



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

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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 *Altierruca* 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 Brünlich 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)

Name	Stratigraphic range	Localities
<i>V. alaskana</i> Pilsbry, 1943	Pliocene	Alaska
<i>V. digitali</i> Buckeridge <i>in</i> Buckeridge & Finger, 2001	Upper Miocene	California
<i>V. koikei</i> Tanaka <i>et al.</i> <i>in</i> Koike <i>et al.</i> , 2006	Lower Pliocene	Japan
<i>V. nuciformis</i> Buckeridge, 1983	Lower Eocene-Lower Miocene	New Zealand
<i>V. prisca</i> Bosquet, 1854	Upper Cretaceous	northwest Europe
<i>V. punica</i> Buckeridge & Jagt, sp. nov.	Lower Palaeocene	Tunisia
<i>V. pusilla</i> Bosquet, 1857	Upper Maastrichtian	Belgium, the Netherlands
<i>V. rocana</i> Steinmann <i>in</i> Wilckens, 1921	Maastrichtian	Argentina
<i>V. spengleri</i> Darwin, 1854	Plio-Pleistocene	Mediterranean
<i>V. steenstrupi</i> Brünlich Nielsen, 1912	Middle Danian	Denmark
<i>V. stroemia</i> (O.F. Müller, 1776)	Pliocene-Recent	North Atlantic, northwest Europe
<i>V. t. chatheca</i> Buckeridge, 1983	Upper Palaeocene-Lower Eocene	Chatham Islands,
<i>V. t. tasmanica</i> Buckeridge, 1983	Upper Cretaceous-Lower Oligocene	Australia, New Zealand
<i>V. veneta</i> Carriol & Dieni, 2005	Upper Eocene	northeast Italy
<i>V. withersi</i> Kruizinga, 1939	Lower Pleistocene	Sumba, Indonesia

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).

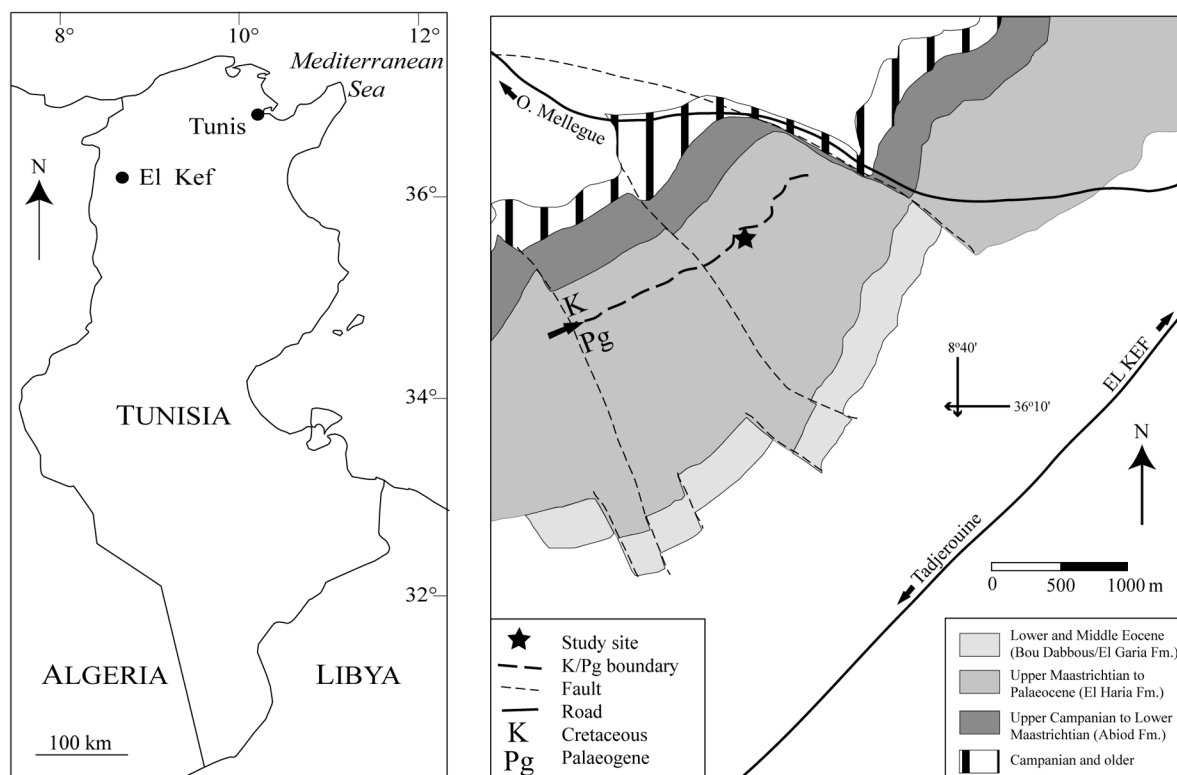


FIGURE 1. Location of the El Haria section, near El Kef (northwest Tunisia), the provenance of the types of *Verruca punica* Buckeridge & Jagt, sp. nov.

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 approximating 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.

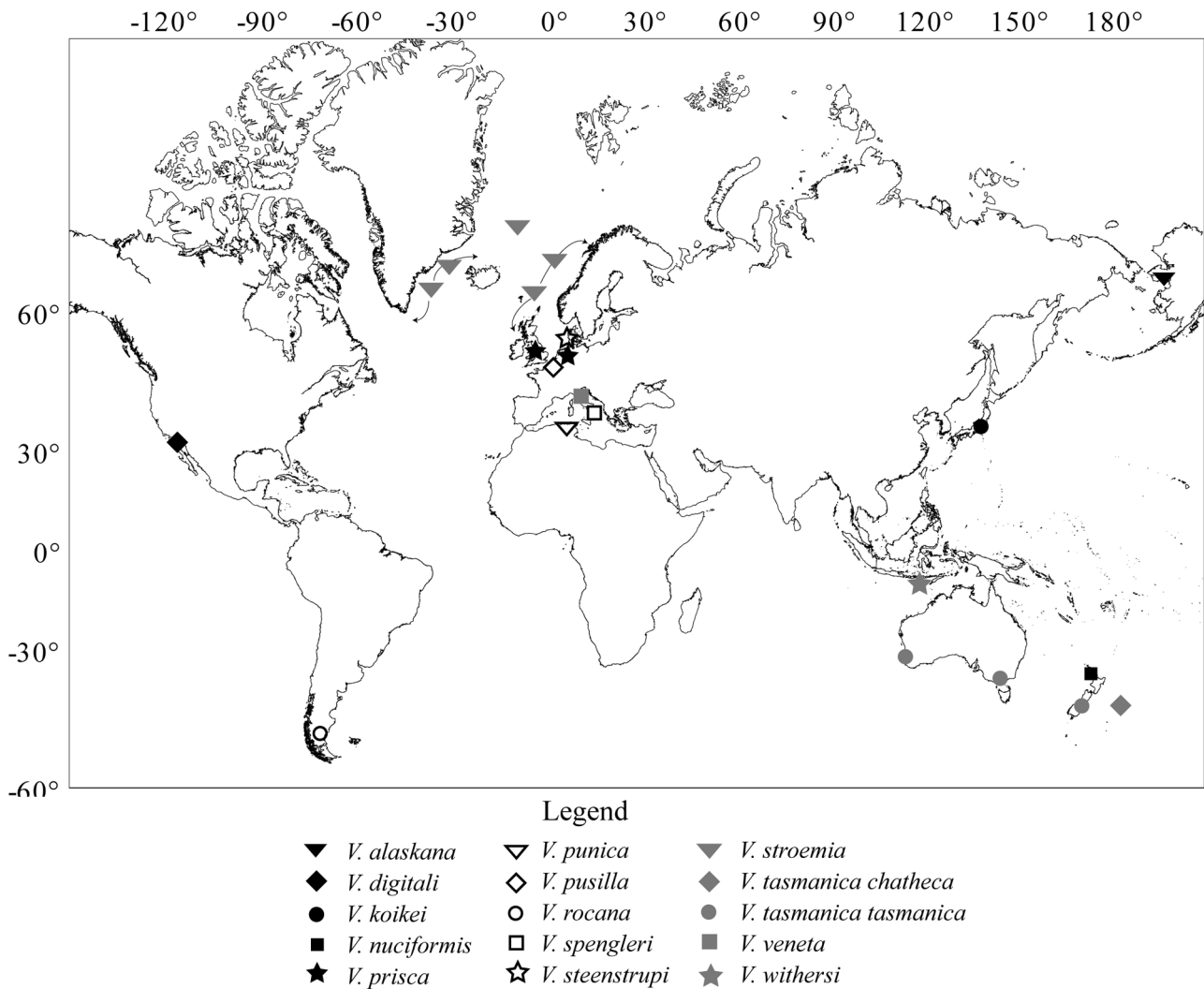


FIGURE 2. Distribution of fossil species assigned to the genus *Verruca* Schumacher, 1817 (sensu stricto); see Table 1 for details.

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).

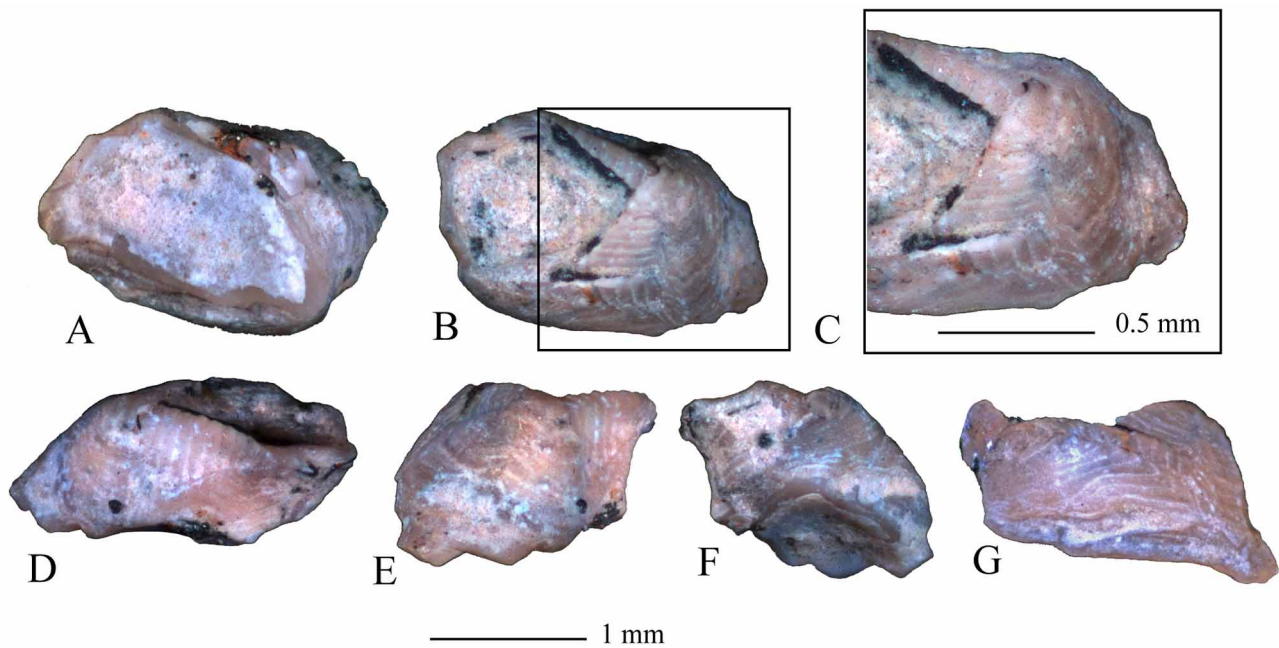


FIGURE 3A–G. *Verruca punica* Buckeridge & Jagt, sp. nov. from the Lower Palaeocene (Danian) El Haria Formation, El Kef area (northwest Tunisia). A, basal view; B, top view, showing pentangular-shaped opercular opening; C, detail of B, showing rostrum; D, lateral view, made up of rostrum, fixed scutum 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.

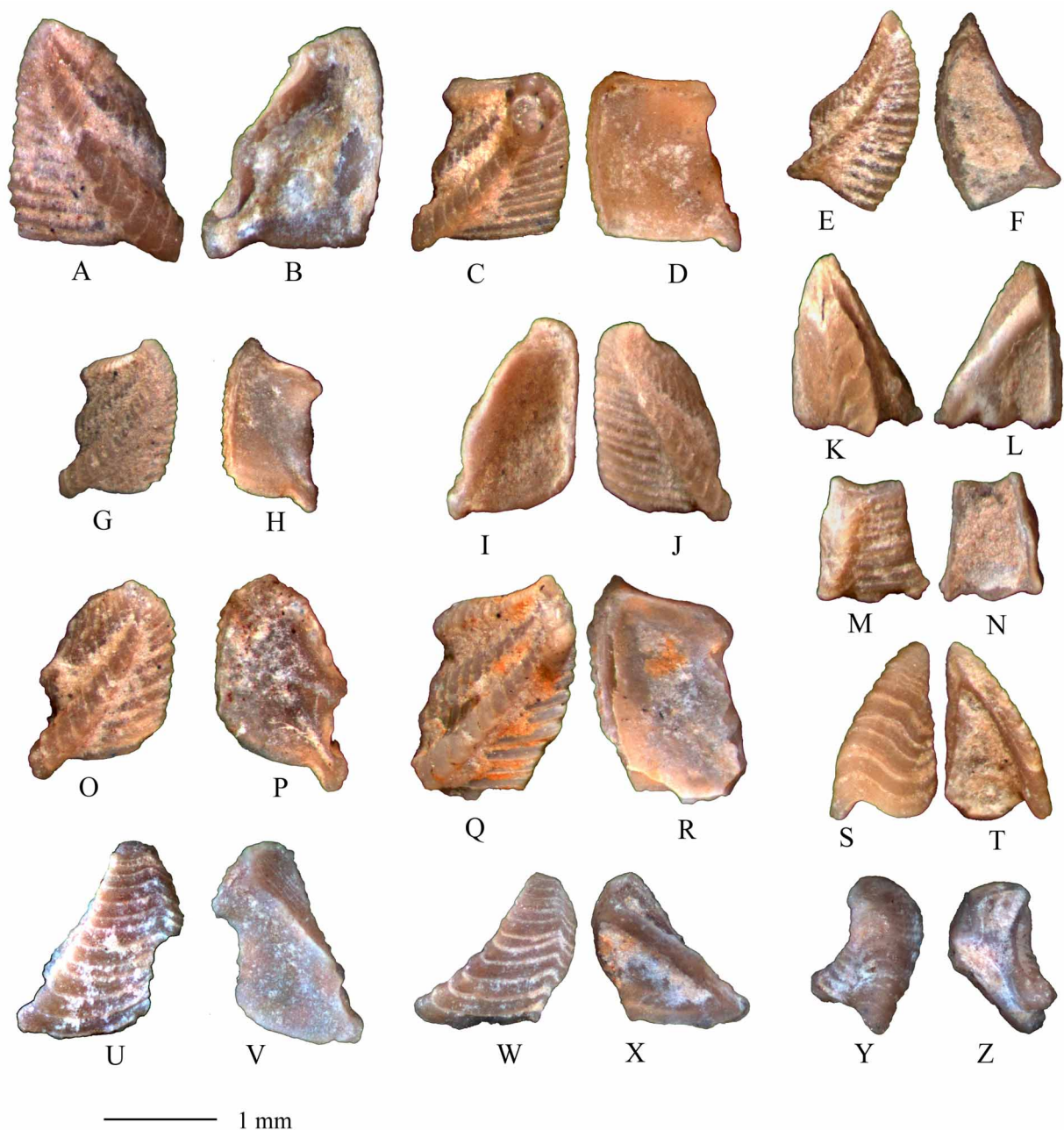


FIGURE 4. Verruciform and scalpelliform cirripede plates from the Lower Palaeocene (Danian) El Haria Formation, El Kef area (northeast Tunisia); A–R. *Verruca punica* Buckeridge & Jagt, sp. nov.; A, B, moveable tergum (NHMM 2007 095, **paratype**), exterior and interior aspects; C, D, moveable tergum (NHMM 2007 096, **paratype**), exterior and interior aspects; E, F, moveable scutum (NHMM 2007 097, **paratype**), exterior and interior aspects; G, H, moveable tergum (NMV P 314992, **paratype**), exterior and interior aspects; I, J, incomplete moveable tergum (NHMM 2007 098), exterior and interior aspects; K, L, incomplete moveable tergum (NHMM 2007 099), exterior and interior aspects; M, N, fixed tergum (NHMM 2007 100, **paratype**), exterior and interior aspects; O, P, incomplete moveable tergum (NHMM 2007 101), exterior and interior aspects; Q, R, incomplete moveable tergum (NHMM 2007 102a), exterior and interior aspects; S, T, *Scillaelepas* sp.?, incomplete carina (NHMM 2007 102b), exterior and interior aspects; U, V, *Scillaelepas* sp.?, lateral plate (NHMM 2007 102c), exterior and interior aspects; W, X, *Scillaelepas* sp.?, lateral plate (NHMM 2007 103), exterior and interior aspects; Y, Z, *Scillaelepas* sp.?, rostromedial plate (NHMM 2007 104), exterior and interior aspects.

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. As there are no obvious molluscs or other suitable hard-shell substrates at the horizon, the verrucids (and bryozoans) are interpreted to have grown on marine algae and/or seagrass leaves, of which there are now no remains (Buckeridge & Finger, 2001).

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References

- Alekseev, A.S. (1974) Podklass Maxillopoda – Maksillopody. Otrial Cirripedia – usonogie raki. Podotrial Thoracica. In: Blank, M.A., Krymgoalts, G.I., Naidin, D.P. & Savtchinskaya, O.V. (Eds.), *Atlas verkhnelovoj fauny Donbassa*, 292–302, 566, pl. 93. Izdatel'stvo 'Nedra', Moskva.
- Alekseev, A.S. (1979) *Verkhemelovye usonogie raki (Cirripedia, Thoracica) evropeiskoi chasti SSSR o sopredel'nykh raionov*. Moskovskii Gosudarstvennyi Universitet im. M.V. Lomonosova, Moskva, 488 pp., 54 pls. (unpublished PhD thesis).
- Berggren, W.A. & Pearson, P.N. (2005) A revised tropical to subtropical Paleogene planktonic foraminiferal zonation. *Journal of Foraminiferal Research*, 35, 279–298.
- Bosquet, J. (1854) Les Crustacés fossiles du Terrain Crétacé du Limbourg. *Verhandelingen uitgegeven door de Commissie belast met het vervaardigen eener geologische beschrijving en kaart van Nederland*, 2, 1–127 [10–137], pls 1–7.

A.C. Kruseman, Haarlem.

- Bosquet, J. (1857) Notice sur quelques Cirripèdes récemment découverts dans le Terrain Crétacé du Duché de Limbourg. *Natuurkundige Verhandelingen uitgegeven door de Hollandsche Maatschappij voor Wetenschappen te Haarlem*, (2)13, ii + 1–36, pls 1–3.
- Brünnich Nielsen, K. (1912) Cirripedierne i Danmarks Danien-Aflejringer. *Meddelelser fra Dansk geologiske Forening København*, 4, 19–42.
- Buckeridge, J.S. (1983) Fossil barnacles (Cirripedia: Thoracica) of New Zealand and Australia. *New Zealand Geological Survey, Paleontological Bulletin*, 50, 1–151, pls 1–13.
- Buckeridge, J.S. (1985) Fossil barnacles (Cirripedia: Thoracica) from the lower Miocene Batesford Limestone, Victoria. *Proceedings of the Royal Society of Victoria*, 97, 139–150.
- Buckeridge, J.S. (1997) Cirripedia: Thoracica: New ranges and species of Verrucomorpha from the Indian and southwest Pacific oceans. In: Crosnier, A. (Ed.), Résultats des Campagnes MUSORSTOM, volume 18. *Mémoires du Muséum national d'Histoire naturelle*, 176, 125–149.
- Buckeridge, J.S. & Finger, K.L. (2001) First record of a fossil verrucid barnacle in California – *Verruca digitalis* sp. nov. (Cirripedia: Thoracica) from the late Miocene. *Journal of Crustacean Biology*, 21, 443–449.
- Buckeridge, J.S. & Newman, W.A. (2006) A revision of the Iblidae and the stalked barnacles (Crustacea: Cirripedia: Thoracica), including new ordinal, familial and generic taxa, and two new species from New Zealand and Tasmanian waters. *Zootaxa*, 1136, 1–38.
- Burmeister, H. (1834) *Beiträge zur Naturgeschichte der Rankenfüsser (Cirripedia)*, viii + 60 pp., 2 pls. G. Reimer, Berlin.
- Carriol, R.-P. & Dieni, I. (2005) Three new Verrucidae (Crustacea: Cirripedia) from the Upper Eocene of the Euganean Hills (Northeast Italy). *Geobios*, 38, 397–406.
- Casadío, S., Griffin, M. & Parras, A. (2005) *Camptonectes* and *Plicatula* (Bivalvia, Pteriomorpha) from the Upper Maastriichtian of northern Patagonia: palaeobiogeographic implications. *Cretaceous Research*, 26, 507–524.
- Darwin, C.R. (1854) *A monograph on the sub-class Cirripedia, with figures of all the species. The Balanidae (or sessile cirripedes); the Verrucidae, etc.*, viii + 684 pp., 30 pls. The Ray Society, London.
- Donovan, S.K. & Jakobsen, S.L. (2004) An unusual crinoid-barnacle association in the type area of the Danian (Paleocene), Denmark. *Lethaia*, 37, 407–415.
- Foster, B.A. & Buckeridge, J.S. (1995) Barnacles (Cirripedia: Thoracica) of seas off the Straits of Gibraltar. *Bulletin du Muséum national d'Histoire naturelle Paris*, (4)17, 163–192.
- Giusberti, L., Fantin, M. & Buckeridge, J. (2005) *Ovulaster protodecimae* n. sp. (Echinoidea, Spatangoida) and associated epifauna (Cirripedia, Verrucidae) from the Danian of northeastern Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 111, 455–465.
- Gray, J.E. (1825) A synopsis of the genera of cirripedes, arranged in natural families, with a description of some new species. *Annals of Philosophy*, new series, 10, 97–107.
- Guasti, E., Kouwenhoven, T. J., Brinkhuis, H. & Speijer, R.P. (2005) Paleocene sea-level and productivity changes at the southern Tethyan margin (El Kef, Tunisia). *Marine Micropaleontology*, 55, 1–17.
- Jagt, J.W.M. (1989) And they never knew what hit them. *Correspondentieblad van de Nederlandse Malacologische Vereniging*, 248, 538–541.
- Jagt, J.W.M. (2004) Een Maastrichts apotheker en zijn fossiele zeepokken: een kwestie van groeiend zelfvertrouwen? *Natuurhistorisch Maandblad*, 93, 334–336.
- Jagt, J.W.M. & Buckeridge, J.S. (2005) A case of homonymy in fossil verrucid barnacles: *Verruca withersi* (Crustacea, Thoracica). *Scripta Geologica*, 130, 187–189.
- Jagt, J.W.M. & Collins, J.S.H. (1989) Upper Cretaceous cirripedes from N.E. Belgium. *Proceedings of the Geologists' Association*, 100, 183–192.
- Jagt, J.W.M., Jaskuła (née Jabłeka), I., Witek, A. & Jagt-Yazykova, E.A. (2008) A new record of the Late Cretaceous cirripede *Eoverruca hewitti* (Verrucomorpha, Proverrucidae) from southern Poland. *Zootaxa*, 1671, 59–68.
- Koike, H., Tanaka, T., Kawase, M., Narita, K. & Karasawa, H. (2006) A first notice of the genus *Verruca* (Crustacea: Cirripedia: Sessilia) from the Pliocene of Japan. *Research Report of the Shinshushinmachi Fossil Museum*, 9, 1–3.
- Kouwenhoven, T.J., Speijer, R.P., van Oosterhout, C.W.M. & van der Zwaan, G.J. (1997) Benthic foraminiferal assemblages between two major extinction events: the Paleocene El Kef section, Tunisia. *Marine Micropaleontology*, 29, 105–127.
- Kruizinga, P. (1939) Two fossil Cirripedia of the Pleistocene marls of Sumba. *Verhandelingen van het Koninklijk Nederlandsch Geologisch-Mijnbouwkundig Genootschap*, 12, 259–264.
- Lamarck, J.B.P.A. de Monet de (1818) *Histoire naturelle des animaux sans vertèbres*, 5, iii + 612 pp. Déterville & J.-P. Verdière, Paris.
- Luterbacher, H.P., Ali, J.R., Brinkhuis, H., Gradstein, F.M., Hooker, J.J., Monechi, S., Ogg, J.G., Powell, J., Röhl, U., Sanfilippo, A. & Schmitz, B. (2004) The Paleogene period. In: Gradstein, F.M., Ogg, J. & Smith, A. (Eds.), *A Geologic Time Scale 2004*, 384–408. Cambridge University Press, Cambridge.

- Marquet, R. (2005) A revision of the Caenozoic Pinnidae from Belgium (Mollusca, Bivalvia). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 65, 241–256.
- Molina, E., Alegret, L., Arenillas, I., Arz, J.A., Gallala, N., Hardenbol, J., von Salis, K., Steurbaut, E., Vandenberghe, N. & Zaghbib-Turki, D. (2006) The Global Boundary Stratotype Section and Point for the base of the Danian Stage (Paleocene, Paleogene, “Tertiary”, Cenozoic) at El Kef, Tunisia – Original definition and revision. *Episodes*, 29, 261–273.
- Müller, O.F. (1776) *Zoologiae Danicae Prodrömus, seu Animalium Danicae et Norvegiae, indigenarum characteres, nomina, et synonyma imprimis popularium*, xxxii + 282 pp. Typis Hallageriis, Holmiae.
- Newman, W.A. (2000) A new genus and species of barnacle (Cirripedia, Verrucomorpha) associated with vents of the Lau Back-Arc Basin: its gross morphology, inferred first juvenile stage and affinities. *Zoosystema*, 22, 71–84.
- Newman, W.A. & Hessler, R.R. (1989) A new abyssal hydrothermal verrucomorphan (Cirripedia; Sessilia): The most primitive living sessile barnacle. *Transactions of the San Diego Society of Natural History*, 21, 259–273.
- Pilsbry, H.A. (1916) The sessile barnacles (Cirripedia) contained in the collections of the United States National Museum; including a monograph of the American species. *Bulletin of the United States National Museum*, 93, xii + 1–366, 76 pls.
- Pilsbry, H.A. (1943) Cirripedia. In: Marine invertebrate faunas of the buried beaches near Nome, Alaska. *Journal of Paleontology*, 17, 94–95.
- Schram, F.R. & Newman, W.A. (1980) *Verruca withersi* n. sp. (Crustacea: Cirripedia) from the middle of the Cretaceous of Colombia. *Journal of Paleontology*, 54, 229–233.
- Schumacher, H.C.F. (1817) *Essai d'un nouveau système des habitations des vers testacés, avec XXII planches*, iv + 287 pp., 22 pls. Schultz, København.
- Seguenza, G. (1876) Ricerche paleontologiche intorno ai Cirripedi terziarii della provincia di Messina. Con appendice intorno ai Cirripedi viventi nel Mediterraneo, e sui fossili terziarii dell'Italia meridionale, Parte II. Lepadidi. *Atti della Accademia Pontaniana*, 10, 369–481.
- Smit, J., Keller, G., Zargouni, F., Razgallah, S., Shimi, M., Ben Abdelkader, O., Ben Haj Ali, N. & Ben Salem, H. (1997) The El Kef sections and sampling procedures. *Marine Micropaleontology*, 29, 65–103.
- Steinmann, G. (1921) Anhang. Über eine *Verruca* von Roca. In: Wilckens, O. (Ed.), Beiträge zur Paläontologie von Patagonien, mit einem Beitrag von G. Steinmann. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 1, 4–5.
- Vervoenen, M. (1994) Taphonomy of some Cenozoic seabeds from the Flemish region, Belgium. In: Herman, J. & Van Waes, H. (Eds.), Elasmobranches et stratigraphie, Volume spécial. *Service Géologique de Belgique, Professional Paper*, 1994/5 (272), viii + 1–115.
- Withers, T.H. (1914) A remarkable new cirripede from the Chalk of Surrey and Hertfordshire. *Proceedings of the Zoological Society London*, 1914, 945–953.
- Withers, T.H. (1923) Die Cirripedien der Kreide Rügens. *Abhandlungen aus dem Geologisch-Paläontologischen Institut der Universität zu Greifswald*, 3, 1–54.
- Withers, T.H. (1935) *Catalogue of fossil Cirripedia in the Department of Geology, Vol. II. Cretaceous*, xiii + 535 pp., pls 1–50. Trustees of the British Museum [Natural History], London.
- Young, P.S. (1998) Cirripedia (Crustacea) from the “Campanha Baciaçores” in the Azores region, including a generic revision of the Verrucidae. *Zoosystema*, 20, 31–92.
- Young, P.S., Zibrowius, H. & Bitar, G. (2003) *Verruca stroemia* and *Verruca spengleri* (Crustacea: Cirripedia): distribution in the north-eastern Atlantic and the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 83, 89–93.