11. Comparative morphology of balanid opercular valves. **A–E** – *Hesperibalanus hesperius* (Pilsbry, 1916). A, E – internal views of terga; B – apical aspect of shell; C, D – internal views of scuta (A–D – USNM 32935; E – USNM 48066), refigured from Pilsbry (1916, pl. 49, figs 1a–c, 7b). **F–I** – *Chirona hameri* (Ascanius, 1767); F, I – internal and external views of tergum; G, H – internal and external views of scutum, refigured after Pilsbry (1916, pl. 53, fig. 1), off Nova Scotia (USNM 9044). **J–M** – *Solidobalanus cornwalli* (Zullo, 1966). J, K – paratype, tergum (UCMP 12167); L, M – paratype, scutum (UCMP 12168), refigured after Zullo (1966, fig. 2). **N, O, R, S** – *Vectibalanus unguiformis* (J. de C. Sowerby, 1846). N, O – scutum (NHMUK IC 1925); R, S – tergum (NHMUK IC 1904). **P, Q** – *Vectibalanus mortoni* sp. nov., tergum, paratype (NHMUK IC 1914). A–D are from the Bering Sea. E is from Kamchatka. M is from Cowlitz Formation, Lewis County, Washington State, USA (Upper Eocene). N, O, R, S are from Venus Bed, Colwell Bay Member, Colwell Bay, Isle of Wight, United Kingdom (Upper Eocene, Priabonian). P, Q are from Barton Formation, Barton, Hampshire, United Kingdom (Bartonian, Upper Eocene, NP16–17). Scale bars equal 1 mm; note: for A–I, no scales were available.

1854a. *Balanus unguiformis* J. de C. Sowerby; Darwin, p. 29, pl. 2, fig. 4a–f.

1854b. *Balanus unguiformis* J. de C. Sowerby; Darwin, p. 296, pl. 8, fig. 8.

1953. *Balanus unguiformis* J. de C. Sowerby; Withers, p. 48.

?1963. *Balanus* (*Chirona*) *unguiformis* Sowerby; Davadie, p. 73, pl. 41, fig. 7.

1966. *Balanus* (?*Hesperibalanus*) *unguiformis* Sowerby; Zullo, p. 202.

1967. *Balanus* (*Hesperibalanus*) *unguiformis* Sowerby; Ross and Newman, p. 4.

1976. *Chirona* (*Chirona*) *unguiformis* (Sowerby); Newman and Ross, p. 50.

1984. *Archaeobalanus unguiformis* (Darwin); Zullo, 1984, p. 1336.

DIAGNOSIS: *Vectibalanus* with smooth to irregularly folded parietes; tergal spur separated from scutal margin by deep V-shaped incision; spur furrow deep, with strongly overfolded tergal margin.

TYPES: The cluster of specimens attached to a bivalve shell (*Cordiopsis* sp.) in the centre of J. de C. Sowerby's (1846) plate 648, fig. 1, is here selected as lectotype (Pl. 1, Fig. 1). The colour and lithology of the matrix (pale grey-green sand) and the bivalve species strongly suggest that this specimen originated in the Venus Bed (Solent Group, Headon Hill Formation, Colwell Bay Member) from Colwell Bay in the west of the Isle of Wight, where the species is abundant. Upper Eocene, Priabonian, probably NP19–20 (Gale *et al.* 2006; King 2016). Its current whereabouts are unknown.

MATERIAL: 55 articulated shells and over 500 isolated valves, Headon Hill Formation (Colwell Bay Member), Bouldnor Formation (Gurnard and Cranmore members), Isle of Wight, United Kingdom.
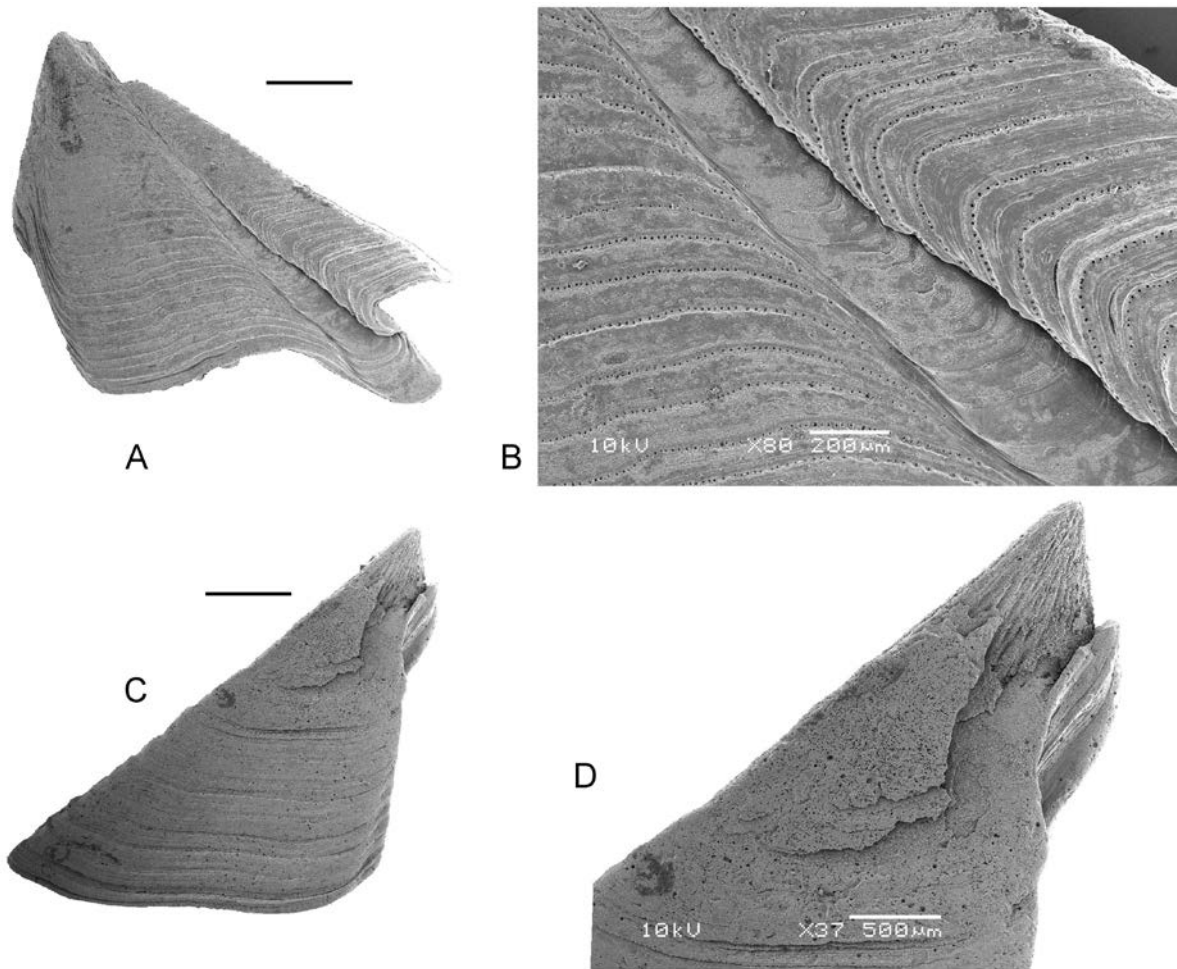
DESCRIPTION: Shell robust, made up of 6 plates, oval to subquadrate in apical aspect (Pl. 2, Figs 5–7, 9, 12), apical margin toothed in large specimens. Orifice diamond-shaped in apical view (Pl. 2, Figs 5, 9), rounded diamond outline in basal view (Pl. 2, Figs 6, 7). Rostral plate broad, weakly convex, occupying 80% of width of shell; carina narrow, 40% of width of shell. In basal view (Pl. 2, Figs 6, 7), interior surface, basal to the sheath, concave; internal ribs fade apically. Compartments (Pl. 4) externally smooth, flat or irregularly folded, lacking regular ribbing (Pl. 4, Figs 2, 4, 6, 8); radii with coarsely denticulate sutural margins (Pl. 4, Figs 1, 3, 5, 9, 10). Parietes tubiferous, with major and minor septa and inner lamina present (Text-fig.

8A, C–E). Longitudinal ribs present on major septa, complex and denticulate at base (Pl. 4, Fig. 10), weakening apically. Sheath height one third of total plate height. Basis calcified, with radial ribs and incipent tubes may be present (Pl. 2, Fig. 8). A single specimen (Pl. 2, Fig. 5) shows original colour banding, developed as alternating basis-parallel rings of buff-pink and cream-pink. A further specimen (Pl. 3, Fig. 6) shows the opercular valves in place; these have a low position in the orifice, and are subparallel to the base.

Scuta (Pl. 8, Figs 9, 10, 13, 14) with isosceles triangular outline, occludent margin straight, longer than basal and scutal margins. Basal margin straight to weakly convex, tergal margin straight to weakly concave. Apical part of scuta with callus, bearing fine ribbing and several broader basal extensions extending to adductor scar. Adductor ridge short, narrow, tergal margin of adductor scar slightly raised. Small lateral depressor pit, margins poorly defined. Terga (Pl. 6, Figs 1–7; Pl. 8, Figs 5–7) elongated, with concave basal margin, weakly convex occludent margin and straight tergal margin. Tergal spur spatulate, moderately elongated, asymmetrical, separated from base of scutal margin by deep V-shaped notch. Spur furrow (Text-fig. 12A, B) deep, scutal margin overfolded. Significant ontogenetic change in tergal outline, with basal margin shortening with growth, and carinal margin elongating. Shell conical, orifice moderately large, toothed, rhombic (Pl. 2, Figs 1, 6, 8, 9); radii broad, with oblique summits.

WALL STRUCTURE: The study of parietal structure in *Vectibalanus unguiformis* (Text-fig. 8A–E) is based on 30 transverse thin sections across wall plates, which show the presence of a sharply demarcated outer wall, which is brown in colour and appears to be constructed of calcite crystals with c-axes oriented orthogonally to the outer surface. The septa have a simple structure, lacking lateral branches. The inner lamina can be seen as a secondary infilling between the inner margins of the septa, as in *Balanus crenatus* (Text-fig. 8G). In one section of *V. unguiformis* (Text-fig. 8E), which shows the basis, the pores appear to be secondarily infilled with calcite crystals which are organised around a median structure. All examples examined possess parietal pores, of approximately even size.

The parietal structure of *V. unguiformis* seen in these thin sections is comparable in most respects with that of more derived balanids, in that longitudinal pores are formed by the development of an inner lamina between the septa. Therefore, there does not seem to be any evidence that they are not

Text-fig. 12. *Vectibalanus unguiformis* (J. de C. Sowerby, 1846). A, B – tergum, external views to show details of spur furrow and surface sculpture (NHMUK IC 1921); C, D – external views of scutum, to show details of thickened apical region and bioerosion (NHMUK IC 1922). Upper Venus Bed, Colwell Bay Member, Whitecliff Bay, Isle of Wight, United Kingdom (see Text-figs 1, 9). Scale bars equal 1 mm (A, C).

homologous with pores in other balanids, although pores could theoretically have evolved independently in different lineages. The structure of the septa is very simple in *V. unguiformis*, comprising a central longitudinal rib from which calcite crystals grow laterally, without complex arborescent processes (compare with *Balanus crenatus*, Text-fig. 8G here, and *Megabalanus*, see Newman *et al.* 1969, fig. 106/3). This simple arrangement is similar to the situation in *Chirona* and *Armatobalanus* (Davadie 1963, pl. 42, fig. 3), which, however, lack longitudinal pores and an inner lamina.

REMARKS: The original illustration of *B. unguiformis* by J. de C. Sowerby (1846, pl. 648, fig. 1) is not accompanied by any details of locality, formation or age. Darwin (1854a, p. 30) evidently obtained this information from the labels of the material that J. de C. Sowerby had described, and other specimens in various collections. He wrote "*Fossil* in the Eocene formations, Isle of Wight, Colwell Bay; Hordwell; Barton (Chama Bed); Headon; Bembridge; Bergh, near Klein Spauwen, Belgium (?). Attached to various shells and wood. Mus J. de C. Sowerby, E. Forbes, F. Edwards, Charlsworth, T. Wright, Bowerbank, Tennant, Bosquet." It is not clear from this information from where the material illustrated by J. de C. Sowerby (1846) originated. Material ascribed to *B. unguiformis* (i.e., any balanomorph from the Eocene–Oligocene of the Hampshire Basin, United Kingdom) is recorded from the Bracklesham Group (Selsey Formation, Lutetian, Middle Eocene), up to

the uppermost Solent Group (Bouldnor Formation, Cranmore Member, Rupelian) (compare Withers 1953).

Vectibalanus unguiformis forma *cylindrica* nov.
(Pl. 2, Fig. 13; Pl. 3, Figs 13, 14; Pl. 5, Figs 1–3)

DIAGNOSIS: Variety of *V. unguiformis* in which the shell is tall and cylindrical, the sheath proportionately tall and the narrow radii have strongly inclined summits.

TYPES: A complete shell from the Venus Bed, Colwell Bay Member, Headon Hill Formation at Colwell Bay, Isle of Wight, is the holotype (NHMUK IC 1874; see Pl. 2, Fig. 13; Pl. 5, Figs 1–3). An articulated marginal and carinomarginal (Pl. 3, Figs 13, 14) from the Corbula Bed, Cranmore Member, Bouldnor Formation, Hamstead, Isle of Wight, is paratype (NHMUK IC 1882).

DERIVATION OF NAME: After the shape of the shell.

DESCRIPTION: Height of shell exceeds width, form cylindrical (Pl. 2, Figs 13; Pl. 5, Figs 1–3); shell with weak transverse sculpture. Radii denticulate, very narrow, especially on carinomarginal, tapering towards base of shell, summits strongly declined (Pl. 2, Fig. 13). Sheath twice as tall as broad (Pl. 3, Fig. 13). Basis not calcified. The paratype (Pl. 3, Figs 13, 14) has grown at a highly inclined angle to the base.

REMARKS: This is a tall form of *V. unguiformis*, and it is possible that the shell morphology was determined by crowded contact with other individuals, because the basal sides of the holotype are vertical and striated. However, the paratype has evidently not grown in such confinement, but shows the same morphological features. The transverse external sculpture of both specimens is different to that of *V. unguiformis*, the basis is not calcified, the radii are very narrow and the sheath is proportionately tall.

Vectibalanus erisma (J. de C. Sowerby, 1846)
(Pl. 3, Figs 7–10, 15, 16; Pl. 5, Figs 4–13; Pl. 7, Figs 1–7)

*1846. *Balanus erisma* J. de C. Sowerby, pl. 648, fig. 2.
1854a. *Balanus unguiformis* var. *erisma* J. de C. Sowerby; Darwin, p. 40, pl. 2, fig. 4b.

DIAGNOSIS: *Vectibalanus* in which the walls of the compartments bear 4–7 robust, rounded ridges and intervening sulci; individual growth increments bear fine denticulae.

TYPES: The remains of a specimen (pyrite decay has broken the material up) originally attached to a gastropod shell (*Ampullina* sp.) on the left of J. de C. Sowerby's (1846) plate 648, fig. 2 (see Pl. 1, Fig. 2 here) is selected as lectotype (NHMUK In. 17027) and refigured (Pl. 1, Figs 4, 5). Bartonian, Barton Clay Formation, Barton, Hampshire. The two smaller individuals on the right of the figure (Pl. 1, Fig. 2 here) are paralectotypes, also attached to a shell of *Ampullina* sp. from the same locality (NHMUK In. 17028), also refigured here (Pl. 1, Figs 6, 7).

MATERIAL: Six articulated individuals and numerous compartmental plates from the Barton Formation, Barton (Hampshire) as well as fewer wall plates from the Colwell Bay and Cranmore members, Isle of Wight. Eocene (Bartonian) to Oligocene (Rupelian).

DESCRIPTION: Shell low, conical, apex abraded in fully-grown individuals (Pl. 1, Fig. 3; Pl. 7, Figs 5–7). Radii narrow, except on rostral plate (Pl. 5, Figs 4, 5). Exterior of parietes bearing 3–7 strong apicobasal rounded ribs, separated by shallow grooves (Pl. 3, Figs 8, 9, 16; Pl. 5, Figs 5, 6, 9); growth lines carrying numerous tiny denticles in well-preserved specimens (e.g., Pl. 3, Fig. 9; Pl. 5, Fig. 6). Parietes porous, strong longitudinal ribs on major septa denticulate at base (Pl. 5, Figs 6, 9). Radii with coarsely denticulate sutural margins, surfaces flattened (e.g., Pl. 7, Figs 9, 12). Apical portions of parietes abraded on fully-grown individuals, exposing septa and parietal tubes (Pl. 5, Figs 10, 13; Pl. 7, Fig. 1). In some large specimens, the apex has not detached, but there is a line of weakness at its base (Pl. 7, Fig. 3). Juveniles (Pl. 1, Figs 6, 7) smooth, low, with ribs developing at R–C length of approximately 4 mm. Basis thin, solid (Pl. 5, Fig. 11). A single poorly preserved scutum (Pl. 8, Figs 15, 16) with convex basitergal angle; callus on interior apical part of valve coarsely ribbed.

REMARKS: *Vectibalanus erisma* was considered by Darwin (1854a, p. 40) to be a ribbed variant of *B. unguiformis*, but examination of the original material, and more recently collected specimens, shows that there are significant differences in parietal structure between the two species. In *V. erisma*, the ribbing on the parietes is strong and regularly spaced growth increments bear small denticulae, whereas

in *V. unguiformis,* ribbing, if present, is very irregular and weak and the external parietal surfaces are weakly corrugated or smooth. In *V. erisma,* the apical portions of the compartments have commonly spalled off, exposing the parietal tubes and the inner lamina. The fine denticulae developed along closely spaced growth lines (Pl. 3, Fig. 9) are remarkably similar to those developed the bathylasmatid genus *Hexelasma.*

OCCURRENCE: Barton Clay Formation, occurring in Beds E and H at Barton, Hampshire. Rare in the Colwell Bay Member (Headon Hill Formation) and in the Cranmore Member (Bouldnor Formation) of the Isle of Wight. Eocene (Bartonian) to Lower Oligocene (Rupelian).

Vectibalanus mortoni sp. nov.
(Pl. 7, Figs 8–16; Pl. 8, Figs 1–4, 11, 12)

DIAGNOSIS: *Vectibalanus* with smooth parietes in which the tergum lacks a spur fasciole; the tergal spur is short and bluntly rounded and separated from the base of the scutal margin by a shallow, concave embayment.

TYPES: The tergum figured here (Pl. 8, Figs 1, 2) is the holotype (NHMUK IC 1913). The other figured plates are paratypes (NHMUK IC 1908–1912, 1914, 1915).

MATERIAL: An associated group of 16 valves, representing at least three individuals. 'Middle Barton Beds' (probably Bed E), Highcliffe Member (Barton Formation) of Barton, Hampshire.

DESCRIPTION: Compartments (Pl. 7, Figs 8–16) smooth externally, radii narrow, coarsely denticulate sutural margins; parietal pores and inner lamina present, basal parts of septa weakly denticulate. Longitudinal ribs present on interior surfaces. Scutum (Pl. 8, Figs 11, 12) with outline of isosceles triangle, occludent and tergal margins straight, basal margin weakly convex. Terga (Pl. 8, Figs 1–4) with broad, short spur, lacking spur fasciole, spur separated from scutal margin by shallow concavity.

REMARKS: *Vectibalanus mortoni* sp. nov. differs from *V. erisma* (see above) in the smooth external surfaces of the parietes, and from *V. unguiformis* in the shorter, broad tergal spur, separated from the scutal margin by a shallow embayment (compare Pl. 8, Figs 1, 2, and 5, 6).

Indeterminate balanomorph
(Pl. 3, Figs 11, 12, 17, 18)

MATERIAL: Ten fragmentary compartments, from Beds A3 and B, Barton Clay Formation, Barton, Hampshire (NHM UK IC 1879, 1880).

DESCRIPTION: The solid compartments are all broken to varying degrees, but have a consistent morphology, including a very tall, narrow sheath, adjacent to which the parietes are very thick (Pl. 3, Fig. 11). The base of the sheath is strongly arched; the parietes basal to the sheath are thin. The external surface of the parietes is smooth. From the material it is not possible to identify individual compartments.

DISCUSSION: The morphology and structure of the compartments is quite different to any other Eocene taxa from northwest Europe, but the limited material is too incomplete to identify more precisely.

DISCUSSION

The balanomorph assemblage described from the Paleogene of the Hampshire Basin (United Kingdom), the Paris Basin and the Contentin Peninsula (France) includes seven taxa, of which all except one (i.e., the indeterminate balanomorph) are known from well-preserved material, although opercular plates are unknown for three of these species. These taxa are assigned to the genera *Archaeobalanus* (*A. semicanaliculatus*; Upper Eocene to Lower Oligocene), *Kathpalmeria* (*K. parahesperia*; Lower Oligocene), *Vectibalanus* gen. nov. (*V. erisma, V. unguiformis* and *V. mortoni* sp. nov.; Eocene–Lower Oligocene) and *Lophobalanus* (*L. fresvillensis* sp. nov.; Middle Eocene). Two of these genera, *Kathpalmeria* and *Lophobalanus,* are best known from the Paleogene of the US Atlantic Coastal Plain (Georgia) where *Vectibalanus* gen. nov. may also be present. The Eocene–Oligocene balanomorphs present in the adjacent Hampshire and Paris basins are completely different at genus and species level. This not surprising for the Eocene (Bartonian) material, as the molluscan assemblages of the two basins are very different in this interval, but is more surprising in the Lower Oligocene (Rupelian) in which the molluscs are rather similar (Pomerol 1982).

Vectibalanus gen. nov. and *Archaeobalanus* are

the oldest balanomorphs to possess parietal pores, but these are only locally developed and of variable size in the latter genus. In *Vectibalanus* gen. nov., the pores are of similar size and developed throughout the parietes of all compartments. Cladistic analysis of a selection of balanomorph genera places *Vectibalanus* gen. nov. as sister taxon to the more derived Balanoidea (Balanidae), in which parietal structure is considerably more diverse and complex (Pitombo 2004), and the Balanidae appeared in the Middle Oligocene. The order of appearance of balanomorph taxa thus appears to be broadly congruent with phylogeny (Text-fig. 9). It is interesting that the development of tubiferous wall structure is likely to have enabled both rapid growth and protection against predation, likely leading to the Neogene adaptive radiation of the Balanidae (Stanley and Newman 1980). Both *Archaeobalanus* and *Vectibalanus* gen. nov. are positioned at the very base of this radiation.

The sudden appearance of balanomorphs in the Middle Eocene (Lutetian) and lower Bartonian (42–38 Ma) and their abundance in the Priabonian and Stampian (37–33 Ma; Upper Eocene–Lower Oligocene) is a feature of northwestern European successions. In the US Atlantic coastal plains, balanomorphs appear in the Priabonian (NP19/20; Zullo and Kite 1985; Cicimurri and Knight 2019), coincident with the abundant occurrences in the Solent Group of the United Kingdom documented in the present paper. Balanomorphs are completely absent in virtually identical facies of the older Eocene and Paleocene strata in Europe and the eastern USA. Their sudden appearance in the Upper Eocene can perhaps be attributed to a northerly immigration from Tethys.

Vectibalanus unguiformis is restricted to intervals of lower salinity, as characterised by co-occurring ostracod and molluscan assemblages that are indicative of salinities of 10–30 ppt, and is the oldest known balanomorph to have adapted to brackish environments.

Acknowledgements

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