Verruca punica, a new species of verrucomorph barnacle (Crustacea, Cirripedia, Thoracica) from the Lower Danian (Palaeocene) of Tunisia

JOHN S. BUCKERIDGE1, JOHN W. M. JAGT2 & ROBERT P. SPEIJER3

1Earth & Oceanic Systems Research Group, RMIT University, Melbourne, VIC 3001, Victoria, Australia.
E-mail: john.buckeridge@rmit.edu.au
2Natuurhistorisch Museum Maastricht (SCZ), de Bosquetplein 6-7, NL-6211 KJ Maastricht, the Netherlands.
E-mail: john.jagt@maastricht.nl
3Department of Earth and Environmental Sciences, K.U.Leuven, Celestijnenlaan 200E, B-3001 Leuven, Belgium.
E-mail: robert.speijer@kuleuven.be

Abstract

The discovery of a near-complete shell wall of a small verrucid barnacle from the Lower Danian (Palaeocene) portion of the El Haria Formation as exposed in the El Kef area (northwest Tunisia), permits its description as a new species with characters that, although conforming primarily to Verruca sensu stricto, show some similarities to Altiverruca Pilsbry, 1916, a genus that is not yet known from the fossil record. The present material extends the known geographic distribution of fossil verrucids, and constitutes one of the earliest species of Verruca to be documented subsequent to the Cretaceous/Palaeogene (K/Pg) boundary mass extinction event.

Key words: Barnacles, Verrucomorpha, Verruca, Tunisia, Danian, new species

Introduction

The verrucomorph barnacles are a group of sessile crustaceans that possess asymmetrical shells. The earliest known representatives, i.e., the proverrucid genera Proverruca Withers, 1914 (Cenomanian–Upper Maastrichtian of northwest Europe; see Withers, 1935: 324–337, text-figs. 33–36; pl. 43, figs. 1–17; pl. 44, figs. 1–8; pl. 45, figs. 1–6), and Eoverruca Withers, 1935 (Upper Santonian–Upper Campanian of England and southern Poland; see Withers, 1935: 338–340, text-figs. 37, 38; pl. 44, figs. 9–18; Jagt et al., 2008, figs. 2, 3), had a shell wall comprising carina, rostrum, fixed tergum and fixed scutum plus two latera. Verruca Schumacher, 1817 is characterised by a shell wall comprising only four plates, the latera having been lost. Although the first records are from the Santonian of Western Australia (Buckeridge, 1983), Verruca had reached a wide geographic distribution by the late Campanian-Maastrichtian, being known from Europe and Western Australia. The present record is one of the earliest of verrucid barnacles following Cretaceous-Palaeogene (K/Pg) boundary perturbations, and demonstrates that such were amongst the first taxa to recover from the crisis. Another record is that of material referred to as V. cf. prisca Bosquet, 1854 from the lowermost two metres of the Danian portion of the Scaglia Rossa Formation in the Forada creek section, Prevenetian Alps, northeast Italy (see Giusberti et al., 2005: 459, fig. 1; pl. 1, figs. 6–10; pl. 2, figs. 8, 9). Specimens of slightly younger (i.e., Middle Danian) age from Fakse (Jylland, eastern Denmark) were originally considered to represent a distinct species, V. steenstrupi, by Brünnich Nielsen (1912) (see also Donovan & Jakobsen, 2004, fig. 3c, d, as V. prisca?). Withers (1935: 341) was of the opinion that this was synonymous with V. prisca, but in the absence of moveable rostra and scuta this cannot be demonstrated beyond doubt. For the time being, V. steenstrupi is here considered to be a valid species (see Fig. 2, Table 1).
The material studied was handpicked from a sample collected from the lowermost Palaeocene in the El Kef section (northwest Tunisia; Fig. 1), where the global boundary stratotype section and point (GSSP) of the Danian Stage (and thus of the Palaeocene/Palaeogene) is situated (Molina et al., 2006).

**Institutional abbreviations:** NHMM, Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands; NMV, Museum Victoria, Melbourne, Australia.

### TABLE 1. Fossil species assigned to *Verruca sensu stricto* described to date, arranged alphabetically (data from Brünich Nielsen, 1912; Steinmann in Wilckens, 1921; Withers, 1935; Kruizinga, 1939; Alekseev, 1974, 1979; Buckeridge, 1983, 1985, 1997; Buckeridge & Finger, 2001; Donovan & Jakobsen, 2004; Young et al., 2003 and Koike et al., 2006)

<table>
<thead>
<tr>
<th>Name</th>
<th>Stratigraphic range</th>
<th>Localities</th>
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<tbody>
<tr>
<td>V. alaskana</td>
<td>Pliocene</td>
<td>Alaska</td>
</tr>
<tr>
<td>V. digitali Buckeridge</td>
<td>Upper Miocene</td>
<td>California</td>
</tr>
<tr>
<td>in Buckeridge &amp; Finger, 2001</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. koikei</td>
<td>Lower Pliocene</td>
<td>Japan</td>
</tr>
<tr>
<td>in Koike et al., 2006</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. nuciformis</td>
<td>Lower Eocene-Lower Miocene</td>
<td>New Zealand</td>
</tr>
<tr>
<td>Buckeridge, 1983</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. punicia</td>
<td>Upper Cretaceous</td>
<td>northwest Europe</td>
</tr>
<tr>
<td>Buckeridge &amp; Jagt, sp. nov.</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. pusilla Bosquet, 1857</td>
<td>Upper Maastrichtian</td>
<td>Belgium, the Netherlands</td>
</tr>
<tr>
<td>V. rocana Steinmann in Wilckens, 1921</td>
<td>Maastrichtian</td>
<td>Argentina</td>
</tr>
<tr>
<td>V. spengleri Darwin, 1854</td>
<td>Plio-Pleistocene</td>
<td>Mediterranean</td>
</tr>
<tr>
<td>V. steenstrupi</td>
<td>Middle Danian</td>
<td>Denmark</td>
</tr>
<tr>
<td>Brünich Nielsen, 1912</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. stroemia (O.F. Müller, 1776)</td>
<td>Pliocene-Recent</td>
<td>North Atlantic, northwest Europe</td>
</tr>
<tr>
<td>V. t. chatheca</td>
<td>Upper Palaeocene-Lower Eocene</td>
<td>Chatham Islands</td>
</tr>
<tr>
<td>Buckeridge, 1983</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. t. tasmanica</td>
<td>Upper Cretaceous-Lower Oligocene</td>
<td>Australia, New Zealand</td>
</tr>
<tr>
<td>Buckeridge, 1983</td>
<td></td>
<td></td>
</tr>
<tr>
<td>V. veneta Carriol &amp; Dieni, 2005</td>
<td>Upper Eocene</td>
<td>northeast Italy</td>
</tr>
<tr>
<td>V. withersi Kruizinga, 1939</td>
<td>Lower Pleistocene</td>
<td>Sumba, Indonesia</td>
</tr>
</tbody>
</table>

**NOTES:** As demonstrated by Jagt & Buckeridge (2005), *V. withersi* sensu Schram & Newman, 1980 is not a cirripede, while *V. withersi* sensu Kruizinga (1939) is a valid species of the *cookei* group. The type material of *V. rocana* is from the so-called ‘Roca Beds’ along the Río Negro in Argentina; although Withers (1935: 347) assigned an early Palaeocene (Danian) age to this, it is perhaps better interpreted as Late Maastrichtian following Casadío et al. (2005), who confirmed the diachronous nature of the Jaguël and Roca formations. In the type area of the Maastrichtian Stage (southeast Netherlands, northeast Belgium), *V. prisca* ranges from the Upper Campanian to the Upper Maastrichtian, while *V. pusilla* appears restricted to the Upper Maastrichtian. The type material of both taxa has recently been traced (Jagt, 2004) and will be described in detail elsewhere (Jagt, in prep.).

### Systematics

**Subclass Cirripedia Burmeister, 1834**

**Superorder Thoracica Darwin, 1854**

**Remarks.** Buckeridge & Newman (2006) have recently revised the systematics of the Thoracica, and proposed four very distinct orders. Within the Sessilia, the suborder Verrucomorpha was demonstrated to have had a scalpelliform ancestor, arising from this order via the Brachylepadomorpha Withers, 1923 during the Middle to Late Jurassic.
Order Sessilia Lamarck, 1818

Suborder Verrucomorpha Pilsbry, 1916

Family Verrucidae Darwin, 1854

Diagnosis. Wall asymmetric, comprising four immovable dissimilar calcareous plates: carina, rostrum, scutum and tergum; second scutum and tergum together form a movable operculum; basis membranous or calcareous.

Remarks. In addition to the Verrucidae, the Verrucomorpha comprises two other families, the earliest of which, the Proverrucidae Newman, 1989 (Newman and Hessler, 1989), (Cenomanian-Upper Maastrichtian), is characterised by the presence of extra (lateral) plates in the shell wall, and the extant Neoverrucidae Newman in Newman & Hessler, 1989, which is a true ‘link’ with early non-verrucomorph barnacles, as it retains several basal whorls of imbricating plates, demonstrating phyletic proximity to a scalpelliform ancestor (Newman, 2000; Buckeridge & Newman, 2006).

Genus Verruca Schumacher, 1817

Diagnosis. Verrucids with shell depressed; apices of rostrum and carina marginal; operculum parallel to base; myophore well developed, projecting parallel to base.

Type species. Lepas stroemia Müller, 1776, by original designation.

Distribution. Late Cretaceous (Santonian) to Recent, cosmopolitan.

Remarks. Verruca is a widely distributed genus (Fig. 2; Table 1), although it generally is not a common fossil (with some notable exceptions of closely spaced individuals on pinnid and ostreid bivalves as well as on gastropods, marine algae, and bioimmured complete individuals in the attachment area of ostreid and gryphaeid bivalves (see Withers, 1935; Jagt, 1989; Jagt & Collins, 1989; Vervoenen, 1994; Buckeridge and Finger, 2001; Marquet, 2005)). This probably reflects the fragility of the shells, and the likelihood that they will quickly disarticulate and disperse upon death. The earliest records are from the Upper Cretaceous (Santonian to Maastrichtian) and Lower Palaeocene (Danian) of northwest Europe, southern Argentina and Western Australia (see Table 1). Not surprisingly, these show the greatest similarity to the present taxon from Tunisia. Buckeridge & Finger (2001), Carriol & Dieni (2005) and Koike et al. (2006) added three Cenozoic species of Verruca, from California, northeast Italy and Japan, respectively, bringing the total of known fossil species (and subspecies) to 15 (Table 1). Young (1998) reviewed the Verrucidae, but did not take fossils into account.

The recognition of Verruca sensu stricto as the most generalised form within the Verrucidae is thus reflected in the fossil record, as it has not only the earliest appearance datums, but also the greatest geographic distribution. Of the remaining verrucid genera, only Metaverruca Pilsbry, 1916 and possibly also Costatoverruca Young, 1998 are known as fossil, and these range from the Upper Eocene to Recent (Buckeridge, 1983; Carriol & Dieni, 2005).

Verruca punica Buckeridge & Jagt, sp. nov.
(Figs 3A–G; 4A–R)

Type material. Holotype NHMM 2007 094, a specimen lacking moveable scutum and moveable tergum; basis unknown; height 1.1 mm, length 2 mm, width 1.2 mm. Paratypes NHMM 2007 095, 2007 096, 2007 097 and 2007 100, and NMV P314992.

Material examined. In addition to the types (see above), sample AFN 601 yielded four moveable terga, one moveable scutum, a single fixed scutum, one fixed tergum, a single carina plus >20 incomplete plates (NHMM 2007 098, 2007 099, 2007 101 and 2007 102a), all handpicked by one of us (RPS) in the Spring of
1988 from washed microfossil residues of the AFN sample set collected in 1982 by a crew of the Cretaceous-Palaeogene Boundary Working Group at El Haria, some 5 km southwest of El Kef (Smit et al., 1997).

**FIGURE 1.** Location of the El Haria section, near El Kef (northwest Tunisia), the provenance of the types of *Verruca punica* Buckeridge & Jagt, sp. nov.

**Diagnosis.** Moderately small *Verruca*, elongate, with a relatively smooth shell and large pentangular orifice; moveable tergum quadrangular, carinal margin slightly longer than basal margin, with prominent apico-basal rib extending beyond the basal margin, and two secondary articular ribs, upper rib upwardly inflected; moveable scutum with a prominent, apico-basal rib, and a secondary rib on the upper margin.

**Description.** Shell small, slightly compressed laterally; apex of carina produced so that carina lies beneath the operculum that is subparallel to the base (Fig. 3C); longitudinal ribbing very weak to imperceptible but with clearly formed transverse growth striae; orifice large, pentangular; rostrum broad, comprising approximately one third of shell wall, two ribs interlocking with carina, one with a quadrangular fixed scutum; fixed tergum narrow (width less than one third height); moveable tergum subrhomboidal, first (= upper) articular rib raised, rounded and slightly produced at scutal margin; second articular rib slightly depressed, closer to apico-basal (primary) rib than to upper, protrudent with other ribs to produce sinuous scutal margin; apico-basal rib rounded in section, elevated, gently arcuate, concave on upper margin, widening towards base, where it extends beyond basal margin by a distance approximately half the basal width; upper carinal angle c. 90°; carinal-basal angle c. 110°, upper scutal angle c. 80°; internal surface with slight apical depression for adductor muscle attachment, otherwise weakly undulating. Moveable scutum triangular, almost twice as long as wide, exterior with a sharply raised apico-articular ridge which has a beaded appearance due to intersection with transverse growth ridges; secondary rib on movable scutum on a gently concave tergal margin; basal margin very slightly convex, occludent margin broadly arcuate; apical angle c. 50°; basi-rostral angle c. 90°, basi-tergal angle c. 120°; external apico-basal striae on both the moveable tergum and scutum is either absent or very weak.

**Etymology.** In allusion to the Punic wars (264–241 BC, 218–201 BC and 149–146 BC), in which Rome crushed Carthaginian power, and obliterated Carthage, on the coast of northern Tunisia.
FIGURE 2. Distribution of fossil species assigned to the genus *Verruca* Schumacher, 1817 (sensu stricto); see Table 1 for details.

**Geographic and stratigraphic setting.** Sample AFN 601 was taken 15 m above the K/Pg boundary in the so-called KS section at El Kef (co-ordinates: 36N08°57’/08E38°39’; see Fig. 1). This is within the El Haria Formation, which straddles the Cretaceous-Palaeogene boundary and comprises shales and marls deposited in the Tunisian Trough (Smit *et al*., 1997; Molina *et al*., 2006). About 13 m above sample AFN 601 a set of four white, marly limestones interrupt the clay-marl sequence and form a subtle pale ridge along the main SW-NE aligned valley. Microfossil assemblages (planktic and benthic foraminifera, dinoflagellate cysts, and ostracods) from the interval comprising the cirripede material studied here document an open marine, oligotrophic environment and deposition at outer neritic to bathyal depths (~200 m) during the early Palaeocene (Kouwenhoven *et al*., 1997; Guasti *et al*., 2005). There was no macrofauna associated with sample AFN 601, but it does come from a 5–10 m interval with common and unusually large (up to 2 mm) agglutinated foraminifera.

Biostratigraphically, the sample is allocated to the lower part of calcareous nannofossil zone NP2 and planktic foraminiferal zone P1b (Guasti *et al*., 2005). This level correlates with the middle of Chron 29N and has an age of ~64.9 Ma (Luterbacher *et al*., 2004) to ~64.4 Ma (Berggren & Pearson, 2005).
FIGURE 3A–G. Verruca punica Buckeridge & Jagt, sp. nov. from the Lower Palaeocene (Danian) El Haria Formation, El Kef area (northwest Tunisia). A, basal view; B, top view, showing pentangular-shaped opercular opening; C, detail of B, showing rostrum; D, lateral view, made up of rostrum, fixed scutum and fixed tergum; E, rostral view; F, carinal view; G, lateral view, made up of carina and rostrum (left to right). All views are of specimen NHMM 2007 094 (holotype).

Remarks. The above description of the shell, as being “slightly compressed laterally”, is based upon a single, almost complete specimen (the holotype). The wall plates in this specimen show no evidence of deformation (e.g. stress cracks) and conform to the few disarticulated wall plates available for study. However, it is possible that further collecting may show the shell to have generally been more circular in plan; because of this, this character is not included in the diagnosis. The moveable tergum and scutum possess no clearly preserved apico-basal striae, however it is most likely that these would be present; their absence is likely due to modification (partial dissolution) of any fine ornamentation on calcareous remains during diagenesis.

The first true verrucomorphs were probably very much like the modern relic taxon Neoverruca brachylepadoformis Newman, in Newman & Hessler, 1989, which possesses a five-plated wall and confirms a monophyletic origin of the balanomorph barnacles from the Scalpelliformes (Newman & Hessler, 1989; Buckeridge & Newman, 2006). However, Neoverruca differs from Verruca sensu stricto by the possession of a medial latus interposed between the fixed tergum and fixed scutum, and the presence of several whorls of imbricating plates that elevate the wall above the substratum, thus having the appearance of a scalpelliform. Verruca punica Buckeridge & Jagt, sp. nov. is clearly a verrucid, and although there are some very minor fractures at the base of the shell wall, these are considered artifacts of preservation rather than the remains of any imbricating plate.

The description provided here is based upon the assumption that all the recovered material that is ‘verrucid’ is from the same species. Unfortunately, the only ‘near-complete’ specimen lacks opercula, and there are no other complete carina or rostra in the sample. There are, nonetheless, some excellent examples of moveable terga and some moveable scuta, and association of these could fit the opercular opening of the single shell. Unfortunately, this single shell is slightly smaller than would be required to accommodate most of the opercula recovered. However, size difference alone is not seen as an impediment to this association. If further material is located, and is able to demonstrate that there is more than one taxon, then the holotype, without opercula, will need a revised diagnosis. The approach adopted here is thus parsimonious, and in reality is the norm rather than the exception in much of palaeontology.
There are also fragments of other cirripedes present (Fig. 4S–Z), and although these are incomplete, they are not verrucid. Rather they can be interpreted as scalpelliform, and likely belong either to *Calantica* Gray, 1825, or *Scillaelepas* Seguenza, 1876.

*Verruca punica* Buckeridge & Jagt, sp. nov. may be distinguished from other Late Cretaceous and early Palaeocene verrucids by the absence of longitudinal ribbing on the exterior and a laterally compressed, rather than subcircular shell (Fig. 3A). In particular, the rather produced carina differentiates it from all other species of *Verruca* and in this character it shows similarity to *Altiverruca* and *Metaverruca*. However, it is distinguished from the former (see e.g., Young, 1998) by having an operculum that is subparallel to the basis, and from the latter by the elongate shape, simpler wall plates (i.e., fewer interlocking ribs) and shape of the operculum, which is D-shaped in *Metaverruca* (see Foster & Buckeridge, 1995; Buckeridge, 1997). The Pliocene *Verruca alaskana* also has a produced plate in the shell wall, resulting in an elongated, rather than rounded shell, but in that species, the produced plate is the rostrum. Unlike most extant species of *Verruca*, the shell of *V. punica* Buckeridge & Jagt, sp. nov. is imperforate. An impunctate shell is a character that is apparently shared with the fossil taxa *V. t. tasmanica*, *V. t. chatheca*, *V. nuciformis*, *V. prisca*, *V. pusilla* and *V. rocana*, although perforations are present in the Miocene *V. digitali* (Buckeridge & Finger, 2001) and the Pliocene *V. koikei* (Koike et al., 2006).

Although verrucid remains have been recovered as disarticulated plates, especially from friable coquinas (where they are easily separated from other shells; e.g., *Verruca tasmanica tasmanica* and *V. tasmanica chatheca*), most fossil verrucids are found articulated and attached to shelly substrates. In part this is an artifact of collecting, as verrucid fragments are small and often overlooked. Of the few that are known from fine-grained sediments similar to those at El Kef, *Verruca digitali* is of note: it is locally very abundant, and occurs as sheets along with associated bryozoans in a shale. Unlike most extant species of *Verruca*, the shell of *V. punica* Buckeridge & Jagt, sp. nov. is imperforate. An impunctate shell is a character that is apparently shared with the fossil taxa *V. t. tasmanica*, *V. t. chatheca*, *V. nuciformis*, *V. prisca*, *V. pusilla* and *V. rocana*, although perforations are present in the Miocene *V. digitali* (Buckeridge & Finger, 2001) and the Pliocene *V. koikei* (Koike et al., 2006).

Acknowledgements

We thank Jessica Reeves, EOS Research Fellow (RMIT University), who kindly photographed the specimens and drafted Figures 1 and 2, and Stijn Goolaerts (Katholieke Universiteit Leuven) for supplying additional cirripede material from Tunisia. RPS acknowledges support by the Research Fund of the K.U. Leuven, while JWMJ is grateful to the European Community-Access to Research Infrastructure action of the Improving Human Research Potential Programme (ABC grant), which allowed him to visit the Institut royal des Sciences naturelles de Belgique (IRScNB, Brussels) and study the original cirripede material of Bosquet (1854, 1857) in November-December 2003.

References


NEW FOSSIL VERRUCID BARNACLE FROM TUNISIA

Zootaxa 1844  © 2008 Magnolia Press · 45

A.C. Kruseman, Haarlem.


Burmeister, H. (1834)

Lamarck, J.B.P.A. de Monet de (1818)

Gosse, J. (1868)

Bosquet, J. (1857)


Darwin, C.R. (1854)


