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Preservation of internal pleurites in a new palaeocorystid crab (Crustacea, Brachyura, Raninoidia) from the Cenomanian (Upper Cretaceous) of Poitou-Charentes, France

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Abstract

A new palaeocorystid crab, *Joeranina houssineaui* **n. sp.**, is described from upper Cenomanian strata in southwest France. Being apparently derived from *J. broderipii*, the new species inhabited a sandier substrate environment than its predecessor. The incomplete holotype reveals portions of the internal pleurites, which are rarely seen in extinct crabs.

Key words: Podotremata, Joeranina, new species, internal pleurites

Introduction

Palaeocorystoid crabs are common in Albian and Cenomanian (mid-Cretaceous) sedimentary rocks worldwide, and in Europe in particular. Their phylogenetic relationships have recently been revised by Van Bakel *et al.* (2012), who concluded that the family Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929 was the most specialised family that was characterized by a back-burrowing mode of life. A major step in developing a shape advantageous to such a mode of life involved a series of coherent adaptations: narrowing of the body, minimizing the posterior thoracic sternal surface, developing arthrodial cavities in a more axial position, and exposing the pleurites. The pleurites are still internal in palaeocorystids, and until now, they were not known from the fossil record. A new member of the genus *Joeranina* Van Bakel, Guinot, Artal, Fraaije & Jagt, 2012 is described herein based upon four specimens, one of which partially reveals the internal pleurites. The genus has a wide stratigraphical and geographical distribution, with representatives known from Greenland, England, France, Spain, Switzerland, Syria, USA, Canada, Colombia, Japan and Madagascar.

Material, locality and stratigraphy

The present lot comprises four near-complete carapaces with well-preserved cuticle. One of these retains portions of the ventral surface and of the axial skeleton.

The quarry which yielded these specimens, the 'Carrière du Mas', is situated 3 km northeast of Roullet-Saint-Estèphe, Poitou-Charentes, southwest France (co-ordinates 45.607688°N/0.061712°E). The quarry floor currently exposes middle Cenomanian marls, overlain by beds of hard limestone which form the basis of the upper Cenomanian (unit C4; see Vullo *et al.* 2007: fig. 1). Above follows approximately 4.5 m of grey-bluish mudstones referred to as *argiles tégulines* (unit Dm), which are slightly silty to sandy at the base and rich in oysters such as *Rhynchostreon suborbiculatum* (Lamarck, 1801) and *Ceratostreon flabellatum* (Goldfuss, 1833). The crabs described herein originate from the uppermost part of this unit, the level yielding them being 3–4 cm thick and approximately 20 cm below the top of the section. Relicts of a coarse, yellow, calcareous-quartzitic sand, replete with fossils such as shark teeth, other fish remains, oysters such as *Pycnodonte biauriculatum* (Lamarck, 1819) and lingulid brachiopods, are located above. This sandy unit is covered by limestones (3.5 m in thickness) which yield rare echinoids. Vullo *et al.* (2007: fig. 1) gave details of these stratigraphic units.

The crab-bearing level is bioturbated (subhorizontal *Thalassinoides*-type burrows), containing phosphatic nodules with remains of decapod crustaceans. Specimens described herein were surface collected during the time when human exploitation created a plateau precisely at the crustacean level.

The following abbreviations are used:

- MAB Oertijdmuseum De Groene Poort, Boxtel, the Netherlands;
- MNHN Muséum national d'Histoire naturelle, Département Histoire de la Terre and Département Milieux et peuplements aquatiques, Paris, France.

P1, P2 pereiopods 1 and 2; mxp3, third maxillipeds.

Systematic palaeontology

Section Podotremata Guinot, 1977 Subsection Raninoidia De Haan, 1839 Superfamily Palaeocorystoidea Lőrenthey *in* Lőrenthey & Beurlen, 1929 Family Palaeocorystidae Lőrenthey *in* Lőrenthey & Beurlen, 1929 Genus *Joeranina* Van Bakel, Guinot, Artal, Fraaije & Jagt, 2012

Type species. Corystes broderipii Mantell, 1844, by original designation.

Species included. Joeranina broderipii (Mantell, 1844) [as Corystes broderipii], J. colombiana Bermúdez, Gómez-Cruz & Vega in Bermúdez et al., 2013, J. gaspari Van Bakel, Guinot, Artal, Fraaije & Jagt, 2012, J. harveyi (Woodward, 1896) [as Palaeocorystes harveyi], J. houssineaui n. sp., J. japonica (Jimbō, 1894) [as Eucorystes japonicus], J. kerri (Luque, Feldmann, Schweitzer, Jarmillo & Cameron, 2012) [as Notopocorystes kerri], J. paututensis (Collins & Wienberg Rasmussen, 1992) [as Notopocorystes (Cretacoranina) paututensis], J. platys (Schweitzer & Feldmann, 2002) [as Eucorystes platys] and J. syriaca (Withers, 1928) [as Notopocorystes syriacus].

Joeranina houssineaui n. sp.

(Figs. 1, 2)

Diagnosis. Carapace small, elongated, widest at quarter from front; axial carina blunt; front narrow; orbital margin broad, with 2 short supramarginal fissures, bounding triangular median lobe; lateral margins sinuous, with prominent spine at level of hepatic region; cervical groove weak, gastric pits widely spaced; low hepatic, admedial protogastric swellings; pterygostome convex; thoracic sternum narrow, sternite 5 with incomplete lateral depression; dorsal surface granular, branchial regions pitted.

Etymology. Named in honour of Romain Houssineau (Puymoreau, La Bénate, France), who collected and kindly donated the type material.

Material examined. MAB k.3272, holotype, carapace with endostome, pterygostome and partially preserved thoracic sternum and axial skeleton; MAB k.3273, MNHN.F.A49778 and MNHN.F.A49779, paratypes, carapaces, all with well-preserved cuticle, from the upper Cenomanian of 'Carrière du Mas', Roullet-Saint-Estèphe (Poitou-Charentes, southwest France).

Description. Carapace small (length of holotype, as preserved, 14 mm, width 9 mm), elongated, outline subhexagonal, maximum width 25% of total carapace length from front; dorsal surface convex in cross section, with blunt median carina; gently arched longitudinally. Orbitofrontal width approximately 70% maximum carapace width, postfrontal area slightly depressed; front narrow, tip not preserved, grooves defining anterior mesobranchial region extended onto front; orbits large, deep, horizontal in dorsal view, oblique in frontal view, supraorbital margin with 2 short, distinct notches, median portion developed as triangular tooth, outer orbital spine directed slightly outwardly; suborbital margin with distinct notch. Anterolateral margins short, rounded in cross section, with salient, outwardly directed hepatic spine, subtle epibranchial spine. Posterolateral margins well defined,

rimmed, long, sinuous, divergent. Posterior margin straight or weakly concave, narrower than orbitofrontal width. Dorsal regions indistinct; cervical groove weakly defined, shallow; protogastric region defined by admedial, triangular protuberance directed anteriorly; hepatic region elongated, inclined, with small, indistinct protuberance; mesogastric region elongated, triangular, with wide base. Cardiac region large, wide, well defined by distinct, crescent-shaped branchiocardiac grooves. Gastric pits distinct, well separated. Subhepatic area narrow, elongated, grooved along thin but distinct pleural line. Pterygostome large, convex, with indistinct groove medially, buccal collar broad, granular. Mxp3 coxae large, flabelliform. Epistome triangular, laterally grooved, medially keeled; endostome elongated, posterolaterally extended, weakly excavated, ending anteriorly in prominent, narrow oxystomian mouth. Abdominal somite 1 short, granular; remainder of abdomen unknown. Thoracic sternum incompletely preserved; narrow; sternite 1 small, triangular; sternite 2 narrow, elongated; sternites 4, 5 large; sternite 6 smaller, with episternites distinctly raised; sternites 8 tilted, narrow, vertical, compressed medially, forming median line. Sutures distinct, crescent shaped. P1–P3 arthrodial cavities large, lateroventrally directed, in ventral view parallel to body axis; P4 arthrodial cavities slightly smaller, more medially placed; P5 arthrodial cavities small, subdorsal. Dorsal carapace surface granular, granules most prominent on entire median carina, postfrontal area, anterolateral area, along posterolateral margin; branchial area non-granular, pitted.

Remarks. Several characters support assignment of the new species to *Joeranina*, rather than to any other palaeocorystid genus: the anterior mesogastric process is marked by frontal furrows; presence of hepatic and admedial protogastric protuberances; complete cervical groove; presence of an entire axial carina that is well defined and raised; cuticle microstructure with granules and pits (see Van Bakel *et al.* 2012: 36).

Several features of *J. houssineaui* **n. sp.** distinguish it from all congeners. The frontal furrows are shallow (conspicuously deep in congeners), the cervical groove is weakly defined (well defined, also laterally, in congeners), the medial portion of the cervical groove is widely arched (narrower, more U-shaped in most other congeners, but rather similar in *J. harveyi* [see Woodward 1896: fig. 4]; and *J. platys* [see Schweitzer *et al.* 2009: fig. 7a, b]), and the medial carina is prominent and strongly granular (more subtle and less granular in congeners). These differences are considered to fall within the range of variation of *Joeranina* and therefore there is no need to erect a new genus to accommodate the new species.

Additional differences between *Joeranina houssineaui* **n. sp.** and *J. broderipii* (Albian–?Cenomanian, southern England, northern and central France, Switzerland) are branchiocardiac grooves that are relatively wider in the former; hepatic and protogastric protuberances being less acute in the new species; post-frontal and anterolateral areas are more clearly granular in *J. houssineaui* **n. sp.**; notches in the supraorbital margin are much shorter in the new species; only one anterolateral tooth is seen in *J. houssineaui* **n. sp.** but two in *J. broderipii*; thoracic sternites 1, 2 are narrower and crown-shaped in *J. houssineaui* **n. sp.**, and the lateral depression in sternite 5 is incomplete, lacking a ridge (Van Bakel *et al.* 2012: 136) in *J. houssineaui* **n. sp.** but with prominent ridge in *J. broderipii* (Van Bakel *et al.* 2012: fig. 56b). The other species from Europe, *J. gaspari* (Albian, northern Spain), is also characterized by longer frontal furrows, and two anterolateral teeth, rather than one. The thoracic sternites are similar to those of *J. broderipii*, and thus differ from those of *J. houssineaui* **n. sp.** (see above).

Joeranina syriaca (Cenomanian, Syria) is known from a single, fragmentary specimen that lacks the strong, granular median carina, and has anterolateral teeth that are broader at their base than in the new species. J. japonica (Cenomanian–Santonian, Japan) has a stronger and more outwardly directed anterior lateral spine, a straighter posterolateral margin, and narrower branchiocardiac grooves as J. houssineaui **n**. **sp.** and it seems to lack the distinct granulation seen in the new species. J. paututensis (upper Santonian or lower Campanian, West Greenland) is characterized by better-defined carapace grooves and a narrower rostrum than in the new species.

The North American *J. platys* (Albian, Oregon) differs by the characters outlined above, but is similar to the new species in that it has a single anterolateral tooth. The median carina in *J. platys* is granular anterior to the cervical groove, while in *J. houssineaui* **n. sp.** it is granular over the entire length. The posterolateral margins are more strongly divergent in *J. platys* (Schweitzer & Feldmann 2002: fig. 15). *J. harveyi* (Cenomanian, British Columbia, Canada) has more and better-developed lateral spines than in the new species (Woodward 1896: fig. 4).



FIGURE 1. *Joeranina houssineaui* **n. sp.**, upper Cenomanian, 'Carrière du Mas', Roullet-Saint-Estèphe, Poitou-Charentes, southwest France. A, MAB k.3272 (holotype), dorsal view of carapace. B, MNHN.F.A49778 (paratype), dorsal view of carapace. C, MNHN.F.A49779 (paratype), dorsal view of carapace. D, E, MAB k.3273 (paratype), left lateral and dorsal views of carapace. All specimens whitened with ammonium chloride sublimate prior to photography. Scale bars 3 mm.



FIGURE 2. *Joeranina houssineaui* **n. sp.**, upper Cenomanian, 'Carrière du Mas', Roullet-Saint-Estèphe, Poitou-Charentes, southwest France. MAB k.3272 (holotype); A, left lateral view; B, ventral view; C, anterior/frontal view; D, posterior view; E, right lateral view. **1–8**, thoracic sternites 1–8; **a1**, abdominal somite 1; **aP1–aP5b**, arthrodial cavity of P1–P5; **ep**, epistome; **en**, endostome; **i**, intestine; **o**, orbit; **om**, oxystomian mouth; **p14–p17**, pleurite 4–7; **pt**, pterygostome. Specimen whitened with ammonium chloride sublimate prior to photography. Scale bar 3 mm.

In South America, *J. colombiana* (middle Albian, Colombia) has a wider carapace, and the anterolateral margin bears a strong spine. The older *J. kerri* (upper Aptian–middle Albian, Colombia) has a much narrower cardiac region, lacks distinct gastric pits, has a better-defined gastric region, and longer orbital notches than in the new species (Luque *et al.* 2012; Bermúdez *et al.* 2013).

The new species would seem to have evolved from *J. broderipii*, and to have inhabited a sandier substrate than its predecessor.

Remarks on internal pleurites. The axial skeleton is rarely preserved and/or exposed in fossil Brachyura. The pleurites are partially exposed In Raninoidea (Van Bakel *et al.* 2012: fig. 42), whereas in the majority of brachyurans the axial skeleton is entirely internal and virtually unknown in fossil representatives. Collins & Smith (1993: 265; text-fig. 3a, b) described and illustrated an 'almost entire endophragmal skeleton' which they ascribed to *Silvacarcinus laurae* Collins & Smith, 1993. Although not properly placed to date, this isolated axial skeleton nevertheless does not belong either to *Silvacarcinus* Collins & Smith, 1993 or to the Raninoidia (Guinot *et al.* 2008: 708; Van Bakel *et al.* 2012: 70).

The branchiostegite is incompletely preserved on both sides in the holotype of *Joeranina houssineaui* **n**. **sp**., allowing the internal arrangement of the axial skeleton to be assessed. The posterior part of the branchiostegite is not preserved on the right side of the body (Fig. 2E), thus revealing internal pleurites 5 and 6 (pleurites 4–8 are for P1–P5). The branchiostegite is nearly completely missing on the left (Fig. 2A), allowing a larger portion of the axial skeleton to be seen, namely internal pleurites 4–7. The radial arrangement of the pleurites is obvious, pleurite 7 being smaller and nearly horizontal, pleurite 8 concealed and apparently greatly reduced in size. The lower margin of internal pleurites 5 and 6 shows an outgrowth, for the connection of the carapace with the axial skeleton, where the original margin of the branchiostegite used to be. A similar device is formed by outgrowths on exposed pleurites in Raninoidea (Van Bakel *et al.* 2012: 132, fig. 44a, b).

The pleurites are entirely internal in the new species. Exposure of pleurites is a key evolutionary step in Raninoidia. It is hypothesized that *Cretacoranina* Mertin, 1941, considered the most derived amongst palaeocorystids (Van Bakel *et al.* 2012: 21, 45), may have had the most ventral portion of the pleurites exposed.

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