

***Perumegabalanus calzai* gen. et sp. nov., a new intertidal megabalanine barnacle from the early Miocene of Peru**

(Short title: **A new intertidal barnacle from Burdigalian deposits of Peru**)

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With 9 figures

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Abstract

Living members of the tribe Austromegabalanini are large-sized balanid barnacles (Crustacea: Cirripedia: Neobalanoformes) that live in temperate and cold waters of the Southern Hemisphere. During the Neogene, however, the austromegabalanines also inhabited the Northern Hemisphere, as well as some low-latitude tropical environments. This paper describes a new taxon of austromegabalanines, *Perumegabalanus calzai* gen. et. sp. nov., from the shallow-marine, nearshore, lower Miocene (19 to 17 Ma, Burdigalian) deposits of the Chilcatay Formation (East Pisco Basin, southern Peru). The shell of *P. calzai* gen. et. sp. nov. has thick, ornamented, multitubiferous parietes and a vesicular sheath that we interpret as indicative of an intertidal habitat. The compresence, in the early Miocene of southern Peru, of two genera of austromegabalanines (i.e., *P. calzai* gen. et. sp. nov. and the recently described *Austromegabalanus carrioli*), supports the hypothesis of an early diversification of this tribe at low latitudes.

40 **Key words**

Adaptation, Austromegabalanini, Balanidae, Chilcatay Formation, East Pisco Basin, evolution, functional morphology, palaeobiogeography, palaeoecology, predation.

1. Introduction

45 Unlike most lineages of crustaceans, cirripedes adopted a sessile lifestyle. By doing this, they
traded their ability to move (at least autonomously) for the advantage of settling in a favourable
location. The main disadvantages of this strategy rely in losing the possibility to flee from
predators and to rapidly relocate elsewhere if environmental conditions deteriorate or become
unsuitable. As a consequence of this, through geological time, cirripedes evolved peculiar
50 solutions to cope with the disadvantages of a sessile lifestyle. Their ability to adapt to different
environmental pressures, especially in the intertidal environment (CRISP & BOURGET 1985),
inspired Darwin his view of organic evolution (CRISP 1983). The earliest confirmed cirripede is
of Silurian age, while the earliest known modern neobalanoform is of Late Cretaceous age
(BUCKERIDGE & NEWMAN 2006; KOČÍ et al. 2017). Following the Cretaceous-Tertiary extinction
55 event, opportunistic barnacles rapidly diversified and, by the Neogene, they had become a
common component of continental-shelf benthic assemblages (e.g., BUCKERIDGE 1983, 2012;
FOSTER 1987; FOSTER & BUCKERIDGE 1987; COLETTI et al. 2018). Currently, barnacles are one
of the most ubiquitous group of shallow-marine organisms, occurring from the poles to the
tropics and including both cosmopolitan and endemic taxa. Endemic barnacles are mostly
60 present in the Southern Hemisphere and include the tribe Austromegabalanini (Balanomorpha:
Balanidae: Megabalaninae) (NEWMAN 1979). These large-sized acorn barnacles are assigned to
two extant genera, *Austromegabalanus* and *Notomegabalanus*, and two extinct genera,
Fosterella and *Porobalanus* (e.g., NEWMAN 1979; BUCKERIDGE 1983, 2015). The two extant
genera are currently restricted to the cold and temperate waters of the Southern Hemisphere, but
65 fossil representatives of both *Austromegabalanus* and *Notomegabalanus* are known also from the
Northern Hemisphere, as well as from tropical palaeolatitudes (COLLARETA et al. 2019, and
references therein). The two extinct genera, *Fosterella* and *Porobalanus*, are only known from

mid- and high-latitude deposits of the Southern Hemisphere (BUCKERIDGE 2015). This palaeobiogeographic pattern suggests a complex history of spreading and adaptation to different environmental settings. With the aim of further enhancing our knowledge of the evolution and distribution patterns of cirripedes, this paper describes a new genus of megabalanine barnacles discovered in an early Miocene barnacle-rich deposit of the Peruvian East Pisco Basin (COLETTI et al. 2018), providing information on its palaeoecology and its significance for the palaeobiogeography of the tribe Austromegabalanini.

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2. Material and Methods

2.1. Stratigraphic and palaeoenvironmental framework

The study area is located in the Ica Desert of southern Peru (Fig. 1A), where the sedimentary succession of the East Pisco Basin (one of the Cenozoic forearc basins of the Peruvian coast) is exposed. The infill of this basin can be subdivided into five stratigraphic units: the lower-middle Eocene Caballas Formation (DEVRIES 2017); the middle to upper Eocene Paracas Formation (DUNBAR et al. 1990; DEVRIES 2017; COLETTI et al. in review); the upper Eocene to lower Oligocene Otuma Formation (DEVRIES et al. 2017); the upper Oligocene to lower Miocene Chilcatay Formation (DEVRIES & JUD 2018; DI CELMA et al. 2018b); the middle Miocene to Pliocene Pisco Formation (MUIZON & DEVRIES 1985; DI CELMA et al. 2017; BOSIO et al. 2019, in press). All these units are bounded by regionally extensive unconformities, and as such, they represent transgressive sequences in the basin; moreover, intraformational unconformities are also present (DUNBAR et al. 1990; DI CELMA et al. 2018a).

The base of each sequence consists of coarse shallow water deposits testifying the early phases of transgression. These horizons are often rich in barnacles, especially those marking the

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base of the Chilcatay Formation (DUNBAR et al. 1990; COLETTI et al. 2018, in review; COLLARETA et al. 2019). At the study areas of Ullujaya and Zamaca (Fig. 1A), the Chilcatay Formation (the barnacles of which are the subject of this paper) is comprised of massive, mixed (siliciclastic-bioclastic) sandstones, sandy siltstones, and diatomaceous and tuffaceous siltstones.

95 Internally, an intraformational unconformity (CE0.2) divides the Chilcatay strata into two allomembers, designated Ct1 and Ct2, in ascending stratigraphic order (DI CELMA et al. 2018b, 2019) (Fig. 1B). Different facies associations can be recognised in each allomember. The lower allomember includes a massive boulder-bearing sandstone that alternates with conglomerates (Ct1c facies association, comprising the base of Ct1), a medium- to fine-grained sandstone with

100 conglomerate beds (Ct1a facies association, comprising the middle part of Ct1), and clino-bedded strata of coarse mixed sediments (Ct1b facies association, comprising the top of Ct1) (Fig. 1B). These facies associations record deposition in shoreface (Ct1c), offshore environment punctuated by mass-transport events (Ct1a), and a mixed siliciclastic-carbonate subaqueous delta perched on the basin margin (Ct1b) (DI CELMA et al. 2018b, 2019). The upper allomember

105 consists of massive, thoroughly bioturbated sandstones (Ct2a facies association) changing upwards into massive siltstones (Ct2b facies association) (Fig. 1B). These facies associations record deposition in shoreface (Ct2a) and offshore (Ct2b) settings (DI CELMA et al. 2018b, 2019).

Invertebrate macrofossils from the Chilcatay strata exposed at Ullujaya and Zamaca are

110 represented by barnacles (belonging to at least three taxa, including the newly described megabalanine species *Austromegabalanus carrioli*), echinoids, bivalves, calcareous tubeworms, and crabs (BIANUCCI et al. 2018; COLETTI et al. 2018; DI CELMA et al. 2018b, 2019; COLLARETA et al. 2019). At the study sites, the Chilcatay deposits are also rich in fossils of marine

vertebrates, mostly cetaceans and elasmobranchs, with subordinate turtles and bony fish
115 (BIANUCCI et al. 2018; DI CELMA et al. 2018b, 2019; LANDINI et al. 2019). This faunal
assemblage indicates a coastal community of warm-temperate waters and, coupled with
sedimentological observations, suggests a semi-enclosed, estuarine embayment connected with
the open-ocean system (BIANUCCI et al. 2018; LANDINI et al. 2019).

Biostratigraphic and geochronological data indicate that the Chilcatay strata cropping out at
120 Ullujaya and Zamaca were deposited between 19 and 17 Ma, i.e., during the Burdigalian (DI
CELMA et al. 2017, 2018a, b, 2019; BOSIO et al. in press).

2.2. Specimen preparation, analytical procedures, repository, and anatomical terminology

Barnacle specimens collected at Ullujaya and Zamaca were at first studied under stereoscopic
125 microscope and hand lens to determine their external morphology. Two specimens from Ullujaya
and two specimens from Zamaca were later embedded in epoxy resin and cut at different levels
(i.e., near the base of the parietes, just above the base of the sheath, and close to the apex of the
shell) by using a Buehler IsoMet low-speed precision-cutting machine. Seven of the obtained
slices were then prepared as thin sections and assessed under a Leica transmitted light optical
130 microscope (OM). One slice and the sutural edge of the ala of an isolated carina were gold-plated
and observed with a VEGA TS Univac 5136XM Tescan Scanning Electron Microscopy (SEM).

All the studied specimens of the new taxon described herein are currently stored in the fossil
invertebrate collection of the Departamento de Paleontología de Vertebrados, Museo de Historia
Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru (hereinafter: MUSM).

135 The terminology for describing the shell anatomy (Fig. 2) follows PRABOWO & YAMAGUCHI
(2005) and COLLARETA et al. (2019), except when explicitly stated otherwise.

3. Systematic Palaeontology

Subclass Cirripedia BURMEISTER, 1834

140 Superorder Thoracica DARWIN, 1854

Order Balanomorpha PILSBRY, 1916 (=Order Sessilia LAMARCK, 1818, *sensu* BUCKERIDGE & NEWMAN 2006)

Infraorder Neobalanoformes GALE (*sensu* KOČÍ et al. 2017, to accommodate Neobalanomorpha GALE in GALE & SØRENSEN 2015)

145 Family Balanidae LEACH, 1817

Subfamily Megabalaninae NEWMAN, 1979

Tribe Austromegabalanini BUCKERIDGE, 2015

Included genera: *Austromegabalanus* NEWMAN, 1979; *Notomegabalanus* NEWMAN, 1979;

Fosterella BUCKERIDGE, 1983; *Porobalanus* BUCKERIDGE, 2015; *Perumegabalanus* gen. nov.

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Perumegabalanus gen. nov.

Derivation of the name: The generic name originates from the combination of “Peru”, in reference to the geographic location of the type locality, and “*Megabalanus*”, the type genus of
155 subfamily Megabalaninae. Gender masculine.

Type and only known species: *Perumegabalanus calzai* sp. nov.

Diagnosis: Austromegabalanines with truncated conical shell; orifice rounded-rhomboidal, toothed; parietes thick; radii very narrow with summits subparallel to the basis; sheath vesicular, less than half the total height of shell, the pores being large, subspherical, and irregularly

160 arranged; paries with multiple longitudinal tubes which are compressed-ovate to rounded-
rectangular in transverse section and, when large, partitioned by auxiliary septa; basal plate
tubiferous, vesicular; interlamine figures complex, arborescent, long, narrow, with spear-like
heads; main axis with several short and straight secondary processes and fine secondary
abutments; tertiary processes crescent moon-shaped, distally asymmetrical with whorl-like
165 structures that seemingly drape the interlamine figures.

Stratigraphic and geographic range: Early Miocene (19 to 17 Ma, Burdigalian; see above for
more details) of southern Peru (East Pisco Basin).

Perumegabalanus calzai sp. nov.

170 Figs. 3-8, 9B

2018 Balanidae indet. – COLETTI et al., p. 582, fig. 8D-F.

Holotype: MUSM INV 624, articulated shell (compound rostrum, two carinolatera¹, two
175 carinolatera², and a carina) lacking the opercula, adjacent to a smaller conspecific specimen
(consisting of two articulated compartments and a partial basal plate) and overgrown over about
30 juvenile barnacle shells (possibly, juveniles of *Perumegabalanus calzai* gen. et sp. nov.) (Fig.
3).

Holotype dimensions: Carino-rostral diameter at shell apex – 11.7 mm; carino-rostral diameter
180 at base – 25.3 mm; height of the shell, with exclusion of the basal plate – varying between 19.6
mm (at carina) and 11.9 mm (at rostrum); height of the shell, including basal plate – varying

between 27.8 mm (at carina) and 23.5 mm (at rostrum); transverse width of the radii at shell apex, measured on the rostrum – 2.7 mm.

Type locality and horizon: Ullujaya, Ocucaje area, Ica Desert, southern Peru (approximate
185 geographic coordinates: 14° 35' 03" S; 75° 38' 36" W). The type horizon, whose deposition dates back to the late early Miocene (i.e., Burdigalian), belongs to the Ct1 allomember of the Chilcatay Formation (as defined by DI CELMA et al. 2018b) and takes place ca. 38 m above the base of the stratigraphic section measured by DI CELMA et al. (2018b), within the lower portion of the *Ct1b* facies association.

190 **Derivation of the name:** Named after Luciano CALZIA (†2016), Italian geologist, football player, and dear friend.

Referred specimens: MUSM INV 625, an almost complete shell, with a largely worn-out external aspect, from Ullujaya (ca. 8 m above base of the section measured by DI CELMA et al. (2018b), corresponding to their marker bed D, within the *Ct1a* facies association); MUSM INV
195 626, a cluster of four shells (two complete and two incomplete), preserved as gypsum casts, from undifferentiated Chilcatay strata exposed at Zamaca (DI CELMA et al. 2019); MUSM INV 627, an isolated carina from undifferentiated Chilcatay strata exposed at Zamaca (DI CELMA et al. 2019); MUSM INV 628, an almost complete shell from the upper portion of the *Ct1b* facies association exposed at Zamaca (DI CELMA et al. 2019); MUSM INV 629 and MUSM INV 630,
200 two almost complete shells from Ullujaya (25 m above base of the section measured by DI CELMA et al. 2018b, within the *Ct1a* facies association); MUSM INV 631, an almost complete shell from the basal portion of the *Ct2a* facies association exposed at Zamaca (DI CELMA et al. 2019). All the specimens referred to *Perumegabalanus calzai* gen. et sp. nov. lack opercula and

come from the Chilcatay strata exposed at the Ullujaya and Zamaca areas (Ica Desert, lower Ica
205 Valley).

Diagnosis: *Perumegabalanus* gen. nov. is currently monotypic; diagnosis as per genus until new species are described.

Description: Shell truncated conical and relatively short; basal diameter significantly larger than diameter of orifice (Figs. 3, 4A-C). Orifice typically rounded rhomboidal, elongated parallel to
210 the carino-rostral axis, and moderately toothed (Fig. 4A-C). In large mature individuals, the orifice shows apical abrasion, being enlarged by erosion (Fig. 4B). Consequently, parietes are roughly trapezoidal in adult individuals (Fig. 4C). Compartments thick, especially basally, where they can exceed 10 mm in thickness. Parietes externally ornamented with fine longitudinal ribs, corresponding to the axes of the parietal longitudinal septa (Fig. 4C), and larger bulging
215 protuberances (Fig. 3A-D) creating a rough and irregular surface. The latter structures are especially common in large-sized specimens at the base of parietes. In abraded specimens, the protuberances are often almost completely eroded, with only slightly raised patches of shell material testifying their presence (Fig. 4C). The external surface of the parietes is frequently worn, locally exposing the complex interplay of parietal tubes and septa. Radii very narrow
220 transversely and barely sunken from the paries, with weak transverse growth striae (Fig. 4C); summits almost parallel to base (Figs 3A, 4C). Sutural edges of the compartments with alae (Fig. 4D) having transverse septa with slender, obliquely oriented, secondary denticles on the upper side only (Fig. 5A). In sectioned specimens, it is possible to observe the tubes that permeate the radii (Fig. 5B, C). Articulation between radius and ala involving a sheath projection that covers
225 the distal edge of the ala – a character shared by megabalanines and concavines according to PITOMBO (2003) (Fig. 5D). Sheath short (i.e., less than half the total height of shell), with

numerous, fine, closely spaced, transverse growth lines (Fig. 4D); appressed, except for its basalmost portion, which is moderately depending. The resulting body chamber is thus subcylindrical. Sheath vesicular, with millimetre-sized subspherical pores (Figs 4D, 6A, B).

230 Pores develop between the growth lamellae of the sheath (i.e., the “lames palléales” *sensu* DAVADIE 1963), either as isolated cavities or as clusters in which each is separated from the adjacent ones by irregular septa (Fig. 6A, B). Fine longitudinal ribs, representing the inner terminations of the interlamine figures, occur on the inner surface of the shell below the sheath (Fig 4D). Basal plate calcareous, multilayered, with an irregular, vesicular, honeycomb-like

235 structure (Fig. 6C), thickening towards the periphery, and very thin and often not preserved in its central part. Internal surface of the basal plate displaying fine ribs similar to those below the sheath. Outer surface of the basal plate ornamented by weak concentric growth folds and radiating striae. Most of the observed basal plates are short and flare peripherally extending downwards the volcano-like shape of the capitulum. When it happens, the external surface of the

240 basal plate reproduces the ornamentation pattern with fine longitudinal ribs and larger bulging protuberances that characterises the exterior of the overlying compartments (making the identification of the boundary between the wall plates and the basal plate difficult). Alternatively, the basal plates might appear either as distinctly planate (i.e., disc-like), modeled against an adjoining barnacle shell, or draping an unpreserved flat substrate. In several cases, the basal plate

245 entombs smaller clustering barnacle shells (?young individuals of *P. calzai* gen. et sp. nov.) that were overgrown by a larger individual (Fig. 3E). Parietes are multitubiferous; longitudinal tubes separated from each other by longitudinal septa and further, irregularly, partitioned by auxiliary septa (Fig. 6D). Auxiliary septa are drape-shaped and composed of the same kind of microgranular calcite that constitute the longitudinal septa and their partial secondary infill (Fig.

250 7A, B). Although, in thin section, the auxiliary septa often appear as small bridges intersecting at variable angles the larger longitudinal septa (Fig. 7C), via SEM observations it is clear that they are shaped as folded drapes that mantle and cross the parietal longitudinal tubes, dividing them into several rows of smaller cavities (Fig. 7A, B). Towards the inner lamina, the auxiliary septa become thicker and more regularly organised, forming a sort of wall that runs orthogonal to the
255 longitudinal septa, resulting in the apparent duplication of the inner lamina (Fig. 7D). Consequently, in the more regularly organised portions of the parietes, it is possible to recognise two main rows of tubes: an outer one (generally further subdivided by the auxiliary septa; Fig 7D) and an inner one (bounded by the interlaminar figures; Fig. 7D). Differently from other balanids that achieve a multitubiferous wall by perforation either of the outer (e.g., *Fosterella*) or
260 inner lamina (*Megabalanus vinaceus*), as well as by regular branching of the longitudinal septa (e.g., several species of *Fistulobalanus*), *P. calzai* gen. et sp. nov. does this via the partitioning of the parietal tubes by irregular auxiliary septa. Branching of the longitudinal septa and creation of subsidiary parietal tubes (sensu PRABOWO & YAMAGUCHI 2005) is also occasionally observed in *P. calzai* gen. et sp. nov., close to the basal margin of the parietes (Fig. 8A). Close to the
265 summit of the parietes, longitudinal tubes are partly infilled by concentric rings of biogenic calcite (Fig. 7C). In *Austromegabalanus*, when observed in transverse thin sections, these secondary infills appear darker than the biogenic calcite that constitutes the longitudinal septa, and the concentric pattern is remarkably strong (COLLARETA et al. 2019). In *P. calzai* gen. et sp. nov., in turn, the infills have the same optical properties of the surrounding calcite that forms the
270 longitudinal and auxiliary septa (Fig. 7C), and they exhibit a similar microgranular structure. The secondary infills observed in *P. calzai* gen. et sp. nov. are also distinctly less conspicuous than those typical of *Austromegabalanus*. Interlaminar figures complex and arborescent, stemming

from the outer lamina and pointing inwards, with their main axis running at the center of the longitudinal septa (Fig. 8A-C). Similar to *Fosterella*, the interlamine figures of *P. calzai* gen. et sp. nov. are long and narrow, having a spear head appearance (Fig. 8); they display short and straight secondary processes provided with crescent moon-shaped tertiary processes (Fig. 8D). Similar to *Austromegabalanus carrioli*, the tertiary processes of *P. calzai* gen. et sp. nov. are more strongly developed on the side facing the exterior of the shell, so that each interlamine figure appears as draped by whorl-like structures (Fig. 8D). However, this feature is variably developed in the sectioned specimens of *P. calzai* gen. et sp. nov., and overall way less prominent than in *A. carrioli*. Similar to several other species of extinct and extant megabalanines (e.g., *Austromegabalanus psittacus*, *A. pisconensis*, *Fosterella tubulatoides*, and *Notomegabalanus decorus*), fine and short secondary abutments stem from the root of each secondary process (Fig. 8A). Inner lamina very thin below the sheath and slightly thicker in the upper part of the capitulum, where it is bordered by the sheath (Fig. 8A-C); presenting faint growth bands and mantling the inner tip of interlamine figures.

For summarising, *Perumegabalanus calzai* gen. et sp. nov. is recognised as a balanid by the complex, arborescent interlamine figures and the calcareous basis (BUCKERIDGE 1983). It is further recognised as a megabalanine by the co-occurrence of tubiferous radii and sheath projections extending over the adjacent alae (PITOMBO 2003). It is further recognized as an austromegabalanine by the sutural edges of alae having secondary denticles on the upper side only (BUCKERIDGE 2015). *Perumegabalanus calzai* gen. et sp. nov. mainly differs from *Austromegabalanus* and *Notomegabalanus* by the shorter, volcano-shaped shell and multitubiferous parietes that are generally strongly ornamented externally. It further differs from *Fosterella* and *Porobalanus* by having irregularly multitubiferous parietes achieved via the

partitioning of the parietal tubes by auxiliary septa and by having a calcareous basis with a vesicular structure. The observation of auxiliary septa that partition the parietal tubes also allows to distinguish *Perumegabalanus calziai* gen. et sp. nov. from the enigmatic balanid *Titobustillobalanus* (CARRIOL & ÁLVAREZ-FERNÁNDEZ 2015), whose assignment at the
300 subfamily level is to date uncertain.

Colour: Specimens of *Perumegabalanus calziai* gen. et sp. nov. are primarily whitish or yellowish. However, a few specimens have retained a pinkish pigmentation which is considered original. This is not unlike several extant species of *Austromegabalanus* and *Notomegabalanus* (e.g. *Notomegabalanus decorus*). Those specimens of *P. calziai* gen. et sp. nov. that are preserved
305 as gypsum casts (e.g., Fig. 4A) are generally translucent and range in colour between honey beige and dark brown.

Ichnological observations: The external surface of the shells of *Perumegabalanus calziai* gen. et sp. nov. is often punctuated by drill holes of predatory origin (Figs. 3B, 4C). Nearly half of the examined specimens present several predation holes, most of which are incomplete (i.e., they do
310 not reach the inner body chamber), thus clearly reflecting unsuccessful predation attempts, presumably by carnivorous gastropods (KLOMPMAKER et al. 2015).

Comments: The nature of the pores in the wall compartments of *Fosterella* had, until the discovery of *Perumegabalanus calziai* gen. et sp. nov., been a defining feature of the former genus. The discovery of similar structures in the closely related *P. calziai* gen. et sp. nov.
315 necessitates a re-examination of *Fosterella*, because although vertical pores in or near the sheath had been noticed, their permeation of the sheath had not been formally discussed. This aspect is addressed below.

Fosterella BUCKERIDGE, 1983

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Fosterella tubulata (WITHERS, 1924)

Fig. 9A

1924 *Balanus* (*Megabalanus*) *tubulatus* – WITHERS, p. 28; pl. VII, figs. 1–10.

325 1976 *Megabalanus tubulatus* – NEWMAN & ROSS, p. 69

1979 *Notomegabalanus tubulatus* – NEWMAN, p. 293

1983 *Fosterella tubulatus* – BUCKERIDGE, p. 111

2015 *Fosterella tubulata* – BUCKERIDGE, p. 563

330 *Fosterella chathamensis* BUCKERIDGE, 1983

1983 *Fosterella chathamensis* – BUCKERIDGE, p. 109

Notes on the parietal and basal plate pores in *Fosterella*: Parietes with multiple longitudinal
335 tubes which are compressed-ovate to rounded-rectangular in transverse section, arranged radially
and, when large, partitioned vertically by auxiliary septa; basal plate thin, with a single row of
small, rounded radial pores. Interlamine figures complex, arborescent, long, narrow, with
spear-like heads; sheath with a single row of ovate pores (Fig. 9A). Both *F. tubulata* and *F.*
chathamensis conform to these observations.

340 **Comments:** The vesicular sheath and the multitubiferous parietes of *Fosterella*, with their
complex, spear-headed, interlamine figures, place this genus very close to *Perumegabalanus*

calzai gen. et sp. nov. However, in *Fosterella* the basal plate is non vesicular and exhibits a single row of comparatively small, radially arranged pores, while in *P. calzai* gen. et sp. nov. the basal plate is vesicular (Fig. 6C). The two genera may be further distinguished by the
345 multitubiferous state of the mural plates which in *Fosterella* is mostly achieved by the regular perforation of the outer lamina by several rows of parietal tubes, while in *P. calzai* gen. et sp. nov. it is achieved via irregular partitioning of the parietal tubes by auxiliary septa. Furthermore, the sheath in *Fosterella* is permeated by relatively small, rounded vertical pores (Fig. 9A); in turn, in *P. calzai* gen. et sp. nov., the pores that occur within sheath the are larger and often
350 irregularly arranged in clusters (Fig. 9B).

4. Discussion

Multitubiferous parietes occur in several groups of Neobalanoformes. Among extant non-epizoic sessile barnacles, this structure is common in the superfamily Tetracitoidea (e.g., members of
355 *Austrobalanus*, *Newmanella*, *Tetracito*, *Tetracitella*, *Lissacito*) and rarer in the supefamily Balanoidea (e.g., *Semibalanus*, *Fistulobalanus*, and *Megabalanus vinaceus*). All the multitubiferous tetracitoids are intertidal genera, generally occurring in a band below the upper intertidal zone (usually occupied by chthamaloidea) and above the shallow subtidal zone dominated by balanoids (DANIEL 1972; FOSTER 1973; NEWMAN & STANLEY 1981; EGAN &
360 ANDERSON 1988; YIPP & SHIN 1990; BOLAND 1997; GOMEZ-DAGLIO & SYOC 2006; CHAN 2007; WONG et al. 2014). Similarly, *Fistulobalanus* and *Semibalanus* are also mainly intertidal genera (CONNELL 1961; ZULLO 1984; RANGELEY & THOMAS 1988; PRABOWO & YAMAGUCHI 2005; CHAN 2007), while *Megabalanus vinaceus* has been reported to occur between the intertidal zone down to 3 metres of water depth (GOMEZ-DAGLIO 2003). The only known extant

365 balanids provided with a vesicular sheath are assigned to the genus *Fistulobalanus*; the latter is
an epiphyte barnacle that usually encrusts the roots and stems of mangroves (Magnoliophyta:
Rhizophoraceae) in the intertidal zone (PRABOWO & YAMAGUCHI 2005; CHAN 2007).
Consequently, it is reasonable to hypothesise that *Perumegabalanus* was also an intertidal
species. Indeed, the shell architecture of *Perumegabalanus calziai* gen. et sp. nov. appears as
370 well-suited for an existence in the intertidal zone. Tubiferous parietes represent an excellent
solution for building a thick shell while saving calcium carbonate (which reflects positively on
growth velocity and energy consumption) without compromising structural strength (STANLEY &
NEWMAN 1980; NEWMAN & STANLEY 1981; CRISP & BOURGET 1985; BUCKERIDGE 2008;
ASTACHOV et al. 2011). Multitubiferous parietes might represent a further step in this direction,
375 providing a competitive advantage in intertidal settings, where space is limited and hydrodynamic
energy is high (STANLEY & NEWMAN 1980; NEWMAN & STANLEY 1981). Evidence of fierce
space competition in the environment of *P. calziai* gen. et sp. nov. is provided by the presence of
small barnacle shells entombed below the base of larger individuals (Fig. 3E). A thick
multitubiferous structure also provides a certain degree of insulation from the strong thermal
380 excursions that are likely to occur in the intertidal zone (YIPP & SHIN 1990; BUCKERIDGE 2012;
WONG et al. 2014). Moreover, a thick shell represents a good defence against carnivorous
gastropods that are among the most common predators of barnacles (PALMER 1982;
BUCKERIDGE 2008; SANFORD & SWEZEY 2008; BUCKERIDGE & REEVES 2009; KLOMPMAKER et
al. 2015). In the intertidal zone carnivorous gastropods have a limited time to complete their
385 attack, because they need to succeed before the low tide. In such an environment, having an
armour that is able to resist drilling for a long amount of time may result in higher chances of
survival for the barnacle. Furthermore, predator gastropods preferentially attack barnacles along

the sutures between the plates, where the shell is thinner (PALMER 1982; KLOMPMAKER et al. 2015); consequently, narrow radii and a strong external ornamentation can hinder the ability of
390 gastropods to locate the vulnerable areas and increase the probabilities of dislodgement of the
predators during drilling (PALMER 1982). The combined action of a thick shell, narrow radii, and
heavy ornamentation would have made the drilling of the shells of *P. calziai* gen. et sp. nov. very
long and complicated. Not surprisingly, the examined specimens are punctuated by a large
number of failed predation holes (Figs 3B, 4C).

395 It must be stressed that, while almost all extant multitubiferous acorn barnacles live in the
intertidal zone, at least one of the extinct multitubiferous genera, *Fosterella*, was probably a mid-
shelf dweller. Although *P. calziai* gen. et sp. nov. and *Fosterella* are morphologically very
similar, remains of the latter genus have been found associated with molluscan assemblages that
indicate a subtidal setting at water depths comprised between 6 m and 400 m (BUCKERIDGE
400 2015). In turn, remains of *P. calziai* gen. et sp. nov. occur in the *Ct1a* and *Ct1b* facies
associations together with abundant ostreids and pectinids (COLETTI et al. 2018). Both facies
associations are interpreted as composed of material formed in a very shallow setting (COLETTI
et al. 2018; DI CELMA et al. 2018b). Furthermore, *P. calziai* and *Austromegabalanus carrioli* are
very common in the basal conglomerate of the *Ct1c* facies association (personal observation by
405 A.C., G.B., and M.U.). This deposit represents a transgressive lag overlying a wave-ravinement
surface, and as such, was deposited in a very shallow water setting (DI CELMA et al. 2019;
LANDINI et al. 2019). *Titobustillobalanus*, which also shares with *P. calziai* gen. et sp. nov. both
the multitubiferous structure and the vesicular sheath, has an extremely limited fossil record
consisting of a single occurrence from the upper Pleistocene of Atlantic Spain. However, it is

410 noteworthy that the holotype of this enigmatic genus was found in a prehistoric site together with
intertidal molluscs gathered by primitive humans (CARRIOL & ÁLVAREZ-FERNÁNDEZ 2015).

Since *Fosterella* and *Porobalanus* appeared only in the middle and early Pliocene,
respectively (BUCKERIDGE 2015), *P. calzai* gen. et sp. nov. is by far the oldest known
austromegabalanine provided with multitubiferous parietes. Compared to the condition observed
415 in the aforementioned genera, the multitubiferous arrangement of *P. calzai* gen. et sp. nov.
appears more irregular and chaotic. This may suggest that *P. calzai* gen. et sp. nov. could
represent the ancestor of the late Neogene multitubiferous genera of Austromegabalanini. In the
light of this hypothesis, the multitubiferous parietes of *P. calzai* gen. et sp. nov. would be
homologous to those of *Fosterella* and *Porobalanus*. However, this interpretation might be
420 challenged by the different position of the tube rows in the shells of these extinct taxa (i.e., the
tube rows take place between the inner and the outer lamina in shells of *P. calzai* gen. et sp.
nov., versus the multitubiferous condition of the outer lamina in shells of *Fosterella* and
Porobalanus). Furthermore, since the fossil record of multitubiferous Austromegabalanini
exhibits a wide gap (i.e., from the late early Miocene to the early Pliocene), it seems reasonable
425 to hypothesise that the multitubiferous condition might have emerged multiple times (and
therefore independently) in the evolutionary history of this tribe, with *Perumegabalanus* only
representing the first known attempt in this direction.

The discovery of a second austromegabalanine taxon (the first one being *A. carrioli*), in the
early Miocene of the Chilcatay Formation of Peru lends further support to the
430 palaeobiogeographical reconstruction proposed by COLLARETA et al. (2019). According to
COLLARETA et al. (2019), austromegabalanines originated and had their earliest diversification
phase at tropical latitudes, then dispersed at higher latitudes, and eventually survived only in the

Southern Hemisphere. Although the discovery of *P. calzai* gen. et sp. nov. does not represent a conclusive evidence in favour of this hypothesis, it emphasises a previously unknown diversity
435 of large-sized megabalanine barnacles in the warm-temperate early Miocene waters of the Pacific coast of South America.

5. Conclusions

A new large-sized balanid barnacle, *Perumegabalanus calzai* gen. et sp. nov., from the early
440 Miocene (19 to 17 Ma, Burdigalian) of the Chilcatay Formation (East Pisco Basin, southern Peru), is described and assigned to the megabalanine tribe Austromegabalanini. Among austromegabalanines, this new taxon is characterised by the presence of multitubiferous parietes, where the parietal tubes are irregularly partitioned by auxiliary septa, and by a vesicular sheath. Based on morphofunctional considerations and actualistic observations, the peculiar shell
445 architecture of *P. calzai* gen. et sp. nov. is here interpreted as well-suited for an existence in the intertidal zone. In the Chilcatay strata, two taxa of Austromegabalanini (i.e., *Austromegabalanus carrioli* and *P. calzai* gen. et sp. nov.) coexist, representing some of the geologically oldest records of austromegabalanines worldwide – an observation that strongly supports the hypothesis of a circumequatorial origin for this successful lineage of acorn barnacles.

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Figure captions

635 [Possible position for the eight figures: Fig. 1, possibly 2 columns wide, between lines 85 and
90; Fig. 2, possibly 2 columns wide, between lines 125 and 130; Fig. 3, possibly 2 columns wide,
between lines 173 and 174; Fig. 4, possibly 1 column wide, between lines 207 and 208; Fig. 5,
possibly 2 columns wide, between lines 230 and 235; Fig. 6, possibly 2 columns wide, between
lines 260 and 265; Fig. 7, possibly 2 columns wide, between lines 290 and 295; Fig. 8, possibly
640 2 columns wide, between lines 345 and 346; Fig. 9, possibly 2 columns wide, between lines 387
and 388]

Fig. 1. Geographical and stratigraphical framework of the study areas. **A)** Location of the
Ullujaya and Zamaca localities of the Ica Desert (East Pisco Basin), where the holotype and
645 referred specimens of the new taxon described in the present paper were found. **B)** Schematic
stratigraphic column of the sedimentary succession exposed at the study areas, with the main
subdivisions and units to which the present paper refer (not to scale). Abbreviations: ambr =
allomember; Fm = Formation. Redrawn and modified after DI CELMA et al. (2019).

650 **Fig. 2.** Generalised structure of a megabalanine barnacle shell. **A)** Model of a complete shell in
external view (modified after BUCKERIDGE 1983). **B)** Internal structure of the paries, the
adjoining radius, and the sheath as revealed by a transverse section above the basal margin
(the recognised features, including the presence of auxiliary septa and pores within the sheath,
as well as the emergence of two main rows of tubes indicated by numbers 1 and 2, are
655 modelled after the condition recognised in shells of the new megabalanine taxon described in

the present paper). **C)** Model of a complete shell in transverse section (modified after DAVADIE 1963) Abbreviations: R = rostrum; CL¹ = carinolatera¹; carinolatera² = CL²; C = carina. **D)** Close-up of an interlaminar figure, presenting the nomenclatural scheme utilised in the present work (after COLLARETA et al. 2019).

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Fig. 3. MUSM INV 624, *Perumegabalanus calzai* gen. et sp. nov., holotype specimen collected at Ullujaya (East Pisco Basin, southern Peru) in lower Miocene deposits of the Chilcatay Formation (*Ct1b* facies association of DI CELMA et al. 2018b). Adjacent to MUSM INV 624, there is a smaller conspecific specimen (consisting of two articulated compartments and a partial basal plate) (panels B–D). In addition, about 30 juvenile barnacle shells (?juveniles of *P. calzai* gen. et sp. nov.) are overgrown by MUSM INV 624 (panel E). **A)** Rostral view. **B)** Left lateral view, the transparent arrow head indicates a failed predation hole observable on the plate. **C)** Carinal view. **D)** Apical view. **E)** Basal view.

670 **Fig. 4.** Macroscopic features of the shell of *Perumegabalanus calzai* gen. et sp. nov. **A)** MUSM INV 626, a cluster of four shells (two complete and two incomplete), preserved as gypsum casts, from undifferentiated Chilcatay strata exposed at Zamaca. **B)** Apical view of MUSM INV 625, an almost complete shell, with a largely worn out external aspect, from the *Ct1a* Chilcatay strata exposed at Zamaca. Abbreviations: R = rostrum; CL¹ = carinolatera¹; carinolatera² = CL²; C = carina. **C)** Lateral view of MUSM INV 625, exhibiting almost completely eroded bulging protuberances (thin black arrows) and a drill hole of predatory origin (black arrowhead). **D)** Internal view of MUSM INV 627, an isolated carina from

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undifferentiated Chilcatay strata exposed at Zamaca, displaying the sutural edge of an ala (thin black arrow) and the vesicular structure of the sheath (black arrowhead).

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Fig. 5. Photomicrographs of the shell of *Perumegabalanus calzai* gen. et sp. nov., detailing the anatomy of the shell structures that allow for articulation between adjacent compartments. **A)** SEM image of the sutural edges of an ala of MUSM INV 627, showing the presence of secondary denticles on the upper side. **B)** Transverse thick section through a radius of MUSM INV 631, an almost complete shell from the *Ct2a* Chilcatay strata exposed at Zamaca, exhibiting well-developed tubes (SEM image). **C)** Transverse thin section through a radius of MUSM INV 628, an almost complete shell from the *Ct1b* Chilcatay strata exposed at Zamaca, exhibiting well-developed tubes (OM image). **D)** Transverse thin section through a wall plate of MUSM INV 628, sectioned above the base of the sheath, showing the lateral margin of sheath extending over the adjacent ala and the tubiferous condition of the radii, indicated by the black arrowhead (OM image).

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Fig. 6. Photomicrographs of the shell of *Perumegabalanus calzai* gen. et sp. nov., detailing the internal architecture of the mural and basal plates. **A-B)** Transverse thin sections through two wall plates of MUSM INV 628, sectioned above the base of the sheath, displaying vesicles within the latter structure (OM images). **C)** Thin section through the basal plate MUSM INV 629, an almost complete shell from the *Ct1a* Chilcatay strata exposed at Ullujaya (OM image). **D)** Transverse thin section through a wall plate of MUSM INV 628, sectioned above the base of the sheath, whose paries exhibits a multitubiferous condition achieved by

695

700 partitioning of the parietal tubes by the auxiliary septa, one of which is indicated by a black
arrowhead (OM image).

Fig. 7. Photomicrographs of the shell of *Perumegabalanus calzai* gen. et sp. nov., depicting the
auxiliary septa and partial secondary infills of the parietal tubes. **A)** Transverse thick section
705 through a wall plate of MUSM INV 631, an almost complete shell from the *Ct2a* Chilcatay
strata exposed at Zamaca, showing the presence of auxiliary septa, indicated by the white
arrowheads, within the parietal tubes (SEM image). **B)** Close-up of the pattern of the structure
of one of the auxiliary septa depicted in the previous panel (SEM image). **C)** Transverse thin
section through a wall plate of MUSM INV 628, sectioned close to the apex of the shell,
710 showing the presence of auxiliary septa and partial secondary infills (black arrowheads)
within the parietal tubes (OM image). **D)** Transverse thin sections through a wall plate of
MUSM INV 628, sectioned above the base of the sheath, showing: *i*) the apparent duplication
of the inner lamina that originates from the local organization of the auxiliary septa to form a
sort of wall that runs orthogonal to the longitudinal septa (black arrowheads); and *ii*) the
715 consequent emergence of two main rows of tubes, an inner one and an outer one, indicated by
the numbers 1 and 2, respectively (OM image).

Fig. 8. Photomicrographs of the shell of *Perumegabalanus calzai* gen. et sp. nov., detailing the
morphology and variability of the interlaminar structures. **A)** Transverse thin section through
720 a wall plate of MUSM INV 630, an almost complete shell from the *Ct1a* Chilcatay strata
exposed at Ullujaya, sectioned near the base of the shell, showing the interlaminar figures,
with secondary abutments (thin black arrows), mantled by the inner lamina (white

arrowhead), and the branching of a longitudinal septum (black arrowhead) (OM image). **B)** Transverse thin section through a wall plate of MUSM INV 628, sectioned above the base of the sheath, showing the interlaminar figures, the inner lamina, characterised by faint growth bands (white arrowhead), and the sheath (black arrowhead) (OM image). **C)** Transverse thin section through a wall plate of MUSM INV 628, sectioned close to the apex of the shell, showing the interlaminar figures, the partial secondary infills of the longitudinal septa (black arrowheads), and the inner lamina (white arrowhead) (OM image). **D)** Transverse thin section through a wall plate of MUSM INV 628, sectioned close to the apex of the shell, close-up of an interlaminar figure, showing the asymmetrical tertiary processes (white arrowhead) whose distal portions form whorl-like structures (black arrowheads) (OM image).

Fig. 9. Transverse thick sections of *Fosterella tubulata* and *Perumegabalanus calzai* gen. et sp. nov. depicting the structure of the multitubiferous paries and vesicular sheath. **A)** Wall plate from an uncatalogued specimen of *F. tubulata* exhibiting the regularly arranged rows of small supplementary parietal tubes that perforate the outer lamina (black arrowhead), the primary longitudinal tubes (white arrowhead), and the ovate pores within the sheath (black arrows); the outer boundary of the sheath is marked by a thick grey line (OM image). **B)** Wall plate from a specimen of *P. calzai* gen. et sp. nov. (MUSM INV 631) showing the longitudinal tubes that are irregularly partitioned by auxiliary septa (white arrowhead) and the large irregular pores perforating the sheath (black arrows) (SEM image).

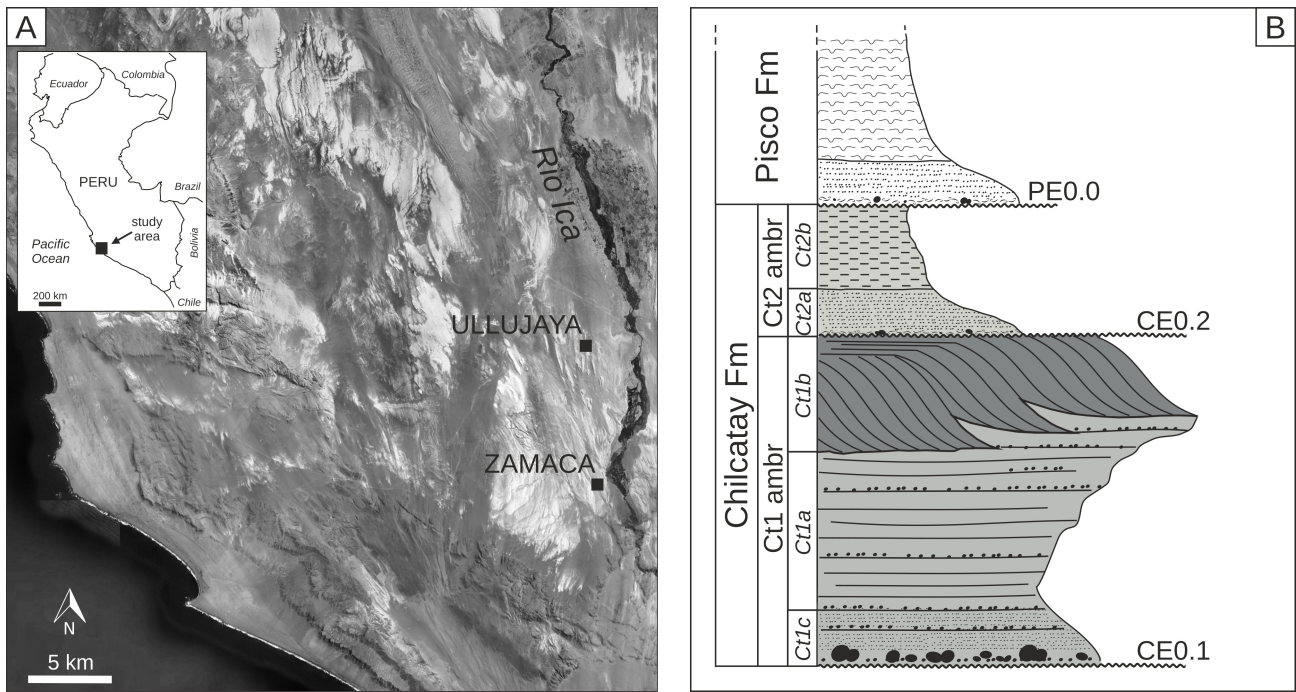


Figure 1

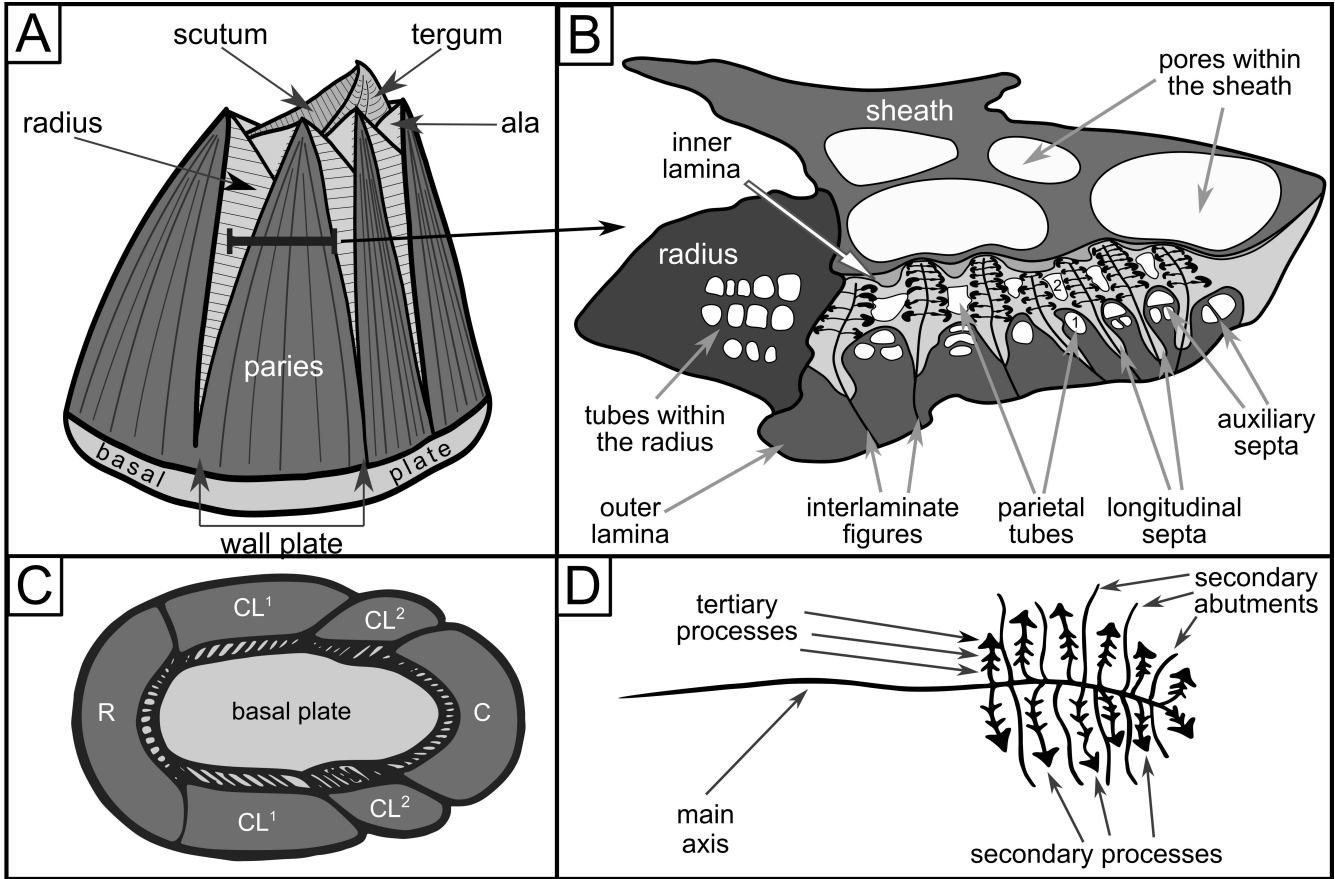


Figure 2

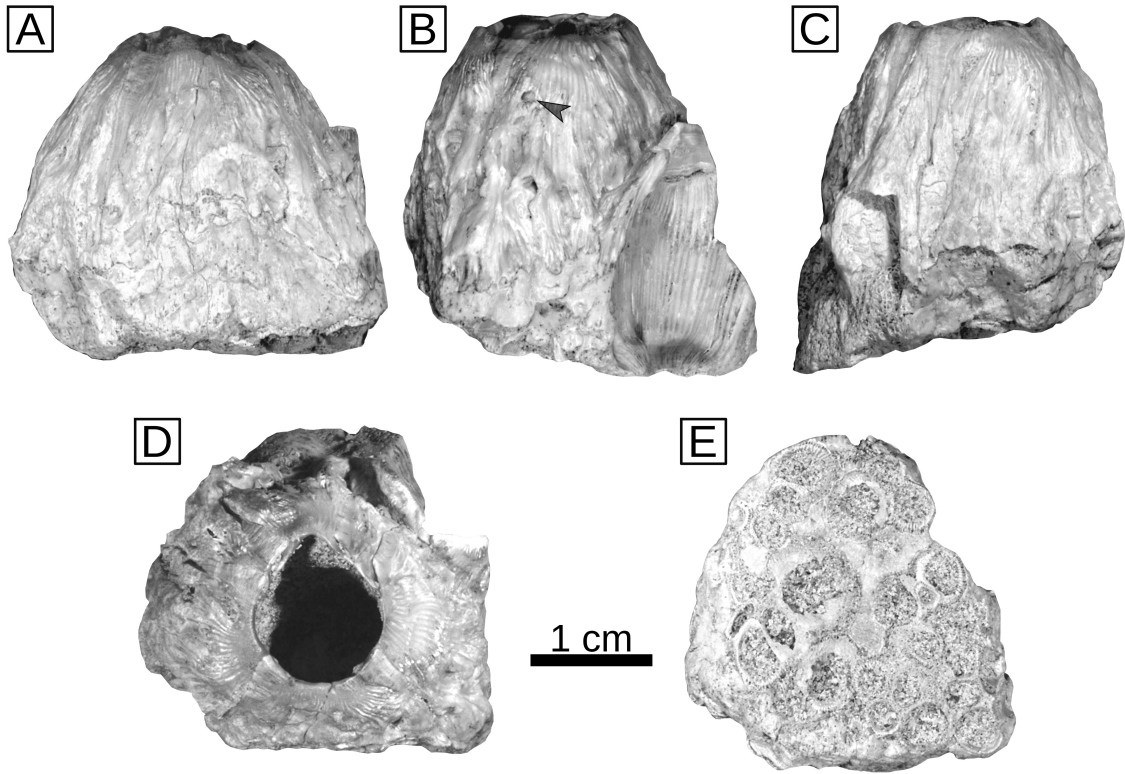


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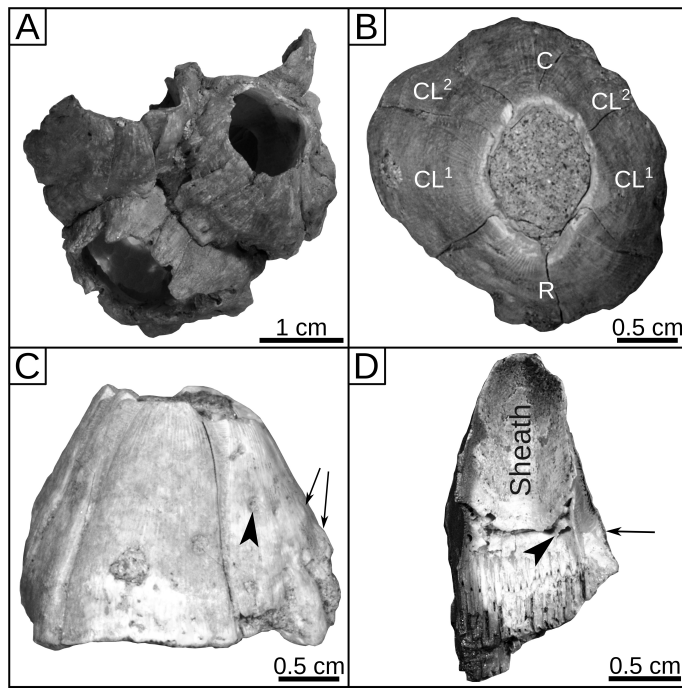


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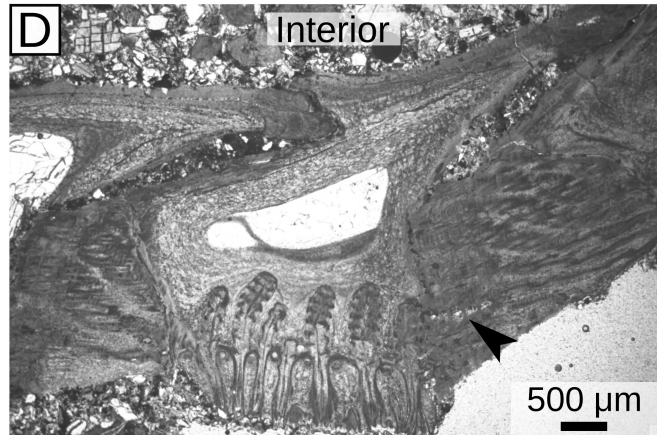
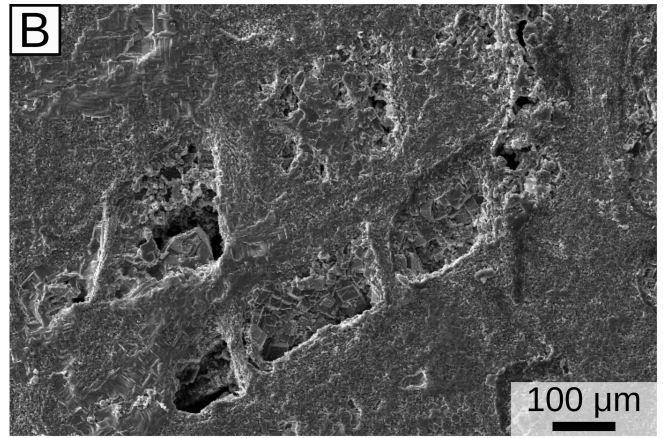
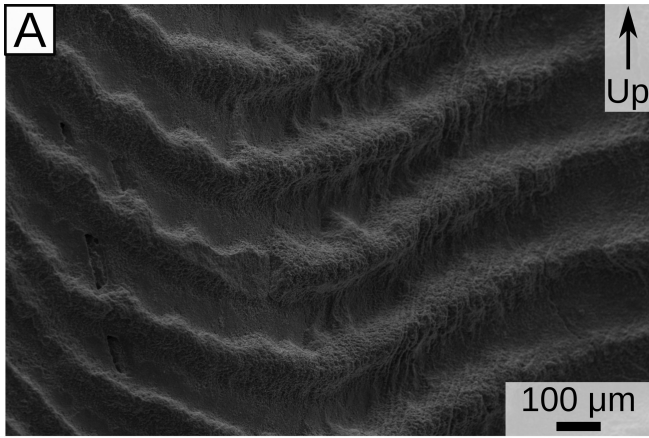


Figure 5

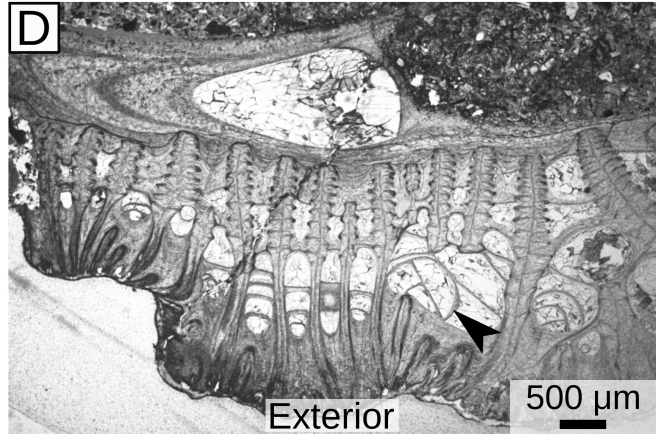
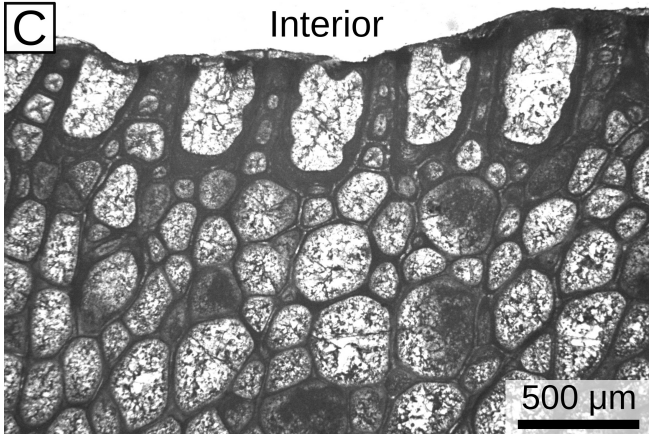
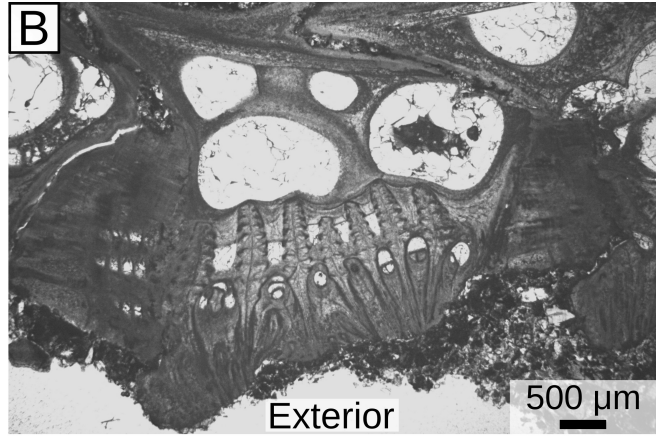
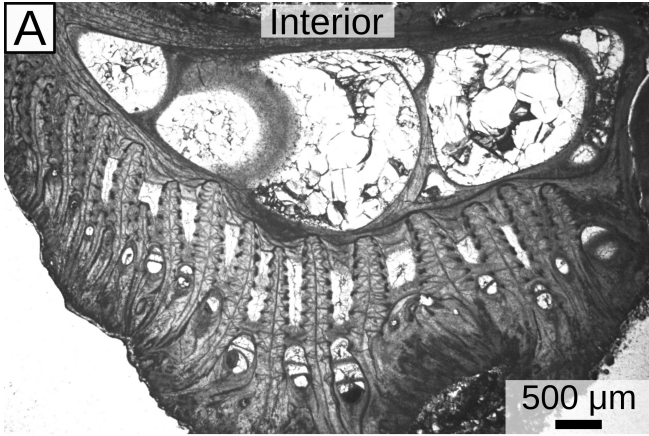


Figure 6

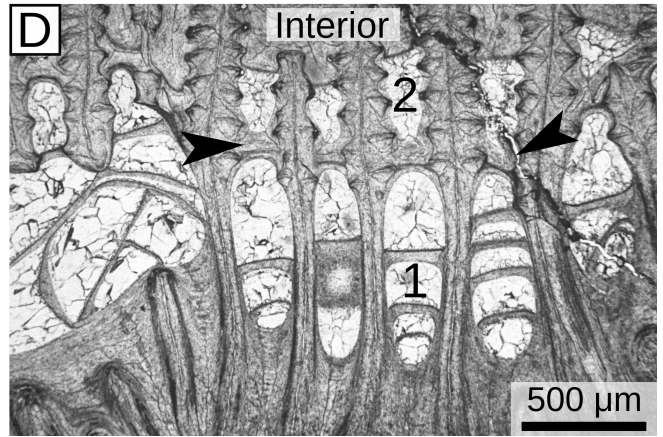
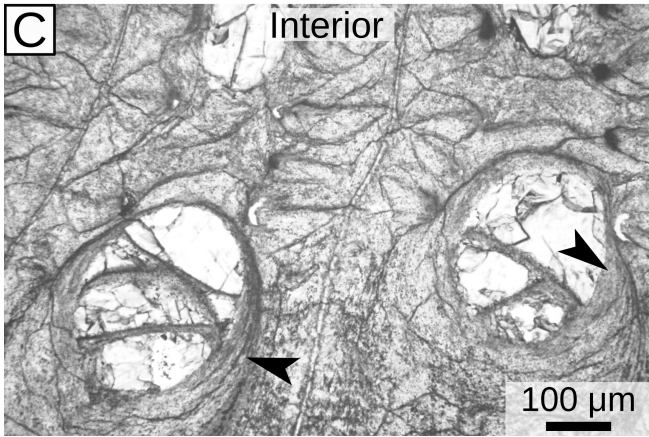
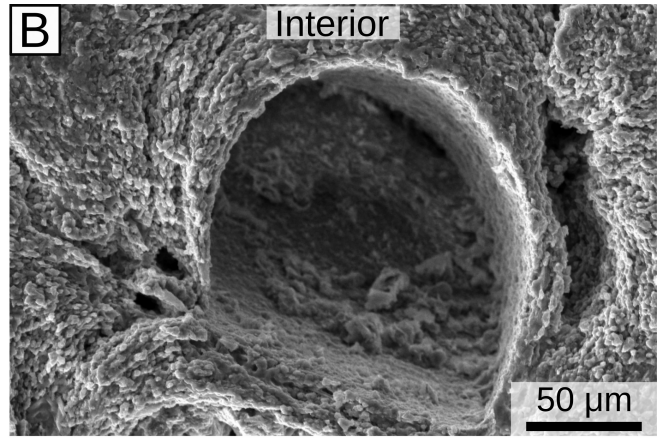
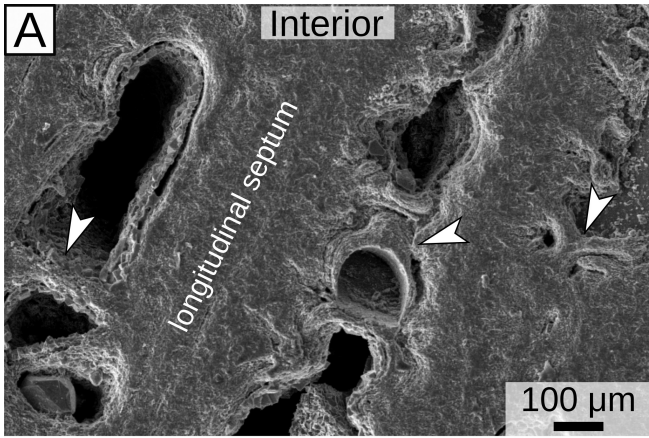


Figure 7

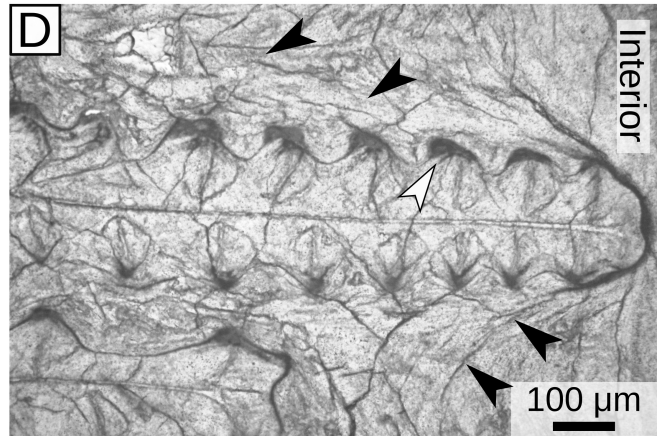
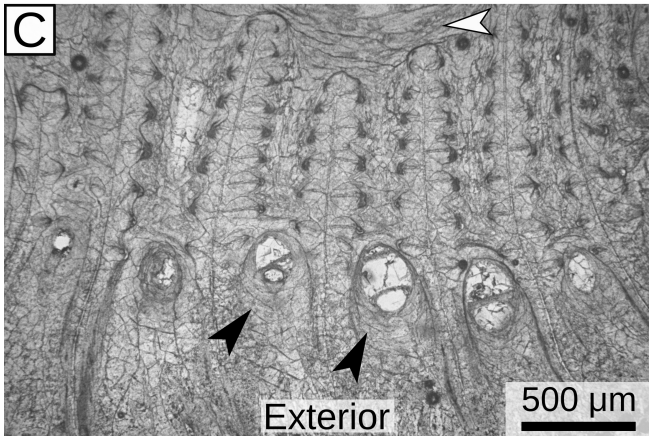
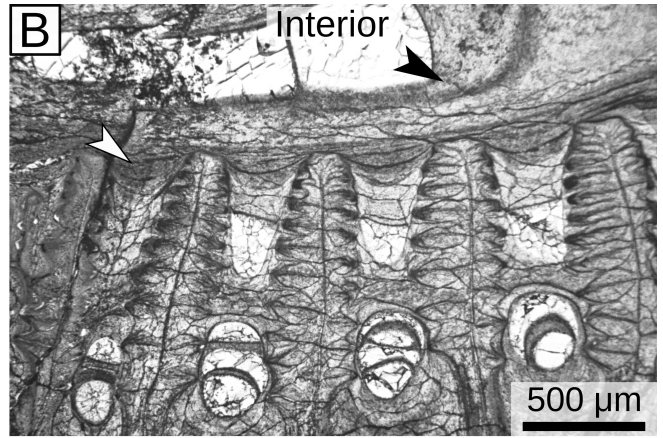
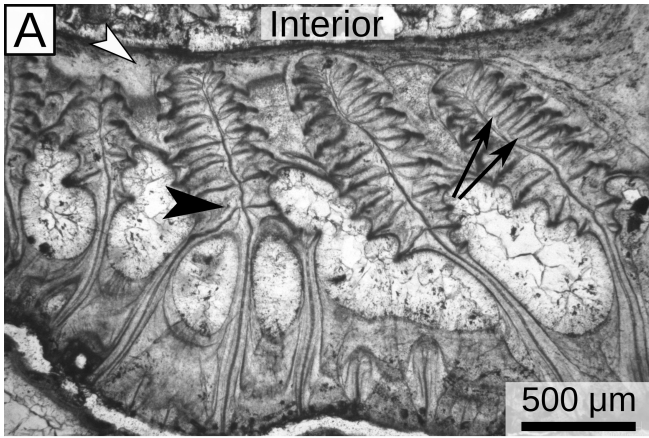


Figure 8

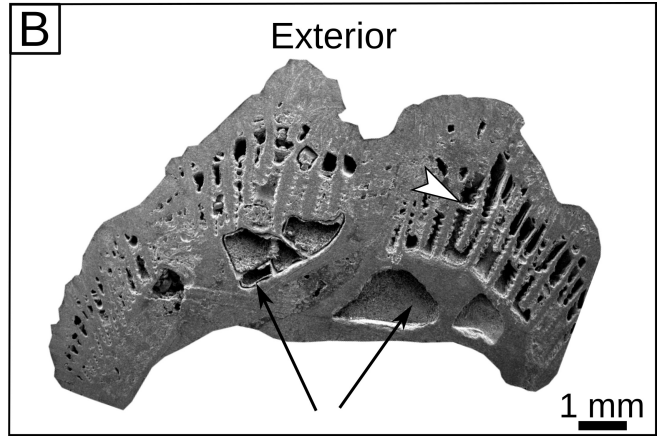
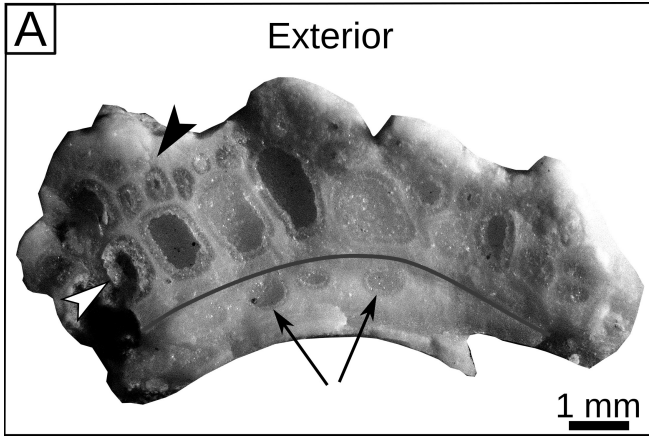


Figure 9