Fossilia, Volume 2020: 13-15

Lower Miocene (Burdigalian) acorn barnacles (Cirripedia: Sessilia) from the Chilcatay Formation of southern Peru: palaeoenvironmental, palaeobiogeographical and evolutionary significance

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Keywords:
Austromegabalanini;
Austromegabalanus carrioli*;*
barnamol;
Perumegabalanus calziai*;*
East Pisco Basin.

Bullet-Points Abstract

- We report on a recently described barnacle-rich facies from the East Pisco Basin.
- Barnacles are associated with an abundant, mollusc-rich hard-substrate biota (i.e., a barnamol).
- The Chilcatay barnacle facies depicts a very shallow, high-energy, nearshore assemblage.
- Two new species of austromegabalanines have been described from this Burdigalian assemblage.
- Austromegabalanines likely originated at low latitudes and in warm marginal-marine waters.

Introduction and Setting

In contrast to most crustaceans, cirripedes have adopted a sessile lifestyle. By doing this, they traded off mobility (at least autonomously) for the advantage of settling in a favourable location. The main disadvantages of this strategy are the inability to flee from predators and to rapidly relocate elsewhere if environmental conditions deteriorate or become unsuitable. Thus, cirripedes evolved *ad hoc* solutions to cope with the disadvantages of a sessile lifestyle (see e.g. Newman, 1996 for a general overview). The earliest confirmed cirripede is of Silurian age (Wills, 1963), while the earliest known modern neobalanoform is of Late Cretaceous age (Kočí et al., 2017). Following the Cretaceous-Tertiary extinction event, opportunistic acorn barnacles rapidly diversified and, by the Neogene, they had become a common component of continental-shelf benthic assemblages (Buckeridge, 1983). They are frequently found at middle and high latitudes, but they can also thrive at low latitudes, especially in nutrient-rich environments. The aim of this ongoing research effort is to investigate, from both palaeoenvironmental and palaeobiological perspectives, a recently discovered lower Miocene barnacle facies from southern Peru, in anticipation that the material will shed light on a key turning point of barnacle history: the early Neogene.

Geological Setting

The study area is located in the Ica Desert of southern Peru, 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 Eocene to Pliocene stratigraphic units – including the upper Oligocene-lower Miocene Chilcatay Formation – which are bounded by regionally extensive unconformities. As such, they represent transgressive sequences in the basin (Di Celma et al., 2017). Furthermore, intraformational unconformities are also present. The base of each sequence consists of coarse-grained, shallow-water deposits testifying the early phases of transgression. These horizons are commonly rich in barnacles, especially those marking the base of the Chilcatay Formation. At the study sites of Ullujaya and Zamaca, the Chilcatay succession has been resolved

Corresponding autor's contact: alberto.collareta@unipi.it
How to cite: Collareta et al. (2020). Lower Miocene (Burdigalian) acorn barnacles (Cirripedia: Sessilia) from the Chilcatay Formation of southern Peru: palaeoenvironmental, palaeobiogeographical and evolutionary significance. *Fossilia*, Volume 2020: 13-15. https://doi.org/10.32774/FosRepPal.2020.0604
FOSSILIA - Reports in Palaeontology

into two smaller packages of strata (allomembers) each separated by an intraformational unconformity. The lower package (i.e., the Ct1 allomember) comprises a massive boulder-bearing sandstone that alternates with conglomerates (*Ct1c* facies association, comprising the base of Ct1), a sub-horizontal package of medium- to fine-grained sandstones and siltstones punctuated by beds of coarse-grained sandstones and conglomerates (i.e, the *Ct1a* facies association), and an overlying stack of clinoformed beds of coarse-grained mixed bioclastic calcarenites (*Ct1b* facies association). The overlying Ct2 allomember consists of massive and intensely bioturbated sandstones (*Ct2a* facies association) changing upwards into massive siltstones (*Ct2b* facies association).

RESULTS AND DISCUSSION

Invertebrate macrofossils from the Chilcatay strata exposed at Ullujaya and Zamaca include barnacles (belonging to at least three taxa), as well as echinoids, bivalves, calcareous tubeworms and crabs (Di Celma et al., 2018). At the study sites, the Chilcatay deposits also contain abundant remains of marine vertebrates, mostly cetaceans and elasmobranchs, with subordinate turtles and bony fish (Bianucci et al., 2018). Biostratigraphic and geochronological data indicate that the Chilcatay strata cropping out at Ullujaya and Zamaca were deposited during the Burdigalian, between 19 and 17 Ma (Di Celma et al., 2018). The Chilcatay barnacle facies depicts a very shallow, high-energy, nearshore assemblage where barnacles were associated with an abundant, mollusc-rich hard-substrate biota (i.e., a barnamol) (Coletti et al., 2018). This deposit represents a prototype of most modern barnacle facies and differs from rarer barnacle-rich assemblages (e.g. barnacle-coralline algae associations, barnalgal) that are generally related to deeper settings (Coletti et al., 2018).

So far, of the three barnacle taxa recognised from the Chilcatay Formation, two have been studied in depth, and both belong to the balanid tribe Austromegabalanini (Newman, 1979), whose living members (assigned to the genera *Austromegabalanus* and *Notomegabalanus*) are characteristic of temperate and cold waters of the Southern Hemisphere. The most abundant austromegabalanine remains from the Chilcatay belong to the newly established species *Austromegabalanus carrioli* (Collareta et al., 2019). Among Austromegabalanini, this species is defined by a peculiar architecture of the interlaminate figures, whose asymmetrical and whorl-shaped tertiary processes have distal portions that seemingly connect adjacent interlaminate figures (Fig. 1A-C). As with the extant Peruvian species *Austromegabalanus psittacus*, *A. carrioli* inhabited very shallow-water littoral and subtidal shelf settings; however, differing from all extant and most extinct austromegabalanines, *A. carrioli* inhabited a warm-temperate environment. Another taxon of austromegabalanines, *Perumegabalanus calziai*, is characterised by the presence of thick, ornamented, multitubiferous parietes, where the parietal tubes are irregularly partitioned by auxiliary septa, and by a vesicular sheath (Coletti et al., 2019) (Fig. 1D-F). Based on morphofunctional considerations, the peculiar shell architecture of *P. calziai* is here interpreted as well suited for an existence in the intertidal zone. Indeed, a thick multitubiferous structure provides a certain degree of insulation from the strong thermal excursions that are likely to occur in the intertidal zone. Moreover, the combined action of a thick shell, narrow radii, and heavy ornamentation would have made the drilling of the shells of *P. calziai* long and complicated – a good defence against drilling carnivorous gastropods that are among the most common predators of barnacles in the intertidal band. Not surprisingly, the examined specimens are commonly punctuated failed predation holes referred to the ichnogenus *Oichnus*.

CONCLUDING REMARKS

The study of the lower Miocene barnacle-rich facies from Ullujaya demonstrates that barnacle palaeontology can be a powerful tool for palaeoenvironmental reconstruction. The discovery of two austromegabalanine taxa in the lower Miocene of the Chilcatay Formation of Peru represents one of the geologically earliest records of Austromegabalanini worldwide and suggests that the austromegabalanines originated and had their earliest diversification phase at tropical latitudes, then dispersed at higher latitudes, and eventually survived only in the Southern Hemisphere. Not least, our discoveries emphasise a previously unknown diversity of large-sized balanid barnacles in the warm-temperate early Miocene waters of the Pacific coast of South America.

ACKNOWLEDGEMENTS

We are grateful to Giovanni Bianucci, Claudio Di Celma, Elisa Malinverno, and Mario Urbina. The results and intrepretations reported herein have been published in an unabridged way by Coletti et al. (2018, 2019), Di Celma et al. (2018), and Collareta et al. (2019).

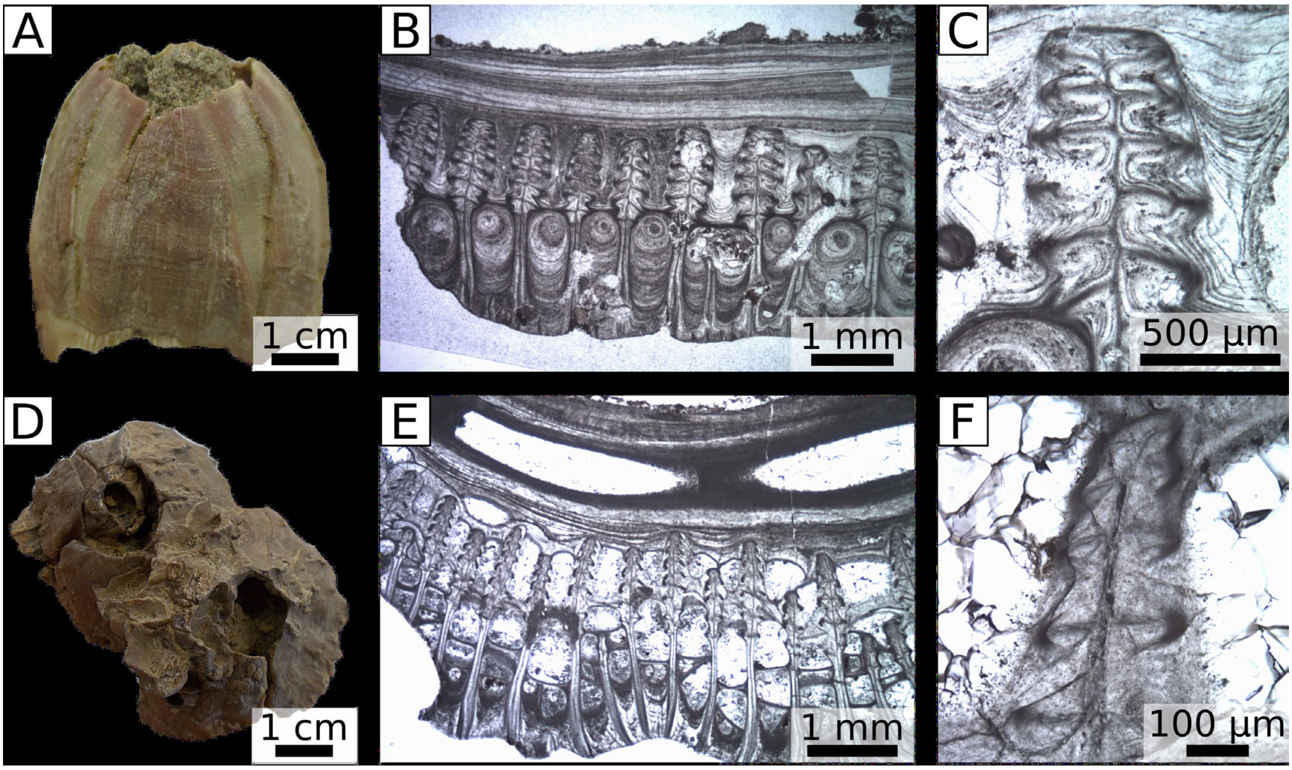

Fig. 1. Austromegabalanine barnacles from the barnacle facies of Ullujaya (Peru). **A**. *Austromegabalanus carrioli*, complete shell. **B**. *Austromegabalanus carrioli*, interlaminate figures. **C**. *Austromegabalanus carrioli*, detail of an interlaminate figure. **D**. *Perumegabalanus calziai*, complete shell. **E**. *Perumegabalanus calziai*, interlaminate figures. **F**. *Perumegabalanus calziai*, detail of an interlaminate figure. Modified after Coletti et al. (2018).

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