

A new basal balanomorph cirripede (Thoracica, Brachylepadidae) from the Upper Cretaceous and its bearing on the evolutionary origins of the group

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ABSTRACT:

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A tiny, sessile brachylepadid barnacle, *Microcorona girodi* gen. et sp. nov., is described from lower and upper Campanian chalks of the Hannover area (northern Germany) and upper Maastrichtian biocalcarenes of southern Limburg (the Netherlands). The new taxon possesses a fused wall, comprising a rostrum, a carina, paired marginal plates and surrounding imbricating plates; an upper latus is absent. Cladistic analysis supports the interpretation that the new taxon is a sister group to all post-Mesozoic balanomorph barnacles (Neobalanomorpha). In the Hannover area, the new brachylepadid encrusted brachiopod shells, echinoid tests and serpulid tubes in a deep water (>200 m) habitat. The single specimen from the upper Maastrichtian of the southern Netherlands was bioimmured by an exogyrine oyster in a shallow-water (<50 m) setting, thus demonstrating that early balanomorphs were able to occupy a wide range of habitats.

Key words: Cirripedia; Balanomorpha; Chalks; Biocalcarenes; Germany; The Netherlands.

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INTRODUCTION

Balanomorphs (acorn barnacles) are the most diverse and abundant representatives of the Cirripedia, having originated in the Late Cretaceous and undergone a major radiation during the Cenozoic, adapting to numerous marine habitats from brackish estuaries to the intertidal zone and the deep sea (Stanley and Newman 1980). Their success has been attributed to evolution of a robust, closely articulated or fused shell wall, and the modification of the paired terga and

scuta into an operculum, which is opened for feeding, reproduction, respiration and excretion (Anderson 1983, 1994). Darwin said that we lived in the 'Age of Barnacles', most of which are in fact balanomorphs.

The homology of balanomorph wall plates has been a topic of controversy. Darwin (1854) identified the wall plates set between the carina (C) and rostrum (R) in balanomorphs as homologous with the lateral plates of stalked forms (i.e., laterals, carinolaterals, rostromaterals). Subsequently, Yamaguchi and Newman (1990) argued that replication of the



carinolatus had taken place during evolution of the balanomorphs, and that the structure of the wall was therefore C, CL1, CL2, RL, R (the upper latus having become incorporated into the operculum). Gale and Sørensen (2014) offered an alternative explanation, because all lateral plates, with the exception of the upper latus, had been lost in brachylepadids, the stem-group to the balanomorphs. They suggested that the wall plates of derived brachylepadomorphs and balanomorphs represented newly evolved structures (probably modified peduncular plates), and called these plates marginals (M), carinomarginals (CM) and rostromarginals (RM). Marginals are present between the carina and rostrum of the four-plated Cretaceous brachylepadid genera *Epibrachylepas* Gale in Gale and Sørensen, 2014 and *Parabrachylepas* Gale in Gale and Sørensen, 2014, and rostro- and carinomarginals are found in the eight-plated *Pachydiadema* Withers, 1935 (Gale and Sørensen 2014). Later (Cenozoic) balanomorphs developed a consistent overlap pattern between the wall plates and a well-defined sheath, comprising a smooth, closely articulated ring on the apical interior of the wall, permitting precise articulation of the operculum.

The history of supposed Cretaceous examples of balanomorphs is chequered. The earliest record, of *Chthalamus darwini* Bosquet, 1857, from southern Limburg (the Netherlands), proved to be a contaminant, actually belonging to the living *Ch. stellatus* (Poli, 1791) (see Jagt and Carriol 2008). In 1935, T.H. Withers described a supposed catophragmid balanomorph, *Catomerus (Pachydiadema) cretacea*, from the marginal upper lower Campanian of Ivö Klack, southern Sweden, based upon large isolated plates. Extensive new material of this species was later collected, and formed the basis of a detailed reconstruction which permitted it to be interpreted as an eight-plated primitive balanomorph (Gale and Sørensen 2014). Kočí *et al.* (2017) refuted this interpretation and suggested that *P. cretacea* was probably a robust stalked cirripede (lepadomorph or scalpellomorph).

Subsequently, Chan *et al.* (2021) recognised *P. cretacea* as a basal balanomorph and placed it in the superfamily Pachydiademataceae (correctly Pachydiadematoidea) but included *Epibrachylepas* and *Parabrachylepas* in the Brachylepadomorpha. A supposed Cenomanian balanomorph (Chionelasmataceae), *Archaeochionelasmus nekvasilovae* Kočí, Newman and Buckeridge in Kočí, Kočová Veselská, Newman, Buckeridge and Sklenář, 2017 was described on the basis of a single specimen from the Czech Republic, but Gale and Skelton (2018) argued that this was a fragment of a rudist bivalve.

Gale and Vidovic (2023) undertook cladistic analysis of 14 verrucomorph, balanomorph and brachylepadid cirripedes and generated a consensus tree which showed brachylepadids as a paraphyletic sister group to the balanomorphs. They therefore abandoned the order Brachylepadomorpha and placed the brachylepadids in the Balanomorpha.

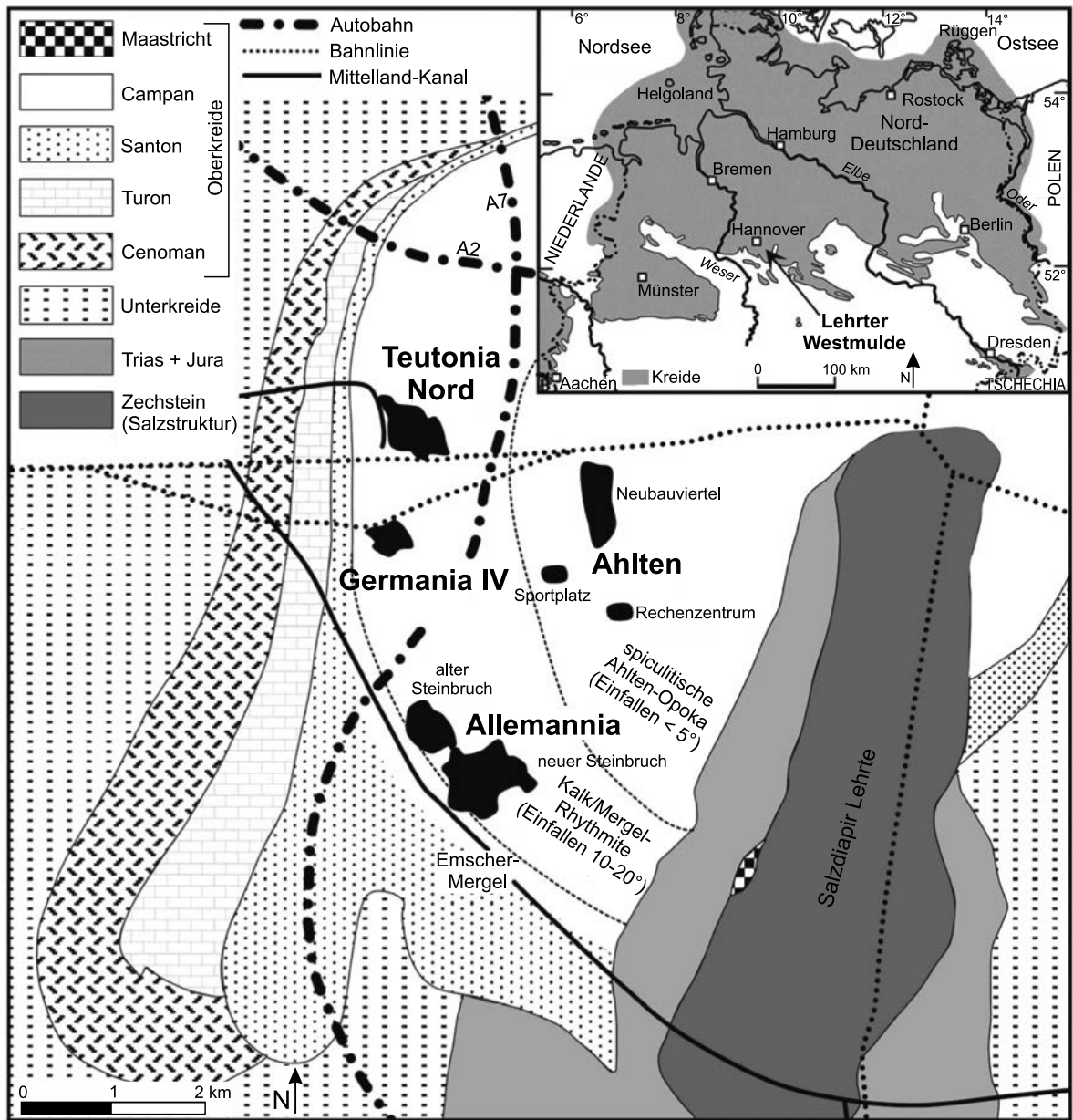
It was therefore of considerable interest to discover a handful of specimens of a new, tiny sessile barnacle (maximum 2 mm in C-R length) from the lower and upper Campanian chalks of Höver and Misburg, near Hannover (northern Germany). Three of these were collected by Dr. Peter Girod of Berlin, who generously made the material available for study. These specimens are cemented onto brachiopod shells, echinoid tests and serpulid tubes, and the marginals, carina, rostrum and imbricating plates are fused together; the opercular plates are missing. Two additional specimens from the Hannover area are in the collection of Dr. Ralf Krupp (Burgdorf, Germany). A further bioimmured individual, from the upper Maastrichtian of southern Limburg (the Netherlands), retains the slightly displaced opercular plates. In the present paper, we describe this material as a new genus and species and discuss its phylogenetic significance.

LOCALITIES AND STRATIGRAPHY

Most specimens come from the lower Campanian (*senonensis* Zone; see Ernst 1975; Niebuhr 2013; Niebuhr *et al.* 2023) and upper Campanian (*vulgaris/basiplana*, *vulgaris/stolleyi* and *minor/polyplocum* zones) chalks that are exposed in the large working and disused quarries in the Hannover area, northern Germany (Text-fig. 1). A single specimen is from upper Maastrichtian coarse-grained biocalcarenes (Maastricht Formation, Meerssen Member; Jagt and Jagt-Yazykova 2012; Vellekoop *et al.* 2022) of southern Limburg, the Netherlands.

PHYLOGENETIC ANALYSIS

The relationships of verrucomorph and balanomorph taxa were investigated using a list of 48 morphological characters taken from Gale and Vidovic (2023; see Tables 1 and 2) and 17 taxa, five of which are extant, including the newly described *Microcorona girodi* gen. et sp. nov. The consensus tree, based on unconstrained heuristic analysis, demonstrates that all three orders form a well-supported (100% bootstrap) monophyletic group, with



Text-fig. 1. Map to show the distribution of Mesozoic strata in the Hannover area and the position of the various working and disused quarries (adopted from Girod *et al.* 2023). Material of the new brachylepadid originates from lower and upper Campanian chalk at Höver (Allemannia quarry, Holcim [Deutschland] GmbH) and Misburg (Nord- and Südgrube of Heidelberg Materials ABG).

an unresolved basal trichotomy [*Pedupycnolepas* Gale, 2014b, Pycnolepadidae+Verrucomorpha (65%), Brachylepadidae+Balanomorpha (72%)]. Thus, taxa previously identified as brachylepadomorphs fall either as basal to the Balanomorpha (paraphyletic Brachylepadidae) or Verrucomorpha (paraphyletic Pycnolepadidae). In this tree (Text-fig. 2), *Microcorona girodi* gen. et sp. nov. appears

as sister group to the Neobalanomorpha, supported by a 100% bootstrap.

Institutional abbreviations

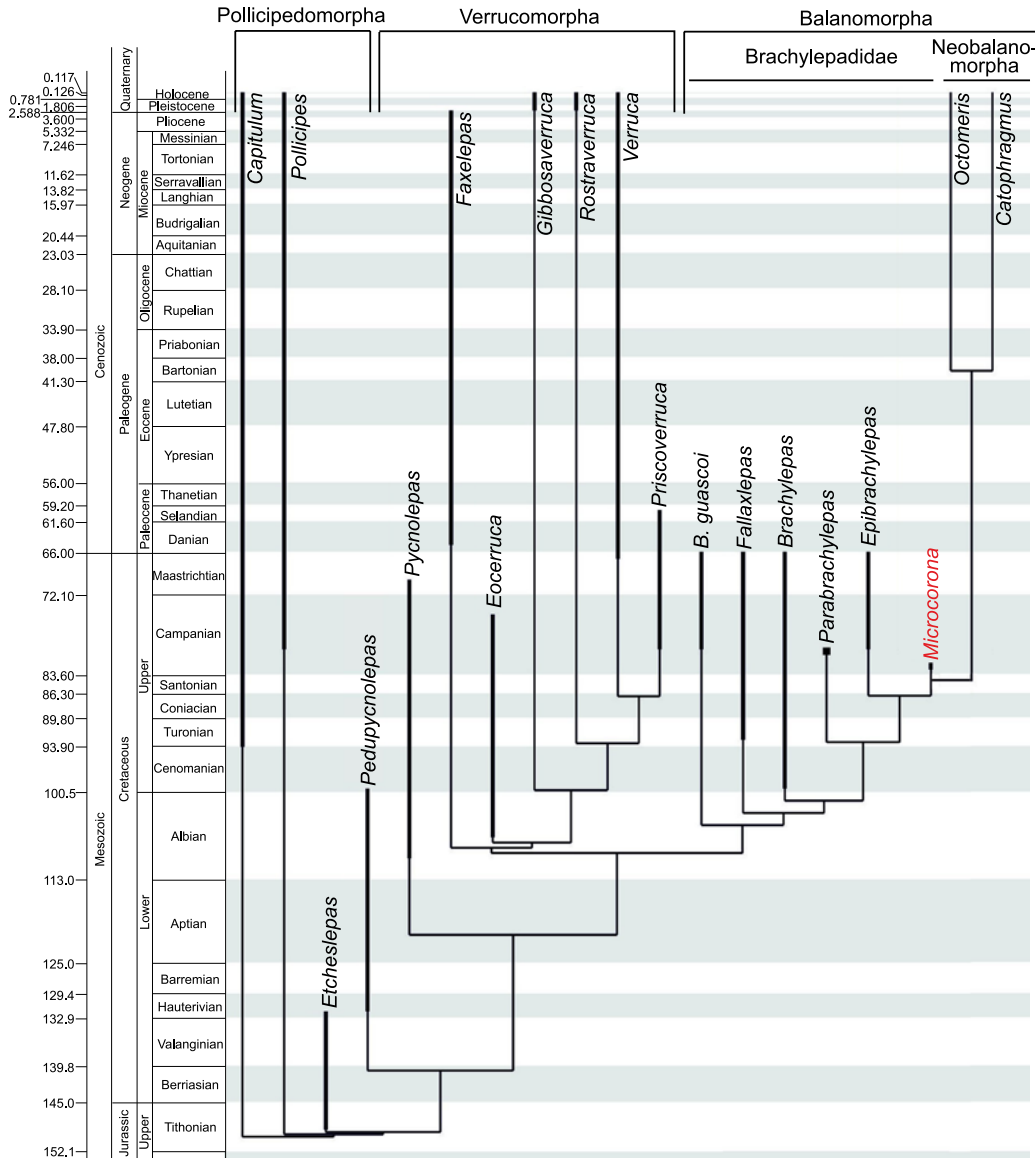
MB – Museum für Naturkunde, Berlin, Germany.
 NHMM – Naturhistorisch Museum Maastricht, Maastricht, the Netherlands.

Number	Character
1	Capitulum bilaterally symmetrical (0); slight asymmetry (1); strong asymmetry (2)
2	Capitulum tall, laterally compressed (0); low, broad as high (1)
3	Capitulum composed of >12 plates (0), 12 plates (1), 8 plates (2); 6 plates (3)
4	Peduncular plates bear inner shelf (0); ball and socket articulation (1); no shelf, smooth interior (2)
5	Peduncular plates small (0); large, form alternating rows around capitulum (1)
6	Tall carina 2-3× breadth (0); low, hemiconical (1); low, asymmetrical (2)
7	Rostrum half height of carina (0); equal height (1)
8	Rostrum and carina do not articulate (0); articulate on one side only (1)
9	Rostrum and carina symmetrical (0); slanted (1); strongly asymmetrical (2)
10	Carinolatera present (0); absent (1)
11	Rostrolatera present (0) absent (1)
12	Inframedian latera present (0) absent (1)
13	Subrostrum present (0) absent (1)
14	Subcarina present (0) absent (1)
15	Minor latera present (0) absent (1)
16	Upper latus present (0); absent (1)
17	Upper latus tall, triangular (0); low, equilaterally triangular (1)
18	Upper latus with angled basal margin (0); straight basal margin (1)
19	Scuta taller than broad (0); broader than tall (1)
20	Scuta and terga symmetrical (0); weakly asymmetrical (1); strongly asymmetrical (2)
21	Terga rhombic (0); kite-shaped (1)
22	Scuta and terga possess narrow apicobasal ridges (0); broad apicobasal ridge on FT and FS
23	Scuta and terga with weak articulation (0); scutal auricle fits into tergal notch (1); articulation interpenetrant (2)
24	No secondary ribs on scuta and terga (0); interpenetrant ribs present (1)
25	Articular ridge absent on scuta (0); present (1)
26	Articular ridge weakly developed (0); strongly developed (1)
27	Articular furrow absent on scuta (0); present (1)
28	Articular furrow weakly developed (0); strongly developed (1)
29	Occludent regions of F scuta and F terga not differentiated (0); occludent wing present (1)
30	Occludent margin at acute angle to FS margin of FT (0); right angles (1)
31	Tergal notch shallow (0); deeply inset (1)
32	Carina-FT contact simple (0); with interpenetrant ribs (1)
33	Rostrum-FS contact simple (0); interpenetrant (1)
34	Scutum and tergum of pair in same plane (0); strongly angled (1); one of pair fixed (2)
35	Pairs of scuta and terga parallel (0); splayed, to form operculum (1)
36	Scutal adductor on FS indistinct (0); sharply defined, impressed (1)
37	Myophore absent (0); present (1)
38	Myophore forms tongue (0); forms horizontal sheet (1)
39	Depressor muscle insertion in band on basal margins of scuta and terga (0); discrete insertion sites on basal margins (1)
40	Tergal depressor insertion absent (0); present (1)
41	Tergal depressor insertion weak, set on mid-lower carinal margin (0); strong, toothed, set on summit of carinal margin (1)
42	Rostrosutal depressor insertion absent (0); present (1)
43	Lateral scutal depressor insertion absent (0); present (1)
44	Marginals absent (0); marginals present (1)
45	Rostromarginals absent (0) present (1)
46	Carinomarginals absent (0) present (1)
47	Marginals over- and underlap rostrum and carina (0); over- and underlap (1)

Table 1. Character list.

Taxon	<i>Etcheslepas</i>	<i>Pedypycnolepas</i>	<i>Pycnolepas</i>	<i>Faxelepas</i>	<i>Eoverruca</i>	<i>Gibbosaverruca</i>	<i>Rostratoverruca</i>	<i>Verruca</i>	<i>Fallaxlepas</i>	<i>Brachylepas</i>	<i>Parabrachylepas</i>	<i>Epibrachylepas</i>	<i>Octomeris</i>	<i>Catophragnus</i>	<i>B. guascoi</i>	<i>Priscoverruca</i>	<i>Capitulum</i>	<i>Pollicipes</i>	<i>Microcorona</i>
1	0	0	0	1	1	2	2	2	0	0	0	0	0	0	0	2	0	0	0
2	0	0	0	0	0	0	1	1		1	1	1	1	1	1	1	0	0	1
3	0	2	2	2	3	3	3	3	2	2	2	2	1	1	2	3	0	0	2
4	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
5	0	0	0	0	0				1	1	1	1	2	2	1		2	2	2
6	0	1	1	1	1				1	1	1	1		1	1		0	0	1
7	0	0	0	0	0	2	2	2	0	1	1	1	1	1	1	2	0	0	1
8	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	0	1
9	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0
10	0	0	0	1	1	2	2	2	0	0	0	0	0	0	2	2	0	0	0
11	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
12	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
13	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
14	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
15	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
16	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	1
17	0	0	0	0	1	1	1	1	0	0	0	0	1	1	1	1	0	0	1
18	0	0	0	0					0	0	1	0					0	0	
19	0	1	1	1					1	1	1	1			1		0	0	
20	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
21	0	0	0	1	1	2	2	2	0	0	0	0	0	0	0	2	0	0	0
22	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	1
23	0	0	0	0	1	1	1	1	0	0					0	1	0	0	
24	0	1	1	1	1	1	1	1	1	1	1	2	2	2	1	1	0	0	2
25	0	0	0	0	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0
26	0	0	0	0					1	1	1	1	1	1	0		0	0	1
27									0	0	0	1	1	0					1
28	0	0	0	0					1	1	1	1	1	1	0		0	0	1
29									0	0	1	1	1	0					1
30	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0
31	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0
32	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0
33	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0
34	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	1	0	0	0
35	0	0	0	0	0	0	0	2	2	2	0	1	1	1	2	0	0	0	1
36	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1
37						0	1	1								1			
38						0	1	1								1			
39							0	1								0			
40	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1
41	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1
42	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
43	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1
44	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	1
45	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0	1
46	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1

Table 2. Data matrix for cladistic analysis.



Text-fig. 2. Consensus cladogram to show the inferred phylogenetic position of *Microcorona* gen. nov. The arrow on the right shows the earliest known occurrence of neobalanomorph species.

SYSTEMATIC PALAEOLOGY

Order Balanomorpha Pilsbry, 1916

DIAGNOSIS: Symmetrical sessile cirripedes in which the rostrum and carina are of similar size, and the terga and scuta form an operculum positioned in an orifice. There is a strong articulation between the terga and scuta.

REMARKS: The definition of the order has recently been modified to include the Brachylepadidae (Gale

and Vidovic 2023). Brachylepadids form a paraphyletic stem group to the Neobalanomorpha Gale in Gale and Sørensen, 2014, which is here resurrected as a suborder.

Family Brachylepadidae Woodward, 1901

MODIFIED DIAGNOSIS: Capitulum low, carina and rostrum short, hemiconical; primary wall surrounded by imbricating plates conjoined by peg-and socket articulations. Rostro- and carinomarginals absent.

INCLUDED GENERA: *Brachylepas* Woodward, 1901, *Fallaxlepas* Gale, 2020, *Epibrachylepas* Gale in Gale and Sørensen, 2014, *Parabrachylepas* Gale in Gale and Sørensen, 2014, and *Microcorona* gen. nov.

REMARKS: The restricted family, admittedly paraphyletic, is demarcated by the low profile of the capitulum and the highly specialised articulation (peg and socket) between alternate rows of imbricating plates. The family is exclusively Late Cretaceous in age, extending from the lower Cenomanian to the upper Maastrichtian (Gale and Vidovic 2023). *Neobrachylepas* Newman and Yamaguchi, 1995, which is morphologically convergent with the brachylepadidae, is now placed in the superfamily Neolepadoidea, subfamily Neobrachylepadinae (Chan *et al.* 2021). *Plesiobrachylepas* Carriol in Carriol, Bonde, Jakobsen and Høeg, 2016 has recently been transferred to the Neobrachylepadidae (Gale and Vidovic 2023).

Microcorona gen. nov.

TYPE SPECIES: *Microcorona girodi* gen. et sp. nov.

urn:lsid:zoobank.org:act:A1C85F0E-9629-46D6-B875-B0DD73EFAA5A

DIAGNOSIS: Tiny (R-C < 2 mm), low, oval-subrhombic shell made up of fused carina, two marginal plates and rostrum. The carina overlaps the marginal plates, which in turn overlap the rostrum. Two or three tiers of triangular-rectangular imbricating plates, fused to wall. Scutum triangular, elongated, tergum short, equilaterally triangular. Upper latus absent.

DERIVATION OF NAME: Latin *micro-*, meaning tiny, and *corona* meaning crown, in allusion to the size and shape of the shell.

REMARKS: *Microcorona girodi* gen. et sp. nov. possibly evolved from *Epibrachylepas* or a closely related genus by the development of imbricate articulations between the marginals, carina and rostrum, and fusion of these plates, plus the surrounding imbricating plates. In the opercular valves, the upper latus was lost.

Microcorona girodi gen. et sp. nov.

(Text-figs 3A–L and 4, item 7)

2023. Brachylepadidae indet.; Jagt *et al.*, p. 614, fig. 16.

urn:lsid:zoobank.org:act:B2E884A-A84B-4B59-A859-A4BFAFCDBA8D

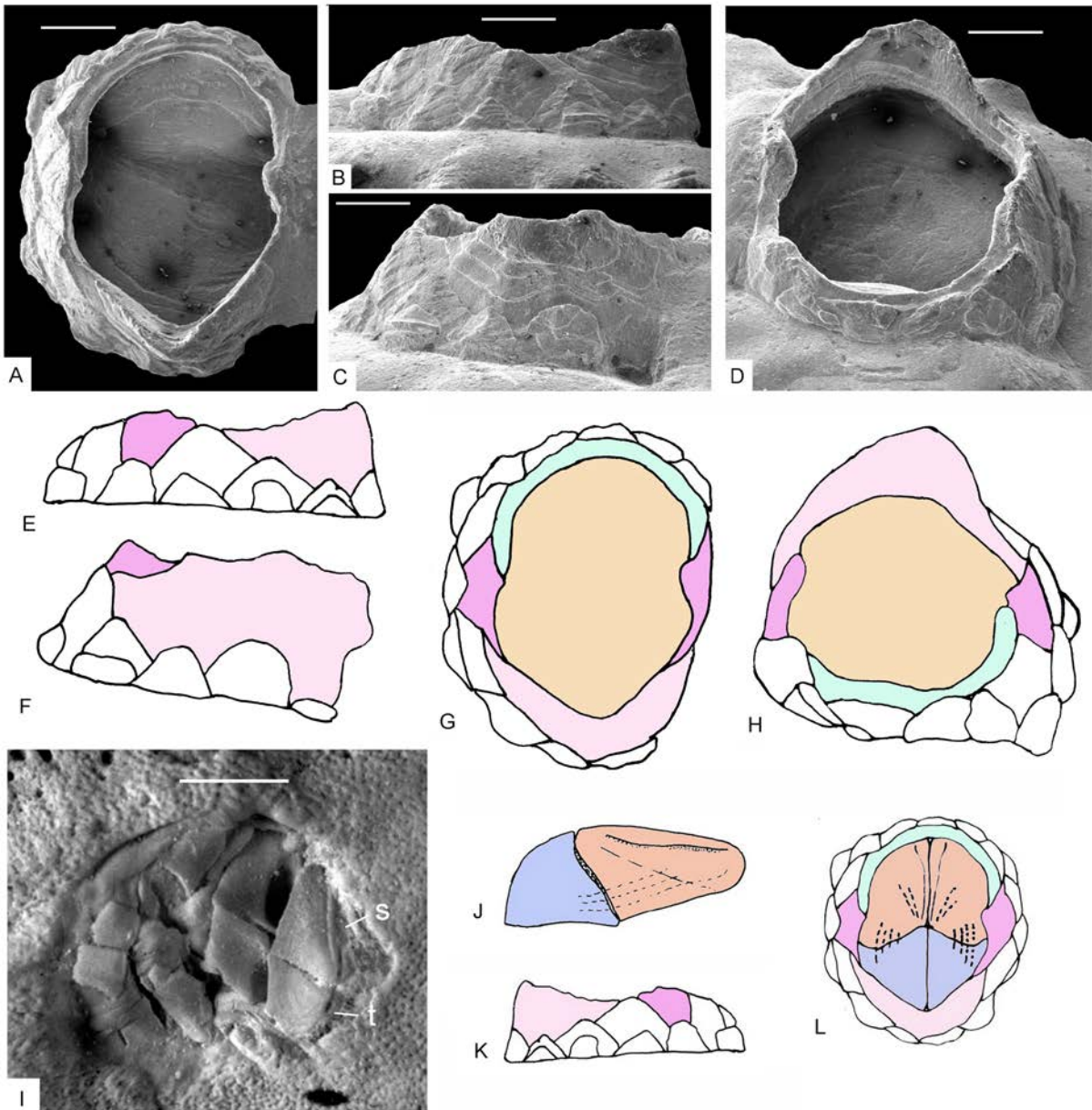
DIAGNOSIS: As for genus.

DERIVATION OF NAME: Named after Dr. Peter Girod (Berlin), who collected the holotype and presented this to the Museum für Naturkunde (Leibniz Institut, Berlin).

TYPES: The holotype (Text-fig. 3A–H) is a well-preserved individual attached to, and partly overgrown by, a serpulid annelid (MB.A.6823), collected from *senonensis* Zone in the lower Campanian of Alemannia Quarry at Höver, near Hannover. The paratype (Text-fig. 3I) is a bioimmured specimen from the upper Maastrichtian (Maastricht Formation, Meerssen Member, base of subunit IVf-3) at the former Blom Quarry, Berg en Terblijt, southern Limburg, the Netherlands (NHMM JJ 2451).

ADDITIONAL MATERIAL: We have also examined two additional specimens in the Girod Collection and two more in the Krupp Collection, all from the Campanian of Misburg, Germany.

DESCRIPTION: Shell very small, oval to rounded rhombic in apical view, quadrangular in lateral aspect (Text-fig. 3A–H). Height half to third of length. Maximum rostrocarinal dimension 2 mm, transverse dimension 1–1.5 mm. Wall comprising carina, rostrum and paired marginal plates; carina concavo-convex, upright; apex narrow, rounded (Text-fig. 3B, E) or weakly reflexed dorsally (Text-fig. 3C). Carina overlapping marginal plates (Text-fig. 3B, E). Marginal plates triangular, symmetrical, apices rounded and/or slightly inflexed over orifice (Text-fig. 3A, G). Rostrum low, wall thin, concavo-convex, overlapped by marginal plates (Text-fig. 3A, D, G, H). Irregularly shaped Imbricating plates in 2 or 3 whorls, closely adpressed and fused to wall; plates of inner row larger, quadrangular or triangular, extending nearly up to apical margin of wall. Outer rows extending up to lower 3rd of wall, irregularly imbricate. Sutures between all plates fused. Orifice hourglass-shaped (Text-fig. 3A), broadest towards dorsal margin. Opercular plates articulated in bioimmured specimen (Text-fig. 3I); scutum triangular, basitergal angle 90°; occludent margin gently convex, elongated; ventral margin of scutum rounded. Tergum short, nearly equilaterally triangular, occludent margin strongly arched. Scars for insertion of tergal depressor muscles visible on basal internal margin of tergum. Scutum and tergum with interpenetrant articulation, forming nearly straight margin. Upper latus absent. Surfaces of scutum



Text-fig. 3. *Microcorona girodi* gen. et sp. nov., holotype (MB.A.6823, leg. P. Girod), from the lower Campanian *senonensis* Zone, Alemania Quarry, Höver (Hannover area, Germany); collections of Museum für Naturkunde, Berlin. Photographs: A – apical view; B – lateral view; C – dorsal view; D – oblique ventral view. E–H – interpretative drawings. I – paratype (NHMM JJ 2451), bioimmured by a large exogyrine oyster, showing paired opercular plates, scutum (s) and tergum (t) which are slightly displaced, upper Maastrichtian (Maastricht Formation, Meerssen Member, base of subunit IVf-3), former Blom quarry, Berg en Terblijt, southern Limburg, the Netherlands. J – drawing of external surface of opercular plates. K, L – reconstruction, in lateral (K) and apical views (L). See Text-fig. 4 for colour key. Scale bars equal 0.5 mm (A–H) and 1 mm (I).

and tergum weakly sculptured, with faint commarginal lines; shallow groove parallel with occludent margin of scutum. Basis variably completely calcified (Text-fig. 3A, D), partly calcified or possibly not calcified.

A reconstruction (Text-fig. 3J–L) combines features of the holotype shell (Text-fig. 3A–H) with the

opercular plates of the paratype (Text-fig. 3I). The shell is oval-cylindrical, very low, and the orifice is large and slightly hour-glass shaped.

REMARKS: *Microcorona girodi* gen. et sp. nov. differs from all other brachylepadids in the hour-glass shape of the orifice, the absence of an upper

latus and the overlap and fusion of the wall plates and imbricating plates.

Suborder Neobalanomorpha Gale in Gale and Sørensen, 2014

DIAGNOSIS: Balanomorphs in which the carina is overlapped by the adjacent carinomarginals or marginals. Alae are more strongly developed than in the stem group balanomorphs.

REMARKS: As thus defined, the neobalanomorphs include all the post-Cretaceous balanomorphs, including the superfamilies Pachylasmatoidea, Chthamaloidea, Elminioidea, Coronuloidea and Balanoidea. The relationships between these have been demonstrated from molecular data (Pérez-Losada *et al.* 2014; Chan *et al.* 2017).

PHYLOGENETIC SIGNIFICANCE

In the phylogeny of balanomorph origins presented by Gale and Sørensen (2014), the derived brachylepadid genera *Epibrachylepas* and *Parabrachylepas* develop a marginal plate on each side of the wall, positioned between the carina and rostrum, creating a four-plated, unfused wall (item 6 in Text-fig. 4). Concomitantly, there were important changes in the articulation between the opercular plates (tergum, scutum) which provided better articulation between these plates. The shape of the scutum changed, with the basitergal angle becoming a right angle. In the more derived *Pachydiadema*, two additional marginal plates were added (rostromarginals and carinomarginals) giving an eight-plated wall. The morphological changes which led to all higher balanomorphs (i.e., Neobalanomorpha) involved loss of the upper latus and a permanent change in the overlap of the wall plates, such that the marginal plates overlap the carinomarginals, and the carinomarginals overlap the carina.

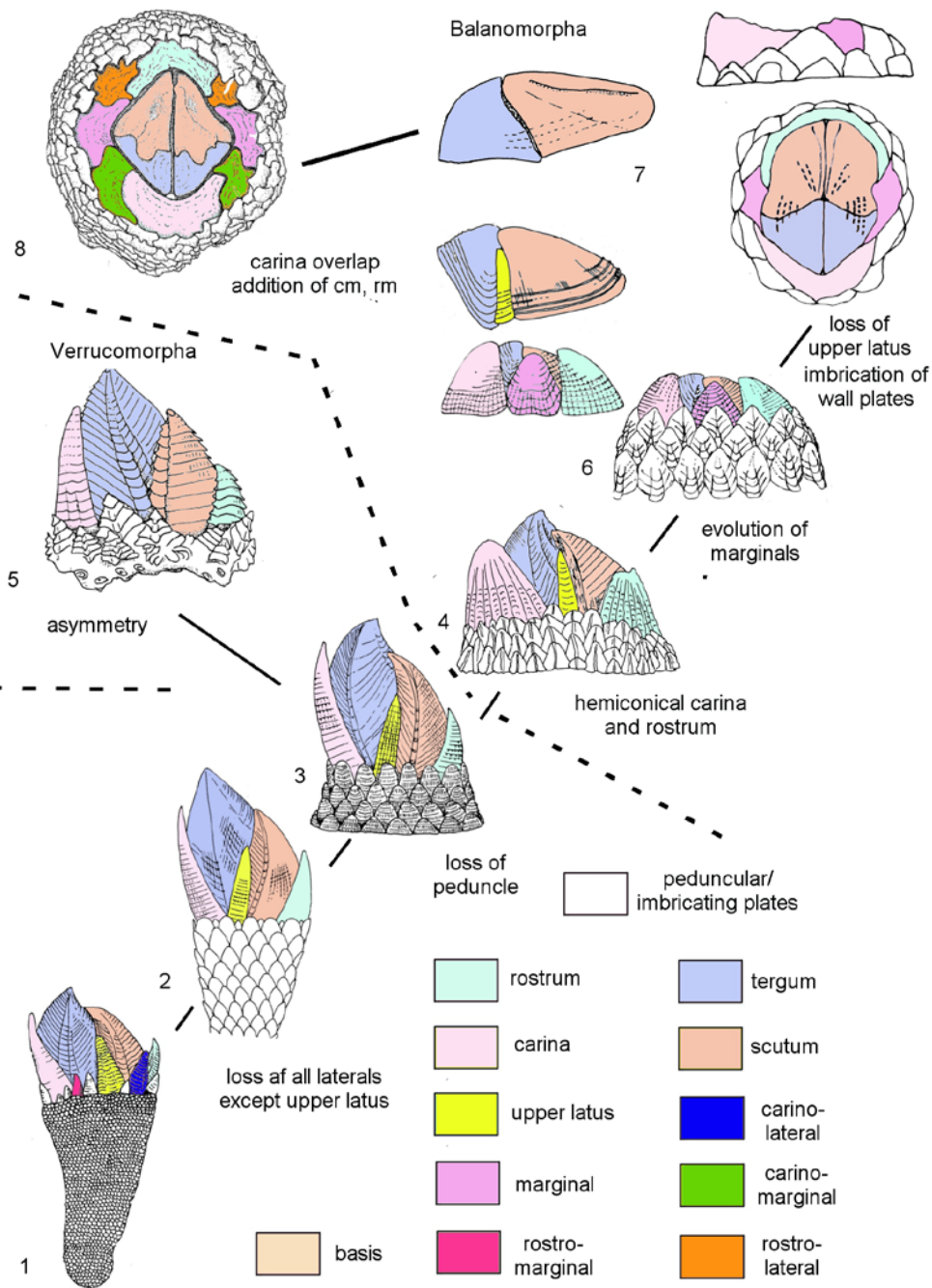
In its four-plated wall, *Microcorona* gen. nov. is at least superficially similar to derived balanomorphs with a similar construction. However, there is a consensus that in neobalanomorphs these originated by progressive plate reduction from an originally eight-plated condition, via a six-plated intermediate, by fusion of various wall plates (e.g., Newman 1967; Palmer 1982; Ross and Newman 1996), although evidence for this is sometimes not clear. This fusion usually involved the rostrum and rostromarginals forming a rostral plate, but other

combinations do occur (Ross and Newman 1996, fig. 2) very rarely, such as the fusion of the carinomarginals with the carina (Ross and Newman 1996, fig. 2). It is also possible that some of these taxa never developed more than four plates, retaining the condition from early post-metamorphosis ontogeny; balanomorphs initially deposit a wall composed of a rostrum, a carina and two marginals (Glennier and Høeg 1993; Chan *et al.* 2021) and only later add rostromarginals and carinomarginals, variably fused or lost in six- and eight-plated forms. Thus, the wall of juvenile (post-metamorphosis) balanomorphs appears to retain its morphology from an ancestral four-plated brachylepadid. The reduction in wall plate numbers can perhaps be related to selection to reduce gastropod predation at plate boundaries (Palmer 1982). Ross and Newman (1996) also proposed a hypothetical, ancestral four-plated ‘urbalanomorph’, in which the wall comprised the rostrum, two marginals and the carina which is remarkably similar to *Microcorona* gen. nov.

The overlapping relationships of neobalanomorph wall plates is also fairly consistent, specifically with the margins of the carina invariably overlapped by the adjacent plates (either the carinomarginals or the marginals) and the rostrum overlapped by the rostromarginals. Gale and Sørensen (2014) interpreted the Late Cretaceous (Campanian) *Pachydiadema cretacea* as having the carina overlapping the carinomarginals, although the rostrum was overlapped by the rostromarginals, as in many other balanomorphs. A similar condition exists in *Microcorona* gen. nov. in which the carina clearly overlaps the marginals (Text-fig. 3). It seems fair to assume that there was considerable flexibility in the relationships of the wall plates during early evolution of the balanomorphs, before the consistent patterns of the crown group were established.

Imbricating plates which surround the wall are homologous with peduncular plates of stalked cirripedes (Ross and Newman 1996, 2001; Gale and Vidovic 2023) and are present in the Brachylepadidae and retained in some basal Chthamaloidea (families Waikalasmatidae, Catophragmidae and Chionelasmatidae). In many forms, these are numerous and form a palisade composed of rows of alternating, imbricating, unfused plates surrounding the wall (items 4, 6 in Text-fig. 4).

The fusion of the imbricating plates with each other, and onto the parietal wall in *Microcorona* gen. nov. is also unusual, because these simply articulate tightly in brachylepadids (Gale and Sørensen 2014), Pachylasmatoidea (Chan *et al.* 2021) and



Text-fig. 4. Phylogenetic scenario for evolutionary origin of balanomorph and verrucomorph cirripedes, based on data from Gale and Sørensen (2014), Gale (2014b), and Gale and Vidovic (2023). The lineage leading to the Verrucomorpha and Balanomorpha lost all lateral plates except for the upper latus (1–2), and subsequently lost the peduncle (2–3). One branch (3–5) led to the Verrucomorpha, by development of a highly asymmetrical shell, the wall of which incorporated one tergum and one scutum – the other pair formed an opercular lid. Derived brachylepadomorphs (6) and balanomorphs (7) evolved new wall plates called marginals which are positioned between the carina and rostrum, and in *Microcorona* gen. nov. (7) these imbricated and fused to form a solid wall. Some balanomorphs (e.g., 8) evolved an 8-plated wall. 1 – *Etcheslepas durotrigensis* Gale, 2014a, Tithonian, Jurassic, Dorset, United Kingdom. 2 – *Pedupycnolepas articulata* (Collins, 1980), Aptian, Cretaceous, Antarctica. 3 – *Pycnolepas rigida* (J. de C. Sowerby, 1836), Albian, Cretaceous, United Kingdom. 4 – *Brachylepas naissantii* (Hébert, 1855), Campanian, Cretaceous, United Kingdom. 5 – *Eoverruca hewitti* (Withers, 1935), Santonian, Cretaceous, United Kingdom. 6 – *Epibrachylepas newmani* Gale in Gale and Sørensen, 2014, Campanian, Cretaceous, Sweden. 7 – *Microcorona girodi* gen. et sp. nov., Campanian, Cretaceous, Germany. 8 – *Catomerus polymerus* Darwin, 1854 (after Anderson 1983), Recent, south-east Australia.

the chthalamoidean families in which these are present (Catophragmatidae, Waikalasmatidae and Chionelasmatidae). However, the homologous imbricating plates are similarly fused in the basal verrucomorph *Eoverruca hewitti* Withers, 1935 (see Gale 2014b), in which a calcified basis is present. Fusion of the shell plates acts as a restriction to further growth in verrucomorphs because it is no longer possible to expand the plate margins by calcification or to add new plates (Gale 2020). It is thus evident that the specimens of *Microcorona girodi* gen. et sp. nov. are fully grown and achieved a maximum dorsoventral length of 2 mm, which is small for a fully-grown balanomorph barnacle.

In all Pachylasmatoidea, Chthamaloidea, Elminioidea and most Coronuloidea, the basis is membranous, and is calcified only in a few bathylasmatids and most Balanoidea, the most derived balanomorphs (Chan *et al.* 2021). Uniquely amongst brachylepadids, the basis is strongly calcified in *Microcorona* gen. nov. A parallel situation exists in the Cretaceous verrucomorph *Eoverruca* (Gale 2014b; Gale and Vidovic 2023) which is the only member of the order to possess a calcified basis. Calcification of the basis evidently occurred independently a number of times.

An interpenetrant articulation of the scuta and terga evolved progressively in the basal Balanomorphs, involving the development of articular ridges and furrows (Gale and Sørensen 2014, fig. 9; Gale and Vidovic 2023, fig. 5). In the brachylepadid *Epibrachylepas*, the articulation is essentially similar to that in Chthamaloidea. In both, a double interpenetrant structure, involving the tergal notch, scutal auricle, articular ridge and furrow (Gale and Vidovic 2023, fig. 5E, F) is present. However, *Epibrachylepas* also possessed an upper latus, positioned in a shallow groove between the scutum and tergum, which is lost in all Neobalanomorphs (Gale and Sørensen 2014). Although details of the scutum/tergum articulation are not visible in the present material of *Microcorona* gen. nov., the upper latus is absent, which brings the genus close to the neobalanomorph condition. The upper latus was independently lost in verrucomorph cirripedes (Eoverrucidae and Verrucidae; see Gale 2014b, Gale and Vidovic 2023).

A scenario for the evolution of basal balanomorphs (Text-fig. 4) involves the following events:

- loss of peduncle, loss of all lateral plates, with exception of the upper latus (Pycnolepadidae);
- peduncular plates forming skirt around carina and rostrum (Pycnolepadidae, Brachylepadidae);

- carina and rostrum becoming hemiconical (*Brachylepas*);
- marginal plate introduced between rostrum and carina (*Epibrachylepas*, *Parabrachylepas*);
- interpenetrant articulation of scutum and tergum (*Epibrachylepas*);
- marginal plate developing overlap with rostrum, being overlapped by carina (*Microcorona* gen. nov.);
- upper latus lost (*Microcorona* gen. nov. and all more derived taxa);
- introduction of carinomarginals and rostromarginals (*Pachydiadema*, Chthamaloidea);
- consistent overlap of marginals/carinomarginals by carina (Chthamaloidea, Elminioidea, Coronuloidea and Balanoidea);
- loss of imbricating plate skirt (all derived balanomorphs, except families Waikalasmatidae, Catophragmididae and Chionelasmatidae).

Cladistic analysis supports the position of *Microcorona* gen. nov. as basal to all neobalanomorphs (Text-fig. 2), and close to the hypothetical ‘urbanomorph’ ancestor of Ross and Newman (1996). However, the new genus displays a number of autapomorphic features which parallel those which evolved independently in more derived balanomorphs, including the calcified basis and fused wall plates. Additionally, the overlapping relationships of the wall plates in *Microcorona* gen. nov. differ significantly from those in more derived taxa.

PALAEOECOLOGY

There is a broad consensus that balanomorphs originated in shallow-marine habitats, specifically, associated with rocky shorelines (e.g., Anderson 1983; Gale and Sørensen 2014); the presence of a primitive balanomorph in a deep-water (>200 m) Upper Cretaceous chalk facies in the Hannover area, attached to shelly substrates is therefore rather unexpected. However, cirripedes are opportunists which have remarkable abilities to adapt to diverse habitats, and deep-water benthic species at the present day all depend on hard substrates for attachment sites (Anderson 1994).

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