Venipagurus mariae gen. et. sp. nov. (Decapoda, Anomura, Venipaguroidea superfam. nov.) from the Lower Lias of Dorset, England

Joe S. H. Collins

The Natural History Museum, Cromwell Road, London SW7 5BD and
8 Shaw's Cottages, Perry Rise, London, SE23 2QN, U. K.

Abstract

Hitherto, the earliest known pagurid remains have been of chelae preserved in an ammonite from the Lower Jurassic (Pliensbachian) of Germany. Thus, recognition of carapaces from the Jurassic, Lower Lias (Sinemurian) of Dorset, England, not only represent the earliest known evidence, but substantiates the assumption of a calcified carapace origin for pagurids. The new material is described herein as *Venipagurus mariae* gen. et sp. nov. and is placed in a new superfamily, Venipaguroidea.

Key words: New hermit crab, Lower Jurassic (Sinemurian), Dorset, England

Introduction

Recent analyses by Ahyong and O'Meally (2004) and Ahyong *et al*. (2009) have shown that the Anomura and Brachyura are sister clades and it is evident this was well established by the Lower Jurassic. Hitherto, the earliest known *in situ* pagurid remains have been of *Palaeopagurus* sp., based on chelipeds preserved in an amaltheid ammonite, *Pleuroceras solare* (Phillips), from the Lower Lias (Pliensbachian) of Banz, southern Germany (Jagt *et al*., 2006, p. 365). Of similar age are two species, *Palaeopagurus deslongchampii* Van Straelen, 1924 (1925 imprint) (extending to the Toartian) and *Goniochirus laevis* Van Straelen, 1924 (1925 imprint), both from May-sur-Orne, Calvados, France, which were described from isolated claws. Recognition of fully calcified carapaces regarded as primitive pagurids, here described as *Venipagurus mariae* gen. et sp. nov., from the Lower Jurassic, Lower Lias of Dorset, England, considerably affects opinions on the early development of the Paguroidea.

Van Bakel *et al*. (2008) studied four species in as many genera of Upper Jurassic (late Oxfordian and late Kimmeridgian) pagurids founded entirely on cephalic shields (the genera since unplaced at family level in De Grave *et al*. (2009). These shields provided considerably more reliable characters in determining the relationships of hermit crabs, than the numerous occurrences of isolated chelae otherwise known at the time, records of which Williams and McDermott (2004, p. 87) considered questionable. The number and diversity of the shields led to a considerable advance in the knowledge of the early development of pagurids and a plausible phylogenetic development was discussed in detail. The lower Pliensbachian (extending to Hauterivian) crab *Eocarcinus praecursor* Withers, 1932, from Gloucestershire and

Yorkshire (England), had long been considered an intermediary form between macrurans and brachyurans. In this guise van Bakel *et al*. (2008, fig. 6), overlooking the more or less contemporary *Palaeopagurus* sp. of Jagt *et al*. (2006), and Van Straelen's species (1924, imprint 1925), adopted it as the root form giving rise to both brachyurans and anomurans. While the conclusions of van Bakel *et al*. appeared logical, in the very short time interval between *Venipagurus* and *Eocarcinus* it is inconceivable that *Venipagurus* could have achieved the contrasting characters of *Eocarcinus*. However, as a result of extensive re-examination of *Eocarcinus praecusor*, Feldmann and Schweitzer (2010, p. 248), concluded that *Eocarcinus* had sufficient distinctive characters to support the, "position that *Eocarcinus* was not fully carcinized". Thus, while doubt is cast on *Eocarcinus* being ancestral to Brachyura, the situation is neatly resolved in as much as *Eoprosopon klugi* Förster, 1986, from the Pliensbachian of Germany, has recently been established as the earliest known undoubted brachyuran (Schweitzer and Feldmann, 2010). Therefore, while the ancestry of the brachyurans through *Eoprosopon* may be considered established, it is clear that pagurids evolved from a separate and distinct lineage.

While throwing new light on the development of the pagurids, the advent of *Venipagurus* does little to solve their origins. In view of the sub-rectangular carapace outline, together with virtual absence of grooves and the presence of longitudinal ridges of *Venipagurus*, descent from *Pseudopemphix* Würst, 1903, as considered by van Bakel *et al*. (2008, p. 139), would seem untenable. It is possible a solution may be found among the remarkably rich number of macrurans in the Upper Trias in the eryonid *Pseudocoleia mazzolini* Garassino and Tepuzzi, 1993, from the Upper Norian(?) – Lower Rheatian (?) of Lombardy,

northern Italy.

From the size point of view, the carapace of *Venipagurus* falls within the range of junior forms of *Pseudocoleia mazzolinii*; immediate resemblance is afforded by the lateral ridges and vestiges of the median ridge, extended in a short rostral spine in *Venipagurus*. Garassino and Terpuzzi (1993, p. 21) considered *P. mazzolinii* to be closely related to *Coleia* Broderip, 1835, species of which occur in the Lower Lias of Dorset, England. Similar to *Coleia*, the gastric region of *Venipagurus* occupies the anterior fourth of the carapace, but the 'cervical' ridge of *Pseudocoleia* becomes the typical cervical groove in *Venipagurus* and *Coleia*, which in the latter reaches the margin in a distinct cleft. The posterior transverse ridge is lost in both the later species; the lateral carapace margins become rounded in *Coleia*, while in *Venipagurus* they remain parallel within ridges. The branchiostegites are ventral in *Coleia* and the ventral position of the pleural suture is clearly seen in *Coleia barrovensis* (M'Coy) (*vide* Woods 1925, p. 4, fig. 2), whereas in *Venipagurus* the branchiostegites are splayed and the pleural suture is subdorsal, typifying the *lineae anomurica* of the pagurids. A major development is the presence of a long rostrum in *Venipagurus*. Only the Recent *Probeebei* Boone, 1926 (Parapaguridae), has this character, otherwise general carapace features are quite different (Karasawa, pers. com., 2010).

Thus, the separated right-hand branch of van Bakel *et al.* (2008, fig. 6), containing the pagurids, would issue from *Pseudocoleia* with a possible offshoot to contain *Gastrodorus*, a genus now re-located in the Homolodromoidea (De Grave *et al.* 2009). The main stem of the revised branch would then contain all other known pagurids, with precedence given to *Venipagurus* and the Upper Pliensbachian *Palaeopagurus* sp., Jagt *et al.*, 2006, which, latter, provides the earliest known evidence for adoption of ammonites as shelter, if not habitation.

Unfortunately, in the absence of the abdomen of both *Venipagurus* and *Palaeopagurus*, decalcification and development of which plays a vital part in the understanding of pagurids, no finite conclusions can be drawn regarding the habitat of the new species.

The parallel-sided family Pylochelidae Bate, 1888, is generally accepted to represent the earliest hermit crabs (Bate, 1888; McLaughlin *et al.*, 2007; van Bakel *et al.*, 2008; and others), and, indeed this could be the case, but, as figured by McLaughlin, (2003, p. 137, fig. g), by way of *Parapylocheles* Heller, 1862, rather than *Pylocheles*. The figured *Parapylocheles* retains a parallel sided carapace within lateral ridges extending almost to the posterior margin, a trace of a median ridge on the branchial region and, albeit foreshortened, *lineae anomurica* visible in dorsal view. Immediately differentiating characters from *Venipagurus* are: the cephalic shield is extended to the anterior third of the carapace length, a transverse groove is distinct and the rostrum is reduced.

As pointed out by Fraaije (2003), and Jagt *et al.* (2006), the earliest known records of paguroids *in situ* are connected with ammonites. Of these, only two instances have been described; the younger is *Palaeopagurus vandengeli* Fraaije, 2003, which came from the Speeton Clay (Hauterivian) of Speeton, Yorkshire, England.

Concerning the older, *Palaeopagurus* sp., Jagt *et al.* (2006, p. 366), drew attention to the smaller size of the claws relative to the apertural size of the ammonite and concluded that it, 'indicated an early stage in the in the evolution of pagurid evolution'. Indeed, a stage early enough to consider shelter within the ammonite, but not necessarily, habitation. Reports of various Jurassic (Toartian) macruran species seeking shelter within ammonite body chambers were made by Fraaije and Jäger (1995, p. 65), who cited several other authors. Although gastropods were present in the Lower Liassic, it would undoubtedly have been more convenient for calcified pagurids to seek shelter in the comparatively straighter ammonite body-chambers. As decalcification and asymmetric development progressed, gastropods offered alternative accommodation, which was essential with the demise of ammonites! The discovery of the hermited ammonites countermands opinions of Boas (1926, p. 8), and Wolff (1961, p. 28) concerning hermit crabs with a semi-calcified, exposed abdomen hiding in rock cavities and, later, gasteropod shells. The descent of the Pylochelidae from [T]halassinid ancestors (Wolff, 1961, p. 28) would appear improbable.

The rapid diversity of pagurids by Middle to Late Jurassic times is well demonstrated by the cephalic shields studied by van Bakel *et al.* (2008). This diversity is in tandem with the number of species of similar age founded on isolated chelae. As pointed out by van Bakel *et al.* (2008, p. 139), there is a degree of similarity between chelae of the Oxfordian *Goniochirus cristatus* Carter, 1898, and extant Polychelidae, but, until evidence of carapace/chelae association comes to light, speculation remains the only alternative of the taxonomic position of isolated chelae in relation to the carapace remains.

Within a relatively short space of time hermited shells were cohabited by boring, etching or encrusting organisms such as bryozoans or worms, which (as exemplified by Recent occurrences) occur in or around the aperture. The oldest known example of an inferred hermit crab/bryozoan association is from the Middle Bathonian of France (Taylor, 1994, p. 176). Other domiciles—some not yet found fossil—include scaphopod shells, polycheate tubes and holes in rock, etc. (Taylor *et al.*, 1989, p. 1059). There is a tendency for hermit crabs to vacate domiciles shortly before death (Schäfer, 1972); so recognition of (or remains of) co-inhabitants in shelly deposits would indicate the presence of hermit crabs where no other remains occur. Also, the breakdown of the corpse or exuviae would account for the preponderances of the chelae in mixed assemblages. The cephalic shields studied by van Bakel *et al.* (2008) are, apart from non-available claws, evidently the surviving parts of decalcified crabs perhaps domiciled in gastropods.

Stratigraphy

The Upper Sinemurian *Asteroceras obtusum* Zone occurs in the c. 60 m thick succession of the Black Ven Marls accessible to the east of Lyme Regis, Dorset, England, between the upper part of the *Caenisites turneri* Zone, *Micrcoderoceras birchi* Subzone and the *Raricostatum* Zone. The *Asteroceras obtusum obtusum* Subzone (the earliest of three) consists of a conspicuous band of paper shales, the lamination considered be the development of selenite crystals in the bedding planes (Davies, 1956, p. 22). Interbeded in the upper 2 m, or so to the West of Charmouth, are three intermittent layers of Flatstones which yielded the pagurids. This part of the section occurs within Lang's (1926) numerical stratigraphical succession 82 and 83h, the uppermost layer. The specimens' matrix coincides with 83h.

There is a slight variance in the succession at Stonebarrow, about one kilometer east of Black Ven, where Lang (1926, p. 153) chose to distinguish the sequence by adopting Greek lettering, 83θ. The specimen matrix agrees with those specimens from Black Ven.

Description

Infraorder Anomura Macleay, 1838
Superfamily Venipaguroidea superfam. nov.

Diagnosis: Carapace fully calcified; regions not well developed, but sufficient for normal basic lobes to be distinguished. Total length about two fifths longer than the width between the lateral ridges, and about as long as wide between splayed branchiostegites. Not well preserved, the orbitofrontal margin is only marginally narrower than the carapace width; of this, the broadly triangular, produced rostrum takes up about one third, the sides curve into deep, narrow ovate orbits; a short, sharp outer orbital spine curves inwards. A median rostral ridge extends onto the mesogastric lobe. The cervical furrow crosses the midline about one third distance from the front, after which it recurves round weakly tumid protogastric lobes, then runs forwards and outwards before turning sharply to the front. There is a broad transverse depression about one third distant from the front. Distinct *lineae anomuricae* extend the length of the splayed branchiostegites, broadly rounded posterior angles of which are continuous with the angularly concave posterior margin.

Family Venipagururidae fam. nov.
Diagnosis: As for superfamily.

Genus *Venipagurus* gen. nov.
Type species: *Venipagurus mariae* sp. nov. by monotypy.
Diagnosis: As for superfamily.
Derivation of name: Derived from Black Ven—the type locality —and *Pagurus*; coincidently *veni* is also Latin for, 'I came'.

Venipagurus mariae sp. nov.
(Fig. 1)
Material: Holotype, a carapace, BMNH In.53966, Lower Lias, Lower Sinemurian, *Asteroceras obtusum obtusum* Subzone Flatstones 83h (Lang, 1926), Black Ven, c. 300 m east of Lyme

Fig. 1a, b. Dorsal views of carapace of *Venipagurus mariae* gen. et sp. nov., from the Jurassic (Sinamurian). 1a, Holotype, BMNH In.53966, from Black Ven, Dorset England: 1b, paratype, BMNH In.49205 from Stonebarrow, Dorset, England.

Regis, Dorset, England; Paratypes, BMNH In.49205-7, BMNH In.53955, all from Black Ven: In.49224, Stonebarrow, c. 600 m east of Lyme Regis, from Flatstones 83θ.

Derivation of name: The name honours Mary Anning, the renowned 19th century palaeontologist.

Description: Carapace two fifths longer than wide including rostrum, moderately arched transversely, nearly flat longitudinally, highest about the cardiac region. Lateral margins are bounded by pronounced, more or less parallel – sided ridges. Taking up the median fifth of the frontal margin which occupies almost the entire carapace width, a triangular, ridged rostrum is produced marginally beyond the outer orbital angles, its sides, bounded by a groove, curve into convex upper orbital margins which are bounded by a thin groove and terminate in a minute oblique spine separated from lateral ridge by thin sulcus. The cephalic shield is short, about as broad as long. The shield and rostrum take up about the anterior third of the carapace length. The basal margin, bounded by a groove, is deeply indented medially and broadly rounded laterally into splayed branchiostegites, which give an apparent length/width ratio of 1:1. Becoming transversely ovate the base of the rostrum is finely separated from a subparallel-sided, ridged mesogastric lobe. Crossing the midline in a sharp V, the deep cervical furrow loops round ovate protogastric lobes then, dividing, the anterior branch (hepatic furrow) defines a narrowly ovate hepatic lobe, while the posterior branch crosses the margin, joins the *linea anomurica* and runs straight to the lateral margin immediately behind a small pear-shaped subhepatic lobe. A broad depression represents the transverse furrow. There is a short transverse ridge on the urogastric lobe and two, the anterior weaker, on the cardiac region; the intestinal lobe is vaguely tumid. Sinuous *linea anomurica* extending the length of the branchiostegites recurve sharply downwards posteriorly; a ridge bounds the angularly concave posterior margin. The dorsal surface is smooth and glossy.

Acknowledgements

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