

# New stalked and sessile cirripedes from the Eocene Mo Clay, northwest Jutland (Denmark)

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## ABSTRACT

New taxa of thoracican cirripedes are recorded from the Eocene Mo Clay of northwest Jutland, Denmark, namely *Stipilepas molerensis* Carriol n. gen., n. sp., a scalpelliform gooseneck barnacle, and *Plesiobrachylepas jutlandica* Carriol n. gen., n. sp., a brachylepadomorph sessile form. This material is of importance in that the former not only represents the first extinct example of the tribe Ashinkailepadini, it also is the second fossil neolepadine, while the latter adds to the diversity of the family Brachylepadidae, which previously embraced only three genera. The geological context of these taxa is outlined and their phylogenetic interest discussed.

## RÉSUMÉ

*Nouveaux cirrripèdes pédonculé et sessile de l'Éocène de Mo clay, nord-ouest du Jutland, Danemark.*

De nouveaux taxons de cirrripèdes thoraciques ont été découverts dans l'Éocène de Mo Clay au nord-ouest du Jutland, Danemark. Il s'agit de *Stipilepas molerensis* Carriol n. gen., n. sp., un cirrripède pédonculé scalpelliforme et de *Plesiobrachylepas jutlandica* Carriol n. gen., n. sp., un cirrripède sessile brachylepadomorphe. Ce matériel est important car le premier taxon représente, non seulement le premier taxon fossile attribuable à la tribu des Ashinkailepadini, mais aussi le second taxon fossile appartenant aux Neolepadinae; le second taxon, quant à lui, agrandit la diversité de la famille des Brachylepadidae qui ne comptait jusque-là que trois genres. Le contexte géologique de ces nouveaux taxons est établi et leur intérêt phylogénétique est discuté.

## KEY WORDS

Barnacles,  
Phylogeny,  
Eocene,  
northern Europe,  
new genus,  
new species.

## MOTS CLÉS

Balanes,  
Phylogénie,  
Éocène,  
nord de l'Europe,  
genres nouveaux,  
espèces nouvelles.

## INTRODUCTION

The fauna and flora, comprising both marine taxa and terrestrial species from nearby land masses, of the 'Mo Clay' have been the subject of numerous studies. Crustacean assemblages from this unit include isopods, decapods (shrimps, crabs) and maxillopods (cirripedes). The last-named, studied in the present paper, are represented by two new species, in two new genera. One of these is attributable to the Ashinkalepadini, a tribe of the Neolepadinae and the other one to the Brachylepadidae. At present, the representatives of these two groups are restricted to hydrothermal vents and seeps in the Pacific and Indian oceans.

All specimens described herein are deposited in the collections of the Statens Naturhistorisk Museum (Geological Museum; prefix MGUH) at Copenhagen.

## GEOLOGICAL SETTING AND PALAEONTOLOGY

The 'Mo Clay' is a *c.* 60-metre thick marine diatomite of Early Eocene age, assigned to the Fur Formation (Pedersen & Surlyk 1983). It was laid down in a narrow strip within the North Sea Basin and yields an excellently preserved pelagic fauna, with none or only few benthic animals present to disturb the laminated sediment and its fossil content (Bonde 1979, 1987; Thomsen & Danielsen 1995; Heilmann-Clausen 2006; Bonde *et al.* 2008).

The diatomite proper is exposed only in a limited area in the western Limfjorden region, particularly on the islands of Mors and Fur in northwest Jutland (Andersen & Sjørring 1992; Heilmann-Clausen 2006), but it has also been recognised in boreholes south towards Harre in northern Salling and even further towards the northwest in a narrow strip of the North Sea (Thomsen & Danielsen 1995). Towards the south in Jutland, the diatomite is replaced by a more clayey facies without diatoms, the Ølst Formation (Heilmann-Clausen 2006). At a few well-defined horizons of the Mo Clay lime precipitated in lenticular boulders or, in a single case, as an continuous limestone layer (Pedersen & Buchardt 1996). In these boulders and at this level, fossils are particularly well preserved, with bird skeletons occasionally associated with feathers (Bonde 1987), pigmentation, chromatine grains, and 3D preservation of skulls and bones, mainly of birds (Kristoffersen 2002; Lindow 2007).

The diatomite itself, referred to as Mo Clay (Danish: *moler*), is composed of about 65% of diatom tests (opal), 25% of smectite and 10% of volcanic dust. The Mo Clay is very porous and when dry is of a light sandy colour and may even float on water. In the lower part much of the sediment has a fine, primary lamination, while there are only few laminated horizons in the upper part, in which most of the sediment is homogenised and several horizons show ash-filled burrows. The limestone boulders are more or less confined to well-laminated sequences, and have a calcium carbonate content of about 65%, probably precipitated due to bacterial activity at very shallow depths below the surface (Pedersen & Buchardt

1996). Evidently they were formed prior to skeleton dissolution, because in the Mo Clay proper skeletons are preserved only as very detailed imprints.

The entire formation contains a series of about 200 volcanic ash layers (Bøggild 1918; Larsen *et al.* 2003) bearing witness to the violent opening of the Norwegian-Greenland Sea (Morton & Parsons 1988), with some of ash falls having been recognised in Austria, far away from their East Greenland-Faroy source area (Egger & Brückl 2006). These ash layers enable an absolute dating of the Mo Clay to *c.* 55.5–54 Ma (Knox 1997). The easily recognised ash layers were numbered by Bøggild (1918); layers –33 to +140 are within the Fur Formation, while layers –34 to –39 are now assigned to the Stolleklint Clay, just below the Mo Clay and lacking diatoms. These layers permit the subdivision of this unit into two members. The lower is the Knuden Member, the type locality of which is Knuden Cliff on Fur, with negative-numbered ash layers (of which there are just few), while the upper, with 140 ash layers, is the Silstrup Member, named after a cliff at Thy on the northern coast of Limfjorden.

The heat emitted from the volcanic activity in the crust made the entire rift zone bulge to a height of perhaps 1 km above sea level, especially close to the 'hot spot' comprising the combined East Greenland and Faroy basalt areas. In this way the 'Thule landbridge' between the Greenland-American region and northwest Europe was established for some time during the earliest Eocene, at least until the cooling of the oceanic lavas made them shrink and sink to a depth of 1 km or more below sea level, so that the land bridge was interrupted. It probably formed, for many millions of years, an important underwater threshold between the North Atlantic proper and the Norwegian Sea, with the rather shallow and narrow gorges on both sides of the Faroy forming a connection between the two water masses and faunal regions, and eventually widening to become the base of the Gulf Stream reaching this far north. As Spitsbergen was, at the time of Mo Clay deposition, positioned close to the corner of northeast Greenland, and the Barents Shelf may well have been dry land forming another land bridge connecting North America with northern Europe (i.e. the Scandinavian-Russian Shield), it appears that the entire basin was a landlocked sea. In addition, the 'English Channel' area was closed, and the eastern end in the Polish-Baltic region most likely was also closed by land. The latter view is based mainly on 'negative evidence', i.e. the lack of Lower Eocene deposits; however, regional geology indicates that there was no marine connection towards the southeast (Bonde 1979; Heilmann-Clausen 2006). Just prior to the deposition of the Mo Clay, when the earliest phase of the ash series was laid down (Stolleklint Clay) during the short Eocene thermal maximum event, the ocean basin was even smaller under a low water stand, and it certainly must have been completely land locked (Schmitz *et al.* 1996; Heilmann-Clausen 2006; Bonde *et al.* 2008).

The distribution of the ash layers across northwest Europe, thinning out towards the south and southeast (Egger & Brückl 2006), appears to indicate that northerly to northwesterly winds were very frequent, if not dominating, and they would

have created a southerly ocean current along the southwest coast of the Scandinavian landmass. This again would have led to a long coast-parallel zone of upwelling, which was the base for the rich planktonic life and the deposition of diatomaceous ooze (Bonde 1974, 1979). At present, such surface currents with upwelling systems always have counter currents below in deeper water, and thus they form a three-layered and rather stable system preventing most organic particles and oxygen to reach the sea floor, where bottom water may be very poor, stagnant, anoxic and perhaps even slightly acidic and containing hydrogensulphide. In short, no benthic life apart of sulphur bacteria, very slow putrefaction, and well-preserved fossils undisturbed by scavengers, in stark contrast to the rich life at the surface.

In addition to marine organisms also a rich fauna from the surrounding land masses is preserved, namely about 200 species of insects (Archibald & Markakin 2006), and *c.* 30 species of land birds (Kristoffersen 2002; Lindow 2007). Amongst pelagic faunal elements fish are the most important component comprising more than 50 species (Bonde 1987), and the two commonest species (both salmoniforms) are found also at coeval levels in oil wells of the North Sea. All of these belong to groups which today are marine, oceanic fishes, such as mackerel and tuna, gempylids, zeiforms, carangids, *Exellia*, polymixiids, lampridiforms, paralepidids, argentinoids (the commonest small-sized fish), tarpons, eels, and a possible whale fish (Bonde *et al.* 2008). The most unexpected ones are four species of osteoglossoids ('bony tongues'), a group which currently inhabit only fresh water on the southern continents; however, from the Eocene, several other marine forms are known.

Pteropod shells, 2 mm across, cover some surfaces in a section in the lower part of the Mo Clay; these have previously been referred to as *Valvatina raphistoma* Stolley, 1900, later *Spiratella mercinensis* (Watelet & Lefèvre, 1880). There are also a few pelagic crustaceans such as uncommon shrimp, and very rare swimming crabs and isopods. Epipelagic elements include cirripedes, numerous mytilid mussels, perhaps two species, and may be also a quite common buccinid snail ('*Cassidaria*' Lamarck, 1816, not identified to species), although the latter could perhaps be benthic, just as a rare naticid and a few uncommon bivalves (Bonde 1987). The brittle star '*Ophiura furiae*' Rasmussen, 1972 is common in a narrow section low in the Mo Clay, and three species of starfish, much rarer, are known from the same section (see Bonde 1987). At quite a few horizons in the upper part of the formation, 4-5 types of trace fossil are quite common as borrows filled in with dark ash in the light diatomite, or *vice versa* (Pedersen & Surlyk 1983), and occurring more regularly distributed throughout the unit are tubes of *Pectinaria*-like polychaetes (Bonde 1987).

Of pelagic flora mainly diatoms are preserved, of which about 120 species and subspecies have been documented, and also silicoflagellates and dinoflagellates. There are also a considerable number of land plants, which have been washed in from surrounding land masses probably more than 100 km away, such as leaves, fruits, twigs and branches, mainly gymnosperms but also some angiosperms. Prominent amongst the latter are large, lanceolate leaves of *Macclintockia* Heer, a plant

of uncertain affiliation, that is characteristic of the so-called 'arcto-tertiary flora' of the Eocene in northwest Europe and Greenland (see Bonde *et al.* 2008). Frequently large branches and trunks are found, some of them identified as *Sequoia*, the largest over 9 m long; these are in surprisingly few cases infested with teredinid borings, but are of great importance for cirripedes, as described below.

## SYSTEMATIC PALAEONTOLOGY

Superorder THORACICA Darwin, 1854

Order SCALPELLIFORMES

Buckeridge & Newman, 2006

Family EOLEPADIDAE Buckeridge, 1983

Subfamily NEOLEPADINAE

Yamaguchi, Newman & Hashimoto, 2004

Tribe Ashinkailepadini

Yamaguchi, Newman & Hashimoto, 2004

Genus *Stipilepas* Carriol, n. gen.

DIAGNOSIS. — Neolepadine with capitular plates ornamented by growth ridges crossed by fine longitudinal ribs; scutum with occludent portion divided into two parts by apico-basal line, lacking apico-basal ridge; width of median latus exceeding height; peduncle with scales that are wider than high.

TYPE SPECIES. — *Stipilepas molerensis* Carriol, n. sp.

ETYMOLOGY. — From Latin *stipes* (trunk), in allusion to the substrate.

AFFINITIES. — *Stipilepas* n. gen., similar to *Ashinkailepas* Yamaguchi, Newman & Hashimoto, 2004, the other genus in the tribe Ashinkailepadini, has peduncle scales that are wider than high and are arranged in a small number of tiers, and capitular plates with longitudinal ornament. The new genus differs from *Ashinkailepas* in having much thinner external ornament and in a scutum in which the occludent portion is divided into two parts, lacking an apico-basal ridge; median latera are wider than high.

*Stipilepas molerensis* Carriol, n. sp.

(Figs 1B-D, 2, 3; Table 1)

DIAGNOSIS. — As for genus.

ETYMOLOGY. — After the Mo Clay Formation, 'moler' in Danish.

TYPE LOCALITY AND HORIZON. — Mors, northwest Jutland, Denmark; Mo Clay Formation.

ENVIRONMENTAL SETTING. — Recent species of the Neolepadinae are restricted to hydrothermal vents and seeps in the Pacific and Indian oceans, occurring bathyal and upper abyssal waters. In contrast, *Stipilepas molerensis* Carriol n. gen., n. sp. occurred in an 'ordinary' North Sea habitat, on logs.

TYPE MATERIAL. — The holotype is MGUH 30522 (Fig. 2C); paratypes are MGUH 30523 (Fig. 2D), MGUH 30524 (Fig. 2A), MGUH 30525 (Fig. 2B), MGUH 30526 (Figs 1B[26], 3A), MGUH 30527 (Figs 1B[27], 3B), MGUH 30528 (Figs 1B[28], 3E), MGUH 30529 (Figs 1D[29], 3D), MGUH 30530 (Figs 1C[30], 3F), MGUH 30531 (Fig. 1C[31]), MGUH 30532 (Fig. 1C[32]) and MGUH 30533 (Fig. 3C).



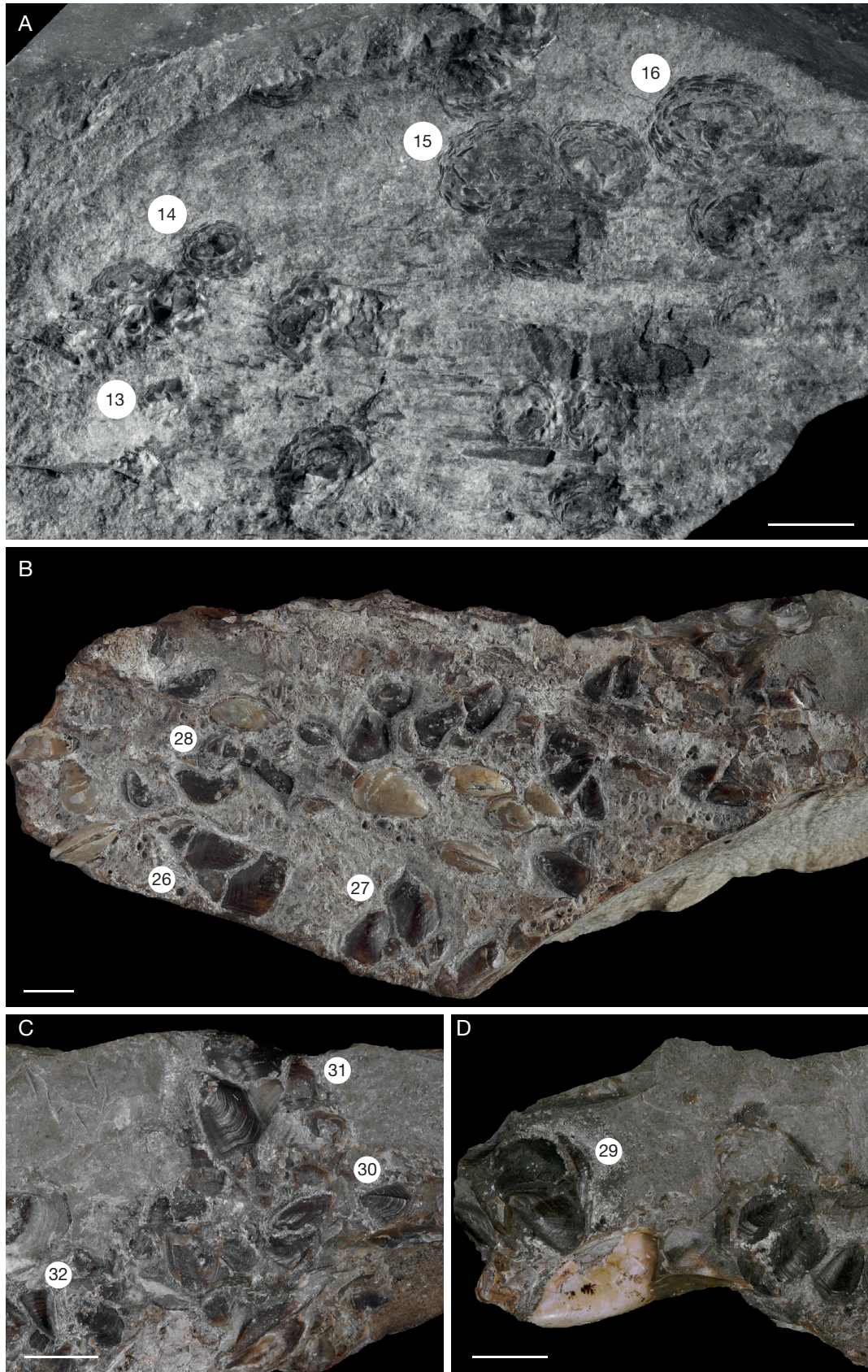


FIG. 1. — **A**, Sample with 18 fossils of *Plesiobrachylepas jutlandica* Carriol n. gen., n. sp. of which paratype MGUH 30513 [13] viewed from the right side, and paratypes MGUH 30514 [14], MGUH 30515 [15] and MGUH 30516 [16] viewed by below; **B-D**, *Stipilepas molerensis* Carriol n. gen., n. sp.; **B**, sample with fragments of capitulum and isolated plates of which paratypes MGUH 30526 [26], MGUH 30527 [27] and MGUH 30528 [28]; **C**, sample with fragments of capitulum and isolated plates of which paratypes MGUH 30530, MGUH 30531 and MGUH 30532; **D**, sample with fragments of capitulum and isolated plates of which paratype MGUH 30529 [29]. Scale bars: 5 mm.



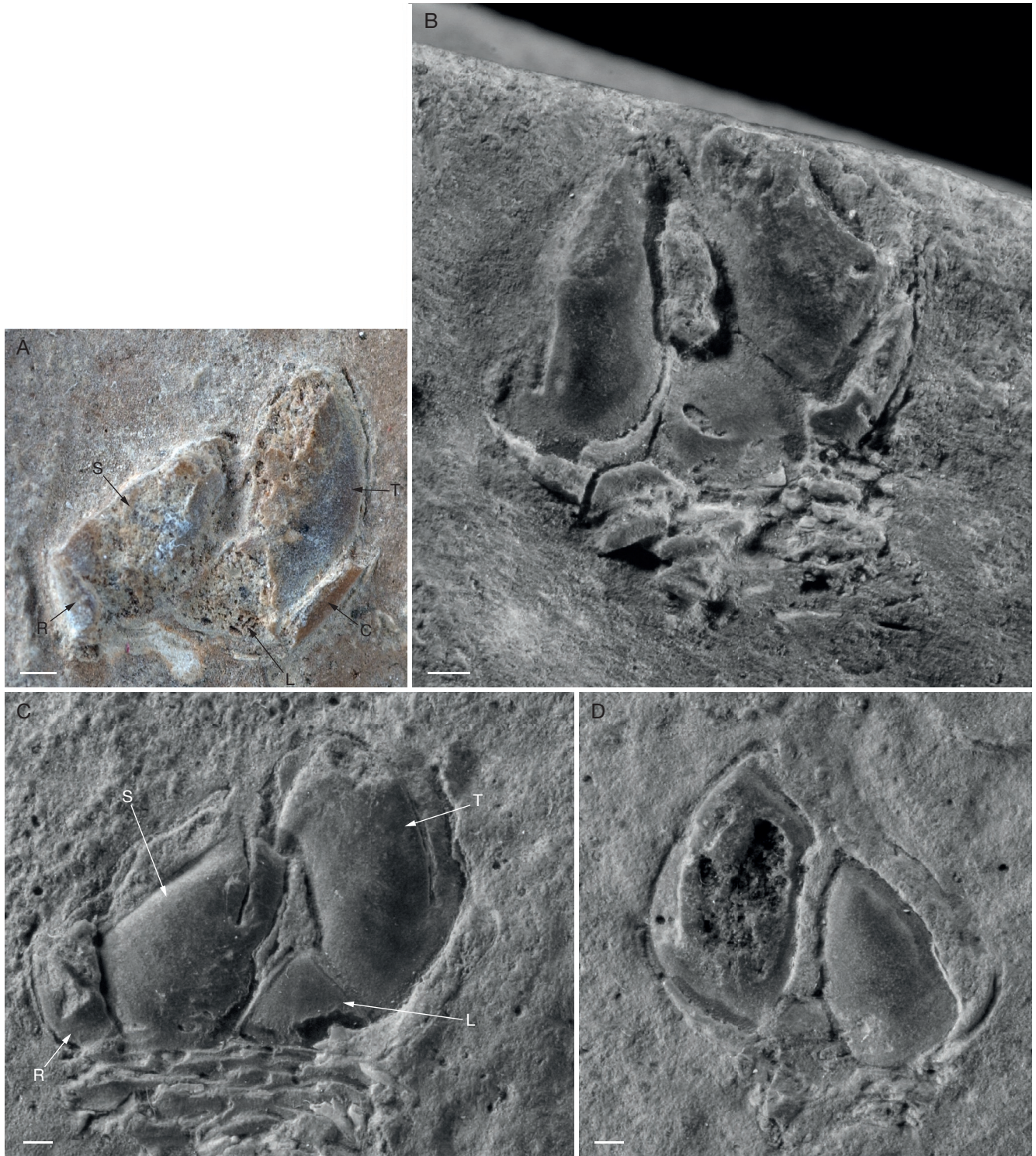


FIG. 2. — *Stipilepas molerensis* Carriol n. gen., n. sp.: **A**, paratype MGUH 30524, right side; **B**, paratype MGUH 30525, right side; **C**, holotype MGUH 30522, right side; **D**, paratype MGUH 30523, left side. Abbreviations: **C**, carina; **T**, tergum; **L**, median latus; **S**, scutum; **R**, rostrum. Scale bars: 1 mm.

#### DESCRIPTION

Tergum (Fig. 3F) wide, subquadrangular. Apico-basal ridge thin, very low, situated less than half the valve width from the carinal margin. Occludent margin straight. Scutal margin sinuous. Upper carinal margin longer than the others, straight. Lower carinal margin convex to straight. Valve rounded and protuberant along

occludent margin, this rounded margin is followed by a depression extending from the apex to about the middle of the scutal margin, a faint secondary ridge, extending from tergal apex to scutal margin, marking the limit of the depression. Outer surface ornamented with major and minor, thin transverse growth ridges and thin longitudinal ridges radiating from the apex.



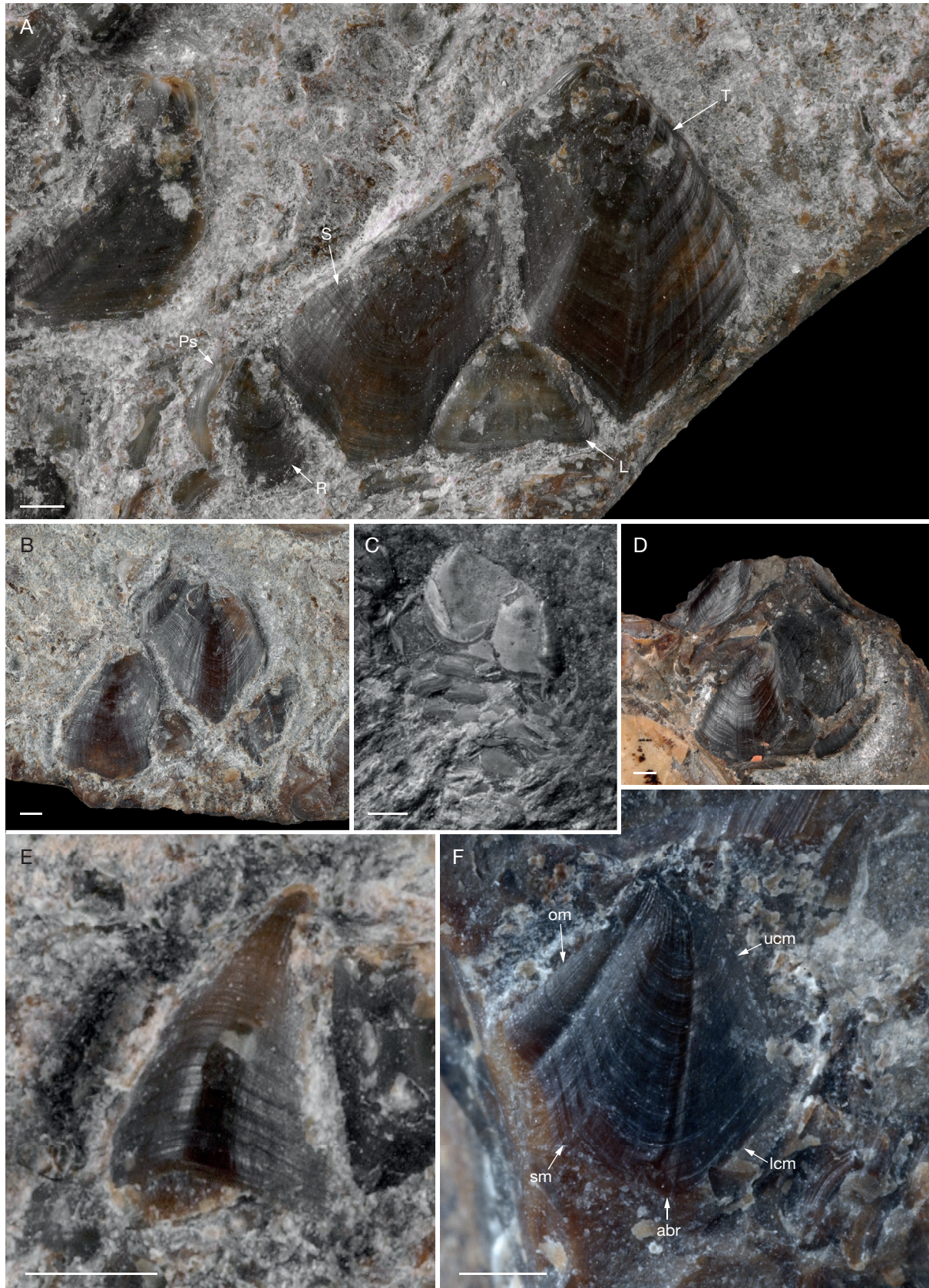


FIG. 3. — Paratypes of *Stipilepas molerensis* Carriol, n. gen., n. sp.: **A**, MGUH 30526 showing the right plates of its operculum, its rostrum and some scales of the peduncle; **B**, MGUH 30527 showing its carina and the right plates of its operculum; **C**, MGUH 30533 seen of the left side; **D**, MGUH 30529 showing its carina and the right plates of its operculum; **E**, MGUH 30528, carina; **F**, MGUH 30530, right tergum. Abbreviations: **abr**, apico-basal ridge; **L**, median latus; **lcm**, lower carinal margin; **om**, occludent margin; **Ps**, peduncle scale; **R**, rostrum; **S**, scutum; **sm**, scutal margin; **T**, tergum; **ucm**, upper carinal margin. Scale bars: 1 mm.





FIG. 4. — *Plesiobrachylepas jutlandica* Carriol n. gen., n. sp.: **A**, internal mould of wood log with 36 fossils of which paratypes MGUH 30519 [19], MGUH 30520 [20] and MGUH 30521 [21]; **B**, wood log with 13 fossils of which holotype MGUH 30517 [17] and paratype MGUH 30518 [18]. Scale bars: 1 cm.



TABLE 1. — Measurements (in mm) of *Stipilepas molerensis* Carriol n. gen., n. sp.

Specimen	Plate	Height	Width
<b>Holotype</b>			
MGUH 30522	scutum	6.2	—
	median latūs	2.5	3.5
	tergum	7.0	—
<b>Paratypes</b>			
MGUH 30523	scutum	5.6	—
	tergum	7.3	—
MGUH 30524	tergum	7.5	—
MGUH 30525	scutum	5.6	—
	median latūs	2.9	3.0
MGUH 30526	rostrum	3.5	1.5
	scutum	7.5	4.0
	median latūs	3.0	3.5
	tergum	8.0	5.0
MGUH 30527	scutum	> 6.0	4.0
	median latūs	2.5	2.0
	tergum	7.0	5.5
MGUH 30528	carina	2.5	1.9

Median latūs (Figs 2C, 3A) short, an isosceles triangle, wider than high, with convex scutal and tergal margins, overlapping scutum and tergum. Outer surface ornamented with major and minor, thin transverse growth ridges.

Scutum (Figs 1C; 3A, D) subrhomboidal in outline and, similar to tergum, ornamented with major and minor, thin transverse growth ridges and some thin longitudinal ridges radiating from the apex. The scutum is bent along a line extending from the apex to the baso-lateral angle and, less strongly, along a second line extending from the apex to a point of the basal margin distant, from the rostral angle, of two-thirds the length of this margin. In the part included between these two lines the growth ridges are curved downwards. There is no distinct ridge associated with the change in direction of the growth ridges along the apico-basal axis. Occludent, tergal and lateral margins convex to straight, basal margin sinuous.

Carina (Fig. 3E) and rostrum have the same shape and are difficult to tell apart when found isolated. Carina (or rostrum) strongly convex transversely, widening from the apex to the basal margin, not carinate, ornamented externally with major and minor growth lines.

Peduncle with scales (Figs 2B, C, 3C), wider than high, externally marked by thin growth lines, with apex rounded. These scales are difficult to count; nevertheless, it is possible to consider their number of tiers by whorl about six. Peduncle length equal to or shorter than that of capitulum.

#### REMARKS

*Stipilepas molerensis* Carriol n. gen., n. sp. is the first extinct taxon that is attributable to the Ashinkailepadini and, in addition to ?*Neolepas augurata* Buckeridge & Grant-Mackie, 1985 from the Lower Jurassic of New Caledonia, the second known fossil taxon that is referable to the Neolepadinae.

TABLE 2. — Measurements (in mm) of *Plesiobrachylepas jutlandica* Carriol n. gen., n. sp. Abbreviations: **H.**, height; **W.**, width; **M. axis**, major axis; **m. axis**, minor axis.

Specimen	Shell			Plate		
	Diameter	M. axis	m. axis	Name	H.	W.
<b>Holotype</b>						
MGUH 30517	6.5	—	—	scutum	c. 2.8	—
				median latūs	c. 1.2	—
<b>Paratypes</b>						
MGUH 30518	—	5.8	—	—	—	—
MGUH 30513	—	—	—	rostrum	0.9	0.6
				tergum	1.1	1.1
				scutum	0.9	0.6
MGUH 30514	—	4.3	3.5	—	—	—
MGUH 30515	—	7.3	5.5	—	—	—
MGUH 30516	—	8.3	6.0	—	—	—
MGUH 30519	—	3.6	2.8	—	—	—
MGUH 30520	4.4	—	—	—	—	—
MGUH 30521	—	5.2	4.8	—	—	—

Superorder SESSILIA Lamarck, 1818  
Suborder BRACHYLEPADOMORPHA Withers, 1923  
Family BRACHYLEPADIDAE Woodward, 1901

Genus *Plesiobrachylepas* Carriol, n. gen.

DIAGNOSIS. — Operculum including a pair of median latera, large relatively and not very high, as well as paired scuta and terga; wall consisting of rostrum and carina surrounded by whorls of imbricating plates, without basal interlocking device, arranged in a few tiers (three).

TYPE SPECIES. — *Plesiobrachylepas jutlandica* Carriol, n. sp.

ETYMOLOGY. — From Greek *plesio*, meaning near.

AFFINITIES. — In having imbricating plates without a basal interlocking peg, *Plesiobrachylepas* n. gen. differs from other brachylepadids, but it has this character in common with *Neobrachylepas* Newman & Yamaguchi, 1995. It can be distinguished from the latter in having fewer tiers of imbricating plates and subrhomboidal scuta, terga without apico-basal ridge, and relatively large and triangular median latera.

*Plesiobrachylepas jutlandica* Carriol, n. sp.  
(Figs 3A, 4, 5; Table 2)

DIAGNOSIS. — As for genus.

ETYMOLOGY. — After Jutland (Jylland), Denmark.

TYPE LOCALITY AND HORIZON. — Mors, northwest Jutland, Denmark; Mo Clay Formation.

ENVIRONMENTAL SETTING. — *Plesiobrachylepas jutlandica* Carriol, n. sp. attached to logs.

TYPE MATERIAL. — The holotype is MGUH 30517 (Figs 4B[17], 5D); paratype are MGUH 30518 (Figs 4B[18], 5B), MGUH 30513 (Figs 1A[13], 5C), MGUH 30514, MGUH 30515, MGUH 30516 (Fig. 1A[respectively 14, 15 and 16]), MGUH 30519 (Figs 4A[19], 5A), MGUH 30520 (Figs 4A[20], 5A) and MGUH 30521 (Figs 4A[21], 5E).



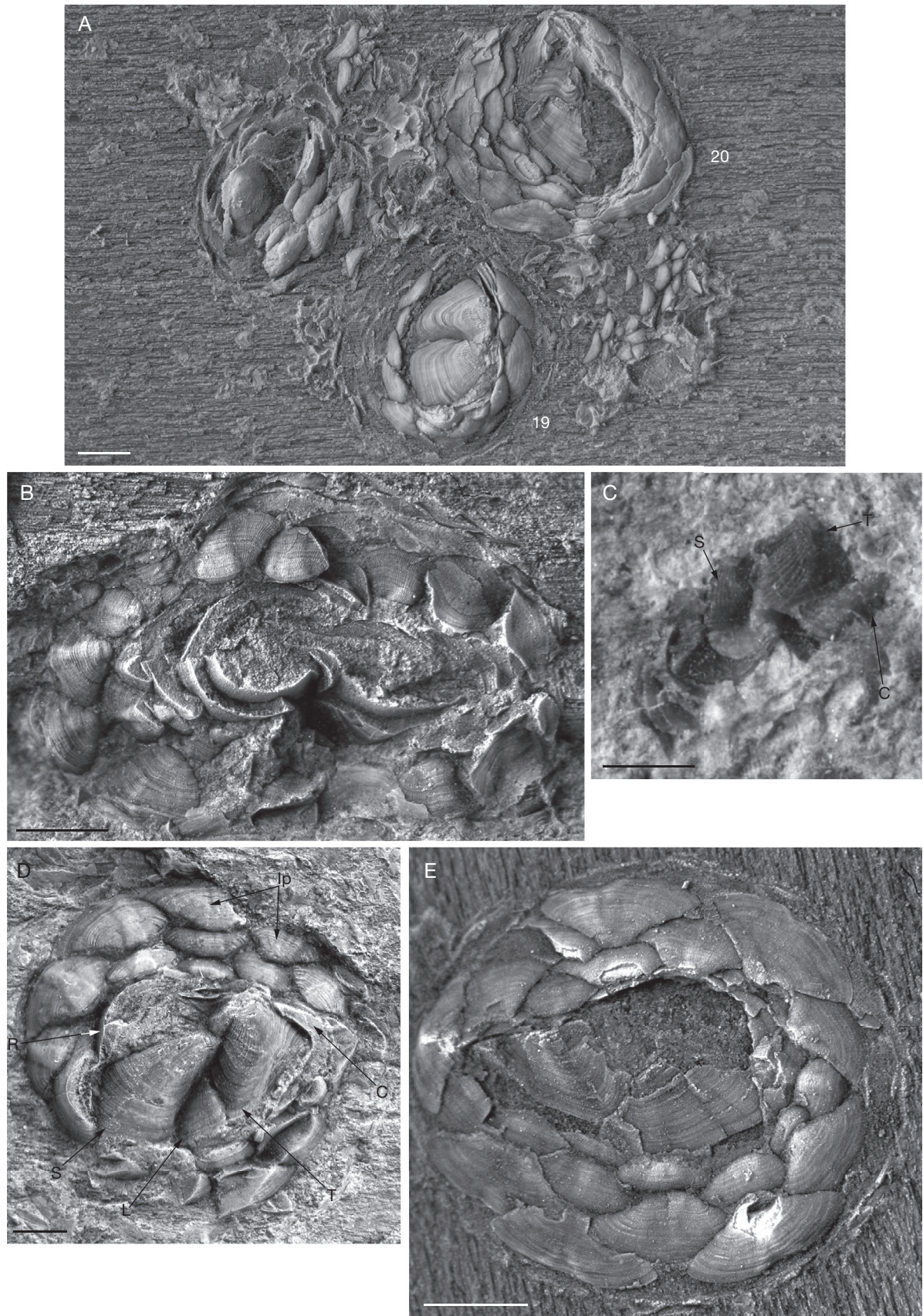


FIG. 5. — *Plesiobrachylepas jutlandica* Carriol n. gen., n. sp.: **A**, paratypes MGUH 30519 [19] and MGUH 30520 [20], viewed by above; **B**, paratype MGUH 30518 viewed by above; **C**, paratype MGUH 30513 viewed by the right side; **D**, holotype MGUH 30517 viewed by above; **E**, paratype MGUH 30521 viewed by above. Abbreviations: **C**, carina; **Ip**, imbricating plates; **L**, median latus; **R**, rostrum; **S**, scutum; **T**, tergum. Scale bars: 1 mm.



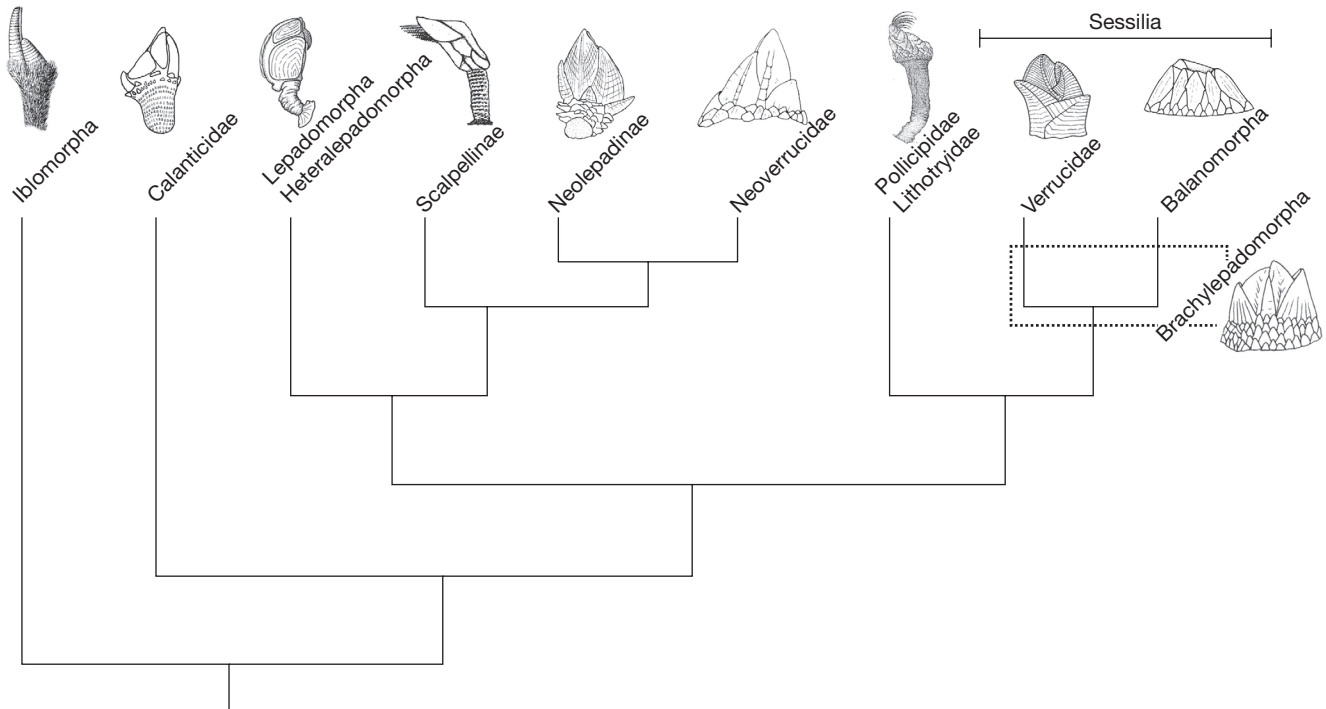


FIG. 6. — Phylogeny of the Cirripedia Thoracica adapted from Pérez-Losada *et al.* (2008). The new species *Stipilepas molerensis* Carriol n. gen., n. sp. is relegated to the Neolepadini, which presently consists of species confined to hydrothermal vents and seeps in the deep sea. The other new species, *Plesiobrachylepas jutlandica* Carriol n. gen., n. sp., is relegated to the Brachylepadomorpha Brachylepadidae, a taxon with many fossil but only one extant species, and assumed to be a paraphyletic stem group to the Sessilia (= Verrucomorpha + Balanomorpha).

#### DESCRIPTION

Tergum (Fig. 5C, D) wide, subquadrangular. Apex hardly curved towards the scutum. No apico-basal ridge. Occludent margin concave. Scutal margin sinuous. Upper carinal margin convex, as long as the lower. Lower carinal margin sinuous. Valve rounded and protuberant along the occludent margin forming a scutal auricle (terminology according to Gale & Sørensen 2014). Outer surface ornamented with thin transverse growth ridges and thin longitudinal ridges radiating from the apex.

Median latus (Fig. 5D) relatively large, an isosceles triangle, taller than wide, scutal and tergal margins straight. Outer surface ornamented with thin transverse growth ridges and thin longitudinal ridges.

Scutum (Fig. 5D) subrhomboidal, ornamented with thin transverse growth ridges and thin longitudinal ridges radiating from the apex. Plate plicated longitudinally in the centre, but no apico-basal ridge; occludent margin as long as the tergal margin, occludent margin straight to convex, tergal margin straight, basal margin as long as the lateral margin, basal and lateral margins straight.

Carina and rostrum: the present state of preservation does not allow to determine whether or not the carina and rostrum abut at their lateral margins. Paratype MGUH 30513 (Fig. 5C) has a carina which is transversely convex, widening from the apex to the basal margin, and with an external ornament of growth lines and thin longitudinal ridges.

Imbricating plates (Fig. 5), are wider than high and are marked externally by thin growth lines and thin longitudinal

ridges; occasionally the plate shows a longitudinal median prominence which widens from the apex to the basal margin, apex rounded. Imbricating plates, without basal interlocking device, are arranged in 12-14 tiers of 3 plates each.

#### PHYLOGENETIC DATA

Both the Neolepadinae (and, in a wider context, the entire Eolepadidae) and the Brachylepadidae have featured prominently in recent discussions on thoracican phylogeny. It is now well established on the basis of molecular and larval morphological data sets that the Thoracica form a monophyletic clade which is separate from the equally monophyletic Acrothoracica and Rhizocephala. Within the Thoracica, the consensus is that the Ibliformes represent the first branch on the thoracican tree, a view supported by both molecular and morphological evidence (Buckeridge & Newman 2006; Pérez-Losada *et al.* 2008; Høeg *et al.* 2009a, b). However, interpretation of the evolutionary pathways within the remaining Thoracica is still fraught with difficulties. The traditional phylogeny supported by adult shell plate characters assumes a more or less gradual acquisition of capitular shell plates, and the 8-plated Neolepadinae represents an important stage in this evolutionary process, which is also beautifully recapitulated in the ontogeny of pedunculate thoracicans with more than 8 plates (Newman 1996; Glenner *et al.* 1995; Buckeridge & Newman 2006). Yet, recent molecular evidence is not in support of gradual acquisition of capitular plates. The molecular



phylogenetic analysis of Pérez-Losada *et al.* (2008) (Fig. 6) has shown that both the 5-plated members of the Lepadiformes and the 8-plated members of the Neolepadinae are nested deep within multiplated forms. Thus, both the species with five shell plates, such as members of *Lepas*, and those with eight plates appear to have reached this stage by secondary loss of body armament. This does not necessarily discredit the fact that five shell plates were an evolutionary stage following the four plates seen in *Ibla*, but clearly shows that the Lepadiformes and Neolepadinae are not in any simple way extant examples of this evolutionary stage.

Nested deep within the Thoracica, the origin of the Balanomorphs has also been much discussed and fossils have yielded important insights into the process by which a pedunculate ancestor evolved the sessile balanomorph condition with separation of armament into wall plates and hinged opercular plates (Glenner *et al.* 1995; Newman 1996). Here molecular characters are of little value, especially because the sole extant brachylepadomorph species, *Neobrachylepas relictus* (Newman & Yamaguchi, 1995), is not yet available for this type of phylogenetic analysis. Also here, unpublished molecular evidence (Pérez-Losada *et al.* 2014) indicates that current ideas on shell plate homology and evolution are in need of revision. However, this does not change the fact that fossil species offer the sole informative clues to resolve such issues. We shall not discuss these problems in detail here, but only note that these new fossils, representing the Neolepadinae and Brachylepadomorphs, will obviously add to the data base of characters that can be used in future phylogenetic discussions.

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