

## **Revision of *Dromilites bucklandii* (Crustacea, Decapoda, Brachyura): Type material revealing its real identity, a junior synonym, and a new species**

**Barry W.M. van Bakel, Ninon Robin, Sylvain Charbonnier, and Jeff Saward**

### **ABSTRACT**

Some of the fossil crabs from the lower Eocene London Clay have recently been the subject of several revisions, among them the exquisitely preserved dromiid (sponge) crabs. We examined Milne Edwards' original type material of *Dromilites bucklandii*, which appears different from all subsequently figured specimens by later authors. The type of *D. bucklandii* is conspecific with the much later described *D. simplex* Quayle and Collins, 1981. Specimens typically referred to as *D. bucklandii* by subsequent authors, of whom Bell (1858) is the most referred to, are here formally described as a new species, *D. belli* n. sp. This new species is described based on Bell's figured material and novel specimens, which show marked ontogenetic variation in the carapace areolation. To document ontogenetic variation and sexual dimorphism, we studied size ranges, variation in ornamentation, and sex (which in many occasions could be determined because the abdomen was preserved) for all examined material. These comparisons rely on the new imaging of measured specimens, which had hitherto been unavailable for research. We provide through this study the description and figuring of type material, which had only been coarsely described (and often non-figured) by nineteenth century researchers. This improves our knowledge of extinct brachyurans; we here provide figures of all British type specimens of *Dromilites*.

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## INTRODUCTION

Improving knowledge of fossil diversity may be extremely dependent on the accessibility of the type material, sometimes not figured, and most of the time very generally described by nineteenth century researchers. The fossil crab species *Dromilites bucklandii* has been widely reported by paleontologists in the Eocene of Europe. Authorship of *Dromilites bucklandii* is ascribed to H. Milne Edwards, who described it in 1837 after material from the Eocene of the Isle of Sheppey deposited at the Muséum d'Histoire Naturelle de Paris, and erected the genus *Dromilites* without assigning it any species nor providing its description. Thus considered as a *nomen nudum* for 20 years, the genus *Dromilites* was formally erected in 1858 by Bell, who provided its first description and put the previously described *Dromia bucklandii* Milne Edwards, 1837, as a species of the genus and figured the species with a series of English specimens housed at the Natural History Museum of London. Subsequent studies dealing with *D. bucklandii* always published the species as described in Bell (1858), without referring to Milne Edwards' original type material (e.g., Beurlen, 1928; Glaessner, 1929; Wrigley, 1945; Schweitzer and Feldmann, 2010; Quayle and Collins, 2012). In 1981, Quayle and Collins described a new species, rarer than *D. bucklandii* (sensu Bell, 1858), displaying much flatter and smoother carapace regions that they named *D. simplex*. After examination of the type material of Milne Edwards housed in the MNHN, we evidence here that the species described in Bell (1858) and widely used by subsequent authors is not conspecific to that of H. Milne Edwards (1837a). Further to this observation, we herein study ancient and new specimens of *Dromilites* by providing good imaging and comment on the features and ontogenetic changes of different morphotypes.

## MATERIAL AND METHODS

### Institutional Abbreviations

**HMCMS**: Hampshire Museum's Collections, United Kingdom; **MNHN.F**: Collection de Paléontologie, Muséum national d'Histoire naturelle, Paris, France; **NHMUK PI**: Collection of Invertebrate Paleontology, Natural History Museum, London, United Kingdom; **MAB**, Oertijdmuseum De Groene Poort collections, Boxtel, the Netherlands.

### Anatomical Abbreviations

**CL**, carapace length (exclusive of rostrum); **CW**, carapace width (excluding lateral spines); **FM**, frontal margin width; **OFM**, orbitofrontal margin width; **PM**, posterior margin width.

## SYSTEMATIC PALAEOLOGY

Order DECAPODA Latreille, 1802

Infraorder BRACHYURA Latreille, 1802

Section PODOTREMATA Guinot, 1977

Subsection DYNOMENIFORMIA Guinot, Tavares and Castro, 2013

Superfamily DROMIOIDEA De Haan, 1833

Family DROMIIDAE De Haan, 1833

Subfamily SPHAERODROMIINAE Guinot and Tavares, 2003

Genus DROMILITES H. Milne Edwards in Bell, 1858

- |       |   |
|-------|---|
| 1837b | <i>Dromilite</i> H. Milne Edwards; H. Milne Edwards, p. 255 ( <i>nomen nudum</i> ).     |
| 1837c | <i>Dromilite</i> H. Milne Edwards; H. Milne Edwards, p. 115–116 ( <i>nomen nudum</i> ). |
| 1838  | <i>Dromilite</i> H. Milne Edwards; H. Milne Edwards, p. 482 ( <i>nomen nudum</i> ).     |
| 1858  | <i>Dromilites</i> H. Milne Edwards; Bell, p. 27–29.                                     |
| 1929  | <i>Dromilites</i> H. Milne Edwards; Glaessner, p. 139.                                  |
| 1969  | <i>Dromilites</i> H. Milne Edwards; Glaessner, p. R487 and subsequent authors.          |

**Type species.** *Dromia bucklandii* H. Milne Edwards, 1837a, by subsequent designation of Glaessner (1929).

**Included species.** *Dromilites bucklandii* (H. Milne Edwards, 1837a) (as *Dromia bucklandi*) (= *D. simplex* Quayle and Collins, 1981); *D. pastoris* Via, 1959; *D. vicensis* Barnolas Cortinas, 1973; ?*Dromilites cardwelli* (Armstrong, Nyborg, Bishop, Ossó-Morales, and Vega, 2009, as *Pithonoton*); *D. montenati* Robin, Van Bakel, Pacaud, and Charbonnier, 2016; *D. belli* n. sp.

**Remarks.** The nomenclature of *Dromilites* has been quite problematic, as stated by Quayle and Collins (1981), Schweitzer and Feldmann (2010), Guinot et al. (2013), and Robin et al. (2016). Here we follow the nomenclatural resolution of these latter authors (*Dromilites* H. Milne Edwards in Bell, 1858). As for included species, we note that *Pithonoton cardwelli* Armstrong, Nyborg, Bishop, Ossó-Morales, and Vega, 2009, *Dromilites*? by Schweitzer and Feldmann (2012), is discussed and transferred to *Pithonoton* again by Ossó (in press).

*Dromilites bucklandii* (H. Milne Edwards, 1837a)  
Figure 1, Table, and Appendix

- |       |  |
|-------|--|
| 1837a | <i>Dromia bucklandii</i> H. Milne Edwards; H. Milne Edwards, p. 178–179.   |
| 1981  | <i>Dromilites simplex</i> Quayle and Collins; Quayle and Collins, p. 736–737, pl. 104, figs. 1-3, 10 (nov. syn.) |
| 1991  | <i>Dromilites simplex</i> Quayle and Collins; Müller and Collins, p. 62.   |
| 2001  | <i>Dromilites simplex</i> Quayle and Collins; Guinot and Tavares, p. 531.  |
| 2006  | <i>Dromilites simplex</i> Quayle and Collins; Collins and Saward, p. 68, table 1.                                |
| 2009  | <i>Dromilites simplex</i> Quayle and Collins; Rayner et al., p. 55.  |
| 2009  | <i>Dromilites simplex</i> Quayle and Collins; Van Bakel et al., p. 56.   |
| 2010  | <i>Dromilites simplex</i> Quayle and Collins; Schweitzer et al., p. 64.  |
| 2010  | <i>Dromilites simplex</i> Quayle and Collins; Schweitzer and Feldmann, p. 423–425, figs. 4-5.                    |
| 2012  | <i>Dromilites simplex</i> Quayle and Collins; Schweitzer and Feldmann, p. 594.                                   |
| 2012  | <i>Dromilites simplex</i> Quayle and Collins; Quayle and Collins, p. 36, table 1–2.                              |
| 2016  | <i>Dromilites simplex</i> Quayle and Collins; Artal et al., 2016, p. 443.  |

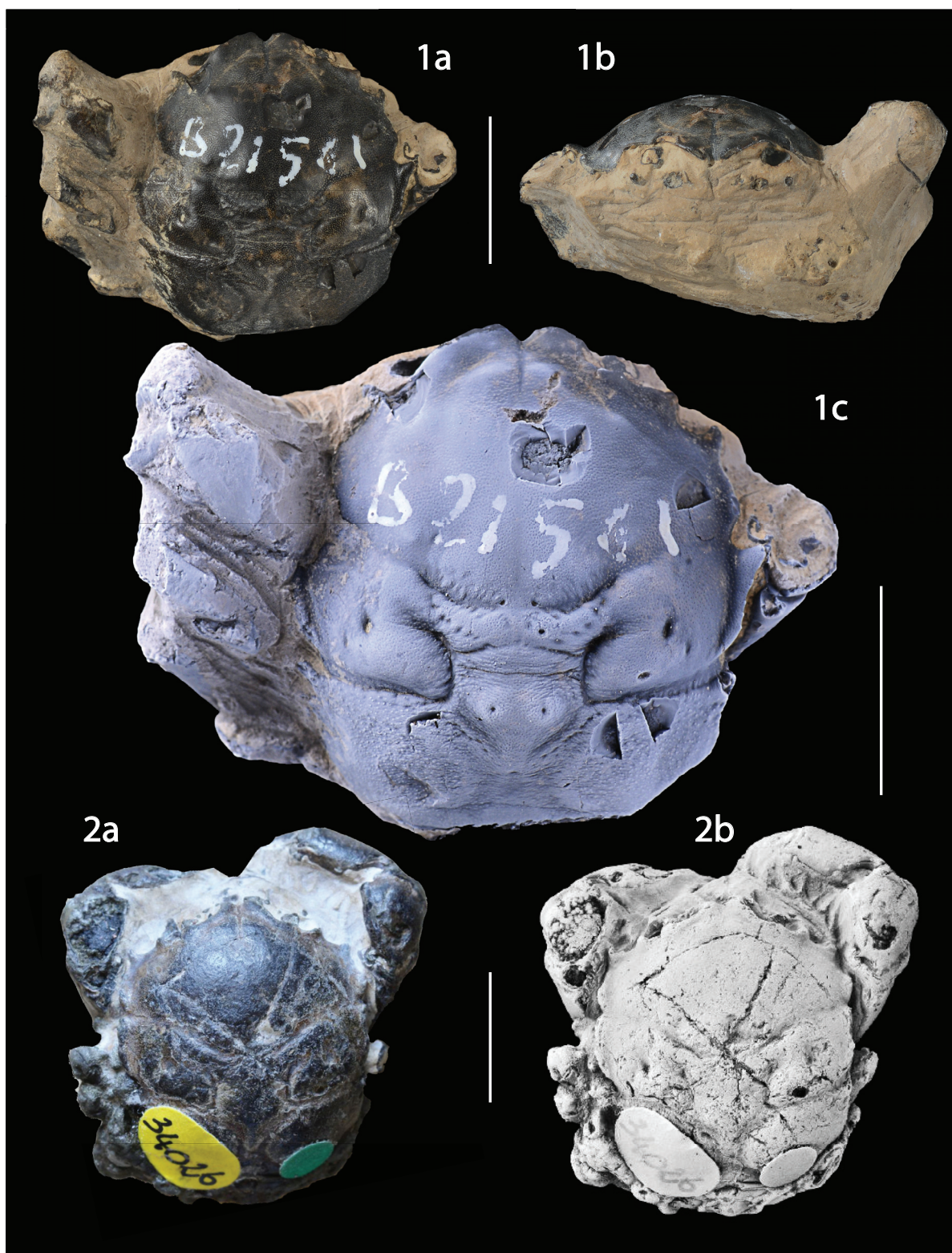
**Type material.** H. Milne Edwards (1837a) did not report if there was more than one specimen included in his type series. Only one syntype is housed in the palaeontological collections of the MNHN, Paris, in H. Milne Edwards' collection (labeled “*bucklandi*”, “Sheppey (Angleterre)”, “Eocène”, with a Milne-Edwards catalog number).

We select this specimen MNHN.F.B21561 to be the lectotype (see Figure 1a-1c).

**Additional material examined.** NHMUK PI IC 34026 (Spencer coll.) (male, London Clay, Highgate, London, 51°34'18.29"N/0°9'0.82"W); NHMUK PI In.28173 (Venables coll.) (London Clay, Bognor Regis, Sussex, 50°46'58.82"N/0°40'23.00"W); NHMUK PI In.61700 (Elmore Formation, Unit 7, Lee-on-the-Solent, Hampshire, 50°48'7.54"N/1°12'8.47"W); NHMUK PI IC 548 (London Clay); MAB.k. 3590 (Isle of Sheppey, foreshore exposure, Kent, United Kingdom, 51°20'36.77"N/1°0'2.76"E), figured in Rayner et al., 2009, p. 55 (Isle of Sheppey foreshore exposure, Kent, United Kingdom) (see Table).

**Remarks on type specimens.** H. Milne Edwards (1837a) described, but did not figure *Dromia bucklandii*. Bell (1858) was the first to use Milne Edwards' species including it in *Dromilites*, and published a plate with figures of specimens currently held at the NHMUK (Wetherell coll.). His description is clearly based on these figured specimens. Specimens conspecific to Bell's species have been referred to as *D. bucklandii* by all subsequent authors, such as Quayle and Collins (1981) and Schweitzer and Feldmann (2010). However, none of these authors have apparently examined the original type material of Milne Edwards. One syntype of *D. bucklandii*, MNHN.F.B21561, is still housed in the MNHN collections (see Figure 1C) and has never been figured or referred to in later works on the species. After careful examination, it appears that this specimen has a rather smooth carapace preserved with the cuticle with regions not strongly inflated or marked with strong tubercles. It is not conspecific to the material figured and described by Bell (1858), as further explained below. This means that Bell (1858) described and figured specimens that did not correspond to *D. bucklandii* (this has no influence on the type species designation of *Dromilites*, which is only a nomenclatural act, and Bell was the first to use the species for this genus).

Quayle and Collins (1981) described *D. simplex*. They discussed (p. 737) that “the absence of marked tuberculation throughout these stages, together with weakly developed, non-bifurcated marginal spines and lack of transverse tubercles on the urogastric lobe immediately distinguishes this species from *D. bucklandii*.” When comparing to *D. bucklandii* they obviously referred to the specimens figured and described by Bell (1858), but not to the type material of H. Milne Edwards. Now having examined both the type material of *D. bucklan-*



**FIGURE 1.** *Dromilites bucklandii* H. Milne Edwards, 1937. **1.** Lectotype MNHN.F.B21561: (London Clay, Isle of Sheppey, Kent, United Kingdom): 1a. carapace in dorsal view, 1b. carapace in frontal view, 1c. carapace coated with ammonium chloride in dorsal view, **2.** Holotype NHMUK PI IC 34026 (London Clay, Highgate, London, UK; Spencer coll.) of *Dromilites simplex*, nov. syn. of *D. bucklandii*: 2a. colored dorsal view, 2b. black and white dorsal view. Scale bars equal 10 mm. Photographs: Lilian Cazes (1) and Barry van Bakel (2).

**TABLE.** Comparative carapace lengths of both examined material of *Dromilites bucklandii* H. Milne Edwards, 1837 and *Dromilites belli* n. sp.

Carapace lengths of the examined material of <i>Dromilites</i>							
<i>D. bucklandii</i>	Carapace length (in mm, excluding rostrum)	Carapace width (in mm, excluding lateral spines)	Sex	<i>D. belli</i> n. sp.	Carapace length (in mm)	Carapace width (in mm, excluding lateral spines)	Sex
NHMUK PI In.61700	14.2	16.22	unknown	MNHN.F.R03853	17.5	18.2	unknown
NHMUK PI In.28173	16.1	15.5	unknown	MAB.k 3583	17.5	19.7	unknown
NHMUK PI IC 548	20.1	14.6	female	MNHN.F.A66911	21.5	19.5	unknown
MNHN.F.B21561	21.5	21.4	unknown	MNHN.F.R03854	29	27	unknown
NHMUK PI IC 34026	22.3	18.5	male	NHMUK PI OR 59089	32	31.5	female
MAB.k 3590	24	21	unknown	Rayner et al., 2009, p.56	33,5	31	female
Rayner et al., 2009, p.55, 'sp. 1'	26	21.5	unknown	MAB.k 3586	25	23	male
			unknown	NHMUK PI OR 59091	35,5	37	male

*dii* and *D. simplex*, we can conclude that the latter is a junior synonym of *D. bucklandii*.

**Description.** Carapace subovate, length slightly exceeding width (holotype dimensions: CL= 21.5 mm, CW= 19.5 mm, FM= 7.5 mm, OFM= 14 mm, PM= 11.2 mm), maximum width at midlength, convex in longitudinal cross section, strongly convex in transverse cross section; orbitofrontal margin prominent, wide, 72% maximum carapace width. Rostrum projected beyond orbits, large, broadly triangular, bilobed, axially notched, frontal margin slightly convex; orbits forwardly, outwardly directed, upper orbital margin concave, outer orbital corner angular. Lateral margin angular in cross section; anterolateral margin weakly convex, with three strong teeth two anterior, one posterior to cervical notch; anterior two teeth pointed triangular; third lateral spine prominent, flattened anteriorly, outwardly directed, posteriorly forming flanged lateral margin with four to five granules. Posterolateral margin short, anteriorly straight, posteriorly strongly curved, anteriorly bearing single small forwardly directed tooth. Posterior margin slightly shorter than orbitofrontal margin, straight, rimmed.

Carapace regions rather smooth, marked by acute, shallow grooves; small epigastric swellings closely spaced, separated by short sulcus, mesogastric region undefined anteriorly, posteriorly only at base, wide, without tubercles, indistinct median groove. Protogastric regions flat; hepatic region inclined. Metagastric region trapezoidal, wide anteriorly, posterior margin inverted V-shape, surface laterally with oblique line of four to five pits,

medially with indistinct paired gastric pits. Urogastric region low, triangular, apex directed forwards. Cardiac region weakly inflated, diamond-shaped, apex pointed posteriorly, centrally bearing two horizontally lined low bumps, pitted; intestinal region large, flat. Branchial region large, subdivided by oblique postcervical, branchial grooves; epibranchial, mesobranchial regions weakly vaulted; metabranchial region large, weakly vaulted.

Cervical groove widely V-shaped, deep, distinct on medial carapace, interrupted at axis by gastric pits, faint laterally, weakly notching carapace margin; branchial grooves more horizontal than cervical groove, acute, distinctly notching lateral margin; post-cervical grooves shallow, indistinct, conspicuously short; branchiocardiac grooves deep, curved, posteriorly converging to intestinal region.

Carapace epicuticle with numerous evenly spaced setal pits, microgranules. Internal mold and its ornamentation unknown.

**Range.** London Clay, Ypresian, lower Eocene.

**Occurrence.** London and Hampshire basins.

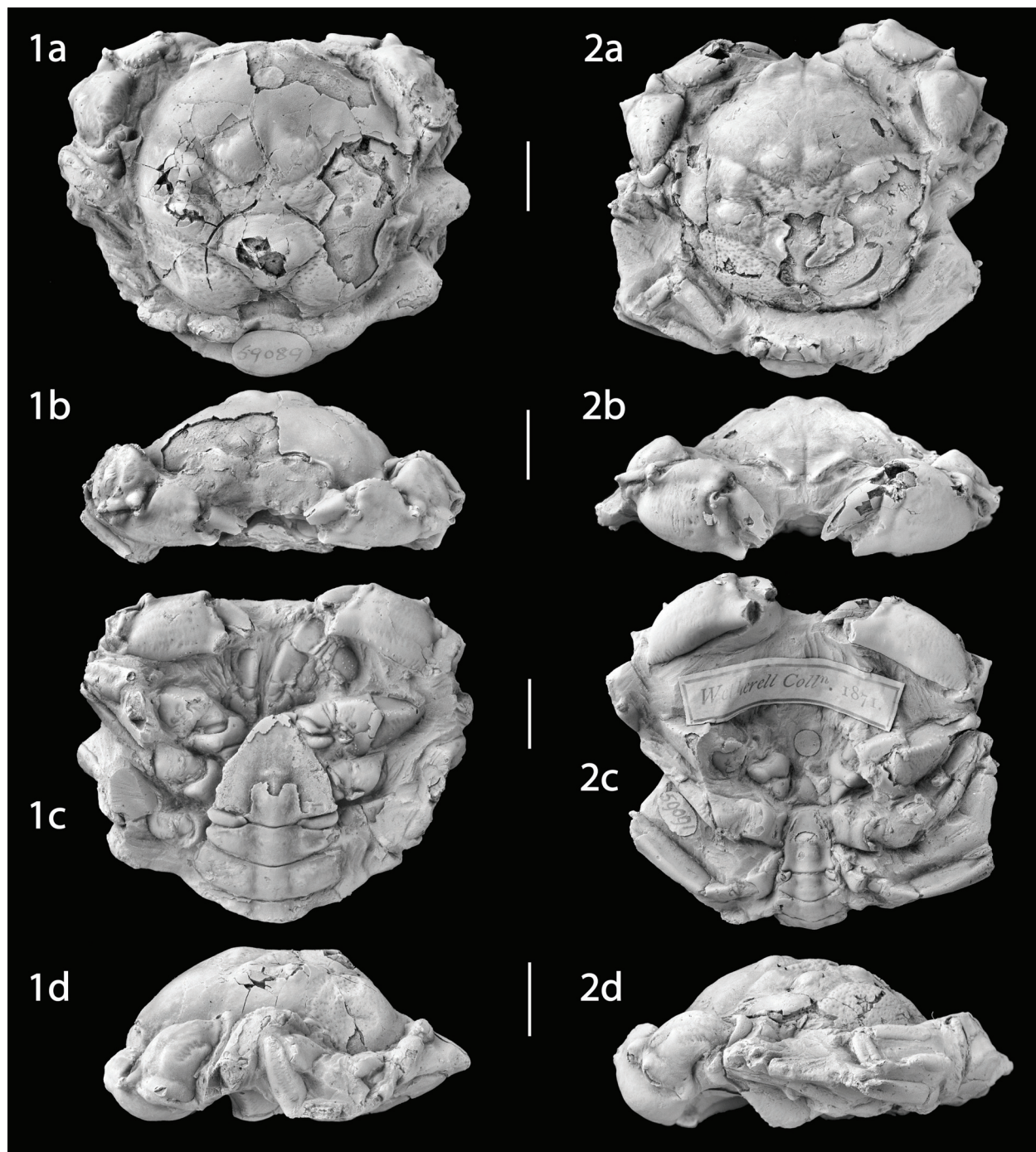
#### *Dromilites belli* n. sp.

Figures 2–3, Table and Appendix

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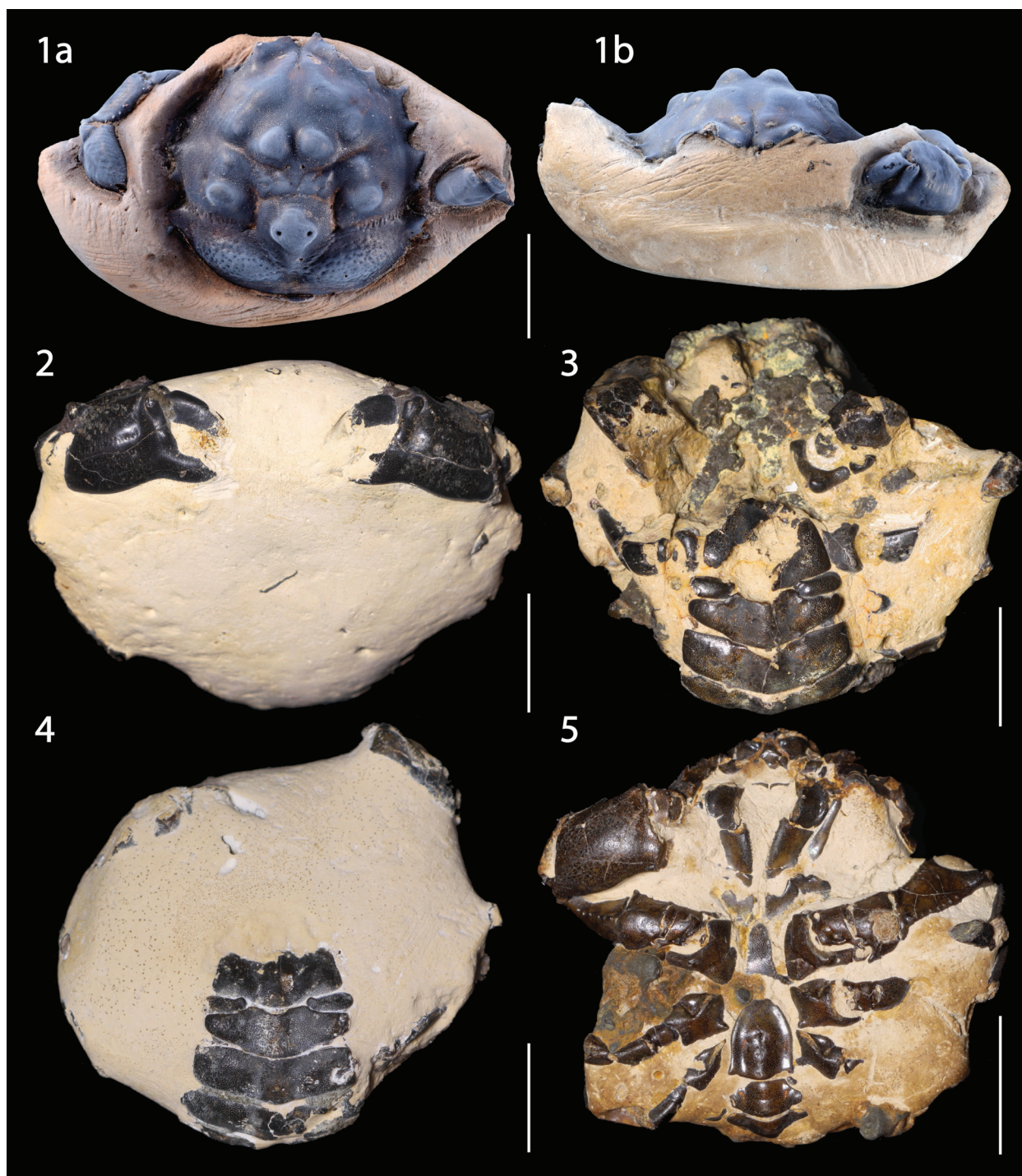
- v. 1858 *Dromilites bucklandi* H. Milne Edwards; Bell, p. 31-32, pl. VI, figs. 1-11.
- v. 1898 *Dromilites bucklandi* H. Milne Edwards; Carter, p. 18.
- v. 1906 *Dromilites bucklandi* H. Milne Edwards; Schröder, p. 7.





**FIGURE 2.** *Dromilites belli* n. sp. type series from the Ypresian of London Clay (Copenhagen Fields, London, United Kingdom). **1.** Holotype NHMUK PI OR 59089 (Wetherell coll.) coated with ammonium chloride (female individual): 1a. carapace in dorsal view, 1b. carapace in frontal view, 1c. carapace in ventral view, 1d. carapace in left-lateral view; **2.** Paratype NHMUK PI OR 59091 (Wetherell coll.) coated with ammonium chloride (male individual): 2a. carapace in dorsal view, 2b. carapace in frontal view, 2c. carapace in ventral view, 2d. carapace in left-lateral view. Scale bars equal 10 mm. Photographs: Philip Hurst, Natural History Museum, London.





**FIGURE 3.** *Dromilites belli* n. sp. type series from the Ypresian London Clay (Division B1, Kent, United Kingdom). **1.** Paratype MAB.k 3583 (Seasalter, foreshore exposure) coated with ammonium chloride: 1a. carapace in dorsal view, 1b. carapace in frontal view; **2.** Paratype MAB.k 3584 (Seasalter, foreshore exposure): claws; **3.** Paratype MAB.k 3585 (Seasalter, foreshore exposure) (female individual): abdomen in ventral view; **4.** Paratype MAB.k 3587 (Seasalter, foreshore exposure) (female individual): abdomen in ventral view; **5.** Paratype MAB.k 3586 (Tankerton, foreshore exposure) (male individual): abdomen in ventral view. Scale bars equal 1cm. Photographs. Lilian Cazes (1) and Barry van Bakel (2-5).

- v. 1925 *Dromilites bucklandi* H. Milne Edwards; Gripp, p. 129.
- v. 1928 *Dromilites bucklandi* H. Milne Edwards; Beurlen, p. 164.
- v. 1929 *Dromilites bucklandi* H. Milne Edwards; Glaessner, p. 139.
- v. 1945 *Dromilites bucklandi* H. Milne Edwards; Wrigley, p. 217.
- v. 1966 *Dromilites bucklandi* H. Milne Edwards; Davidson, p. 211.
- v. 1969 *Dromilites bucklandi* H. Milne Edwards; Glaessner, p. R487, fig. 297.3.
- v. 1977 *Dromilites bucklandi* H. Milne Edwards; Cooper, p. 172.
- v. 1982 *Dromilites bucklandi* H. Milne Edwards; Förster and Mundlos, p. 155.
- v. 2006 *Dromilites bucklandi* H. Milne Edwards; Collins and Saward, p. 68-69, table 1.
- v. 2009 *Dromilites bucklandi* H. Milne Edwards; Rayner et al., p. 56.
- v. 2010 *Dromilites bucklandi* H. Milne Edwards; Schweitzer et al., p. 64.
- v. 2010 *Dromilites bucklandi* H. Milne Edwards; Schweitzer and Feldmann, p. 422-432, fig. 2.

**Etymology.** The species name is dedicated to the British paleontologist Thomas Bell, who erected in 1858 the genus *Dromilites* previously proposed by H. Milne Edwards (in 1837) by assigning species *Dromia bucklandi* and *Dromia lamarckii* to the genus.

**Type material.** Holotype: NHMUK PI OR 59089 (fig. 2.1) and 6 paratypes: NHMUK PI OR 59091 (fig. 2.2), MAB.k 3583-3587 (fig. 3).

**Additional examined material.** MNHN.F.R03853-4 and MNHN.F.A66911 (casts of specimens figured in Bell, 1858, Plate VI, figs. 8-10) (London Clay, Copenhagen Fields, London), 'specimen 1' figured in Rayner et al., 2009, p. 56 (London Clay, Division B1, Seasalter foreshore exposure, Kent, United Kingdom, 51°20'36.77"N/1°0'2.76"E) (see Table).

**Description.** Carapace subcircular, length and width subequal (holotype dimensions: CL = 35.5 mm, CW = 37 mm, FM = 18.5 mm, OFM = 16 mm, PM = 20.5 mm), maximum width at midlength to in posterior half, strongly convex in longitudinal and transverse cross sections; orbitofrontal margin prominent, wide, 43% maximum carapace width. Rostrum projected beyond orbits, broadly triangular, bilobed, axially notched, frontal margin with four triangular sharp teeth, median two from rostrum advanced; orbits forwardly, outwardly directed, upper orbital margin concave, outer orbital corner pointed. Lateral margin prominent; anterolateral margin weakly arched, with four

strong, triangular, broad-based teeth; two anterior, two posterior the cervical notch; third lateral spine largest, flattened, more anteriorly directed. Posterolateral margin rounded in cross section, conspicuously short, strongly curved towards posterior margin, anteriorly bearing single prominent tooth. Posterior margin narrower than orbitofrontal margin, straight, distinctly rimmed.

Carapace regions strongly swollen, distinctly marked by large, rounded tubercles, deep, wide groove system; small epigastric swellings bounding anterior mesogastric process, mesogastric region narrowly triangular, posterior mesogastric region large, wide, strongly vaulted, with two large horizontally lined prominent tubercles, divided by short distinct median groove. Protogastric regions with two low tubercles, one anteriorly, one posteriorly, wider spaced; hepatic region flat, inclined. Metogastric region trapezoidal, wide anteriorly, posterior margin concave, arched, surface wrinkled. Urogastric region undefined. Cardiac region distinctly defined, large, strongly inflated, diamond-shaped, apex pointed posteriorly, large central tubercle bearing two horizontally lined pits; intestinal region small, depressed. Branchial region large, subdivided by oblique postcervical, branchial grooves; epibranchial, mesobranchial regions bearing single large tubercle, mesobranchial tubercle largest, wider spaced, laterally marked by large pit; metabranchial region wide, short, conspicuously swollen, bearing numerous pits.

Cervical groove widely V-shaped, deep, distinct on medial carapace, interrupted at axis by gastric pits, faint laterally, weakly notching carapace margin; branchial grooves subparallel to cervical groove, wider, distinctly notching lateral margin; post-cervical grooves shallow, indistinct, separating branchial tubercles; branchiocardiac grooves conspicuously deep, anteriorly longitudinally directed, weakly concave, posteriorly converging to posterior margin.

Carapace epicuticle with numerous evenly spaced setal pits. Internal mold smooth.

Third maxillipeds long, pediform, coxae large, flabelliform, endopod robust, exopod slender, elongate. Chelipeds well developed, sub-homochelous, merus subtriangular in cross section; manus outer surface smooth, bulbous, spine on proximal upper surface; pollex scoop-shaped, pointed teeth on occlusal surface; dactylus curved. Pereiopods two, three moderately sized, pereiopod four, five reduced, carried subdorsally. Distal ends not preserved, most probably subchelate.



Male sternum narrow, sternite four elongate, rounded, posterior sternites strongly curved. Male pleon narrow, telson longer than wide, reaching base of chelipeds; somite six long, uropods dorsally visible, small; somites four and five short, wide. Female pleon moderately wide; telson conspicuously large, longer than wide, reaching anterior end of coxae of chelipeds; somite five rectangular; somite six with large, triangular uropods.

**Range.** London Clay, Ypresian, lower Eocene.

**Occurrence.** London basin.

**Remarks.** This new species is assigned to *Dromilites* based on the following morphological characters: a carapace slightly wider than long; a bidentate rostrum; the anterolateral margins with widened teeth, an entire cervical groove, the carapace regions well defined, with sharp tubercles, and a prominent cardiac region. *Dromilites belli* n. sp. is morphologically closest to the species *Dromilites montenati* Robin, Van Bakel, Pacaud, and Charbonnier, 2016 in showing comparable highly defined carapace regions with marked tubercles, but differs in displaying four anterolateral (instead of five) and one posterolateral teeth (instead of none), prominent tubercles on the posterior mesogastric region, a less defined urogastric region, a more carved cardiac region with a large central tubercle bearing two horizontally lined pits, epibranchial and mesobranchial regions bearing a single large tubercle (instead of two); and in having cervical and branchial grooves notching the lateral carapace margins less and more distinctly respectively. *Dromilites belli* n. sp. differs from *D. bucklandii*, *D. pastoris* and ?*D. cardwelli* in having less distinct grooves, in particular a much weaker cervical groove, and distinctly vaulted carapace regions with strong tubercles (weakly vaulted carapace regions, without distinct tubercles in *D. bucklandii*, *D. pastoris* and ?*D. cardwelli*) in all size ranges. *D. belli* n. sp. differs from *D. vicensis* in having a relatively shorter carapace (however, ratio length/width varies considerably; see Table), a well-defined mesogastric region, a distinctly vaulted cardiac region, and presence of strong tubercles.

The London Clay dromiid crabs are morphologically very similar. There are a number of differences by which *D. belli* n. sp. and *D. bucklandii* are separated. The anterolateral margin in *D. bucklandii* has three teeth instead of four in *D. belli* n. sp., in which only a single tooth is present between the cervical and branchial grooves. This third anterolateral tooth in *D. bucklandii* is flattened posteriorly, giving a flanged appearance. The posterolateral

margin in *D. belli* is strongly curved, whereas it is anteriorly straight in *D. bucklandii*. This results in a relatively wider posterior margin in *D. bucklandii*. The single posterolateral tooth, just posterior the branchial groove, is subtle in *D. bucklandii*, while it is well-developed in the second species. The carapace regions in *D. bucklandii* are weakly vaulted, whereas they are strongly inflated in *D. belli* n. sp. Also the mesogastric region is undefined in *D. bucklandii* while it is visible in *D. belli* n. sp. Large, coarse tubercles mark the gastric and branchial regions in *D. belli*, while these are absent in *D. bucklandii*. Finally, there are two weak bumps with a pit on the cardiac region of *D. bucklandii*; these are merged into one strongly inflated tubercle in *D. belli* n. sp.

## DISCUSSION AND CONCLUSIONS

A range of carapace sizes belonging both to males and females of *D. bucklandii* and *D. belli* n. sp. have been examined in this study (Table), including specimens of both species which are subequal in size (e.g. MNHN.F.B21561 and MAB.k 3583; 21.5 and 21 mm, respectively; see also Appendix for comparison). Ontogenetic differences are present in these two species, especially in *D. belli* n. sp. These differences have already been discussed in Bell (1858, p. 32: for *D. belle* n. sp.) raising the fact that adult and young individuals might readily be taken for distinct species. Many of the tubercles, which are distinct, and even prominent in the small specimens, are lowered, expanded, in the larger. In the smaller specimens, the frontal and lateral teeth are distinctly more pronounced and spiny than in larger specimens. The claws are more slender in juveniles; in larger specimens the claws are large and robust. On the dorsal carapace, the tubercles are more acute in smaller specimens. In larger individuals, the tubercles on the protogastric and epibranchial regions are weak or even absent. The metabranchial region is strongly inflated in smaller specimens, and somewhat weaker in large individuals. These differences are seen in both sexes, so here considered as ontogenetic variation. This variation does not overlap the two species, ruling out the possibility that the species could be conspecific and that the morphotypes could correspond to sexual or ontogenetic variations. Also, only specimens with well-preserved cuticle are examined; thus the characters of each species, and differences between the two species, are no reflection of preservational incidence. Thus, *Dromilites belli* n. sp. is clearly distinguished from *D. bucklandii*, to which Milne Edwards was actually referring 180 years ago

when he named what would become the type species of this dromioid crab genus.

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## APPENDIX.

Photogrammetric reconstructions of *Dromilites bucklandii* H. Milne Edwards, 1837 lectotype (MNHN.F. B21561, Ypresian of the Isle of Sheppey, Kent, UK) and *Dromilites belli* n. sp. (MAB.k 3583, Ypresian of Seasalter, Kent, UK). Photogrammetry. Lilian Cazes. Animated PDF file available at [palaeo-electronica.org/content/2017/2077-eocene-dromiid-crabs-revised](http://palaeo-electronica.org/content/2017/2077-eocene-dromiid-crabs-revised).