

Rogueus belgodereae, a new raninoid crab (Crustacea: Brachyura: Raninoidea) from the Upper Palaeocene (Thanetian) of Southern France, with comments on early palaeocene decapod crustacean faunules

Barry W.M. van Bakel, Àlex Ossó, and Dominique Téodori

ABSTRACT

Palaeocene crabs are rare globally; crab faunules of this period are mostly described from reefal environments, and little is reported about non-reefal environments. A new raninoid crab is described and formally named from Thanetian (upper Palaeocene) non-reefal deeper water deposits of Boussens, southern France. The new species is assigned to the genus *Rogueus*, from which only two species were previously known, and this new record suggests the genus was widespread in the European Palaeocene. A rich Palaeocene brachyuran assemblage of this locality is preliminarily presented and briefly discussed. It appears that eubrachyuran crabs dominated this palaeoenvironment. Based on the global fossil record, it appears that brachyuran crabs quickly recovered after the K/Pg extinction event and were able to restock both reefal and non-reefal environments, prior to the explosive diversification of decapods during the Early Eocene Climatic Optimum.

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INTRODUCTION

Palaeocene crabs including Thanetian crabs are particularly rare globally (Schweitzer and Feldmann, 2005). The hitherto most extensively known Palaeocene crustacean assemblages have been reported from the reefal environments of Fakse, Denmark (Jakobsen and Collins, 1997) and southern Sweden (Segerberg, 1900). Non-reefal Palaeocene localities have yielded a relatively rich decapod fauna in Texas, USA (e.g., Armstrong et al., 2009); Neuquén Basin, Argentina (e.g., Feldmann et al., 1995); Coahuila, Mexico (e.g., Martínez-Díaz et al., 2017) and West Greenland (Collins and Rasmussen, 1992).

In this paper, we preliminarily report a decapod assemblage, currently under study, recovered in Thanetian (upper Palaeocene) levels of the Lafarge quarry at Boussens (Haute Garonne, France) (Figure 1). This decapod assemblage shows a high diversity of brachyurans, in addition to some callianassid and ctenochelid decapods, and increases the number of Palaeocene brachyurans, especially with regards to non-reefal environments.

The first report of decapods of the Boussens locality was published by Van Straelen (1924), who described *Litoricola macrodactyla* (Van Straelen, 1924) (as *Xanthilites macrodactylus*), and *Zanthopsis jacobi* Van Straelen, 1924 from the "gres à *Micraster tercensis*" in the banks of the Garonne River. However, presence of the latter from Thanetian levels and its specific assignment has been refuted (Ossó et al., 2023, p. 5). Also, Goret et al. (2013), made a brief overview of the Thanetian decapod fauna of Boussens.

The decapod assemblage of Boussens, with a total of about 13 different brachyurans, shows a clear pre-eminence of eubrachyuran crabs and appears dominated by morphotype 7 (Figures 1N, O; 2F), and by *Litoricola macrodactyla* (Geryonidae Colosi, 1923) (Figures 1I, J; 2D), both belonging to Eubrachyura. The former is morphologically reminiscent of the Ypresian *Glyphithyreus almerai* Artal and Van Bakel, 2018 (Panopeidae Ortmann, 1893), which is particularly abundant in the lower Ypresian *Alveolina* limestones of the nearby outcrops of Fontcouverte (Aude, France) (Plaziat and Secrétan, 1971; Artal and Van Bakel, 2018).

From the Boussens assemblage, we describe the raninid *Rogueus belgodereae* n. sp., the third global occurrence of the genus and the second Palaeocene record. We also provide herein a compilation of Palaeocene brachyuran crabs, with only the distinction of their higher systematic placement: Podotremata or Eubrachyura, and of their general palaeoenvironmental occurrence: reefal, or nonreefal (see Table 1). This compilation gives a global overview of the faunal composition in different environments, helps to understand the recovery of Brachyura during the Palaeocene after the K/Pg event and later the explosive diversification during the Early and Middle Eocene.

GEOLOGICAL SETTINGS

The specimen studied herein was collected by one of us (D.T.) in the currently inactive Lafarge quarry, near Boussens, in the municipality of Martres Tolosane, Haute Garonne department, Southern France; co-ordinates 43°11'21.3"N 0°57'46.9"E.

This area is locally called the "Small Pyrenees" and represents a pre-belt at the base of the high peaks of the Pyrenees. The geological unit, formed of anticlinal and synclinal structures folded in the direction of WNW-ESE, is made up of an alternation of sandstones, marls and limestones, which can reach more than 100 m of thickness. The unit is covered in the north by discordant molassic formations and in the south by the overlap of the Pyrenean chain. The Lafarge quarry exploits the marls and limestones of the Lower Thanetian to the Upper Thanetian, the Unit 2 of Tambareau et al. (1995, p. 379). The Small Pyrenean Thanetian corresponds to a period of transgressions open to the Atlantic environment, which favours an important marine faunal contribution. Five marine transgressions have been recorded in the region from the early Palaeocene to the early Eocene, one during the Danian (T1), three during the Thanetian (T2-T4), and one during the lower Ypresian (T5) (Tambareau et al., 1995, figure 2). The crab described in this paper was discovered in lower Thanetian deposits.

Five different levels were recognised in the lower Thanetian (Villatte, 1962; Paris, 1971). These are from the base to the top:



FIGURE 1. Brachyuran crabs from the Thanetian (Upper Palaeocene) of Boussens, Martres Tolosane (France). **A**, *Cherpiocarcinus* sp., MNHN.F.A89305 dorsal view. **B-D**, Crab-morphotype 1, MNHN.F.A89306, B: dorsal view; C: frontal view; D: left lateral view. **E**, **F**, Crab-morphotype 2, MNHN.F.A89307, E: dorsal view; F: frontal view. **G**, Crab-morphotype 3, MNHN.F.A89308, dorsal view. **H**, Crab-morphotype 4 (*?Litoricola*), MNHN.F.A89309, dorsal view. **I**, *Litoricola macrodactyla* (Van Straelen, 1924), MGB 69155, dorsal view. **J**, *Litoricola macrodactyla* (Van Straelen, 1924), MNHN.F.A89310, dorsal view. **K**, Crab-morphotype 5, MNHN.F.A89311, dorsal view. **L**, **M**, Crab-morphotype 6, MNHN.F.A89312, L: dorsal view; M: frontal view. **N**, **O**, Crab-morphotype 7, MNHN.F.A89313, N: dorsal view; O: frontal view. **P**, **Q**, Crab-morphotype 8, MNHN.F.A89314, P: dorsal view; Q: frontal view. **R**, **S**, *Jakobsenius* sp. MNHN.F.A89315, R: dorsal view; S: frontal view. Scale bar equal to 10 mm, except B-D, P, Q, equal to 5 mm.

| TABLE 1. List of Palaeocene brachyuran crabs in reefal and non-reefal environments. (Age and environments accord- |
|---|
| ing with original and subsequent publications data. References are only informative. Asterisk [*] indicates species found |
| in both environments). |
| |

Reefal

....

| Locality/ Country | Genera/species | Podotremata | Eubrachyura | Age | Source | Ν |
|----------------------|--|-------------|-------------|--------------------------|------------------------------------|-----|
| Fakse | Dromiopsis depressus (Segerberg, 1900) | Х | | Danian | See Jakobsen and Collins, 1997 | 1 |
| " | D. rugosa (von Schlotheim, 1820) | х | | " | " | 2 |
| " | D. elegans Reuss, 1858 | х | | " | " | 3 |
| " | D. minor von Fischer-Benzon, 1866 | х | | ű | " ; see also Robin et al., 2016 | 4 |
| " | D. laevior Reuss, 1859 | х | | ű | See Jakobsen and Collins, 1997 | 5 |
| " | <i>Latheticocarcinus transiens</i> (Segerberg, 1900) | х | | ű | " | 6 |
| " | L. spiniga (Jakobsen and Collins, 1997) | х | | " | " | 7 |
| " | L. affinis (Jakobsen and Collins, 1997) | х | | " | " | 8 |
| " | <i>L. adelphinus</i> (Collins and Rasmussen, 1992) | х | | " | u | 9 |
| " | Raniliformis baltica (Segerberg, 1900) | х | | " | " | 10* |
| " | Necrocarcinus senonensis Schlüter in von der Marck and Schlüter, 1868 | х | | " | u | 11 |
| " | <i>Faksecarcinus gracilis</i> (Jakobsen and Collins, 1997) | х | | ű | " | 12 |
| " | <i>Caloxanthus ornata</i> (von Fischer-Benzon, 1866) | х | | ű | " | 13 |
| " | Kromtitis daniensis Collins, 2010 | х | | " | See Collins, 2010 | 14 |
| " | Cyclocorystes incertus (Segerberg, 1900) | | х | " | See Jakobsen and Collins, 1997 | 15 |
| Fakse/ Vigny | <i>Jakobsenius cretaceous</i> (Segerberg, 1900) | | х | " | " ; see also Robin et al., 2016 | 16* |
| Fakse | <i>Titanocarcinus subellipticus</i> (Segerberg, 1900) | | х | " | " | 17 |
| Fakse/ Vigny | <i>Titanocarcinus faxeensis</i> (von Fischer- Benzon, 1866) | | х | " | " ; see also Robin et al., 2016 | 18 |
| Vigny | <i>Dromilites montenati</i> Robin, Van Bakel, Pacaud and Charbonnier, 2016 | х | | ű | See Robin et al., 2016 | 19 |
| " | <i>Dromiopsis mosae</i> Collins, Fraaye and Jagt, 1995 | х | | ű | " | 20 |
| " | <i>Caloxanthus vignyensis</i> Klompmaker, Hyžný and Jakobsen, 2015 | х | | и | " | 21 |
| " | Xanthoidea indet. | | х | " | " | 22 |
| " | <i>Titanocarcinus schweitzerae</i> Robin, Van Bakel, Pacaud and Charbonnier, 2016 | | х | " | " | 23 |
| Kambühel | <i>T. kambuehelensis</i> Verhoff, Müller, Feldmann and Schweitzer, 2009 | | х | ?Selandian- Thanetian | See Verhoff et al., 2009 | 24 |
| | TOTAL | 17 | 7 | | | 24 |

TABLE 1 (continued). Non-reefal

| ocality/ ountry | ener <i>al</i> Decies | odotremata | ubrachyura | ee | əference | |
|--------------------------------------|--|------------|------------|---------------------|-------------------------------|----|
| <u> </u> | <u>ق ي</u> | å | ū | Ă | Ř | z |
| Sweden | Campylostoma bispinosa (Segerberg, 1900) | х | | Danian | See Segerberg, 1900 | 1 |
| " | Arcticocarcinus insignis (Segerberg, 1900) | Х | | " | " | 2 |
| The Netherlands/ Sweden | Raniliformis baltica (Segerberg, 1900) | Х | | " | See Jagt et al., 1993 | 3* |
| The Netherlands | <i>Dromiopsis</i> aff. <i>D. mosae</i> Collins, Fraaye and Jagt, 1995 | х | | " | See Jagt et al., 2014 | 4 |
| " | Lyreididae sp. | Х | | " | " | 5 |
| Texas (USA) | Kieronopsis nodosa Davidson, 1966 | х | | " | see Armstrong et al., 2009 | 6 |
| ű | <i>Pithonoton cardwelli</i> Armstrong, Nyborg, Bishop, Ossó-Morales and Vega, 2009 | х | | ű | и | 7 |
| " | Caloxanthus sp. | х | | " | " | 8 |
| Texas (USA)/Mexico/ Alabama (USA) | <i>Giulianolyreidus johnsoni</i> (Rathbun, 1935) | х | | " | u | 9 |
| Texas/Alabama/ Arkansas (USA) | Notosceles bournei (Rathbun, 1928) | х | | " | " | 10 |
| Texas (USA)/ Denmark | <i>Raninoides treldenaesensis</i> (Collins and Jakobsen, 2003) | х | | " | " | 11 |
| Texas (USA)/Mexico | <i>Tehuacana americana</i> (Rathbun, 1935) | | Х | " | " | 12 |
| Texas (USA) | <i>Costacopluma texana</i> Armstrong, Nyborg, Bishop, Ossó-Morales and Vega, 2009 | | Х | ű | ű | 13 |
| Texas (USA)/Mexico | <i>Paraverrucoides alabamensis</i> (Rathbun, 1935) | | Х | ű | ű | 14 |
| Texas (USA) | <i>Viapinnixa mexiaensis</i> Armstrong, Nyborg, Bishop, Ossó-Morales and Vega, 2009 | | Х | ű | ű | 15 |
| California (USA) | Cyclocorystes aldersoni Squires, 1980 | | Х | | See Squires, 1980 | 16 |
| u | <i>Costacopluma squiresi</i> Nyborg, Vega and Filkorn, 2009 | | Х | | See Nyborg et al., 2009 | 17 |
| Argentina | <i>Archaeogeryon lophos</i> (Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995) | | х | " | See Feldmann et al., 1995 | 18 |
| ű | <i>Lobulata lobulata</i> (Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995) | | Х | ű | ű | 19 |
| " | Rocacarcinus gerthi (Glaessner, 1930) | | Х | " | " | 20 |
| " | <i>Chirinocarcinus wichmanni</i> (Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995) | | Х | ű | ű | 21 |
| ű | <i>Palaeopinnixa rocaensis</i> (Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995) | | Х | ű | и | 22 |
| " | <i>Costacopluma australis</i> Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995 | | Х | " | u | 23 |
| Alabama (USA) | <i>Costacopluma grayi</i> Feldmann, Schweitzer and Portell, 2014 | | х | Lower Palaeocene | See Feldmann et al., 2014 | 24 |
| ű | <i>Stevea martini</i> Feldmann, Schweitzer and Portell, 2014 | | х | " | ű | 25 |
| " | Matutites americanus (Rathbun, 1935) | | х | " | See Feldmann et al., 2019 | 26 |

TABLE 1 (continued).

| scality/ suntry | anera/ ecies | odotremata | lbrachyura | e | sference | |
|---------------------------|--|------------|------------|----------------------|---|----|
| čč | s ë | Рс | Er | Āç | Re | z |
| Alabama (USA) / Mexico | <i>Quasilaeviranina ovalis</i> (Rathbun, 1935) | х | | u | See Tucker, 1998; Martínez-Díaz et al., 2017 | 27 |
| Greenland | <i>Cristella hastata</i> Collins and Rasmussen, 1992 | х | | Lower Palaeocene | See Collins and Rasmussen, 1992 | 28 |
| Jamaica | <i>Trechmannius circularis</i> Collins and Donovan, 2006 | х | | " | See Collins and Donovan, 2006 | 29 |
| North Dakota (USA) | <i>Camarocarcinus arnesoni</i> Holland and Cvancara, 1958 | Х | | Palaeocene | See Holland and Cvancara, 1958 | 30 |
| Senegal | <i>Costacopluma senegalensis</i> (Rémy in Gorodiski and Rémy, 1959) | | Х | Palaeocene | See Gorodisky and Rémy, 1959 | 31 |
| " | ? <i>Branchioplax ballingi</i> Rémy in Rémy and Tessier, 1954 | | Х | ** | See Schweitzer and Feldmann, 2010 | 32 |
| Venezuela | <i>Costacopluma bífida</i> Collins, Higgs, and Cortitula, 1994 | | Х | Palaeocene | See Collins et al., 1994 | 33 |
| " | Costacopluma sp. | | Х | " | See Luque et al., 2017 | 34 |
| Brasil | Raninoides sp. | х | | " | " | 35 |
| " | <i>Costacopluma nordestina</i> Feldmann and Martins-Neto, 1995 | | Х | " | See Feldmann and Martins-Neto, 1995 | 36 |
| " | "Necrocarcinus" sp. | | Х | " | See Távora and Miranda, 2004 | 37 |
| u | <i>"Lobonotus" sturgeoni</i> (Feldmann, Bice, Schweitzer-Hopkins, Salva, and Pickford, 1998) | | х | u | See Távora et al., 2005 | 38 |
| Colombia | Indet. sp. | | Х | ** | See Luque et al., 2017 | 39 |
| India | <i>Goniocypoda rajasthanica</i> Glaessner and Rao, 1960 | | Х | ** | See Glaessner and Rao, 1960 | 40 |
| Greenland | <i>Macroacaena bispinulata</i> (Collins and Rasmussen, 1992) | х | | Middle Palaeocene | See Collins and Rasmussen, 1992; Tucker, 1998 | 41 |
| " | <i>Laeviranina borealis</i> Collins and Rasmussen, 1992 | х | | " | See Collins and Rasmussen, 1992 | 42 |
| " | <i>Camarocarcinus quinquetuberculatus</i> Collins and Rasmussen, 1992 | х | | " | " | 43 |
| " | <i>Verrucoides verrucoides</i> (Collins and Rasmussen, 1992) | | Х | " | " | 44 |
| " | <i>Viapinnixa nodosa</i> (Collins and Rasmussen, 1992) | | Х | " | " | 45 |
| Denmark | <i>Rogueus robustus</i> Collins and Jakobsen, 1996 | х | | Selandian | See Collins and Jakobsen, 1996 | 46 |
| Mexico | Notopoides sp. | х | | " | See Martínez-Díaz et al., 2017 | 47 |
| " | Quasilaeviranina sp. | х | | " | " | 48 |
| ű | <i>Claudioranina latacantha</i> Martínez-Díaz, Aguillón-martínez, Luque and Vega, 2017 | х | | " | ű | 49 |
| " | Claudioranina sp. | х | | " | " | 50 |

TABLE 1 (continued).

| Locality/ Country | Genera/ species | Podotremata | Eubrachyura | Age | Reference | z |
|----------------------|--|-------------|-------------|------------|---------------------------------|----|
| ű | <i>Macroacaena venturai</i> Vega, Nyborg, Fraaije, and Espinosa, 2007 | Х | | " | See Luque et al., 2017 | 51 |
| ű | <i>Viapinnixa perrilliatae</i> Vega, Nyborg, Fraaye, and Espinosa, 2007 | | х | ű | ű | 52 |
| Sardinia (Italy) | Titanocarcinus cf. subellipticus | | х | " | See Dieni, 2010 | 53 |
| Germany | Xanthilites traubi Förster, 1970 | | х | Thanetian | See Förster, 1970 | 54 |
| " | X. interpunctus Förster, 1970 | | х | ? | " | 55 |
| " | <i>Titanocarcinus reisi</i> Böhm, 1891 | | х | " | " | 56 |
| Тодо | Pleolobites erinaceus Rémy, 1960 | | х | ű | See Ossó et al., 2022 | 57 |
| Pakistan | <i>Proxicarpilius planifrons</i> Collins and Morris, 1978 | | х | Thanetian? | See Charbonnier et al., 2013 | 58 |
| ű | <i>Pakicarcinus orientalis</i> (Collins and Morris, 1978) | | х | ű | ű | 59 |
| ű | Glyphithyreus wetherelli (Bell, 1858) | | х | " | See Collins and Morris, 1978 | 60 |
| Boussens | <i>Rogueus belgodereae</i> n. sp. | Х | | Thanetian | This paper | 61 |
| " | Cherpiocarcinus sp. | Х | | " | " | 62 |
| " | Crab sp. 1 | ? | ? | " | " | 63 |
| " | Crab sp. 2 | ? | ? | " | " | 64 |
| " | Crab sp. 3 | ? | ? | " | " | 65 |
| " | Crab sp. 4 <i>Litoricola</i> ? | | Х | " | " | 66 |
| ű | Litoricola macrodactyla (Van Straelen, 1924) | | х | ű | See Van Straelen, 1924 | 67 |
| " | Crab sp. 5 | | х | " | This paper | 68 |
| " | Crab sp. 6 | | х | " | " | 69 |
| " | Crab sp. 7 | | х | " | " | 70 |
| " | Crab sp. 8 | | х | " | " | 71 |
| " | Jakobsenius sp. | | х | " | " | 72 |
| | TOTAL | 27 (3?) | 42 (3?) | | | 72 |

- 1 "Calcaires à Miliolidés et Echinanthus"
- 2 "Marnes gréseuses à moules internes de Mollusques"
- 3 "Calcaires à Miliolidés, Madréporaires et Mollusques"
- 4 "Grès à Echinanthus et Ostrea bellovacensis"
- 5 "Marno-calcaires gréseux à Operculina heberti, Orbitoclypeus seunesi et Micraster tercensis"

The uppermost level, level 5, yielded the crab specimens described in this paper; these were collected in 2015 by one of us (D.T.). The "*M. tercensis* marly limestones", reflects the second

Thanetian transgression (T3) in the aforementioned Unit 2, and indicates an external carbonatic shelf, dated as Thanetian based on the benthic foraminifera associations of *Operculina heberti - Orbitoclypeus seunesi*, and *Glomalveolina primaeva -Fallotella alavensis*, which correspond to the *G. primaeva* biozone, correlated with the NP6-NP8 and P3-P4 planktonic zonations (Tambareau et al., 1995:, p. 379, figures 2, 3). The presence of *Pycnodonte leymeriei* Villatte, 1962 in these marly limestones of the *M. tercensis* complex, documents a deep-water deposit (Villatte, 1962). The studied specimens come from the base of this level, which is rich in echinoids (*Micraster (Pseudogibbaster*)



FIGURE 2. A, General view of Lafarge quarry, Boussens, municipality of Martres Tolosane, Haute Garonne (France), in the background, the south, with the Pyrenees. **B**, crab-morphotype 5 in situ, from the upper Thanetian (T4) (star). **C**, close-up of the extraction front of the "gres à *Micraster tercensis*" level, before the abandonment and renaturation of the quarry. **D**, *Litoricola macrodactyla* (Van Straelen, 1924) in situ. **E**, **G**, *Rogueus belgodereae* sp. nov. in situ. **F**, crab-morphotype 7 in situ.

tercensis (Cotteau, 1863), *Hemiaster stella* (Morton, 1830), *Gauthieria pseudomagnifica* (Cotteau, 1877), *Dorocidaris bazerquei* (Lambert, 1908), *Hemiaster (Linthia?) canaliculatus* Cotteau, 1856 and internal moulds of molluscs. This level also provides many remains of the brachyuran *Litoricola macrodactyla* (Van Straelen, 1924) and other crabs (Figure 2), preliminary reported in the present paper. Overlying levels corresponding to the third Thanetian transgression (T4), of *Glomalveolina levis* biozone, which also yielded some crabs (Figure 1K, 2F; Tambareau et al., 1995, figure 2).

SYSTEMATIC PALAEONTOLOGY

Institutional abbreviations for specimens referred to herein: **MNHN.F** = Collection de Paléontologie, Muséum national d'Histoire naturelle, Paris, France.

We follow the higher Brachyura classification scheme of Guinot et al. (2013, table 1), and Jagt et

al. (2015, table 1), and the classification of the Gymnopleura of Van Bakel et al. (2012, table 1) and Van Bakel et al. (2021, figure 7).

Infraorder BRACHYURA Linnaeus, 1758 Section PODOTREMATA Guinot, 1977 Subsection GYMNOPLEURA Bourne, 1922 Superfamily RANINOIDEA De Haan, 1839 Family LYREIDIDAE Guinot, 1993 Subfamily LYREIDINAE Guinot, 1993 (=ROGUEINAE Karasawa, Schweitzer, Feldmann and Luque, 2014)

Genus ROGUEUS Berglund and Feldmann, 1989

Type species. *Rogueus orri* Berglund and Feldmann, 1989, by monotypy.

Species included. *Rogueus orri, R. robustus* Collins and Jakobsen, 1996, and *R. belgodereae* n. sp.

Remarks. Remarks on *Rogueus*, and on the type species *Rogueus orri*, were made by Van Bakel et al. (2012, p. 84, 85). These authors considered

Rogueus an early member of the subfamily Lyreidinae and noted the similarity of the front with that of *Marylyreidus* Van Bakel, Guinot, Artal, Fraaije and Jagt, 2012.

Karasawa et al. (2014, p. 227) stated in their cladistic analysis that Rogueus lacked the ambiguous character of a well-developed outer orbital spine. We observe that the type species shows a distinct outer orbital spine (Berglund and Feldmann, 1989, figures. 2.1; 2.2) as well as the other two included species (see above). Also, Karasawa et al. (2014, p. 227) stated that Rogueus exhibits an autapomorphic character, namely an anterolateral spine with a subspine, and stated that therefore a new monogeneric subfamily should be erected for Rogueus. However, subspines are a commonly observed character in Raninoidea: in Amphoranina Nyborg, Pasini, Garassino, Van Bakel, Vega and Nyborg, 2020; Doraranina Gustafson, Nyborg and Van Bakel, 2019; Ranina Lamarck, 1801; Pseudorogueus Fraaye, 1995; Bicornisranina Nyborg and Fam, 2008; and Rogueus this character is present. The overall appearance of Bicornisranina and Pseudorogueus are similar to that of Rogueus, however, they are assigned to Raninoidinae Lőrenthey in Lőrenthey and Beurlen, 1929 (Nyborg and Fam, 2008; Van Bakel et al., 2012; Karasawa et al., 2014) based on the diagnosis of in particular the orbitofrontal margin.

The unique character set ascribed to the Rogueinae ("(...)wide fronto-orbital width, a bifid rostral tip, the lack of intra-orbital spines and orbital

fissures, and possession of a lyreidine-like sternum") are all plesiomorphic characters in the Lyreididae (Van Bakel et al., 2012, p. 75) and the genus fits well within Lyreidinae; therefore, we consider Rogueinae synonymous to Lyreidinae. Basal members of the Lyreidinae appear to have a wide orbitofrontal margin (Van Bakel et al. 2012), which accounts for *Rogueus. Rogueus* does not show a basal condition of the thoracic sternum as in Marylyreidinae; the anterior extensions of thoracic sternite 4 are well developed and connected to pterygostome (sternum/pterygostome junction).

Collins and Jakobsen (1995, p. 64) discussed that the earlier age of the Danish species suggested a European origin and subsequent westerly migration of the genus. The new material described herein is slightly younger than *R. robustus* from Denmark and suggests that the genus was widespread in Europe in the Palaeocene.

Rogueus belgodereae n. sp. Figure 3A-C

zoobank.org/AF048BFB-6114-444C-BECC-662D65C4B05C

Etymology. Named after Valérie Belgodere (Pechbonnieu, France), who has supported the second author (D.T.) and his passion, for more than 30 years.

Diagnosis. *Rogueus* with short, stout anterolateral spines, a widened orbitofrontal margin with anterolaterally directed outer orbital spines, and smooth dorsal carapace surface.

Type. The holotype is MNHN.F.A88045, a well-preserved complete carapace with the cuticle pre-



FIGURE 3. A-C *Rogueus belgodereae* n.sp, A: holotype MNHN.F.A88045. B, paratype MNHN.F.A88046, C, paratype MNHN.F.A88047. Scale bar equals 1 cm.

served; maximum carapace length: 26.5 mm, maximum carapace width (including lateral spines): 19.5 mm, orbitofrontal width: 12.5 mm. Paratypes MNHN.F.A88046 and MNHN.F.A88047 represent partial carapaces with portions of cuticle preserved. All material comes from the Lafarge quarry, Martres Tolosane, Haute Garonne, France.

Description. Carapace of moderate size (length of holotype: 26.5 mm, width 19.5 mm), elongated, width 74% of length, outline subhexagonal, maximum width (excluding anterolateral spine) at approximately 43% of total carapace length from front; dorsal surface gently convex in transverse cross section, gently arched in longitudinal crosssection. Orbitofrontal width approximately 69% of maximum carapace width; front narrow, tip blunt, bifid; orbits large, horizontally orientated in dorsal view, supraorbital margin sinuous, with a single short, distinct notch, inner portion of orbital margin concave, outer part first convex, then concave towards prominent outer orbital spine, directed slightly outwards. Anterolateral margins short, rounded in cross section, short concave margin continuously curved into robust anterolateral spine, with broad basis, directed anteriorly and outwardly, anterior margin with anteriorly directed sub-spine. Margins posterior to the lateral spines diverging, straight or gently convex. Posterolateral margins long, smooth, gently sinuous, convergent. Posterior margin straight, narrow (approximately 28% maximum carapace width).

Dorsal regions undefined; cervical groove visible axially as arched scars; hepatic region weakly swollen, cardiac region large, wide, defined by crescent-shaped branchiocardiac grooves. Gastric pits minute, well separated.

Dorsal carapace surface appears overall smooth, exocuticle not preserved. Diminutive granules and pits present in frontal region and near base of anterolateral spine.

Remarks. *Rogueus belgodereae* n. sp. differs from the type of the genus, *R. orri* from the lower middle Eocene of southwestern Oregon, U.S.A., in having clearly shorter, more robust lateral spines (slenderer and more elongated in *R. orri*), a stronger, more laterally directed outer orbital spine, and a smoother, less pitted carapace surface microstructure. *Rogueus robustus*, from the middle Palaeocene of northern Sjaelland, Denmark, is readily distinguished from *R. belgodereae* n. sp. by the former clearly having elongated anterolateral spines, a longer anterolateral margin between the outer orbital spine and anterolateral spines, and clearly pitted carapace microstructure. The subdistal spine of the anterolateral spine is distally placed in *R. orri* and *R. robustus*, giving the elongated anterolateral spine a bifurcate appearance; because the anterolateral spine is so short in *R. belgodereae* n. sp. the subdistal spine is positioned halfway the anterolateral spine.

DISCUSSION

The Boussens assemblage presented herein is currently under study, and as preliminary results we recognize 13 different crab species. This means the assemblage constitutes one of the richest Palaeocene brachyuran faunas globally and significantly contributes to the knowledge of brachyurans during the Palaeocene.

Among this fauna, eight species are unquestionably eubrachyurans, and two are podotremes, whereas three of them have an unclear taxonomic placement at the moment.

This faunal composition reasserts the trend observed in the Palaeocene faunas (Schweitzer and Feldmann, 2015, figures 7B, C), in which the podotreme crabs dominated the reefal environments, in a broad sense, indistinctly of whether they are coral, coralgal or bryozoan environments, and the eubrachyuran crabs, in turn, dominated the non-reefal environments (Figure 4). Even though the age calibration of the Palaeocene fossil taxa is not always well documented, it appears that in the late Palaeocene the number of eubrachyuran taxa is higher than the podotremes, with which also concludes the extensive analysis of Schweitzer and Feldmann (2023). More research is needed to verify this observation.

Brachyuran crabs, like most forms of life, suffered the consequences of the K/Pg event (Sch-



FIGURE 4. Faunal composition of the known Palaeocene brachyurans, and its distribution in reefal and nonreefal environments. weitzer and Feldmann, 2023, p. 3, and references therein). However, based on the fossil record, it seems that they quickly recovered and were able to restock both reefal and non-reefal environments (e.g., Schweitzer and Feldmann, 2023, and references therein). Schweitzer and Feldmann (2005) discussed the decapod faunal turnover after the K/ Pg event, and compiled data on families and genera that became extinct or survived, concluding that the decapods were one of the least affected groups by the K/Pg event.

Thus, despite the apparent low diversity of brachyuran families in Palaeocene times, it appears that they constituted a robust fauna that gave rise to the explosive evolutionary diversification of decapods during the Early Eocene Climatic Optimum.

The scant knowledge of marine Palaeocene faunules globally hampers our vision of the brachyuran fauna of that time interval.

CONCLUSIONS

Rogueus belgodereae n. sp. constitutes the third member of this lyreidid crab genus, and the second record for Europe and the Palaeocene. The new species differs most significantly from the other members in having clearly shorter, more robust lateral spines. The crab specimens described in this study originate from the second Thanetian transgression. The genus *Rogueus* was used to erect a distinct subfamily, but we conclude that Rogueinae is synonymous to Lyreidinae.

Our comprehensive compilation of Palaeocene brachyuran crabs, shows a rapid recovery after the K/Pg extinction event. The Boussens decapod assemblage, still undergoing study, comes from a non-reefal environment, which is remarkable for the Palaeocene. Also, with 13 species, it represents one of the richest Palaeocene brachyuran faunas globally; a robust fauna that gave rise to the explosive evolutionary diversification of decapods during the Early Eocene Climatic Optimum. Eubrachyuran crabs dominate this fauna, a composition that differs from similar-aged reefal environments. The faunal assemblage of Boussens presented herein, enriches our knowledge of Palaeocene crustacean faunules.

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