



## A review of the brachylepadomorph cirripede genus *Pycnolepas*, including the first record of an Early Cretaceous species from the Russian Far East\*

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\*Dedicated to the memory of Dr Annie Valérie Dhondt (1942–2006)

### Abstract

To date, twelve species have been assigned to the brachylepadomorph cirripede genus *Pycnolepas* Withers, 1914, some of them on the basis of very limited material. The current status of all these taxa is briefly reviewed. Added are notes on a small collection of isolated capitular valves from middle Albian (Lower Cretaceous) strata in the lower reaches of the Amur River (Vassinskaja protoka, Khabarovsk region); this constitutes the first record of *Pycnolepas* from the Russian Far East (North Pacific Province). It is noted that species of *Pycnolepas* are almost exclusively European in distribution; notable exceptions are *P. articulata* (?lower Aptian; Alexander Island, Antarctica), *P. orientalis* (unspecified Upper Cretaceous, Kuzna-chaj, Azerbaijan; here considered to be a *nomen dubium*), *P. nov. sp.* (upper Paleocene; Turgay Strait, northwestern Kazakhstan), and the present lot which appears to be closely related to *P. rigida* from the lower Albian-middle (?upper) Cenomanian of Europe (England, France). In the absence of other valves (terga, rostra and imbricating plates), for now we refer to this lot as *P. aff. rigida*, and consider it a vicariant species, awaiting the discovery of additional material. In the literature, it has been pointed out that amongst associated faunal elements (in particular, ammonoids and buchiid/inoceramid bivalves) at Vassinskaja protoka and nearby sections along the Amur River, there are species which are closely related to European taxa, and their occurrence appears best explained by vicariance biogeography. The absence of *Pycnolepas* in younger strata in the Russian Far East suggests that no subsequent radiation took place, but collection failure cannot be ruled out either in view of the vastness of the area and the generally small size of cirripede valves.

**Key words:** Cirripedia, Brachylepadomorpha, Brachylepadidae, *Pycnolepas*, revision, Russia, Lower Cretaceous

### Introduction

Currently, twelve species have been assigned to the extinct brachylepadid genus *Pycnolepas*. These range in age from Late Jurassic (Tithonian, 141–135 Ma) to Neogene (early Miocene, 23 Ma), yet some are based on very limited material and placement is more or less preliminary, awaiting the discovery of additional capitular valves and/or imbricating plates. With the exception of *P. articulata* from the ?lower Aptian of Alexander Island (Antarctica), *P. orientalis* from an unspecified Upper Cretaceous level along the Kuzna-chaj River (Azerbaijan; here considered a *nomen dubium*), and *P. nov. sp.* from the upper Paleocene of northwestern Kazakhstan, the genus is essentially European in distribution (Fig. 1). All species are briefly reviewed below, and added is the first record of *Pycnolepas* from the Russian Far East. This material, comprising a single carina and four scuta, is apparently closely related to the northwest European *P. rigida*; we consider it a vicariant

species. This interpretation finds support in the fact that amongst associated macrofossil taxa some show European links, e.g. the inoceramid bivalve *Inoceramus* ex gr. *anglicus* Woods, 1911 and the buchiid bivalve *Aucellina* cf. *aptiensis* d'Orbigny, 1850, plus the ammonoids *Beudanticeras* sp., *Sonneratia?* sp., *Cleoniceras* sp. and *Eogaudryceras* (*Eotetragonites*) *duvalianus* (d'Orbigny, 1840). In the absence of other capitular valves and imbricating plates, we refer to the present material as *P. aff. rigida* for the time being.



**FIGURE 1.** Geographic distribution (solid black dots) of members of the genus *Pycnolepas*; note the disjunct occurrences of early(?) Aptian and middle Albian species in Antarctica and in the Russian Far East, respectively. Dots for southern Sweden and Belgium/the Netherlands in fact represent more than one species, namely *P. ignabergensis* + *P. bruennichi*, and *P. bruennichi*, *P. landenica* + *P. industriosa*, respectively. *Pycnolepas orientalis*, from an unspecified Upper Cretaceous level in Azerbaijan, is here considered a *nomen dubium* (see text); *P. nov. sp.* from the upper Paleocene of Kazakhstan has not yet been described or illustrated.

**Institutional abbreviations:** BAS, British Antarctic Survey, Cambridge (United Kingdom); IRScNB, Institut Royal des Sciences Naturelles de Belgique, Brussels (Belgium); NHM, The Natural History Museum (Department of Palaeontology), London (United Kingdom); NHMM, Natuurhistorisch Museum Maastricht, Maastricht (the Netherlands); SMNH, Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm (Sweden); VSEGEI/CNIGR Museum (Vserossijskij Nauchno-Issledovatel'skij Geologicheskij Institut im. A.P. Karpinskogo/Centralny Nauchno-Issledovatel'skij Geologo-Razvedochny Muzej), Sankt Peterburg (Russia).

## Systematic palaeontology

### Suborder Brachylepadomorpha Withers, 1923

#### Family Brachylepadidae Woodward, 1901

#### Genus *Pycnolepas* Withers, 1914

**Diagnosis.** Sessile; shell laterally flattened; carina (semi-)cylindrical; three to four outer whorls of imbricating plates with inwardly projecting ledge bearing median basal socket (?muscle pit); basis probably membranous (Withers, 1953: 345; Newman *et al.*, 1969: R283).

**Remarks.** We consider *Pycnolepas* (stratigraphic range: Tithonian to early Miocene) to be sufficiently distinct from the only other fossil brachylepadomorph genus, *Brachylepas* Woodward, 1901, to which five or six species from the Upper Cretaceous (Turonian-Maastrichtian) of North America, northwest Europe, the Ukraine and Russia have been assigned (Withers, 1935; Collins, 1973; Alekseev, 1974, 1979; Zullo, 1987; Zullo *et al.*, 1987; Collins & Jagt, 1999; Jagt, 2007). We follow Withers (1935, 1953), Newman *et al.* (1969), Zullo *et al.* (1987), Newman and Yamaguchi (1995) and Newman (2000) in referring to capitular structure (i.e., laterally flattened in *Pycnolepas*, more radially symmetrical in *Brachylepas*, although some species appear more or less transitional in this respect) and especially to the nature of the imbricating plates, to differentiate between these genera. *Brachylepas* (stratigraphic range: Turonian to latest Maastrichtian) appears to be an offshoot of *Pycnolepas*, which failed to cross the Cretaceous-Paleogene (K/Pg) boundary. An extant form, *Neobrachylepas*, is found associated with hydrothermal vents near Tonga (Newman & Yamaguchi, 1995).

**Type species.** *Pollicipes rigidus* J. de C. Sowerby, 1836: 335, pl. 11, fig. 6, by original designation.

**Remarks.** As noted above, twelve species have so far been assigned to this genus. For most of these, at least two different types of capitular valves are known, yet some are based on very limited material only, making placement in *Pycnolepas* more or less preliminary. Terminology used in the descriptions below follows Withers (1935, 1953) and Newman *et al.* (1969). Species are arranged in stratigraphic order.

### *Pycnolepas tithonica* (Withers, 1912)

**Original description.** Withers (1912: 506, pl. 23, fig. 2a, b, as *Brachylepas*(?) *tithonicus*) [see also Withers 1928: 92, pl. 12, figs 13, 14].

**Type.** Holotype is a carina in the M. Remeš Collection (Olomouc), an ‘electrotype’ of which is NHM I.15819.

**Locality and stratigraphy.** Štramberk, Moravia (Czech Republic); White Limestone (Tithonian, 141–135 Ma).

**Remarks.** The single carina known of *P. tithonica* is semicylindrical, strongly convex transversely with steeply inclined sides, non-carinate and comparatively large (length [estimated] 27 mm); ornament consists of regularly spaced, sharp-edged and straight transverse ridges; lacking longitudinal ridges and interspaces smooth. No other capitular valves are known. So far as no other valves and/or imbricating plates are known, assignment to *Pycnolepas* must remain tentative; Withers (1928: 93) noted that there was some resemblance to carinae of *Brachylepas fallax* (Darwin, 1851).

**Occurrence.** Known only from the type locality; no subsequent records.

### *Pycnolepas fimbriata* (Withers, 1912)

**Original description.** Withers (1912: 506, pl. 23, fig. 1a, b, as *Brachylepas*(?) *fimbriatus*) [see also Withers 1928: 91, pl. 12, figs 9–12].

**Type.** Holotype is a carina in the M. Remeš Collection (Olomouc), an ‘electrotype’ of which is NHM I.15818.

**Locality and stratigraphy.** Stramberg (= Štramberk), Moravia (Czech Republic); Red Limestone, Tithonian (141–135 Ma).

**Remarks.** The single carina known of *P. fimbriata* is semicylindrical, strongly convex transversely, non-carinate and comparatively small (length c. 13 mm), with a near-straight basal margin; ornament consists of regularly spaced, prominent, transverse and rounded longitudinal ridges. Two other capitular valves have been referred to this species, albeit with a query. One is a fragmentary tergum (Withers, 1928: pl. 12, fig. 11; Red

Limestone, Nesselndorf = Koprivnice), with a straight apicobasal ridge; the other a fragmentary ?rostrum (Withers, 1928: pl. 12, fig. 12). In the absence of other valves, assignment to *Pycnolepas* must remain tentative; Withers (1928: 93) noted a general resemblance to the carina of *P. rigida*.

**Occurrence.** Known only from the Red Limestone (Tithonian) of Štramberk and Koprivnice, Moravia (Czech Republic); no subsequent records.

### *Pycnolepas articulata* Collins, 1980

**Original description.** Collins (1980: 22, figs 2, 3).

**Type.** Holotype is BAS KG.1657.8b; paratypes are BAS KG.1657.8a, c; all are articulated, near-complete capitula (leg. M.R.A. Thomson).

**Locality and stratigraphy.** Station KG.1657, northern Hyperion Nunataks, southeastern Alexander Island (Antarctica); Fossil Bluff Formation, ?lower Aptian. Associated ammonites and a brachiopod suggest approximate correlation with the Fossil Bluff section, for which an early Aptian age (c. 113–112 Ma) was suggested (Thomson, 1974; see also Crame, 1985).

**Remarks.** The type lot represents the only articulated material of *Pycnolepas* known to date. *Pycnolepas articulata* is a moderately large species with thin, strongly ridged valves; carina subcylindrical, with rounded parietes; tergum subrhomboidal; scutum elongate-triangular, showing one longitudinal ridge more prominent than other ridges on occludent side of apicobasal ridge; rostrum only partially preserved, apparently reaching half the length of scutum; imbricating plates in three or four whorls, subtriangular and with broadly rounded apex, each having narrow basal ridge with shallow, slit-like median socket.

**Occurrence.** Known only from the type locality; no subsequent records.

### *Pycnolepas rigida* (J. de C. Sowerby, 1836)

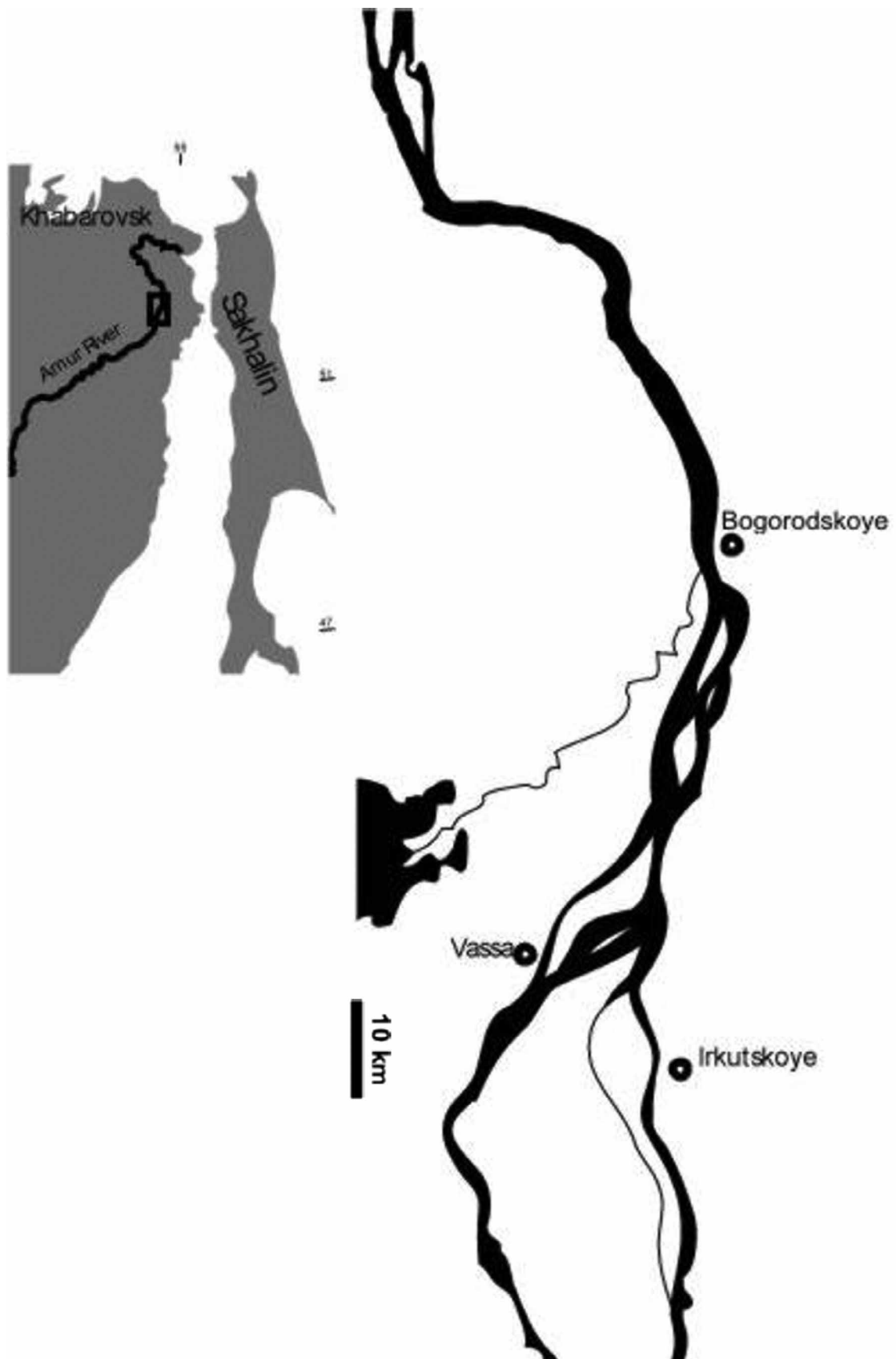
**Original description.** J. de C. Sowerby (1836: 335, pl. 11, fig. 6, as *Pollicipes rigidus*).

**Type.** Lectotype, designated by Withers (1914: 170), is a scutum illustrated by J. de C. Sowerby (1836); current whereabouts unknown.

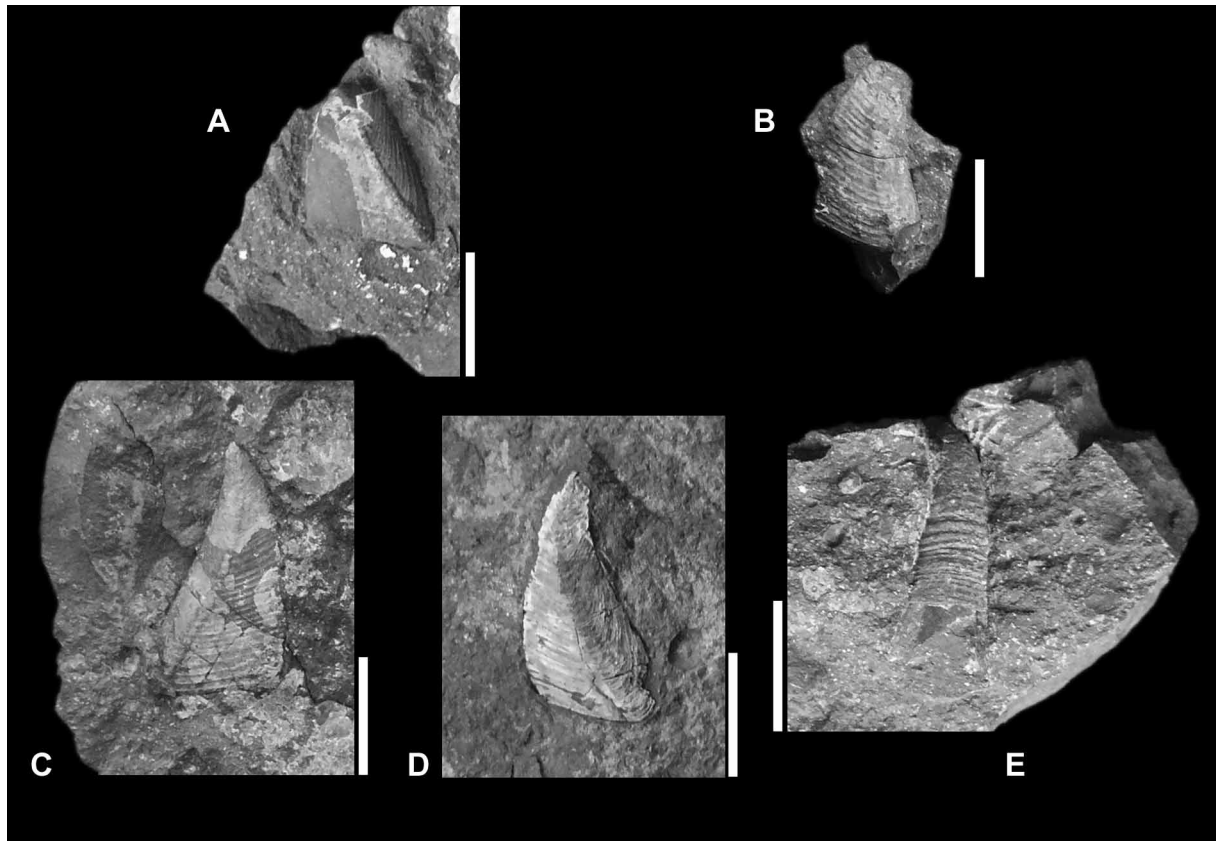
**Locality and stratigraphy.** Folkestone, southeast England; lower Gault (middle Albian).

**Remarks.** Valves of *P. rigida* are transversely, and generally also longitudinally, ridged; scutum elongate-triangular, with basilateral portion produced and with narrow wall-sided ridge curving from apex to basilateral angle; tergum with apical portion much curved towards scutum and with ridge like that of scutum, curving from apex to basal angle; width of imbricating plates exceeding height. Lot NHMM 2006 020 (leg. J.S.H. Collins), comprising isolated scuta, terga, rostra and carinae from the Albian of Bedfordshire (England), shows the wide range of variation of this taxon, expressed in valve proportions (length/width ratio), ornament (in particular, number and strength of longitudinal and transverse ribs) and width of apicobasal ridge (see Withers, 1935).

**Occurrence.** Lower Albian (c. 108–107 Ma) to middle (?upper) Cenomanian (c. 93–92 Ma), England (Bedfordshire, Kent, Cambridge area) and France (Yonne, Haute-Marne); common in the lower Albian *Leymeriella tardefurcata* Zone, ranging throughout overlying Albian zones and extending into the Chalk Marl and higher (Cenomanian, *Schloenbachia varians* and *Holaster* [= *Crassiholaster*] *subglobosus* zones) (Collins, 1980; Carriol & Collins, 2000; Owen, 2002; Smith & Wright, 2003).



**FIGURE 2.** Map showing provenance area in the Khabarovsk region, Russian Far East (inset), and simplified map of the Amur River near Vassa and Irkutskoye, south of Bogorodskoye. Localities 901 and 1024-I are in the same general area, near Vassa, referred to as Vassinskaja protoka.



**FIGURE 3.** *Pycnolepas* aff. *rigida* (J. de C. Sowerby, 1836), all capitular valves from localities 901 and 1024-I, Vassin-skaja protoka, southwest of Bogorodskoye, Khabarovsk region, Russian Far East. A, fragmentary right scutum (VSEGEI/CNIGR Museum, no. 58/13062), locality 901, leg. V.D. Ovchinnikov, 1966 (= Sey *et al.*, 2004: pl. 92, fig. 15a, b); B, fragmentary right scutum (VESGEI/CNIGR Museum, no. 57/13062), locality 901, leg. V.D. Ovchinnikov, 1966 (= Sey *et al.*, 2004: pl. 92, fig. 14a, b); C, left scutum (VSEGEI/CNIGR Museum, no. 128/13062), locality 1024-I, leg. L.P. Ejkhvald, 2000 (= Sey *et al.*, 2004: pl. 92, fig. 16); D, abraded right scutum (VSEGEI/CNIGR Museum, no. 130/13062), locality 1024-I, leg. L.P. Ejkhvald, 2000; E, fragmentary carina (VSEGEI/CNIGR Museum, no. 129/13062), locality 1024-I, leg. L.P. Ejkhvald, 2000. Scale bars equal 10 mm.

### *Pycnolepas scalaris* Withers, 1914

**Original description.** Withers (1914: 187, pl. 8, figs 7–10) [see also Withers, 1935: 364, pl. 47, figs. 16–19].

**Type.** Holotype is NHM I.16679, a rostrum; paratypes are NHM I.16680 (rostrum), NHM I.16681 (upper latus) and NHM I.16682 (scutum).

**Locality and stratigraphy.** Cambridge area, England; Chalk Marl, lower-middle Cenomanian, *Schloenbachia varians* Zone (c. 96–94 Ma).

**Remarks.** Of the type lot (no other valves are known), the small-sized rostrum (length < 2 mm) and upper latus (length 2.4 mm) compare well to other material firmly assigned to *Pycnolepas*, e.g. *P. rigida* and *P. bruennichi*. Rostrum semiconical, ornament of transverse ridges, crossed by longitudinal ridges resulting in short spines; two submedian ridges stronger than others; upper latus acute-angled, triangular, with prominent transverse ridges crossed by longitudinal ridges resulting in short spines. The referred scutum is triangular, slightly convex, with fine transverse ridges, crossed by longitudinal ridges producing short spines; lacking an apicobasal ridge, growth lines not differentiating occludent portion from tergo-lateral portion of valve. Conspicuity of these valves relies primarily on external ornament; tergum, carina and imbricating plates are unknown. Withers (1935: 365) expressed doubts over the assignment to *Pycnolepas*, mainly based on struc-

ture of the scutum, which lacks an apicobasal ridge and appears closer to scuta of some Late Cretaceous calan-  
ticids.

**Occurrence.** Known only from the type locality; no subsequent records.

### *Pycnolepas ignabergensis* Carlsson, 1953

**Original description.** Carlsson (1953: 23, pl. 5, fig. 10; pl. 6, figs 1, 2).

**Type.** Holotype is SMNH Ar. 8742, a left scutum.

**Locality and stratigraphy.** Ignaberga, Skåne (southern Sweden); uppermost lower Campanian (c. 81–80 Ma), *Belemnellocamax mammillatus* Zone (see Christensen, 1975, 1997a, b).

**Remarks.** Of this species, only two scuta and a single tergum are known to date; ornament consists of numerous transverse and longitudinal ridges (comparable to some representatives of *P. rigida*; see e.g. Withers, 1935: pl. 47, fig. 5); comparatively narrow apicobasal ridge. Carina, rostrum, upper latus and imbricating plates unknown.

**Occurrence.** Known exclusively from the type locality; no subsequent records.

### *Pycnolepas industriosa* Jagt, 2007

**Original description.** Jagt (2007: in press).

**Material.** A single rostrum, NHMM 2003 015/1.

**Locality and stratigraphy.** Altembroeck (Voer, northeast Belgium); Gulpen Formation, Vijlen Member, Interval 4, lower upper Maastrichtian (c. 70 Ma, *Belemnitella junior* Zone) (Jagt *et al.*, 1995; Jagt, 2007).

**Remarks.** The sole rostrum known is medium-sized, widely semi-conical, strongly convex transversely and subcarinate; ornament consists of longitudinal and transverse ridges, resembling that of *P. landenica* (see below) which also has a similar L/W ratio. No other capitular valves or imbricating plates known.

**Occurrence.** Known exclusively from the type locality.

### *Pycnolepas orientalis* Kolosváry, 1966 (*nomen dubium*)

**Original description.** Kolosváry (1966: 130, text-fig. 2).

**Type.** Not indicated; current whereabouts of material unknown.

**Locality and stratigraphy.** Kuznataj (= River Kuzna-chaj, Azerbaijan); Upper Cretaceous (exact level not specified).

**Remarks.** The type lot (collected 1958; leg. V.G. Nikitin) of this form consists of isolated capitular valves; Kolosváry referred to these as scutum, carina, carinolaterale, tergum, rostrum and supralaterale. As noted by Collins (1980: 21), the ‘scutum’ in Kolosváry’s fig. 2a clearly is a tergum, while the ‘tergum’ of his fig. 2d is a scutum; that this was intentional can be seen from the description and reconstruction of the capitulum (Kolosváry, 1966: fig. 7). Kolosváry failed to explain why this form should have had three pairs of lateral valves, while the genus *Pycnolepas* has a single pair (see Withers, 1914, 1935). Alekseev (1979: 17) clarified the provenance of the material by noting that (translated), ‘In the same year, G. Koloshvary (Kolosvary, 1966) based on material from Caucasus, received from O.S. Vialov, briefly described the new species *Pycnolepas orientalis* (Azerbaijan, River Kuzna-chaj, Upper Cretaceous) and the new subspecies *Zeugmatolepas mockleri armenicus* (Armenia, Maastrichtian), without pictures giving only schematic drawings’. We consider it best to treat *P. orientalis* as a *nomen dubium* until the types are traced, or new material is collected, so as to allow a proper interpretation of this form.

**Occurrence.** Known only from the type area; no subsequent records.

### *Pycnolepas bruennichi* Withers, 1914

**Original description.** Withers (1914: 181, pl. 7, figs 5–9; pl. 8, fig. 6, as *Pycnolepas brünnichi*).

**Type.** Holotype is NHM I.16625, a right scutum.

**Locality and stratigraphy.** Fakse, Sjælland (eastern Denmark); middle Danian (*Tylocidaris bruennichi* Zone; c. 63 Ma).

**Remarks.** Valves of this species are strongly ridged both transversely and longitudinally; scutum subtriangular, with broad wall-sided apicobasal ridge, occasionally broader than tergo-lateral portion, tergum with apical portion only slightly curved towards scutum and a similar, yet much narrower, near-straight apicobasal ridge. Height of imbricating plates exceeding width. On tergum, longitudinal ridges subdued by prominent growth lines. Thousands of isolated, yet associated, valves are known from the middle Danian of Fakse, and allow the species to be reconstructed; however, upper latera invariably are rare. Postulated to have been attached either to certain scleractinian corals and/or logs (Donovan & Jakobsen, 2004), substrates now dissolved.

Withers (1914) proposed *Pycnolepas bruennichi* as a replacement name for *Pollicipes elegans* Darwin, 1851 (76, pl. 4, fig. 9a–d), *non* Lesson (1830: 441), and later (Withers, 1935) showed *P. bruennichi* to be confined to strata of early Paleocene (Danian) age. Drygant (1966: 116, fig. 8a, b) recorded a single carina from upper Maastrichtian levels at Briukhovichi, Volhynia-Podolia (now western Ukraine) which he assigned to *Pycnolepas elegans* (Darwin). This, however, clearly represents a typical carina of the calanticine *Scillaelepas darwiniana* (Bosquet, 1854), as already noted by Alekseev (1979).

**Occurrence.** Lower and middle Danian of Denmark (Withers, 1914, 1935; Jakobsen, 2003; Donovan & Jakobsen, 2004; Jakobsen & Feldmann, 2004), southern Sweden (Limhamn area), northeast Belgium and the southeast Netherlands (Jagt & Collins, 1988; Jagt, 1996) and the Crimean Peninsula, Ukraine (Alekseev, 1979).

### *Pycnolepas landenica* Withers, 1953

**Original description.** Withers (1953: 348, pl. 60, figs 1–6).

**Type.** IRScNB unregistered, a right scutum.

**Locality and stratigraphy.** Wansin, northeast of Namur, southern Belgium; base of ‘Landenian’ sands (= now Hannut Formation, of early-middle Thanetian [late Paleocene] age, c. 55–53 Ma); see Laga *et al.*, 2002; De Geyter *et al.*, 2006).

**Remarks.** Valves of *P. landenica* have few and comparatively widely spaced transverse and longitudinal ridges; carina narrowly semiconical; rostrum widely semiconical; scutum with apical part very slightly attenuated and incurved, and longitudinal ridges extending straight down from apex; tergum with apico-basal ridge curved, inner occludent and carinal edges narrowly raised. Upper latus and imbricating plates unknown.

**Occurrence.** Known only from the type locality; no subsequent records.

### *Pycnolepas* nov. sp.

**Original description.** Levina *et al.* (2006: 411).

**Type.** Not designated yet; no formal description published to date.

**Locality and stratigraphy.** Sokolovsky quarry, northwestern Kazakhstan (Turgay Strait); upper Paleocene (c. 55–53 Ma).

**Remarks.** This appears to be an undescribed, large species of *Pycnolepas* (Levina *et al.*, 2006; A.S. Alekseev, pers. comm., March 2007).



### *Pycnolepas paronai* (De Alessandri, 1895)

**Original description.** De Alessandri (1895: 266, pl. 3, fig. 8a–f, as *Pollicipes paronai*).

**Type.** Lectotype, designated by Withers (1914:185), is an unregistered scutum, illustrated by De Alessandri (1895: pl. 3, fig. 8a, b), contained in the Luigi Di Rovasenda Collection (now at the Museo Regionale di Scienze Naturali, Torino).

**Locality and stratigraphy.** Chieri, southeast of Torino, northern Italy; lower Miocene (Aquitanian, c. 23–22 Ma)

**Remarks.** All valves of *P. paronai* have numerous, close-set transverse and longitudinal ridges; carina narrowly semiconical; scutum with apical part attenuated, much incurved, and longitudinal ridges fine, wavy and radiating from apicobasal ridge; inner occludent edge very wide, extending more than halfway across valve; tergum with apicobasal ridge straight; inner occludent and tergal edges widely raised. Upper latus and imbricating plates unknown.

**Occurrence.** Withers (1953) recorded material from the lower and middle Miocene (in his terminology: Aquitanian and Helvetian, respectively) of the environs of Torino (Chieri, Baldisero and Sciolze [St. Antonio], northern Italy), which would now be equivalent to the lower Miocene (Aquitanian and Burdigalian; see Kroh, 2005: table 1).

**Occurrence.** Known only from the type locality; no subsequent records.

### Early Cretaceous record from the Russian Far East

From the above it appears that the genus essentially is European in distribution (the record of *P. orientalis* being doubtful, see above), with three notable exceptions: *P. articulata* from the ?lower Aptian of Antarctica, *P. nov. sp.* from the upper Paleocene of Kazakhstan, and the present material from the middle Albian of the Russian Far East (Fig. 1). This small collection comprises five isolated capitular valves, four scuta [three right, one left] and a single carina, from localities 901 and 1024-I, on the left bank of the River Amur, near Vassa (Fig. 2), exposing Albian siltstones, mudstones and sandstones with layers of tuffaceous rocks. Sey *et al.* (2004: pl. 92, figs 14–16) illustrated some of these specimens, identified them correctly as *Pycnolepas* sp., but did not provide a description, nor a discussion.

### *Pycnolepas* aff. *rigida* (J. de C. Sowerby, 1836)

(Fig. 3)

**Localities and horizon.** Localities 901 and 1024-I, near Vassa (Vassinskaja protoka), southwest of Bogorodskoye, Khabarovsk region (Fig. 2); middle Albian (Sey *et al.*, 2004: table 6), zone of *Cleoniceras* sp. and *Inoceramus* ex gr. *anglicus* Woods, 1911. Associated faunal elements include the inoceramid bivalve *I. udylensis* Zonova, 1989 and ammonoids (*Beudanticeras* sp., *Marshallites* sp.).

**Material.** Three right scuta (VSEGEI/CNIGR Museum, nos 57/13062, 58/13062, 130/13062), one left scutum (VSEGEI/CNIGR Museum, no. 128/13062) and a single, fragmentary carina (VSEGEI/CNIGR Museum, no. 129/13062), collected in 1966 and 2000 by V.D. Ovchinnikov and L.P. Ejkhvald, respectively.

**Description.** Scuta are elongately triangular, strongly convex transversely, mainly in apical portion; apex strongly curved towards terga; basilateral portion slightly produced; occludent margin strongly convex; basal margin near-straight, oblique; upper part of tergo-lateral margin concave, lower part rounded, protuberant; apicobasal ridge conspicuous, of variable width, extending from apex to basilateral angle, with perpendicular sides and marked with transverse ridges of highly variable prominence; ornament on occludent and tergo-lat-

eral sides of apicobasal ridge consisting of close-set transverse ridges, variable in number and spacing; no longitudinal ridges seen, but this may be preservation induced; inner side not exposed.

As preserved, VSEGEI/CNIGR Museum, no. 130/13062 (Fig. 3D), not illustrated by Sey *et al.* (2004), is c. 20 mm in length; maximum width (basal margin) is 9.5 mm, apicobasal ridge c. 2 mm at its widest point; ornament strongly abraded. VSEGEI/CNIGR Museum, no. 57/13062 (Fig. 3B) measures 15 mm in length, and 9 mm in width; basitergal angle broken; apparently damaged after publication by Sey *et al.* (2004) and glued; apicobasal ridge flattened, conspicuously wide, with prominent sides. VSEGEI/CNIGR Museum, no. 58/13062 (Fig. 3A) also has suffered extensive damage since it was illustrated by Sey *et al.* (2004: pl. 92, fig. 15a, b), the occludent portion is now missing; as preserved, it measures 13 mm in length and c. 10.5 mm in width, showing an abraded apicobasal ridge. VSEGEI/CNIGR Museum, no. 128/13062 (Fig. 3C) is the best preserved valve in the present lot; it measures 22 mm in length and c. 10 mm in width; apicobasal ridge well developed, 1 mm in width and divided into two by a shallow central furrow.

The carina (VSEGEI/CNIGR Museum, no. 129/13062; Fig. 3E, not illustrated by Sey *et al.*, 2004) is broken apically and basally; semicylindrical, moderately curved inwards, strongly convex transversely, yet not carinate, basal margin slightly concave centrally; ornament of irregularly spaced, raised and slightly undulating ridges; interspaces (near-) smooth. As preserved, it measures 15 mm in length (estimated to have been >20 mm originally), with basal width of at least 6.5 mm.

No other capitular valves or imbricating plates known.

## Discussion

When erecting *Pycnolepas*, Withers (1914) noted the similarity to certain extant species of *Pollicipes*, notably *Po. mitella* (von Linné, 1758) [now placed in *Capitulum* Gray, 1825], suggesting *Pycnolepas* to have evolved from a *Pollicipes*-like form. Much later, Collins (1980) remarked that, with the calanticine *Pollicipes* then first recorded, albeit with a query, from the Albian (Collins, 1974), derivation of *Pycnolepas* from *Eolepas* (?Middle Triassic to Upper Jurassic [Kimmeridgian]; see Buckeridge, 1983) might have to be favoured. The oldest representatives of *Pycnolepas* appear to be *Brachylepas*(?) *fimbriatus* and *B.*(?) *tithonicus*, both described by Withers (1912) from the Tithonian (150–144 Ma) of the Czech Republic. The material on which these taxa are based is too limited to allow meaningful comparisons, but the carinae of both forms do closely resemble those of genuine species of *Pycnolepas*. There is no record of any pre-Tithonian *Pycnolepas* or similar forms, nor are any representatives from pre-Albian strata in Europe known. If correctly interpreted, the genus thus could have originated in central Europe; additional material of both Czech taxa is needed to be certain of this. The next oldest member is *P. articulata* from the ?lower Aptian (119–118 Ma) of Antarctica. This shows all features typical of the genus, and in fact some capitular valves bear a close resemblance to those of the much younger European species. Collins (1980) did not explain the occurrence of *Pycnolepas* in Antarctica, far removed from stratigraphically younger species which are more or less confined to Europe. Current views on palaeogeography during the latest Jurassic-earliest Cretaceous would allow for dispersal across the proto-Indian Ocean (Skelton, 2003; predating the opening of the Atlantic), provided that the genus did in fact originate in central Europe during the latest Jurassic.

A comparison with literature sources and specimens from the Albian of England (NHMM 2006 020, leg. J.S.H. Collins) shows that the present material from the Khabarovsk region is close to *P. rigida* from the lower Albian to middle (or ?upper) Cenomanian of England and France. Withers (1935) provided the most detailed description, noting the fairly wide range of variation of the species. However, in the absence of rostra, terga and imbricating plates, which are needed either to substantiate or refute our assignment, we consider our material to represent a vicariant species, and refer to it as *P. aff. rigida* (see below).

To explain the occurrence of this taxon in Far East Russia, far away from coeval European counterparts, there is a choice between dispersal and vicariance (palaeo)biogeography (Skelton, 1993; Heads, 2005; Hembree, 2006). In the former option, *Pycnolepas rigida*, which appeared during the earliest Albian (c. 113 Ma) in southern England, might have extended its range by long-distance transport during the early Albian, possibly aided by a ?prolonged larval stage and favourable currents. Successful dispersal would then have led to diversification, and once isolated from the parent population, allopatric speciation could take place. In terms of geological time, such events would have been virtually instantaneous and difficult to detect in the sedimentary record (Skelton, 1993). Current interpretations of northern European and Arctic palaeogeography during the Early Cretaceous (e.g., Doré, 1991; Scotese, 1991; Owen, 1996; Amédro & Robaszynski, 2005; Haggart *et al.*, 2006; Owen & Mutterlose, 2006; Soudry *et al.*, 2006) would certainly have ‘allowed’ species to migrate via the Arctic into the North Pacific Province. To test this, either rocks of middle Albian age across the Arctic, or existing museum/institute collections from such stratigraphic levels would need to be screened. Larval dispersal of the ‘island hopping’ type would certainly have left traces (see Skelton & Wright, 1987).

In terms of vicariance (palaeo)biogeography, disjunct distribution may reflect populations that were once continuous rather than the result of long-range dispersal across barriers. Such distribution would then be the result of the disappearance of the taxon in question from intervening areas or of subsequent creation of barriers which prevented populations from mixing and offer an opportunity for allopatric speciation. Vicariant species form part of a group of different taxa, all with similar disjunct distribution patterns. In support of this interpretation, rather than dispersal (see above), to explain the occurrence of *Pycnolepas* in the Russian Far East, it is associated macrofaunal elements which provide important data. Yazykova (2001) and Zonova and Yazykova (2000, 2001, 2004) have previously commented on a number of ammonoid and bivalve taxa and discussed earlier works (Zonova, 1982; Pochialajnen, 1985; Zakharov *et al.*, 1996). Amongst taxa which are either held to be conspecific with, or closely related to, European forms are *Inoceramus* ex gr. *anglicus* [but see also Crame, 1985], *Aucellina* cf. *aptiensis*, *Beudanticeras* sp., *Sonneratia*? sp., *Cleoniceras* sp. and *Eogaudryceras* (*Eotetragonites*) *duvalianus*. Thus, there is evidence of vicariant species in other macrofaunal groups. However, to decide whether or not the present material does represent a distinct species, more material is needed from the Khabarovsk area. The apparent absence of stratigraphically younger representatives of *Pycnolepas* in the North Pacific Province suggests that no subsequent radiation occurred, but given the vastness of the area and small size of cirripede material in general, collection failure cannot be ruled either.

Amongst Cretaceous cirripedes the present example is exceptional. We know of no comparable records, albeit that some species of *Brachylepas* [e.g., *B. fallax*, *B. naissantii* (Hébert, 1855) and *B. guascoi* (Bosquet, 1857)] have been shown to have had wide geographic ranges, so it is quite possible that brachylepadomorph larvae had a long lifespan. A few scalpellomorphs, such as representatives of the genera *Scillaelepas* Seguenza, 1876 (s. lat.), *Arcoscalpellum* Hoek, 1907 and *Cretiscalpellum* Withers, 1922 show extensive geographic, and occasionally also stratigraphic, distribution across Europe, inclusive of European Russia, the eastern Ukraine (Donbass) and Kazakhstan (Mangyshlak) as well (see Alekseev, 1974, 1979). In some instances, attachment to floating logs may also have been conducive to a wide distribution. In the case of the present *Pycnolepas* aff. *rigida*, we can rule this out, since material occurs highly scattered at the Vassinskaja protoka outcrops, and not all capitular valve types are represented in near-equal numbers. Where logs with attached cirripedes sank to the seafloor, we would expect imbricating plates to be represented as well (see Jagt & Collins, 1999).

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