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A new early brachyuran (Crustacea, Decapoda) from the Middle Jurassic of northwest France, epibionts and ecological considerations

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Abstract

The earliest known crabs are of Early and Middle Jurassic age; in general, they are rare. Here we describe a new species of homolodromioid from the late Bathonian of Sarthe (France), based on a single dorsal carapace, *Tanidromites raboeufi* n. sp. This specimen has mostly well-preserved cuticle, and shows two episkeletozoans (bryozoan colonies) on its dorsal side, which is unique amongst early brachyurans (Early and Middle Jurassic). These bryozoans are identified as juvenile colonies of the morphogenus *Berenicea* (sheet-like tubuloporines), typical encrusters of hard substrates. Their presence directly on the carapace crab shows that they were closely cohabitating with this early brachyuran in its palaeoenvironment. One of these colonies appears to have attached to the internal carapace surface, indicative of *post-mortem* settlement and growth. Colony sizes suggest a growth phase of at least several months on the sea floor, implying a certain resistance to decomposition of the crab carapace. This is of note in the light of extant homolodromioids which are known to have extremely fragile carapaces. This association demonstrates that *post-mortem* associations may yield palaeoecological insights into both substrate and colonising organisms.

Contents

Introduction

Epibiosis and epibionts have been defined in numerous ways (West, 1977; Wahl, 1989; Walker and Miller, 1992), focusing either on the organic nature of the coloniser or on that of the colonised substrate. There is a difference of opinion as far as the live condition of the host organism is concerned: compulsory to some authors (Wahl, 1989), not to others (Walker and Miller 1992; Gutt and Shickan, 1998). Our study aims to define the nature of the fossil association observed, and we prefer the use of the terms epibiosis/epibionts because they do not depend on the live/dead condition of the substrate. We here adopt the terminology proposed by Taylor and Wilson (2002) to specify its *syn-vivo* or *post-mortem* nature, by using the terms epizoozoans or episkeletozoans respectively. We also use 'symbiosis' in its original, broad definition (de Bary, 1879), *i.e.* the direct (either brief or long-lasting) association of two living organisms. This definition permits consideration of the widest diversity of associations without regard to the effect, permanency or interdependence of the partner species, which cannot be easily extracted based on fossil associations. This is the most useful definition to study fossil interspecific associations.

As argued by some authors, the paucity of fossil evidence for symbiosis on decapod crustaceans can be attributed to several factors, *i.e.* extrinsic ones, such as the soft (non-durable) composition of most of their modern epizoans (anthozoans, ascidians, bacteria), which do not leave any trace of their presence after their removal and thus have no fossil record (Feldmann, 2003), and intrinsic others such as moulting or grooming habits, repelling any sustainable settlement (Waugh *et al.*, 2004).

Among extant decapod crustaceans, symbiotic bryozoans are frequently recorded in brachyurans (Ryland and Stebbing, 1971; Mori and Manconi, 1990; Cadée, 1991; Becker and Wahl, 1996; Abello and Corbera, 1996; Parapar *et al.*, 1997; Key *et al.*, 1999; Gordon and Wear, 1999; Fernandez-Leborans, 2003; Waugh *et al.*, 2004; McGaw, 2006; Savoie *et al.*, 2007; McDermott, 2007) and in anomurans (Buge and Lecointre, 1962; Schembri, 1982; Walker, 1988; Taylor *et al.*, 1989; Taylor, 1994; McDermott, 2001; Carter and Gordon, 2007, Klicpera *et al.,* 2013).

To date, the oldest confirmed brachyuran is of Pliensbachian (Early Jurassic) age (Förster, 1986); it belongs to the Homolodromioidea Alcock, 1900 (Förster, 1986; Schweitzer and Feldmann*,* 2010a; Haug and Haug, 2014). A new representative of this superfamily, *Tanidromites raboeufi* n. sp., is here recorded from the upper Bathonian (Middle Jurassic) of Crannes-en-Champagne (Sarthe, France). This specimen, with a mostly well-preserved cuticle, shows two episkeletozoans (bryozoan colonies) on its dorsal side, which is unique amongst the earliest brachyurans (Early and Middle Jurassic). Indeed, epibiotic forms were reported on brachyurans from the Late Jurassic of Europe (Oxfordian, Feldmann *et al.*, 2006; Tithonian, Schweitzer and Feldmann, 2009), but never on so old crabs. The true nature of this association (*syn-vivo* versus *post-mortem*) is here considered; it provides new palaeoecological insights into the rare early brachyurans (in this case, *ca* 167 myr old), and some of their sympatric organisms. The scarcity of epizoans on fossil decapod crustaceans and their few studies make the present bryozoans worthy of detailed consideration.

Material and methods

The specimen studied here is housed in the palaeontological collections of the Musée Vert–Muséum d'Histoire naturelle du Mans (Sarthe, France), bearing registration number MHNLM 2013.2.1. It was collected in 2013 by Patrick Raboeuf at La Bigotière, near the village of Crannes-en-Champagne, Sarthe department, Pays-de-la-Loire region, France (Fig. 1). The specimen originates from the Calcaire à *Montlivaultia sarthacensis* Formation, which is dated by ammonites as late Bathonian (Retrocostatum Biozone) (Guillier and Chelot, 1886). This formation, 3 to 4 metres thick, is composed of poorly stratified limestone beds, which yield abundant fossils, such as ammonites, gastropods, bivalves, brachiopods, bryozoans, echinoids, corals and sponges (Guiller and Chelot, 1886; Clément *et al.*, 1987). The studied specimen seems to be the first report of a decapod crustacean from this unit. Palaeogeographical

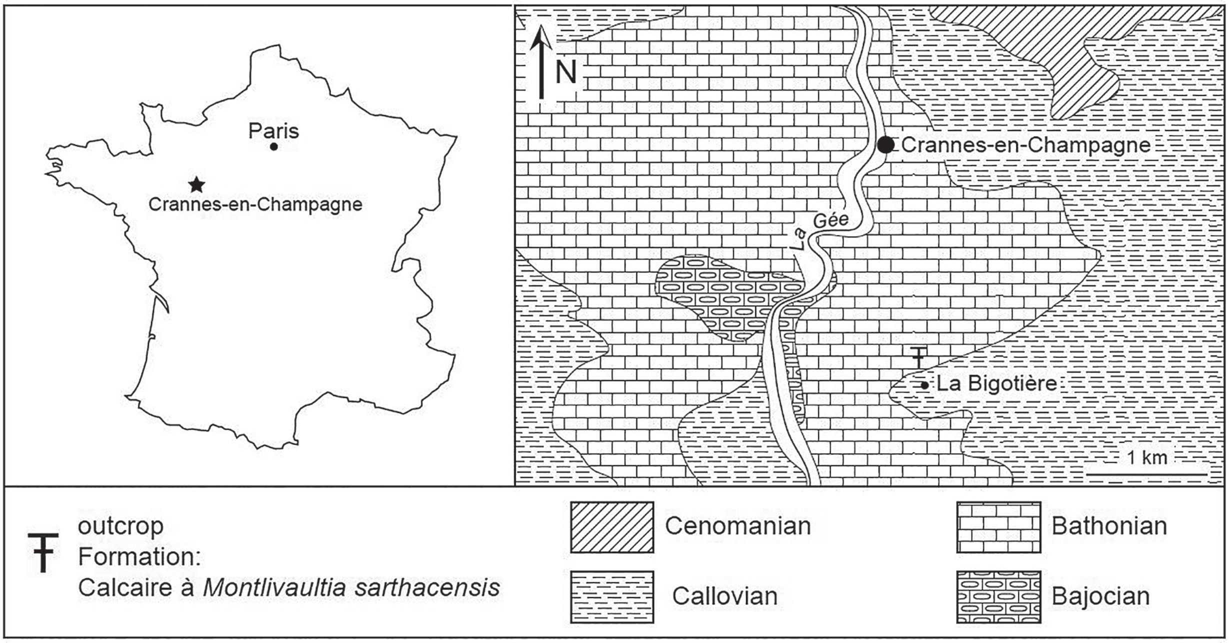

Fig. 1. Geographical and geological setting of the outcrop that yielded specimen MHNLM 2013.2.1 (geological map simplified after Clément *et al.,* 1987).

reconstructions for the Middle Jurassic place the Crannes-en-Champagne area along the western margin of the Paris Basin and adjacent to the Armorican Massif which was probably not completely submerged at that time (Mégnien, 1980; Enay *et al.*, 1993). It was part of a shallow carbonate platform (Clément *et al.*, 1987).

A second brachyuran specimen is here figured for its equivalent epibiotic pattern of bryozoan colonies. Bearing registration number MNHB-MB.A19171, the specimen is identified as *Dromiopsis rugosa* (von Schlotheim, 1820) from the Danian of Fakse (Denmark). It is housed at the Museum für Naturkunde, Humboldt University of Berlin (Germany).

Epibionts were observed *in situ* using a Tescan SEM (VEGA II LSU) at the Direction des Collections (MNHN, Paris), linked to an X-ray detector of type SD3 (Bruker). The systematics used in the present paper follow that used in papers on Late Jurassic cyclostomatous bryozoans (see Taylor, 2009; Zaton *et al.*, 2013) and that of Guinot *et al.* (2013) for the brachyurans.

Institutional abbreviations

FSL, Université Claude Bernard Lyon 1 (France); MAB, Oertijdmuseum De Groene Poort, Boxtel (The Netherlands); MNHB, Museum für Naturkunde, Humboldt University, Berlin (Germany); MNHN.F, Collection de Paléontologie, Muséum national d'Histoire naturelle, Paris (France); MHNLM, Musée Vert-Muséum d'Histoire naturelle du Mans, Sarthe (France).

Results

The brachyuran

Order DECAPODA Latreille, 1802
Infraorder BRACHYURA Latreille, 1802
Section PODOTREMATA Guinot, 1977
Subsection DYNOMENIFORMIA Guinot, Tavares and Castro, 2013
Superfamily HOMOLODROMIOIDEA Alcock, 1900
Family TANIDROMITIDAE Schweitzer and Feldmann, 2008
Genus *Tanidromites* Schweitzer and Feldmann, 2008

Type species. Prosopon insigne von Meyer, 1860, by original designation.

Included species. Tanidromites etalloni (Collins *in* Collins and Wierzbowski, 1985) [as *Coelopus*]; *T. insigne* (von Meyer, 1860) [as *Prosopon*]; *T. lithuanicus* Schweigert & Koppka, 2011; *T. maerteni* Fraaije, Van Bakel, Guinot & Jagt, 2013; *T. montreuilense* Crônier & Boursicot, 2009; *T. pustulosa* (von Meyer, 1860) [as *Prosopon*]; *T. raboeufi* n. sp.; *T. richardsoni* (Woodward, 1907) [as *Prosopon*]; *T. scheffnerae* Schweigert & Koppka, 2011; *T. sculpta* (Quenstedt, 1857) [as *Prosopon*] (= *P. elongatum* von Meyer, 1857; *P. lingulatum* von Meyer, 1860).

Remarks. To describe certain carapace features, such as 'anterior groove', 'hepatic pit' and 'hepatic tubercle', we follow Starzyk (2013; fig. 2); to characterise cuticle microstructure, we follow Waugh *et al.* (2009).

The date of von Meyer's species has been recorded incorrectly on numerous occasions. The type species, *Prosopon insigne*, was not mentioned by von Meyer (1857; 556), although this date appears in virtually all recent publications (Schweitzer and Feldmann, 2008; Crônier and Boursicot, 2009; Hyžný *et al.*, 2011; Schweigert and Koppka, 2011; Fraaije *et al.*, 2013; Starzyk, 2013), even if Glaessner (1929; 321) mentioned the right date of 1860 for *Prosopon insigne*. Besides, von Meyer (1858; 61) proposed the binomen *Prosopon insigne* but no diagnosis, description or illustrations are supplied, making it a *nomen nudum* (ICZN art. 12.1). The name did not become available until it appeared in print in his 1860 work, where a description is given (von Meyer, 1860; p. 193). The same holds true for *Proposon lingulatum* only mentioned in the 1858 paper and accurately published in 1860 (see von Meyer 1860; 205).

Tanidromites raboeufi *n. sp.*

Locality and age. La Bigotière, Crannes-en-Champagne, Sarthe, France; late Bathonian, Retrocostatum Biozone.

Material. Holotype, and sole specimen known, is MHNLM 2013.2.1, a carapace lacking the posterior margin, but with partial preservation of the cuticle; MAB k.3552 represents a cast of this specimen.

Etymology. The specific epithet honors Mr Patrick Raboeuf, who collected and donated the holotype.

Diagnosis. Tanidromites with long anterior carapace portion, outer orbital area rounded, front anteriorly with pseudorostral nodes, rostral margin straight to weakly concave, orbital margin distinctly oblique, epigastric lobes very weak or obsolete, anterior groove absent, mesogastric region weakly defined, cardiac region with two low nodes, post-cervical groove absent, cuticle microstructure with pits.

Description. Carapace of rather large size for genus (maximum preserved length 20.2 mm, width 13.5 mm), distinctly convex in longitudinal and transverse directions, longer than wide, with subparallel margins, may converge slightly posteriorly (Fig. 2A). Margins gently rounded, except anterior of cervical groove where several granules are lined, anteriormost two granules enlarged, outer orbital spine lacking. Rostrum long, sulcate but sulcus not reaching tip, subtriangular, with pseudorostral nodes (Fig. 2C, arrows), resulting in a blunt tip of rostrum. Orbitofrontal margin continuous, straight to weakly concave, not interrupted by rostro-frontal groove, overall having steep angle, without rim (Fig. 2A, C). Orbits weakly defined, very shallow, with rounded outer orbital fossa (Fig. 2B-C).

Epigastric regions obsolete; mesogastric region weakly defined, except anteriorly at the mesogastric process, base appearing broad, triangular; hepatic regions undefined. Cervical pits circular; hepatic pits or tubercles not observed. Cardiac region weakly vaulted, subpentagonal, with two low nodes lined horizontally. Cervical groove entire, sinuous, widely arched medially where it is relatively shallow, deeper laterally (Fig. 2C). Branchiocardiac groove only clearly defined at outer third, subparallel to cervical groove, shallow, as a weakly curved line.

Cuticle partially preserved, very thin, dorsal cuticle microstructure below cervical groove with widely separated setal pits, more densely packed pits anteriorly and just posterior to cervical groove; orbital and subhepatic areas smooth (Fig. 2B-C). Inner mould, where cuticle lacks, smooth. Abdomen, appendages and ventral side not preserved.

Remarks. The specimen is attributed to *Tanidromites* on the basis of the elongate carapace outline with parallel margins, a groove pattern with subparallel cervical and branchiocardiac grooves which extend onto the lateral flanks, the triangular shape of the front and weak development of orbits, and the weak development of the lateral margins. It matches the generic diagnosis given by Schweitzer and Feldmann (2008). The genus is well known from the Middle and Upper Jurassic across Europe; the new species does not extend either its geographical or stratigraphical range (see Starzyk, 2013, for further references). The specimen studied does not show any hepatic pit or tubercle; these characters may differ amongst specimens with or without cuticle preserved, and caution must be taken when comparing these features (for further discussion, see Klompmaker *et al.* 2015).

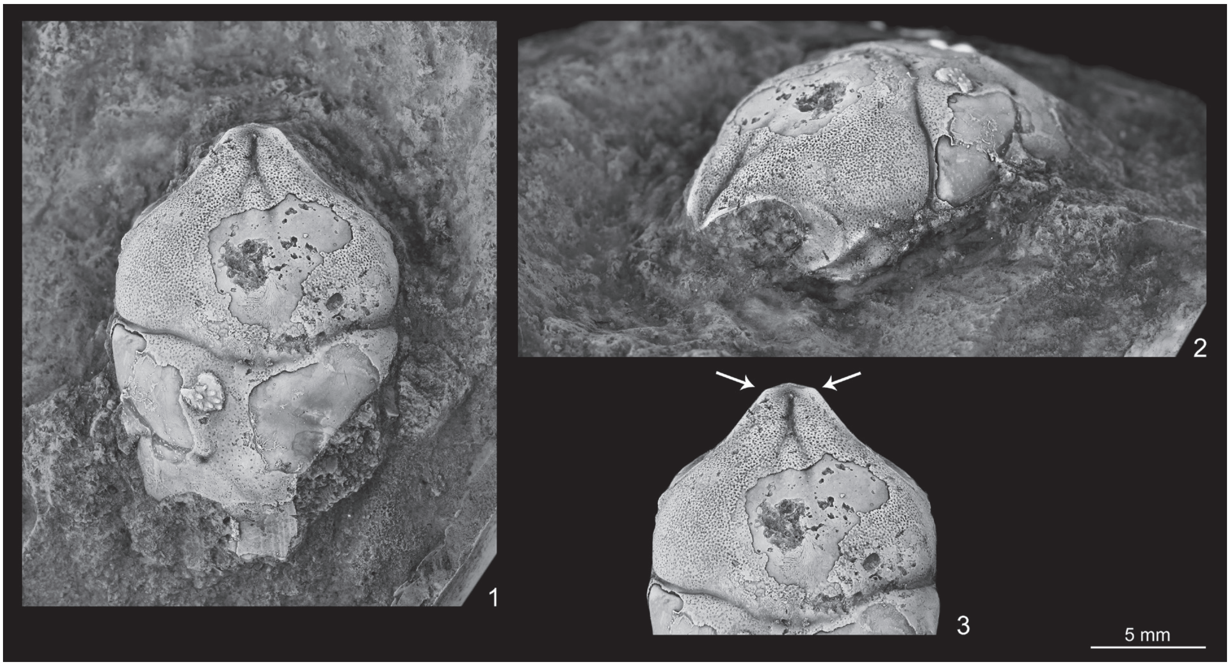

Fig. 2. Tanidromites raboeufi n. sp., MHNLM 2013.2.1, from the upper Bathonian of La Bigotière, near Crannes-en-Champagne, Sarthe, France. (A) Dorsal view; (B) Oblique orbital view; (C) Anterior carapace, showing orbitofrontal margin. Arrows = pseudorostral nodes. Photographs: Barry van Bakel.

Tanidromites maerteni from the lower upper Bajocian of Maizet, Calvados, northwest France, is also known only from the holotype. It differs from *T. raboeufi* n. sp. in having a flatter carapace, much stronger grooves around the mesogastric region, a shallower cervical groove, a clearly defined postcervical groove, an epibranchial lateral spine, and a shorter cardiac region. A hepatic pit is present on the right-hand side of the holotype of *T. maerteni* where cuticle is preserved; thus, this is an additional differentiating feature between these Bathonian and Bajocian species. The tumidity of the carapace may depend on the ontogeny of the crab (see Klompmaker *et al.*, 2012, Klompmaker, 2013) however there is no significant size difference between the two species.

Tanidromites montreuilense from the lower Callovian of Montreuil-Bellay, Maine-et-Loire, northwest France, was described on the basis of three specimens. This species differs from *T. raboeufi* n. sp. in having distinctly defined branchiocardiac, cardiac and postcervical grooves, a well-defined anterior groove, a shorter (in dorsal view) carapace proportion anterior of the cervical groove, stronger pseudorostral spines (Crônier and Boursicot, 2009; pl. 1, figs. 7, 8), and in granules of the anterolateral margin (Crônier and Boursicot, 2009; pl. 1, fig. 3). In addition, both the cuticle and the internal mould of *T. montreuilense* show a granular ornament, unlike the pits seen in *T. raboeufi* n. sp.; however, we must be cautious with a final observation since it is unsure which cuticular layer is preserved in the different specimens.

Several specimens have been described of *Tanidromites richardsoni*. The holotype, from the lower Bathonian at Wotton-under-Edge, southern Cotswolds, England, was refigured by Withers (1951; pl. 15, figs 1-3). This particular specimen has only a few fragments of cuticle preserved, and shows small, yet acute, outer orbital spines. Withers also described a second specimen from the same locality and level, but that one is rather worn at the margins. Donovan (1962) described, but did not illustrate, an additional specimen from Somerset, England; it is unclear from the description whether this specimen has cuticle preserved or not. Donovan (1962; p. 195) noted, "...behind the base of the broken-off antero-lateral spine, on the right side, is clearly visible the base of a second, smaller spine". More recently, Schweigert and Koppka (2011) described a single specimen, without rostrum, from the Sengenthal Formation of Göllersreuth, Franconia, Germany. This specimen is preserved with cuticle; it is stated by Schweigert and Koppka (2011; p. 5) that 'the anterolateral edge bears a prominent spine', and the dorsal surface is covered with pustules. The prominent outer orbital spine, the granular cuticle microstructure, the well-defined epigastric lobes, the weak anterior groove, and a rather wide anterior portion of the rostrum with convex margins (Withers 1951; pl. 15, fig. 1) differentiate *T. richardsoni* from *T. raboeufi* n. sp.

Tanidromites lithuanicus from the middle Callovian, Papartine, Lithuania, is known from the holotype only, which is easily distinguished from *T. raboeufi* n. sp. by its more distinctly defined carapace regions and well-defined cervical and branchiocardiac grooves.

Currently, *Tanidromites pustulosa* from the Tithonian of Štramberk, Moravia, Czech Republic, is known only from the type series (Schweitzer and Feldmann, 2010b; p. 58). The species is relatively short, with a proportionally short rostrum and a steep orbital margin, unlike features displayed by *T. raboeufi* n. sp. In addition, the epigastric lobes are clearly defined in *T. pustulosa* while they are very weak or obsolete in *T. raboeufi* n. sp.

The type species, *T. insigne*, has distinct anterior grooves, well-defined epigastric lobes and mesogastric region, and a wider rostrum without pseudorostral nodes.

Tanidromites etalloni has long been considered a junior synonym of *T. insigne*, but re-evaluation of the holotype and additional material by Starzyk (2013) has recently proved the validity of this species; it is apparently confined to the Kimmeridgian of Poland. It is closely similar to *T. insigne*, and as such shares the same differences in comparison with *T. raboeufi* n. sp., but an additional differential feature is the shape of the outer orbital fossa. This area is rounded near the outer orbital corner in *T. insigne* and *T. raboeufi* n. sp., while it is narrower, and subtriangular, in *T. etalloni* (compare Starzyk, 2013; figs. 4e, 5d).

Tanidromites scheffnerae was established on the basis of a single specimen from the upper Kimmeridgian of Gundelsheim, southern Germany; additional specimens from southern Poland, of middle and upper Oxfordian age, were described and figured by Starzyk (2013). Its carapace lacks a spine or tubercles at the outer orbital angle, has moderately developed epigastric lobes, but lacks pseudorostral nodes. These features differentiate it from *T. raboeufi* n. sp. In addition, the carapace of *T. scheffnerae* is more convex in both directions, however, size difference and thus ontogenetic variation must be taken into account.

The type locality of *T. sculpta* is near Sigmaringen, southern Germany, where it was recovered from Kim-

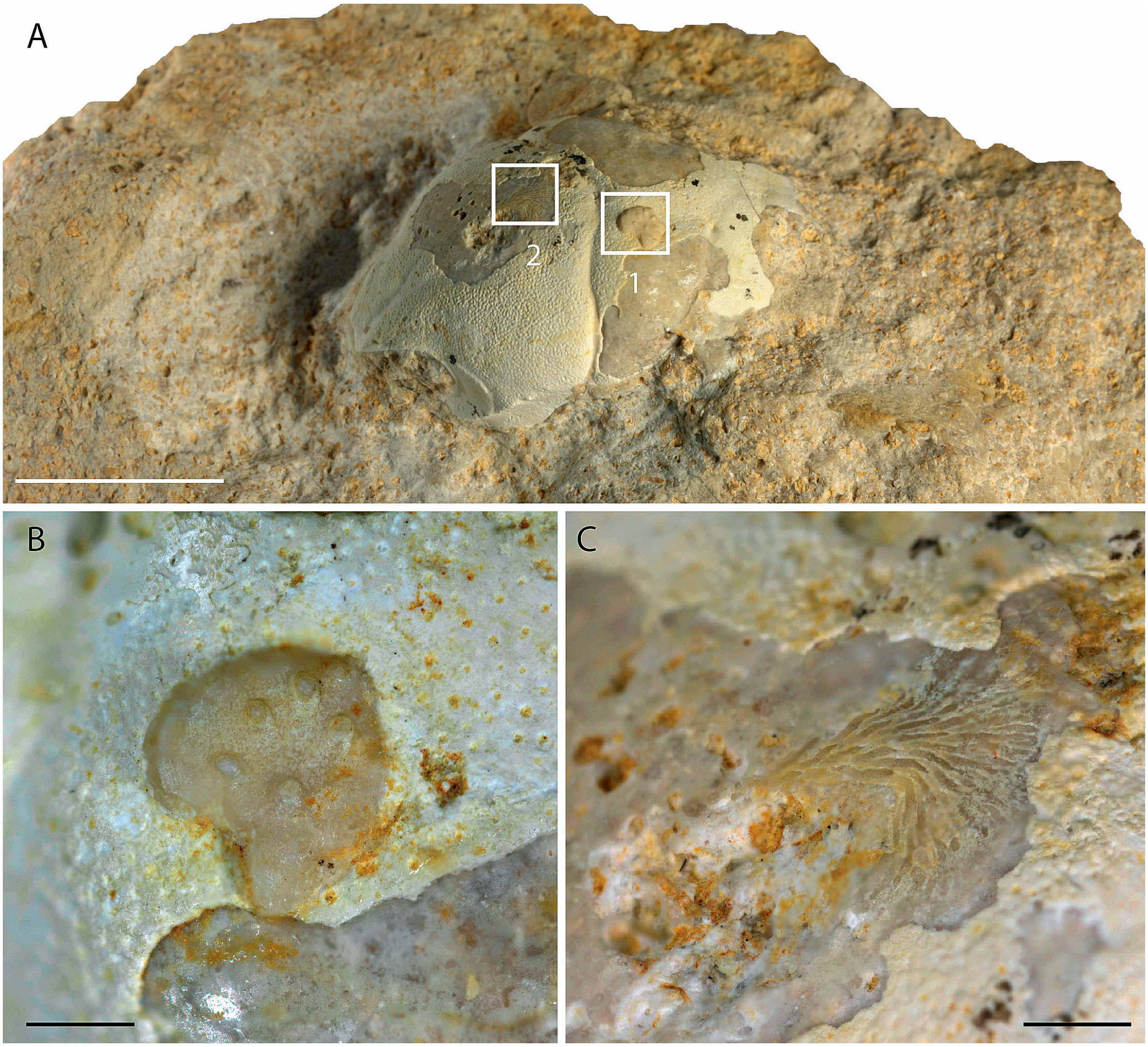

Fig. 3. Occurrence of epibionts on MHNLM 2013.2.1, holotype of *Tanidromites raboeufi* n. sp. (A) General view; boxes: (1) Complete bryozoan colony settled on the outside of the carapace; (2) Underside view of the bryozoan colony settled on the inside of the carapace; (B) Close-up of complete colony on cuticle; (C) Close-up of basal imprint of a colony on carapace portion devoid of cuticle. Scale bars: A = 10.0 mm, B-C = 500 μm. Photographs: Ninon Robin.

meridgian rocks (for details see Schweigert and Koppka, 2011; p. 9). It is known from diverse localities in Poland (Starzyk, 2013; p. 183) and southern Germany (Schweigert and Koppka, 2011). For a detailed discussion of its synonymy and type series, see Schweigert and Koppka (2011; p. 9). This species is flatter in transverse section in its complete size range. The outer orbital fossa of *T. sculpta* is similar to that of *T. etalloni*: narrowing, subtriangular, and lacking a distinct spine in the outer orbital corner. A specimen of *T. sculpta* with cuticle preserved shows an ornament of larger granules, which differs from the pitted cuticle of *T. raboeufi* n. sp.

Epibionts

The holotype of *Tanidromites raboeufi* n. sp. shows two epibionts on the upper and lower sides of the cuticle on the dorsal side of the crab (Fig. 3). We identify these epibionts as juvenile colonies of bryozoans (with circu-

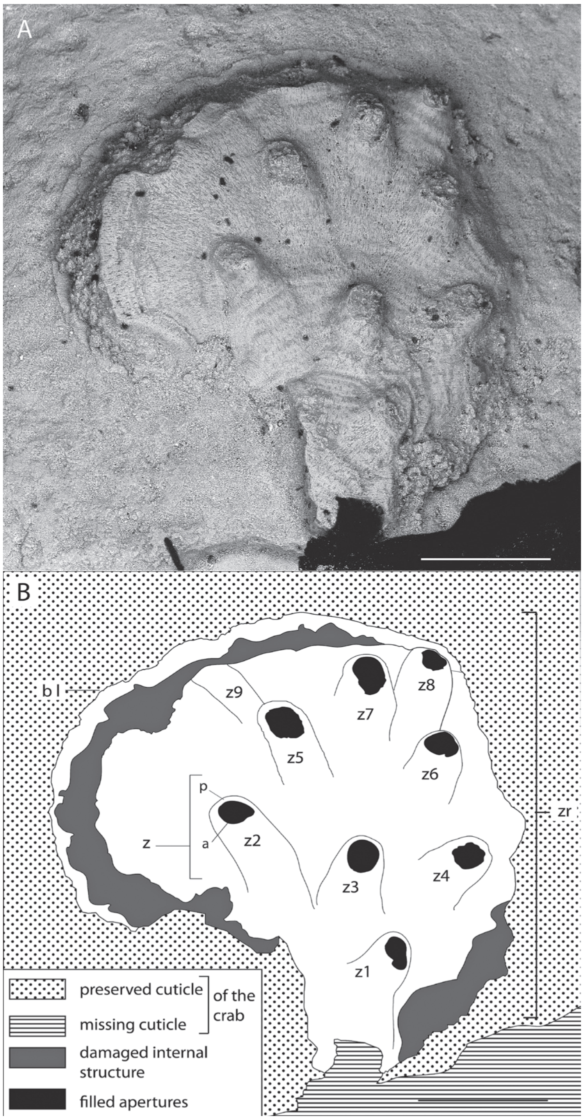

Fig. 4. Complete bryozoan colony. (A) SEM picture; (B) Interpretative line-drawing: a = aperture, an = possible ancestrula, bl = presumed basal lamina, p = peristome, z1-z9 = visible zoecia 1-9, zr = zoarium. Scale bars = 500 μm.

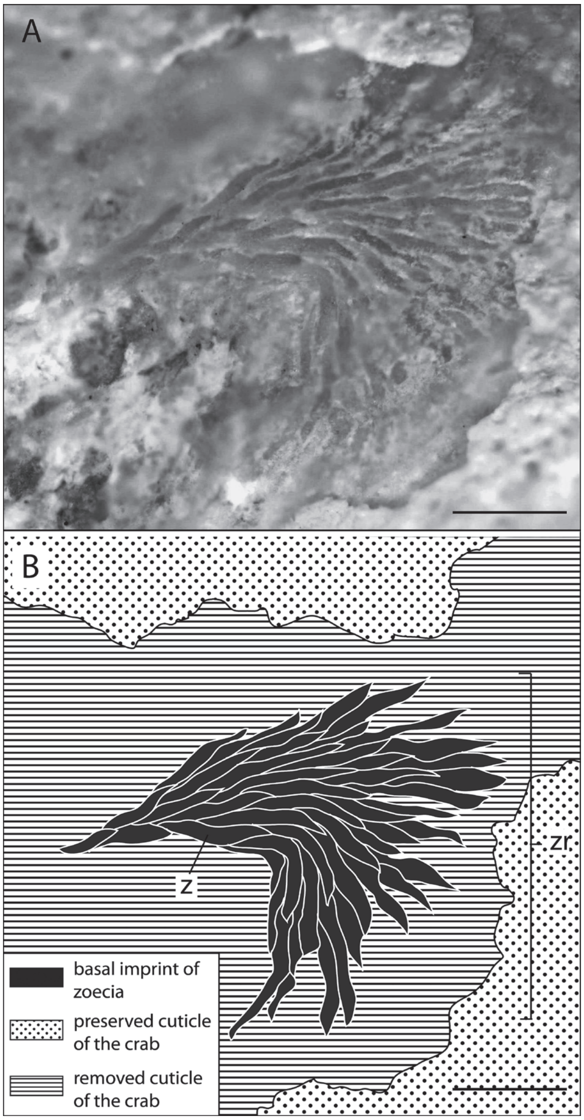

Fig. 5. Basal imprint of bryozoan colony. (A) Optical picture; (B) Interpretative drawing: z = apparent zoecium, zr = zoarium. Scale bars = 500 μm.

lar zooecial apertures; see Hayward and Ryland, 1985).

The first shows a clear three-dimensional structure and is settled directly on top of the preserved cuticle (Fig. 3A, B). On the second colony, all that can be seen are the basal outlines of the zooids as defined by the vertical interzooidal walls; the zooecial chambers are infilled by calcite cement, and the apertures are not visible (Fig. 3A, C). This second colony is settled where the cuticle is missing, broken during the fossil splitting. This kind of preservation correspond thus to the colony visible from the underside, necessarily settled on the inside of the crab carapace.

Phylum BRYOZOA Ehrenberg, 1831
Class STENOLAEMATA Borg, 1926
Order CYCLOSTOMATA Busk, 1852
Suborder TUBULIPORINA Milne Edwards, 1838

Family *Incertae sedis* Morphogenus *Berenicea* Lamouroux, 1821

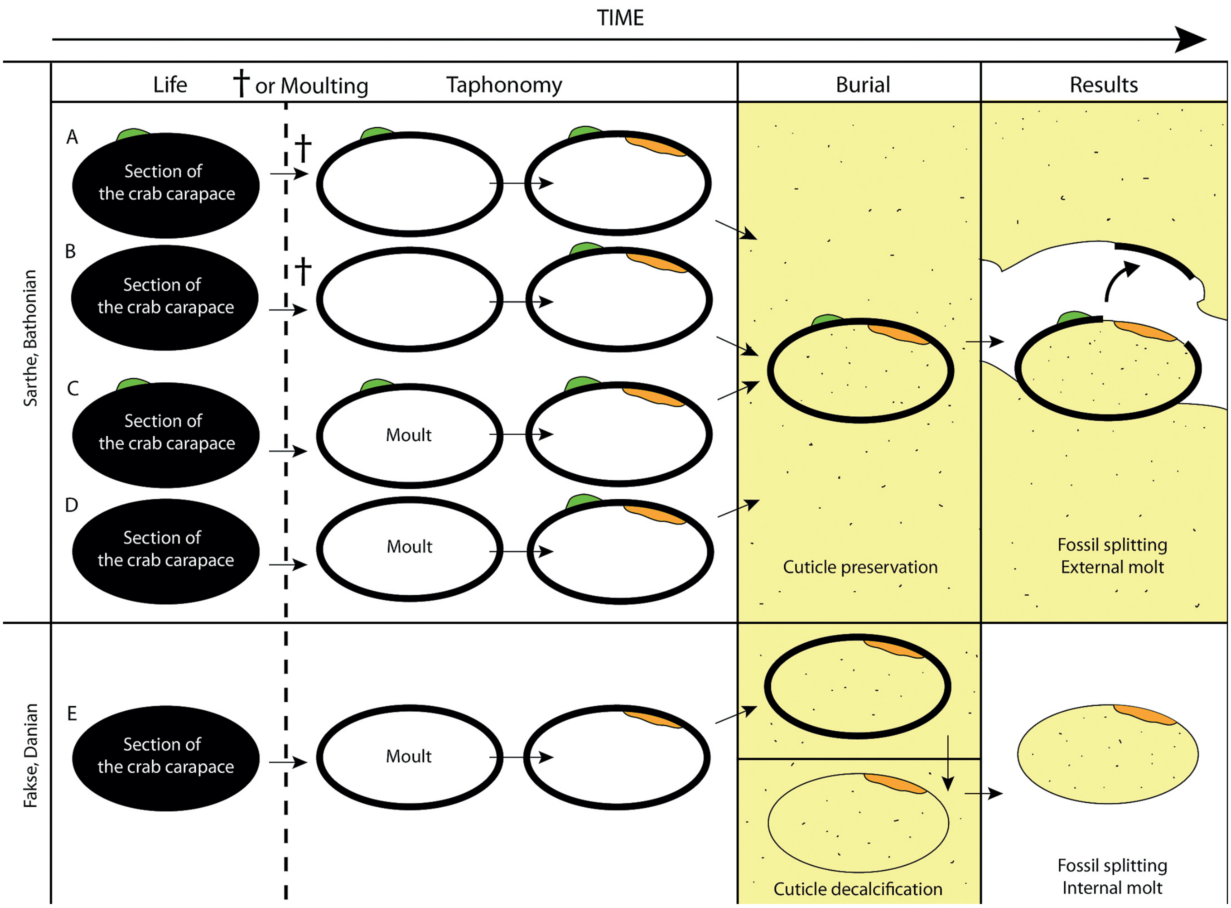

Fig. 6. Schematic representation of all the possible scenarii of association between the observed bryozoans and brachyurans. A, B, C, D. Possible scenarii for *T. raboeufi* nov. sp. from Sarthe, Late Bathonian, western France (MHNLM 2013.2.1.); E. Scenario for *Dromiopsis rugosa* (von Schlotheim, 1820) from Fakse, Middle Danian, eastern Denmark (MNHB-MB.A19171).

(*Sensu* Taylor and Sequeiros (1982): Undetermined bereniciform tubuloporinid)

Description of the complete colony on the outside of the carapace. Tiny spread-out colony (nine visible zooecia), 1.75 mm in length and 1.45 mm in width (Fig. 4A-B); encrusting zoarium apparently unilamellar. Zooecia almost parallel to zoarial surface, arranged in quincunx (Fig. 4A). Tubular, rather short zooecia with circular apertures. Apparent zoecia length 0.4-0.5 mm. Zoecia width rather constant at 0.23 mm (Fig. 3B). Peristomes mostly damaged but probably originally short (Fig. 4B). Approximate apertural diameter 0.11 mm (Fig. 4B). Wrinkled surface towards youngest zooecia (Fig. 3A). Basal lamina visible at periphery of colony (Fig. 4B). Gonozoid lacking.

Description of the colony on the inside of the carapace and visible from the underside. Colony of about 40 zooecia, 2.5 mm in length and 1.5 mm in width (Fig. 5A, B). Colony observable by the basal outlines of the zooids, as defined by the vertical interzooidal walls. Zoocial chambers infilled by calcite cement. Apertures not visible (Fig. 3A, C).

Identification. The complete specimen presents a ramose, encrusting and sheet-like zoarium; zooecia are tubular with circular apertures ascribable to Tubuliporina Milne Edwards, 1838. The colony is devoid of gonozooids. This lack impedes any familial determination for this colony of Jurassic cyclostomatous bryozoans. Such sheet-like tubuliporine may be informally assigned to the morphogenus *Berenicea* Lamouroux, 1821 as proposed by Taylor and Sequeiros (1982) which may correspond to the genera *Rosacilla*, *Reptomultisparsa*, *Dacryopora*, *Microecia*, *Plagioecia*, *Diaper-*

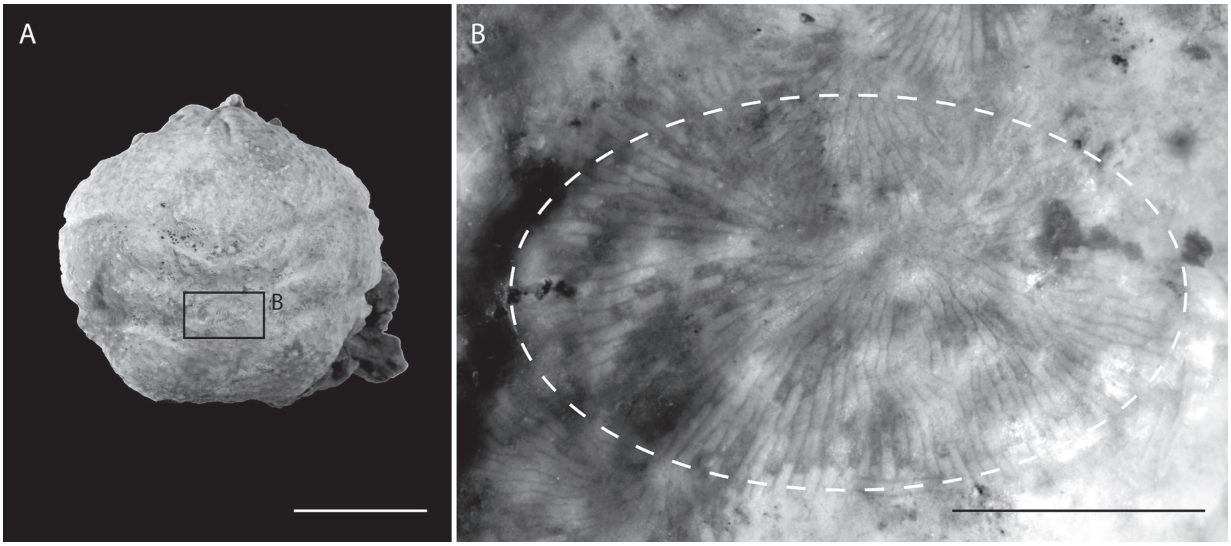

Fig. 7. Carapace of brachyuran crab from the Fakse quarry (Middle Danian, eastern Denmark) and underside view of the bryozoan zoarium similar to that seen on *T. raboeufi* n. sp. (compare Fig. 5). (A) Specimen MNHB-MB.A19171 of *Dromiopsis rugosa*; (B) Radial zoarium (delimited by dashed line) showing underside view of long and narrow zooecia. Scale bars: A = 10.0 mm, B = 2.0 mm. Photographs: Ninon Robin.

oecia, *Atractosoecia*, *Mesonopora* or *Hyporosopora,* which distinguish on the basis of their gonozooid morphology. Although the volume of the colony visible from the underside is here not observable, the basal outlines of zooids evoke a ramose, encrusting and sheet-like zoarium allowing an assignation to the informal morphogenus *Berenicea* too.

Discussion

Epibiosis, carapace resistance and environment

The isolated carapace of *T. raboeufi* n. sp., devoid of appendages, may have either resulted from a moulting or from the decay of a dead organism (Fig 6A-D). The complete colony is clearly fixed on the outside of the carapace, on the preserved cuticle. This one may correspond equally to a *post-mortem* settlement or to a *syn-vivo* one (epizoozoans; Taylor and Wilson, 2003), in other words to a palaeosymbiosis between the crab and the bryozoans (Fig 6A-D; in green). Indeed, bryozoan colonies are well reported on extant alive brachyurans (Ryland and Stebbing, 1971; Mori and Manconi, 1990; Cadée, 1991; Becker and Wahl, 1996; Abello and Corbera, 1996; Parapar *et al.*, 1997; Key *et al.*, 1999; Gordon and Wear, 1999; Fernandez-Leborans, 2003; Waugh *et al.*, 2004; McGaw, 2006; Savoie *et al.*, 2007; McDermott, 2007), sometimes even with true selection of the alive crab by the larva (J.-L. d'Hondt, pers. obs. on cheilostomes). The colony attached to the inside of the carapace and visible from the underside, necessarily settled on an exuvia, or *post-mortem* on the crab carapace. Indeed, if Stenolaemata bryozoans are reported as colonisers of extant brachyuran gills (for instance on *Callinectes sapidus* Rathbun, 1896; see Key *et al.*, 1999), the present case differs strongly by its location in the metagastric region; which may only be permitted by a *post-mortem* settlement on the inside of the empty carapace (Fig 6A-D; in orange).

The settlement of bryozoan colonies on both inner and outer sides of crab carapaces has already been reported by Jakobsen and Feldmann (2004) in the decapod crustacean assemblage from the upper middle Danian of Fakse (eastern Denmark). The authors recorded and figured cheilostome and ctenostome bryozoans on exuviae of *Dromiopsis rugosa* (von Schlotheim, 1820), all devoid of cuticle. These bryozoans and other epibionts (*e.g.* clionid sponges, scleractinian corals, serpulid worms and brachiopods) have been interpreted *post-mortem*. Some of these epibionts are attached to the outer side of the decalcified carapaces (see Jakobsen and Feldmann, 2004, fig. 7.3) but most of them – including bryozoan colonies – are attached to the carapace inner side (see Jakobsen and Feldmann, 2004; Figs. 6-11, 7.1-2).

A newly examined specimen from Fakse (Fig. 7A) shows the radial outline of elongate cyclostomatous zoecia, perfectly flat and visible on the internal molt surface (decalcified cuticle; Fig. 7B). We interpret here this pattern as the underside view of a colony settled on the inside of the carapace (Fig. 6E) what Jakobsen and Feldmann (2004) did not explain. This pattern is thus, in all respect, similar to that observed on the holotype of *T. raboeufi* n. sp. from Sarthe, except in exhibiting no cuticle, completely decalcified during the burial (Fig. 6E). In conclusion, this kind of colonial pattern –flat basal outlines of the zooids, below the cuticle–seems always to correspond to a *post-mortem* settlement on the inside of the carapace or of an exuvia. Thus, they necessarily have to be determinate as episkeletozoans (Taylor and Wilson, 2003), unlike the complete colony preserved on the cuticle outside for which nothing can be concluded.

Regarding the case of *T. raboeufi* n. sp. (Sarthe), as the *post-mortem* colony (on the inside of the carapace) consists of up to 40 zooecia, the decapod carapace shall thus have stayed a certain time on the seafloor to be colonised on the inside by these colonies. Little is known about growth rates of modern cyclostomes, but it appears reasonable that such kind of colony forms in at least a couple of weeks (J.-L. d'Hondt., pers. obs.; P. Taylor, pers. comm.; see also Amui-Vedel *et al.*, 2007 for cheilostomes). A rather 'long' period of settlement is also argued by the important calcification which permitted the colonies good preservation (as observed on the complete colony).

Carapaces of extant homolodromioids are known to be extremely fragile. This is illustrated by extant specimens damaged by simple handling for systematic issues (see Martin, 1991, figs. 4a, 5a; Cleva *et al.*, 2007, figs 5.B, 6.A; Chan *et al.*, 2009, fig. 93). However, our interpretation argues for a rather long exposure of the carapace, showing that the carapace of *T. raboeufi* n. sp. certainly was not that weak and fragile. Feldmann and Gaździcki (1998) studied the cuticular ultrastructure of both fossil and extant homolodromiids, and demonstrated that the exocuticle of the extinct *Antarctidromia inflata* Förster, Gaździcki and Wrona, 1985 (Miocene of King George Island, Antarctica) was thicker than that of extant *Homolodromia paradoxa* A. Milne Edwards, 1880 offering a more rigid and resistant carapace than the fossil representatives. This may also be suggested for Jurassic tanidromitids, permitting external and internal fouling of their unburied carapaces by co-occurring bryozoans. This carapace resistance could simply be ascribed to local paleoenvironmental conditions (*e.g.*, turbulent waves, particular temperatures).

Sheet-like tubuloporinid cyclostomes are broadly reported in the Middle and Late Bathonian of France (Normandy, Sarthe, Ardennes and Aisne) including in the Calcaire à *Montlivaultia sarthacensis* Formation (Guiller and Chelot, 1886). Such encrusting bereniciform colonies would have needed a proper indurated substrate on which to settle. In a calm environment with a carbonate muddy bottom, the isolated carapace (exuvia or carapace of a dead crab) may have appeared as a suitable substrate for these co-occurring larvae of *Berenicea* to settle and grow. However, we may suggest that at the first disturbance of the substrate, the carapace was buried by carbonate muds, the juvenile cyclostomes died and fossilisation started. This may explain the finding of solely small sized colonies on the present brachyuran substrate.

This observation confirm that, during the Bathonian, and particularly in muddy environments, encrusting cyclostomatous bryozoans needed to grow on alive or very steady substrates to succeed in growing to reach the colony mature stages. Such alive substrates may have been brachyurans (too poorly reported in the Late Bathonian of France), or even gastropod shell inhabited by paguroid crustaceans. Gastropod shells encrusted by mature colonies of the bereniciform *Reptomultisparsa incrustans* (d'Orbigny, 1850, and ICZN, 1986), indicating a paguroid dwelling, have rightly been reported in the Bathonian of Sarthe, only 15 km far from La Bigotière (Conlie; Buge and Fisher, 1970).

Conclusion

A new species of early crab, *Tanidromites raboeufi* nov. sp., is described from the upper Bathonian of Sarthe (France). The preservation of juvenile colonies of *Berenicea* (cyclostomatous bryozoans) on both outer and inner sides of its carapace (or exuvia) implies several possible scenarii of associations between these bryozoans and their substrate. The identification of a necessarily *post-mortem* colony composed of 40 zoecia indicates that the carapace of this fossil homolodromioid crab was not so weak and fragile than observed on its extant relatives. The present association is a snapshot of a *post-mortem* meeting (and possibly *syn-vivo* for one of the two colonies) between species cohabitating during the Bathonian. This supports that during Bathonian, and probably in particularly muddy environments, sheet-like tubulinoporines tried to colonise all available hard substrates and that only alive or very steady substrates permitted their growth to an adult stage.

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