



***Litholepas klausreschi* gen. et sp. nov., a new neolepadine barnacle (Cirripedia, Thoracica) on a sponge from the Upper Jurassic lithographic limestones of southern Germany**

Christina Nagler, Joachim T. Haug, Henrik Glenner and John Buckeridge

With 6 figures

Abstract: In this study we describe a unique fossil comprising 13 intact specimens of a pedunculate cirripede attached to a sponge (*Codites serpentinus*). The fossil comes from the Upper Jurassic lithographic limestones of southern Germany. Based on the shape and distinctive sculpture of the plates, a new genus and species *Litholepas klausreschi* gen. et sp. nov. (Eolepadidae: Neolepadinae) is introduced. Although lateral plates are indistinct and the rostrum is unknown, plate disposition and strong external sculpture indicate a position within Neolepadinae though the exact relationships are still uncertain. Representatives of *L. klausreschi* gen. et sp. nov. are considered to have lived either in a parasitic or commensal relationship partially buried within the sponge.

Key words: Cirripedia, Thoracica, Scalpelliformes, *Litholepas klausreschi* gen. et sp. nov., peramorphosis, epibiosis.

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1. Introduction

Barnacles are sessile crustaceans, apart from their swimming larvae. Most adult barnacles bear a number of calcareous shell plates to protect them, resulting in a unique morphology. For much of recorded history, the systematic taxonomy of barnacles has been uncertain, even including any attribution of them to Arthropoda *sensu stricto*. Their crustacean nature was finally revealed in 1830, following J. VAUGHAN THOMSON'S seminal work on nauplius larvae (BUCKERIDGE 2011; BUCKERIDGE & WATTS 2012). Early barnacle larvae are rather "typical" nauplius-larvae as known from many modern e crustaceans. Barnacles are now recognized as a group within Thecostraca, a group comprising cirripedes and a number of parasitic forms (Ascothoracida

and Facetotecta). Extant barnacles are typically marine, from shallow waters to bathyal depths (BUCKERIDGE 2012; HARZHAUSER & SCHLÖGL 2012).

The evolution of cirripedes incorporating fossils was summarized by NEWMAN (1996). Although the earliest known cirripede, *Cyprilepas holmi* WILLS, 1962, is of Silurian age (some 430 mya), barnacles are rather rare fossils until the Mesozoic, only becoming abundant in Jurassic and Cretaceous deposits where, for the most, isolated shell plates are preserved (WITHERS 1928, 1935; BUCKERIDGE 1983; COLLINS et al. 2014; GALE 2014a; GALE & SØRENSEN 2014). Based on molecular as well as fossil data, the Jurassic has been interpreted as an important period for the radiation of barnacles (PÉREZ-LOSADA et al. 2008; HERRERA et al. 2015). Recent work on barnacles of that time includes

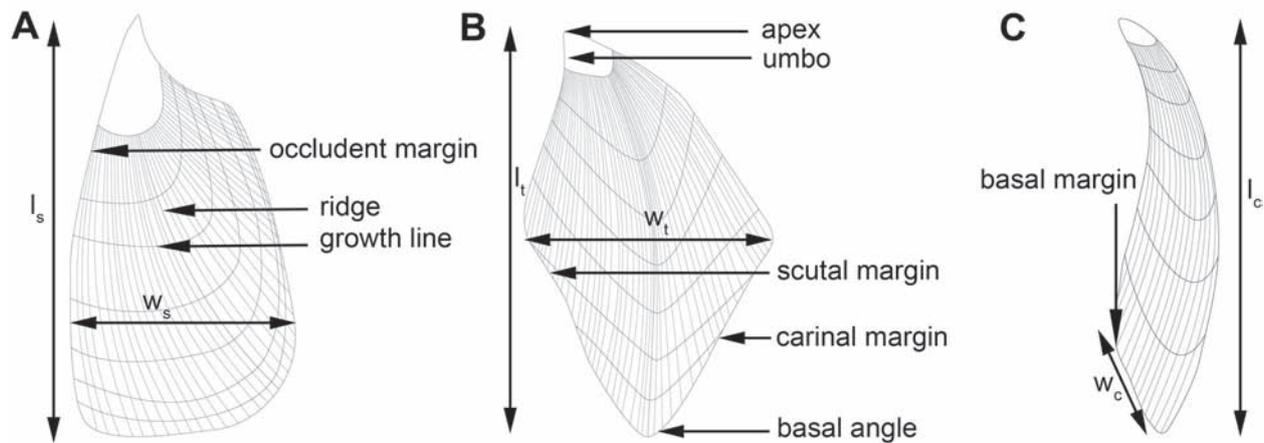


Fig. 1. Generalized drawing of scalpelliform barnacles shell plates from the right. **A** – Scutum, l_s = length of scutum, w_s = width of scutum. **B** – Tergum, l_t = length of tergum, w_t = width of tergum. **C** – Carina, l_c = length of carina, w_c = width of carina. Not to scale.

revisions of major groups such as Eolepadidae (GALE & SCHWEIGERT 2015; KOČI et al. 2015; CARRIOL et al. 2016), Brachylepadidae (GALE & SØRENSEN 2014) and Zeugmatolepadidae (GALE 2014a).

The group Cirripedia includes Acrothoracia, Thoracica and Rhizocephala, the latter two representing sister groups. Thoracica includes the more commonly known forms: goose barnacles and acorn barnacles. The goose barnacles (= stalked or pedunculate barnacles) retain more plesiomorphic traits and therefore roughly resemble the ancestral thoracican. Goose barnacles were previously recognized as a group “Pedunculata”; however, “Pedunculata” has been identified as a non-monophyletic assemblage united by plesiomorphies such as the presence of a peduncle. Instead of “Pedunculata” now four distinct monophyletic groups are recognized, and one of these is the group Scalpelliformes (see BUCKERIDGE & NEWMAN 2006).

We report here new and exceptionally preserved fossil representatives of Scalpelliformes apparently closely related to the extant group Neolepadinae previously known for certain as far back as the Eocene (CARRIOL et al. 2016). On the basis of overall morphology, including strongly sculptured plates and irregular radiating ridges, this material is identified as a representative of Neolepadinae. In total 13 specimens were found, all attached to a sponge from lithographic limestones (*sensu lato*) of the Solnhofen area in southern Germany. This discovery also permits analysis of the palaeoecology and provides a unique case of an ancient epibiosis (“syn vivo” *sensu* ROBIN et al. 2015) between a barnacle and a sponge.

2. Material and methods

2.1. Material

A single slab of lithographic limestone from the Solnhofen lithographic limestones of Blumenberg near Eichstätt, Southern Germany, of early Tithonian age. A large elongate sponge is the most prominent fossil on the slab. This sponge, identified as *Codites serpentinus* v. STERNBERG, 1833, is non-bifurcating and 466 mm long. Attached to the sponge are 13 barnacle specimens that are in the focus of this study (Figs. 1-5).

The slab was in the private collection of UDO RESCH, Eichstätt, Germany, but has been donated to the Stuttgart Natural History Museum (SMNS 70388). The counterpart of the slab is kept in the private collection of ROGER FRATIGIANI, Laichingen, Germany.

Barnacle specimens for ecological comparison (*Pectinoacasta pectinipes* (PILSBRY, 1912)) (Fig. 6D, E) were provided by the Zoological Museum, Natural History Museum of Denmark, Copenhagen (ZMUC). An extant scalpelliform barnacle, used for morphological comparison (*Vulcanolepas osheai* (BUCKERIDGE, 2000)) (Fig. 6B, C), was collected from 1313 metres depth in the Brother’s Caldera, southwest Pacific Ocean; these specimens are held in the EOS Collection, RMIT University, Melbourne.

2.2. Documentation

All fossil and extant barnacle specimens have been figured using macro photography and stereo photography (Figs. 2-4, 4). Stereo photography and macro photography (combined with composite imaging) were performed following HAUG et al. (2011, 2012), under cross-polarized light. We used a Canon EOS Rebel T3i camera, either with a Canon EFS (18-55 mm) lens (for overview images) or a Canon MP-E (65 mm) macro lens (for detail images). Illumination was

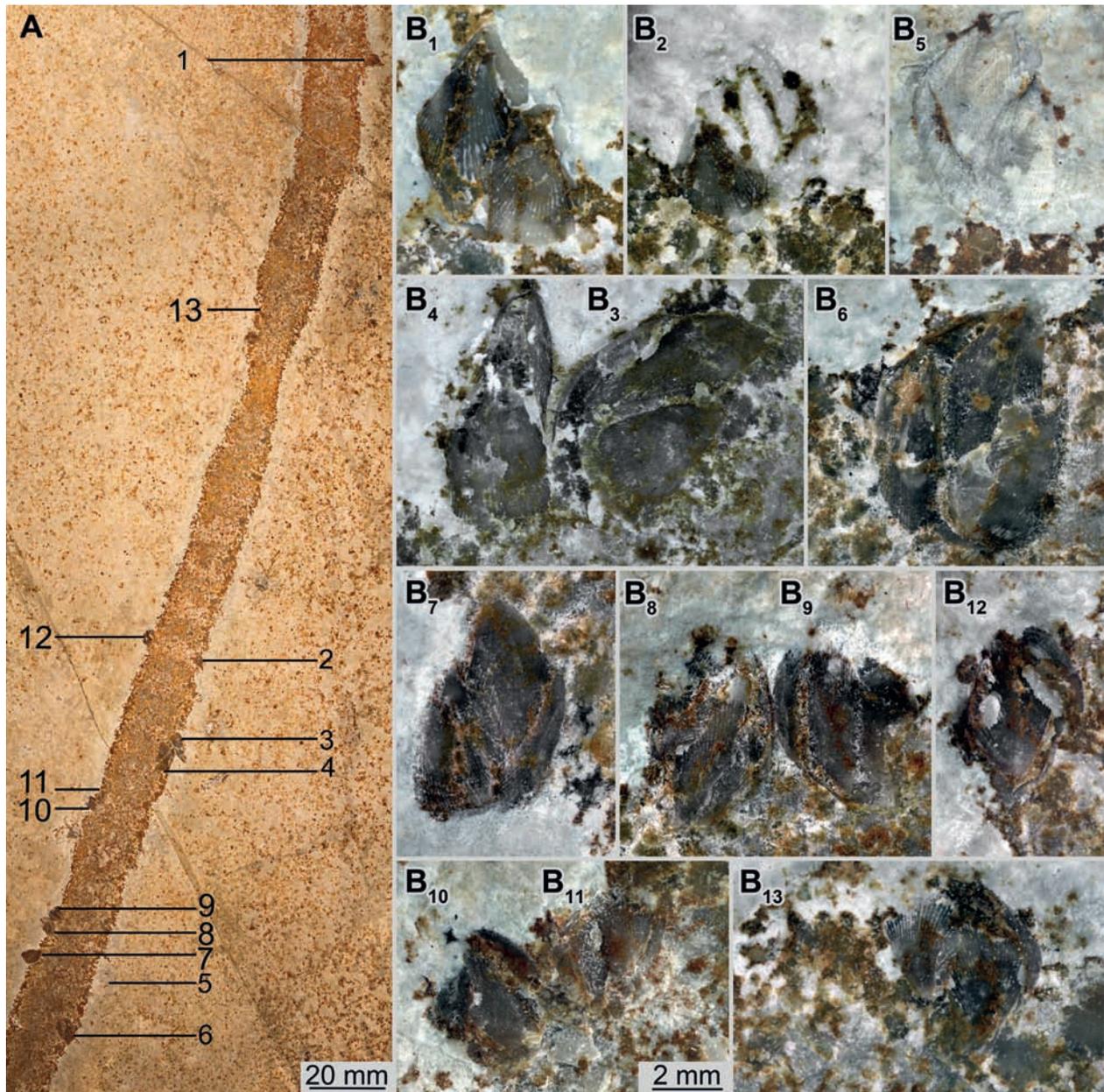


Fig. 2. Overview of the slab (A) and of the individual specimens (B₁-B₁₃) of fossil barnacle *Litholepas klausreschi* gen. et sp. nov. All images macro photographs under cross-polarized light. A – Sponge *Codites serpentinus* v. STERNBERG, 1833 with 13 attached specimens of *L. klausreschi* gen. et sp. nov. (SMNS 70388), numbers indicate the specimens. B₁ – Specimen 1 (SMNS 70388/1) B₂ – Specimen 2 (SMNS 70388/2). B₃ – Specimen 3 (SMNS 70388/3). B₄ – Specimen 4 (SMNS 70388/4). B₅ – Specimen 5 (SMNS 70388/5). B₆ – Specimen 6 (SMNS 70388/6). B₇ – Specimen 7, holotype (SMNS 70388/7), B₈ – Specimen 8 (SMNS 70388/8). B₉ – Specimen 9 (SMNS 70388/9) B₁₀ – Specimen 10 (SMNS 70388/10). B₁₁ – Specimen 11 (SMNS 70388/11). B₁₂ – Specimen 12 (SMNS 70388/12). B₁₃ – Specimen 13 (SMNS 70388/13).

provided by a Canon Macro Twin Lite MT-24EX flash from the two opposing sites.

Additionally, three specimens (5-7) were photographed with image stacks with a distance of 10 µm between single images (Fig. 5). Stereo models of these three specimens were obtained by using the depth map of the image stacks and

calculating a virtual surface (HAUG et al. 2013a).

Stacks of images were processed with the freeware packages CombineZP (ALAN HADLEY), ImageAnalyzer (Meesoft) and ImageJ (WAYNE RASBAND). Assembling of stereo images and final processing (levels, sharpness, and saturation) was performed in Adobe Photoshop CS2.

2.3. Presentation method

We present color highlighted versions of the images directly alongside stereo images for better recognizing the interpreted structures. For this purpose the stereo image was simply copied. Then one color channel of the stereo image was deleted, hence leaving only one half image of the stereo pair. This half image was de-saturated; then structures apparent in the stereo images were marked with the lasso tool in Photoshop CS2 (Adobe) on the de-saturated half image (HAUG et al. 2010, 2012). We marked all visible structures of the shell plates as follows: the carina (c) is highlighted in blue; the tergum (t) is highlighted in green, the scutum (s) is highlighted in cyan and the lateral plate (l) is highlighted in orange. The peduncle (p) is highlighted in purple.

2.4. Reconstruction

Drawings of specimen 5 of *Litholepas klausreschi* gen. et sp. nov. were made with the aid of camera lucida attached to a binocular microscope. Drawings were scanned and electronically tracked using a graphic tablet (Cintiq 12 WX, Wacom), an electronic pen (Wacom Inkling MDP-123), and the software Adobe Creative Suite 2, according to the protocol of COLEMAN (2003). Drawings were finally optimized in Adobe Illustrator while comparing directly to the original. For the reconstruction, growth lines were added to the median latus and the peduncle was added (Fig. 6A).

2.5. Measurements

Measurements of length and width of the body surrounding plates: one carina, two terga and two scuta, two latera (Fig. 2) and the distances between their ridges were performed in ImageJ (WAYNE RASBAND). Due to the preservation, not all specimens could be used. For the measurement of scuta we used specimens 1-7, 9, 10, 12. For measurements of terga we used specimens 1, 2, 4-9. For measurements of carina we used specimens 1, 2, 5-7.

Measurements of the distances between ridges were performed at the basal margin (carina, scuta) and at the basal angle (terga). For the distances between the scutal ridges we used all specimens. For the distances between the tergal ridges we used all specimens except specimen 12. For the distances between the carinal ridges we used all specimens except specimen 3 and 9.

Taxonomy follows BUCKERIDGE & NEWMAN (2006) and the 'World Register of Marine Species' (WoRMS 2016). Basic terms and measurements of the carina, tergum and scutum are shown in Fig. 2. The term 'rostrum' refers in other arthropod groups to different structures (e.g. an extension of various mouthpart in insects (SINGH et al. 2016), a frontal process of the shield in decapods (FELDMANN et al. 2016), the anterior plate of the cephalon of trilobites (DALEY & DRAGE 2016), the mouthparts of chelicerates (FRANZ-GUESS et al. 2016), or the anterior part of the shield of mites (ERMILOV et al. 2016)). In this study we use 'rostrum' for the rostral shell plate of cirripedes and do not implicate any homology to other structures with the same name.

3. Systematic palaeontology

Cirripedia BURMEISTER, 1834

Thoracica DARWIN, 1854

Scalpelliformes BUCKERIDGE & NEWMAN, 2006

Eolepadidae BUCKERIDGE, 1983

Neolepadinae NEWMAN, 1996

Remarks: In revising Eolepadidae, YAMAGUCHI et al. (2004) divided Neolepadinae NEWMAN, 1996 into Ashikailepadinae YAMAGUCHI, NEWMAN & HASHIMOTO, 2004 and Neolepadini NEWMAN, 1996. A carina being present in the new form indicates it is not an iblifform, whereas the presence of a pair of latera as well as a carina suggest an eolepadid in spite of a rostral plate imbricating peduncular plates either being very reduced or lost (presumably in response to the symbiotic situation). Therefore, while the form is likely a new genus as well as a new species, it is nonetheless placed as *incertae sedis* within Neolepadinae.

Litholepas gen. nov.

Etymology: With reference to the Solnhofen lithographic limestones, where it was found.

Type species: *Litholepas klausreschi* sp. nov., monotypic.

Diagnosis: See diagnosis of type species.

Litholepas klausreschi sp. nov.

Figs. 2-5, 6A

2015b *Eolepas quenstedti* (v. AMMON). – SCHWEIGERT, p. 290, fig. 606.

Etymology: In honor of the father of the private collector UDO RESCH, Eichstätt, who found the fossil.

Holotype: The holotype is specimen 7 (SMNS 70388/7) (Figs. 1A, B₇, 4A₁₋₂, 5A).

Paratypes: Paratypes are specimens 1-6 and specimens 8-13 attached to *Codites serpentinus* on the same slab (SMNS 70388) (Figs. 2A, B₁₋₆, B₈₋₁₃, 3, 4B-E).

Type locality and horizon: Blumenberg near Eichstätt; Altmühl Formation (Solnhofen lithographic limestones), Eichstätt Member (see NIEBUHR & PÜRNER 2014); early Tithonian, Hybonotum Zone, Riedense Subzone (age after SCHWEIGERT 2015a).

Diagnosis: A neolepadine barnacle with seven capitular plates: a carina and the paired scuta, terga and median latera. All shell plates, except the lateral plates, with strong, regu-

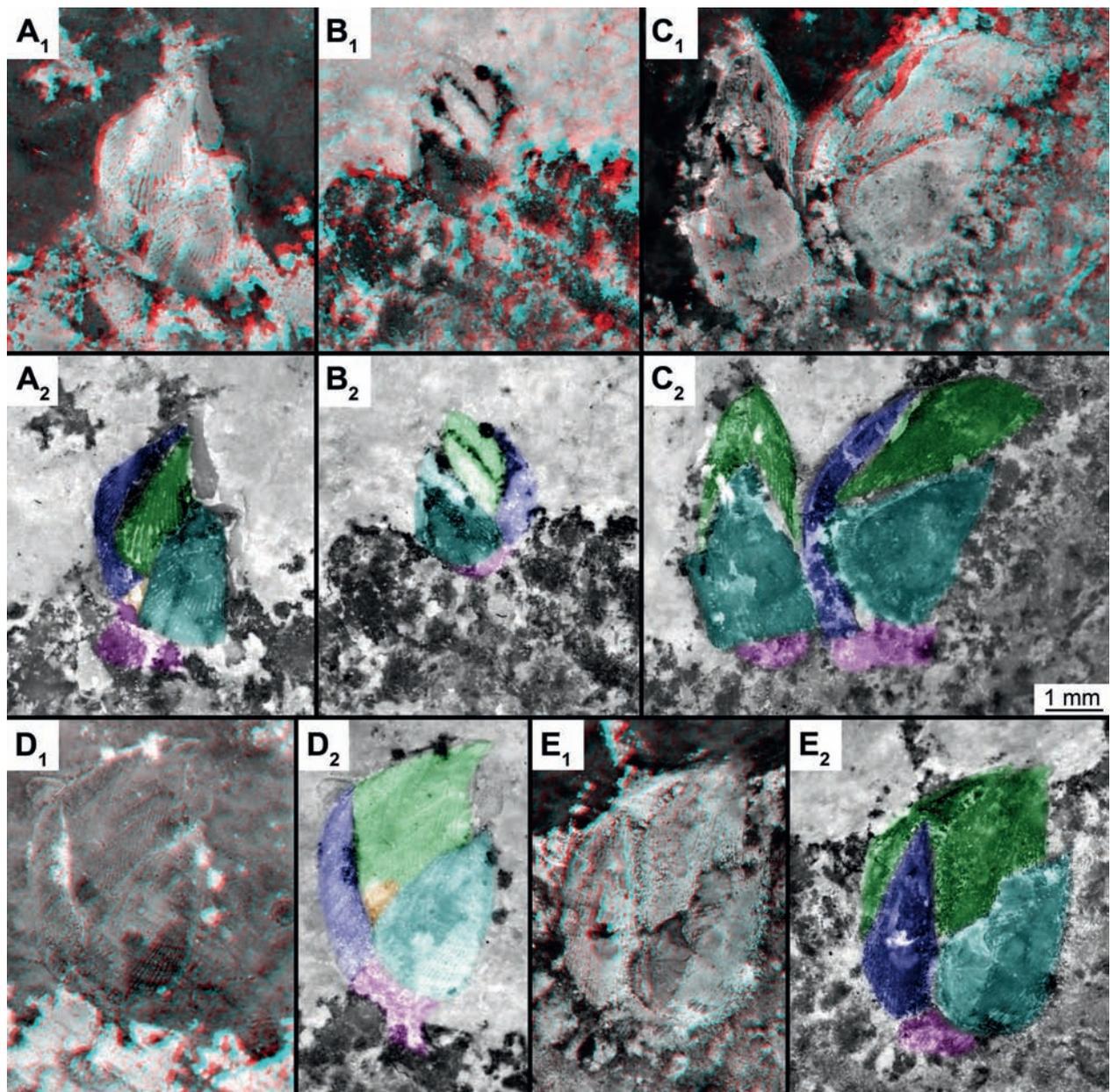


Fig. 3. Stereo images (please use red-cyan anaglyphs to view) and color-highlighted versions of fossil barnacle *L. klausreschi* gen. et sp. nov. (specimens 1-6). Color-markings: Carina highlighted blue, terga highlighted green, scuta highlighted cyan, latera highlighted orange and peduncle highlighted purple. **A**_{1,2} – Specimen 1 (SMNS 70388/1). **B**_{1,2} – Specimen 2 (SMNS 70388/2). **C**_{1,2} – Specimen 3 (SMNS 70388/3) & specimen 4 (SMNS 70388/4). **D**_{1,2} – Specimen 5 (SMNS 70388/5). **E**_{1,2} – Specimen 6 (SMNS 70388/6).

lar, apico-basal striae; carina strongly boomerang-shaped; tergum trapezoid; scutum triangular with pointed apex and apical umbo; latus small, triangular with weak apico-basal striae. Rostrum apparently absent; peduncle long without visible peduncular scales.

Description: The overall arrangement of a barnacle consists of a capitulum, covering the soft body and a peduncle. The capitulum consists of seven calcium carbonate plates: unpaired carina, paired scuta, paired terga and paired median latus (Figs. 1, 3-5, 6A). The surface of each shell plate shows lateral growth lines and longitudinal ridges. Peduncular

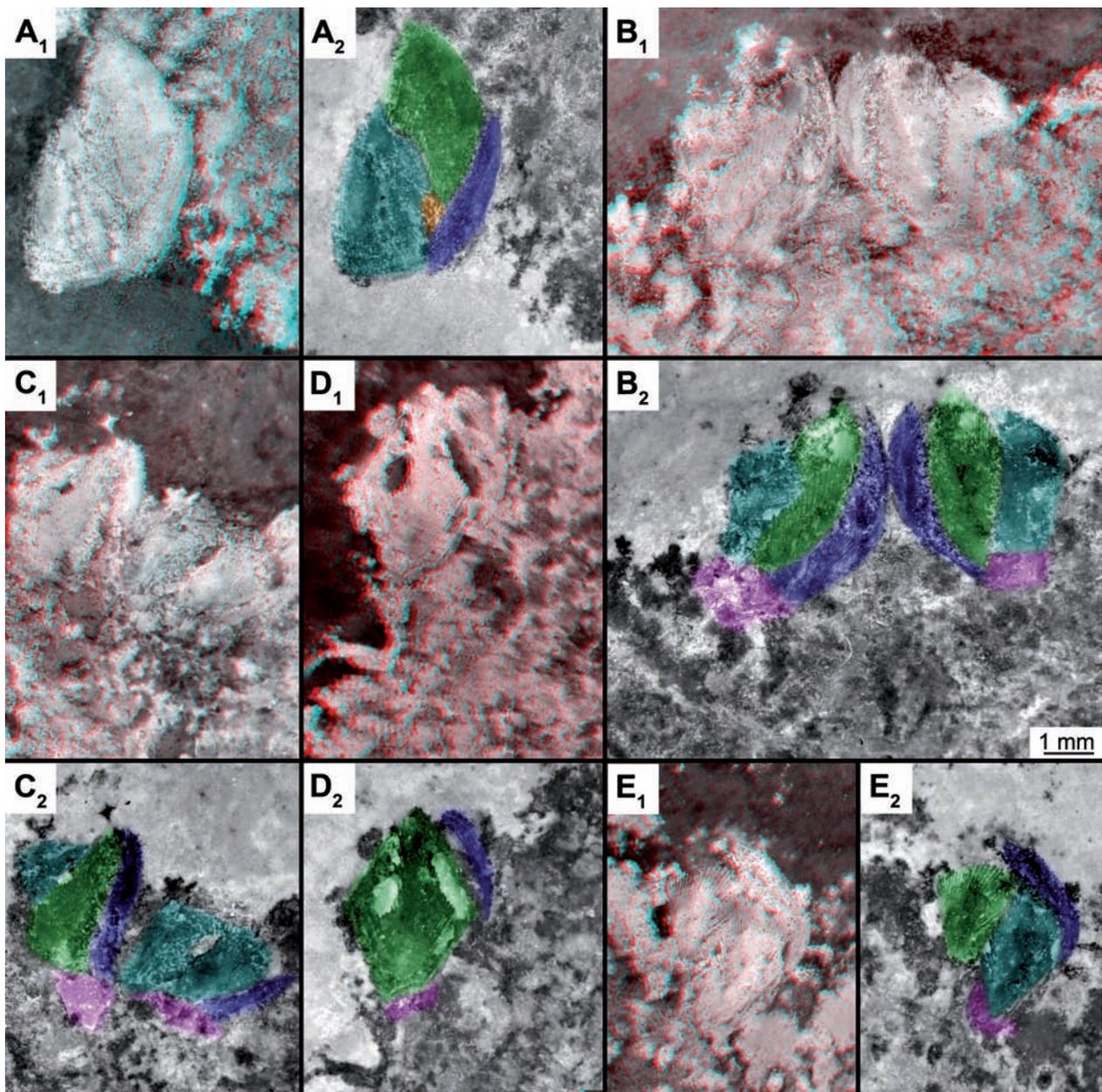


Fig. 4. Stereo images (please use red-cyan anaglyphs to view) and color highlighted versions of fossil barnacle *L. klausreschi* gen. et sp. nov. (specimens 7-13). Color-markings: Carina highlighted blue, terga highlighted green, scuta highlighted cyan, latera highlighted orange and peduncle highlighted purple. **A**₁₋₂ – Specimen 7, holotype (SMNS 70388/7). **B**₁₋₂ – Specimen 8 (SMNS 70388/8) & specimen 9 (SMNS 70388/9). **C**₁₋₂ – Specimen 10 (SMNS 70388/10) & specimen 11 (SMNS 70388/11). **D**₁₋₂ – Specimen 12 (SMNS 70388/12). **E**₁₋₂ – Specimen 13 (SMNS 70388/13).

scales could not be observed, perhaps due to poor preservation.

Carina boomerang-shaped, strongly convex with an apical umbo. It is 4.6 times taller than broad; length = 4.6 ± 1.4 mm, width = 1.1 ± 0.2 mm. The basal margin is almost straight. The longitudinal ridges are distinct and have an av-

erage spacing of $66 \mu\text{m}$ ($62\text{--}73 \mu\text{m}$). The lateral growth lines are V-shaped in the apical part and parallel with the basal margin in the lower part (Fig. 5). A defined apico-basal ridge is present.

Paired plates display considerably more variation in shape and size than the unpaired carina. Scutum trapezoid

to triangular, slightly curved anterior towards the tergum with an apical umbo and a pointed apex. It is nearly 1.7 times longer than wide; length = 3.7 ± 0.7 mm, width = 2 ± 0.4 mm; basal margin broadly curved; occludent margin gently concave; lateral growth lines are strong and L-shaped. The ornamental ridges are on average separated by $89 \mu\text{m}$ ($71\text{--}97 \mu\text{m}$) and also well demarcated. A curved apico-basal ridge is present on the tergal site and it is slightly wider than the ornamental striae (Figs. 3-5).

Tergum rhomboid with an apical umbo; on average two times longer than wide; length = 3.9 ± 0.8 mm, width = 1.9 ± 0.4 mm. The angle between the carinal and scutal margins is acute. The upper and lower carinal margins join in an obtuse angle, almost straight; lateral growth lines are V-shaped and well preserved. The longitudinal ridges are on average separated by $99 \mu\text{m}$ ($80\text{--}120 \mu\text{m}$). A central apico-basal ridge is present (Figs. 3-5).

The basal termination of the carina, scutum and the tergum leave a space between them. In some specimens, this space is occupied by what we interpret as a median latus (specimens 1, 5 and 7, Figs. 2B₁, B₅, B₇, 3A, D, 4A, 5A, B, E, F), which although distorted, appears to be triangular, length = 0.8 ± 0.1 mm, width = 0.5 ± 0.1 mm, characterized by fine apico-basal striae.

No rostrum has been recognized and the close fit between the scutal and tergal margins suggest that no further lateral plates were present; these may however have been pedomorphically lost (see below). Peduncle poorly preserved (Figs. 2-5), long, without recognizable peduncular scales.

Remarks: The new genus and species is identified as a representative of Neolepadinae based on the morphology of the carina, scuta and terga with strong radial sculpture, their position to each other, their length-width ratio and the position and length-width ratio of the lateral plates (see BUCKERIDGE et al. 2013, table 1). *Litholepas klausreschi* gen. et sp. nov. differs from other groups within Neolepadinae by apparently lacking a rostrum and peduncular scales. This fundamental difference is discussed below and not seen as a counter argument for the identification as an ingroup of Neolepadinae.

L. klausreschi is morphologically closest to representatives of *Neolepas* and *Vulcanolepas*, as the basal angle of the scutum is situated approximately at the capitulum-peduncle margin and the basal angle of the tergum is slightly elevated from the capitulum-peduncle margin.

Additionally, modern representatives of *Neolepas* are found adjacent to hydrothermal vents and show a distinct latus that can be observed in the fossils described herein (NEWMAN 1979; GALE 2014b; Figs. 3D, 4A, 5A, B, E, F, 6A-C). In contrast to representatives of *Vulcanolepas*, representatives of *Neolepas* show approximately 16 plates per whorl in the peduncle that project over 1 mm out of the peduncle (30 plates per whorl that project less than 0.4 mm out of the peduncle in representatives of *Vulcanolepas*) (BUCKERIDGE et al. 2013). The second main difference between *Neolepas* and *Vulcanolepas* is the ratio between the length of the rostrum and the length of the median latus (1.5:1 in *Neolepas* vs. 1:1 in *Vulcanolepas*; BUCKERIDGE et al. 2013). Unfortunately, an appreciation of the fine detail of the peduncle in these fossil specimens is not possible. Since the fossil specimens lack a rostrum, it is not possible to assign the fossil barnacle to

either *Neolepas* or *Vulcanolepas*. Furthermore, *Litholepas* possesses an acute scutal apex and an elongated scutum, contrary to the obtuse apex in *Neolepas* and *Vulcanolepas*.

4. Discussion

4.1. Lack of some shell plates – a pedomorphic form?

As pointed out above the species described herein apparently lacks some mineralized elements (i.e. a rostrum and peduncular scales) that other representatives of the larger group have. While this might appear problematic for the systematic interpretation at first sight, this phenomenon is in fact not unusual. Lack of specific plates in barnacles is well known: Some extant forms of Lepadidae have secondarily lost the carina, species of *Arcoscapellum* have lost the rostrum (NEWMAN et al. 1969) and interestingly *Neoscapellum debile* gradually loses lateral plates during ontogeny (YOUNG 2002). Furthermore, a secondary loss of plates has been proposed for representatives of Neolepadinae (PÉREZ-LOSADA et al. 2008). The loss of such plates was reviewed by SHALAEVA & NEWMAN (2016). On the other hand, juvenile stages also lack certain plates. The first sessile stage of extant barnacles is characterized by five plates (paired terga and scuta plus unpaired carina), also known as primordial plates (DARWIN 1852; GLENNER & HØEG 1993; GLENNER et al. 1995; GALE 2014b, 2015). All other plates (latera, rostra, peduncular scales) are developed subsequently during later ontogenetic stages (YOUNG 2001; GALE & SØRENSEN 2014; GALE & SCHWEIGERT 2015). This ontogenetic pattern has been also reported from Carboniferous and Silurian specimens (NEWMAN 1979; BRIGGS et al. 2005).

With these known examples in mind, there are at least three interpretations of the absence of certain plates in the newly described species:

- 1) All specimens represent juveniles and have not yet developed the rostrum and peduncular scales, but would have done so later in ontogeny.
- 2) All specimens are adults and the species has evolved by pedomorphosis. Pedomorphosis is a type of heterochrony, an evolutionary shift of developmental timing. This would mean all individuals remained in a juvenile state, never developing the missing plates.
- 3) All specimens are adults and have secondarily reduced the missing plates (similar to *Neoscapellum debile*). In this case juveniles of the new species would have possessed the missing plates, but these were lost later in ontogeny. Despite the fact that the resulting

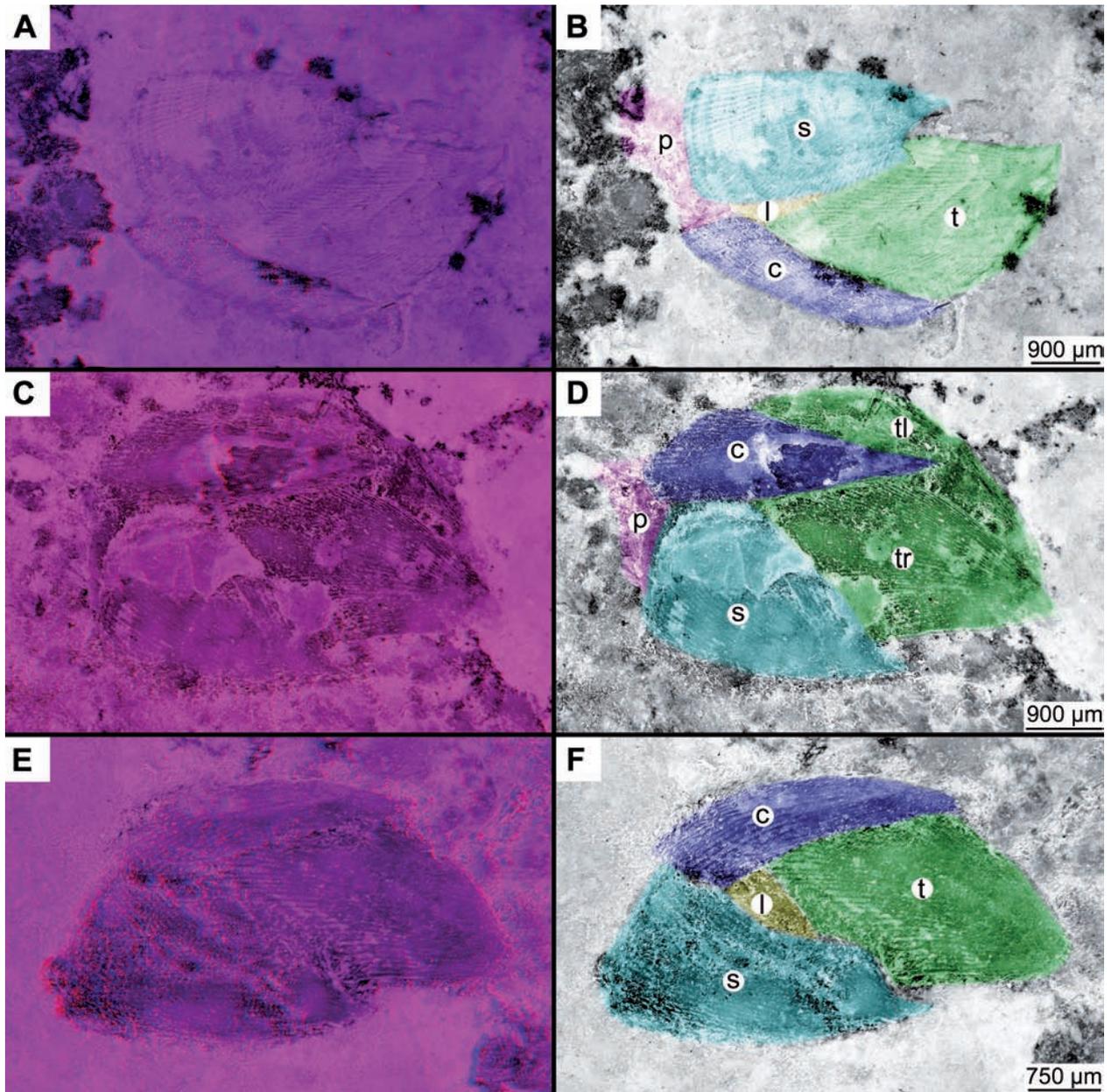


Fig. 5. Stereo images of virtual surfaces based on depth maps of image stacks and color highlighted versions of fossil barnacle *L. klausreschi* gen. et sp. nov. (specimens 5-7). Color-markings: Carina (= c) highlighted blue, terga (= t) highlighted green, scuta (= s) highlighted cyan, latera (= l) highlighted orange and peduncle (= p) highlighted purple. **A, B** – Specimen 5 (SMNS 70388/5). **C, D** – Specimen 6 (SMNS 70388/6), please note two terga, each from one site (tr = tergum right, tl = tergum left). **E, F** – Specimen 7, holotype (SMNS 70388/7).

morphology appears juvenile in certain aspects, this would indeed represent a case of peramorphic heterochrony (adultizing), the morphology with fewer shell plates representing a terminally added new morphol-

ogy. This would identify this case of peramorphosis as hypermorphosis.

Heterochronic shifts appear not to be unusual for the evolutionary lineage of barnacles (HAUG & HAUG

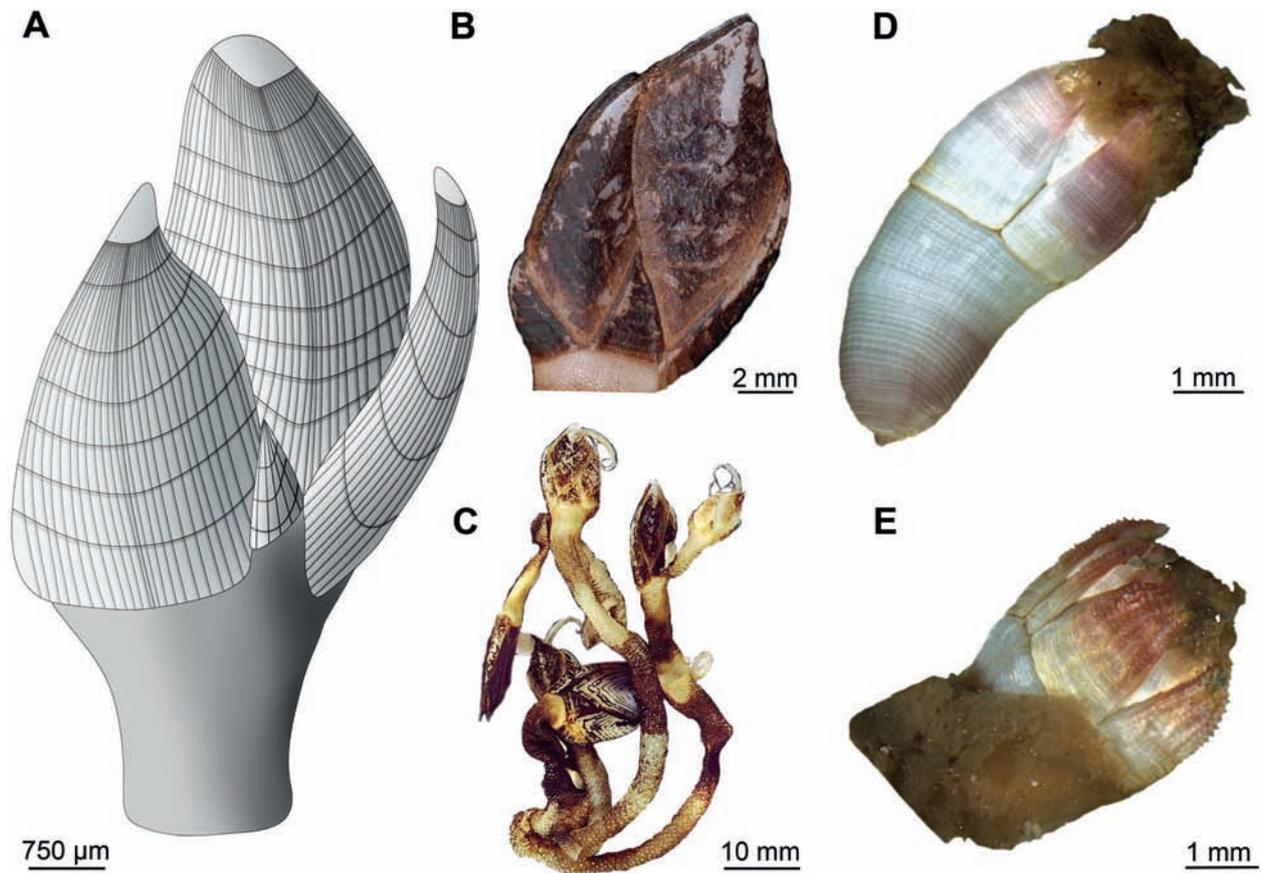


Fig. 6. Reconstruction of fossil barnacle *Litholepas klausreschi* gen. et sp. nov. (A) and comparative photographs of *Vulcanolepas osheai* (B, C) and *Pectinoacasta pectinipes* (D). **A** – Reconstruction of *L. klausreschi* gen. et sp. nov. based on drawing of specimen 7. Please note that there has been some movement of all capitular plates during preservation, especially the latius, which has rotated slightly, thus the reconstruction displays not the original morphological arrangement. **B** – Detail of capitulum of *V. osheai*, indicating original position of the lateral shell plate. **C** – Overview image of *V. osheai*. **D** – Detail of *P. pectinipes*. **E** – *P. pectinipes* with remains of sponge tissue.

2015). Thus, evolutionary novelties in the ontogeny of thecostracans are well known and cirripedes provide a unique opportunity to apply an evolutionary developmental approach (GALE 2015; HØEG et al. 2015).

4.2. Could these specimens represent juveniles?

Deciding whether a fossil organism is adult or not is in fact far from trivial (see e.g. discussion in HAUG et al. 2013b; HAUG & HAUG 2016). It has been claimed that fossil arthropods are recognized as adults by characters of sexual maturity (WOLFE & HEGNA 2014). This is almost impossible in most cases and is also not applicable here; we could not observe any character that was clearly related to sexual maturity. On the basis of the well-developed morphology and strong sculpture

of the plates, the fossils described herein most likely represent adults.

4.3. Could the specimens represent paedomorphic or peramorphic forms?

If the specimens represent paedomorphic forms, the plates that are absent would never have developed. Therefore, this is indeed a possible interpretation. Yet, as pointed out, the absence of the plates may also be the result of a secondary reduction throughout ontogeny. Hence, they could just as well represent peramorphic forms. Given the data we have, we cannot differentiate between the one and the other interpretation. Only the observation of actual juveniles can resolve this issue.

It is well known that the morphology of cirripede

plates is quite variable according to their habitats (COLLINS et al. 2014; GALE 2014a). It has been also proposed that the number, as well as morphology and location in the capitulum of latera might be varying and the presence or absence of a rostrum and subcarina is only nearly constant for a genus (CHEETHAM 1963). The shape and sculpture of scuta and terga has been used for distinguishing species, the morphology of the carina has been used for distinguishing genus (CHEETHAM 1963). This has also been suggested by others (e.g., NEWMAN 1979; GALE & SØRENSEN 2014). Therefore, it is quite reasonable to interpret the new species as a representative of Neolepadinae.

Nonetheless, due to the variable morphology of the plates these small Jurassic barnacles are some of the most difficult of all cirripedes to interpret (GALE 2014a). The morphology of the seven plates (two terga, two scuta, two latera and one carina) of the fossil cirripedes described herein is the basis for placement within Neolepadinae.

5. Palaeoecology

Little is known about the palaeoecology of Jurassic barnacles (GALE 2014a), because most fossils are disarticulated, isolated shell plates (KOČOVÁ-VESELSKÁ et al. 2014). Modern representatives of Neolepadinae are known as hydrothermal vent-dwelling organisms (BUCKERIDGE 2000; PÉREZ-LOSADA et al. 2008; GALE 2015). However, extant vent organisms originated earliest 100 mya (VAN DOVER et al. 2002) and representatives of Neolepadinae are interpreted as originating in a shallow marine environment (BUCKERIDGE & GRANT-MACKIE 1985).

Identifying the fossil specimens as a new species, interpreted as a genus *Litholepas* within Neolepadinae would fit well into the divergence time proposed for these barnacles: Based on molecular and morphological data, representatives of Scalpelliformes evolved about 360 mya. The split within Neolepadinae has been interpreted as having happened approximately 200 mya (PÉREZ-LOSADA et al. 2008). The transition for living at hydrothermal vents would have appeared more recently, around 120 mya (PÉREZ-LOSADA et al. 2008). However, it seems likely that many Jurassic and Cretaceous barnacles were attached to floating objects (DIETL & SCHWEIGERT 2001; GALE 2014a) or moving animals and thus display wide geographical distributions (HARZHAUSER & SCHLÖGL 2012). Fossil scalpelliform cirripedes have been reported from molluscs, echinoids, brachiopods,

bryozoans, algae and corals (WITHERS 1928; CHEETHAM 1963; WHYTE 1976).

Representatives of one Jurassic group (“*Pollicipes*”) have been reported to attach to ammonites and to feed on detritus provided by the ammonite (KEUPP et al. 1999). Due to the energy-taking process of phoresy, this strategy could be interpreted as parasitism without trophic interaction (GOATER et al. 2014) and would be indicating a rare Case 1 of fossil parasitism (direct evidence of parasitism, where the parasite is still attached to the host, see NAGLER et al. 2015, 2016).

Extant representatives of Scalpelliformes are well known epibionts on other marine organisms, e.g. sharks, crabs, sea spiders, sea urchins, molluscs, corals or on rocks (NILSSON-CANTELL 1978; YOUNG 2001; BUHL-MORTENSEN & HØEG 2006; CHAN et al. 2009; DI GERONIMO 2010; REES et al. 2014). Unfortunately, the details of most of the relationships of extant forms are unknown (CHAN & HØEG 2015).

Benthic sponges have been reported to be heavily infested by other benthic invertebrates (ARNDT 1933; URIZ et al. 1992). Furthermore, sponges are important benthic suspension feeders and are believed to slow the water flow and raise the water turbulence, resulting in an increased residence time of possible nutrient particles (GILI & COMA 1998). Cirripedes as epibionts can thus take advantage of the slowed water currents caused by sponges. Sponges also represent erect substrates and microhabitats (BARTHEL & GUTT 1992) that offer new shelter and additional space. Representatives of the extant balanoid “*Acasta* group” are well known to live in symbiotic relationships with sponges (ARNDT 1933; VAN SYOC & WINTHER 1990; KOLBASOV 1993). Individuals of *Pectinoacasta pectinipes* burrow with a calcareous basal plate deep into the sponge tissue (Fig. 6D, E) and are protected by the sponge. Due to the plugging of the sponge’s openings by representatives of *Pectinoacasta*, their host sponge will be harmed by sealing its functional orifices (URIZ et al. 1992). A similar *syn-vivo* lifestyle might have been performed by the fossils described herein. Furthermore, the sponge *Codites* spp. is a representative of Geoiidae within Demospongia (SCHIMPER 1869; WALTHER 1904; DIETL & SCHWEIGERT 2001). Their skeleton is built of a dense, narrow network of spongin fibers and spicules and these sponges are known to be covered by epibionts, such as oysters (WALTHER 1904; KEUPP & SCHWEIGERT 2012, 2015). Although, we cannot observe these spicules in the fossil sponge specimen studied herein, DIETL & SCHWEIGERT (2001) demonstrated sterraster-type microscleres (“Rhaxe”) for *Codites* spp. The absence of peduncular

plates in the fossil barnacles described herein could give a hint for a lifestyle within the sponge, as the barnacles may well have been protected by the sponge. Hence, it is likely, that the barnacles lived not only at, but also within the sponge.

The sponge might also provide a nutrient source for the cirripedes, as reported for fossil and extant coral-barnacle associations (WHYTE 1976). Thus the barnacle could have benefitted from feeding on the sponge, while the sponge gets attenuated. A *syn-vivo* like the above one (one species benefits, while the other suffers) can be interpreted as a form of parasitism (LAFFERTY & KURIS 2002). Nevertheless, it seems clear that *Litholepas klausreschi* lived in a symbiotic relationship, either parasitic or commensalistic, with sponges.

6. Conclusions

The new genus and species *Litholepas klausreschi* is interpreted as an ingroup of Neolepadinae. *Litholepas klausreschi* might represent a paedomorphic or peramorphic form. Further corroboration of the one or other interpretation and their systematic interpretation demands for finding juvenile specimens. These fossils represent the earliest case of a barnacle-sponge-relationship and might represent a case of palaeo-parasitism. They also demonstrate that Jurassic fossil barnacles may be found in direct association with their habitat.

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Addresses of the authors:

CHRISTINA NAGLER (corresponding author), Department of Biology II, Functional Morphology group, University of Munich (LMU), Planegg-Martinsried, Germany; e-mail: christina.nagler@palaeo-evo-devo.info

JOACHIM T. HAUG, Department of Biology II, Functional Morphology group, University of Munich (LMU), Planegg-Martinsried, Germany & GeoBio-Center, LMU Munich;

HENRIK GLENNER, Department of Biology, Marine Biodiversity group, University of Bergen, Bergen, Norway; Center for Macroecology and Evolution, University of Copenhagen, Denmark;

JOHN BUCKERIDGE, Earth & Oceanic Systems Group, RMIT University, Melbourne, Australia.