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SPHAERODROMIIDAE (BRACHYURA: DROMIACEA: DROMIOIDEA) IN THE FOSSIL RECORD

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ABSTRACT

The definition of the genus *Dromilites* has become extended over the past nearly 200 years to include most any dromioid crab from Eocene rocks. We examined type material of *Dromilites* spp. and restrict the genus to four species. The remaining species are removed to other genera or families incertae sedes. The remarkable preservation of the type species and a second species make it possible to assign with confidence *Dromilites* sensu stricto to Sphaerodromiidae. The unique features of this family, which Guinot and Tavares (2003) had erected as a subfamily within Dromiidae, support its elevation to family status. A new genus referred to Sphaerodromiidae embraces a Campanian (Late Cretaceous) species from South Dakota, *Ferricorda kimberleyae* (Bishop, 1987). Sphaerodromiidae now extends into the Late Cretaceous. The fossil record of Dromiidae sensu lato and sensu stricto is currently under investigation.

KEY WORDS: Brachyura, Decapoda, *Dromilites*, Dromioidea, Eocene, Sphaerodromiidae

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INTRODUCTION

Studies over the past decade have shown that many extinct decapod genera are polyphyletic (Schweitzer, 2003, 2005). Revisionary work on the fossil Brachyura is ongoing and is currently focused on the dromiacean crabs (Schweitzer and Feldmann, 2009). Numerous extinct genera have been referred to Dynomenidae and Dromiidae over the past decades (Glaessner, 1969), but none of these genera has been evaluated within the context of new classifications for these groups (Guinot and Tavares, 2003; Guinot, 2008). *Dromilites* H. Milne Edwards, 1837, originally described from well-preserved specimens, is now known to be much less speciose than previously believed and can be confidently referred to Sphaerodromiidae new status, extending the range of that family into the Eocene.

Institutional abbreviations: BMNH and NHM IC, The Natural History Museum, London, UK; M, Természettudományi Múzeum, Föld-és őslénytar, Budapest, Hungary; MGSB, Museo Geológico del Seminario de Barcelona, Spain; SDSM, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, South Dakota, USA; USNM, United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

SYSTEMATICS

Infraorder Brachyura Linnaeus, 1758
Section Dromiacea De Haan, 1833
Superfamily Dromioidea De Haan, 1833
Sphaerodromiidae Guinot and Tavares, 2003 *new status*

Included Genera.—*Dromilites* H. Milne Edwards, 1837 (extinct); *Eodromia* McLay, 1993 (extant); *Ferricorda* n. gen. (extinct); *Sphaerodromia* Alcock, 1899 (extant).

Diagnosis.—Carapace longer than wide or about as long as wide; rostrum projecting beyond orbits; orbital area composed of two contiguous circular depressions, outer depression deeper, essentially continuous with orbit, poorly separated from orbit; lateral rim merging with or separated only by short distance from outer-orbital angle; subhepatic region inflated; cervical groove weak, postcervical and branchiocardiac grooves well defined; male vestigial pleopods on pleonal somites 3-5; female spermatheca positioned posteriorly on sternum, short female sutures 7/8; male P5 coxa extended into immobile structure; telson long, uropodal plates large and readily visible in ventral view, triangular epimeres on sixth somites, rectangular terminations on remaining pleomeres; long anterior process of sternite 4; pereiopods 4 and 5 reduced in size. [See Guinot and Tavares (2003) for additional characters observed from extant specimens.]

Discussion.—Guinot and Tavares (2003) erected Sphaerodromiinae to accommodate two genera within Dromiidae De Haan, 1833. They considered this subfamily to exhibit the most primitive characteristics within the family, including male vestigial pleopods on pleonal somites 3-5, female spermatheca positioned posteriorly on the sternum, short female sutures 7/8, and a male P5 coxa extended into an immobile structure. In addition to these features, Sphaerodromiinae possess a unique combination of characters within Dromiacea De Haan, 1833, which embraces Homolodromioidea Alcock, 1900; Dynomenidae Ortmann, 1892; and Dromiidae (Table 1). The sphaerodromiines have a long telson, visible uropodal plates, triangular epimeres on the sixth pleomeres, rectangular terminations on the remaining pleomeres, a long anterior process on sternite 4, an inflated subhepatic region, and reduced pereiopods 4 and 5 (Fig. 1). The combination of diagnostic characters listed here for Sphaerodromiinae is sufficiently distinct from the other Dromiidae, Dynomenidae, and Homolodromioidea (Table 1) that we elevate it to family status. Removal of Sphaerodromiinae from the Dromiidae renders the latter much less variable than it would be with inclusion of Sphaerodromiinae within it. Sphaerodromiidae thus occupy a unique position within the dromiacean crabs.

Table 1. Comparison of key features of various brachyuran families and *Dromilites*. Homolodromiidae as defined by Guinot (1995) and used by Schweitzer et al. (2009); Dromiidae (excluding Sphaerodromiinae) as defined by Guinot and Tavares (2003); Dynomenidae as defined by Guinot (2008); Sphaerodromiidae as defined by Guinot and Tavares (2003) as Sphaerodromiinae; Goniodromitidae as defined by Schweitzer and Feldmann (2008 [imprint 2007]). Notice the variability within the Dromiidae as defined by Guinot and Tavares (2003).

	Homolodromiidae	Dromiidae	Dynomenidae	Sphaerodromiidae	*Dromilites*	Goniodromitidae
Oldest known occurrence of confirmed taxa	Middle Jurassic (Bathonian)	Eocene	Cretaceous?	Late Cretaceous (Campanian)	Eocene	Late Jurassic (Oxfordian)
Uropod visible	No	Sometimes	Yes	Yes	Yes	?
Male telson longer than wide	Yes	Rarely	No	Yes	Yes	?
Pleonite 6 with triangular epimeres	Yes	No	Yes	Yes	Yes	?
Pleonites 1-5 with long epimeres	Yes	No	No	No	No	?
Anteriorly displaced spermatheca	No	Yes, except *Stebbingdromia*	No	No	No (Fig. 5)	?
Both pereiopods 4 and 5 reduced in size	Yes	Yes	No	Yes	Yes	?
Cervical groove defined	Yes	Weak	Yes	Weak	Yes	Yes
Branchiocardiac groove defined	Yes	Yes	Yes	Yes	Yes	Yes
Postcervical groove defined	No	Sometimes	Sometimes	Yes	Yes	Yes
Augenrest sensu stricto	Yes	No	No	No	No	Yes

Unfortunately, few of the extinct homolodromioid families retain features of the pleon, sternum, and appendages necessary to make direct comparison with Sphaerodromiidae. Armstrong et al. (2009) described a portion of a sternum of *Pithonoton cardwelli* Armstrong et al., 2009, but its incomplete preservation makes it comparable to most dromiaceans. All homolodromioids have well-developed augenrests, deep and usually broad depressions, often protected by spines, that lie distal to the orbit. In sphaerodromiids, the orbital area is composed of two contiguous circular depressions, one of which could be construed as an augenrest, but it is not the same in overall structure as in homolodromioids. It is deeper, essentially continuous with the orbit, and poorly separated from the orbit. Thus, this feature can be used to distinguish Sphaerodromiidae from extinct homolodromioids.

There are several fossil taxa that are referable to Sphaerodromiidae, based upon features of the pleon, sternum, and pereiopods. This yields a range for Sphaerodromiidae of Late Cretaceous to Holocene.

Dromilites H. Milne Edwards, 1837

Type Species.—*Dromia bucklandi* H. Milne Edwards, 1837 [*in* 1834-1840], apparently by subsequent designation of Glaessner (1929b).

Included Species.—*Dromilites bucklandi*; *D. pastoris* Vía, 1959; *D. simplex* Quayle and Collins, 1981; *D. vicensis* Barnolas Cortinas, 1973.

Diagnosis.—Carapace ovate to rectangular, about as wide as long or longer than wide; rostrum bilobed; lateral margins crispate, notched at intersection of cervical and branchiocardiac grooves, with spines; cervical, postcervical, and branchiocardiac grooves deep; carapace with distinct swellings on mesogastric and epibranchial regions; third maxillipeds pediform; first pereiopods short, with or without spine on upper margin of manus, fixed finger with scoop-shaped tip; male sternum narrow; female sternite 4 with long anterior process, short female sternal sutures 7/8, spermatheca situated posteriorly; male pleon narrow; pleonites 4 and 5 short, wide; pleonite 6 with triangular epimeres, uropods large, visible, nested between pleonite 6 and telson, telson much longer than wide, reaching base of coxae of chelipeds; female pleon moderately wide, pleonite 5 rectangular; pleonite 6 with triangular tips; uropods large, visible, nested between pleonite 6 and telson, telson longer than wide, reaching anterior end of coxae of chelipeds.

Material Examined.—In addition to specimens of *Dromilites bucklandi* and *D. simplex* listed below, casts of *Dromilites vicensis*, MGSB 23888, holotype; *D. pastoris*, MGSB 15955, holotype; *D. subglobosa*, M91-127, holotype; *D. fossata*, P. Müller personal collection, were studied.

Nomenclature.—The name *Dromilites* has a rather mysterious origin. H. Milne Edwards (1837 [*in* 1834-1840]) named the species *Dromia bucklandi* for fossil specimens from Tertiary clays of the Island of Sheppey, and he provided a description for it (p. 178-179). Later that year, he published the name *Dromilite*, apparently for this genus and species, in L'Institut, Journal Universel des Sciences et des Societe Savantes en France et a l'etranger, 1ere section, Sciences, mathematiques, physiques, naturelles … on p. 255 and possibly in another publication, Extr. P. V. Soc. Philom. Paris on page 115. The name *Dromilites* was published, also in 1837, in Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde in a note on p. 494 apparently as minutes from a meeting. This note refers to a "Dromien" from the Tertiary of the Isle of Sheppey, clearly the same taxon H. Milne Edwards described as *Dromia bucklandi*, but the species name was not used.

Later, Bronn (1848, p. 439) listed *Dromilithus* and *Dromilithes* as what appear to be synonyms of *Dromite* and also referred *Brachyurites rugosus* (Schlotheim, 1820) to *Dromilite*. Bronn's listed authorship for *Dromilite* clearly indicates that he intended it as the same genus as H. Milne Edwards erected in 1837 for the species *Dromia bucklandi*. Reuss (1858 [imprint 1857]) then placed *B. rugosus* within a new genus, *Dromiopsis*, suggesting that he recognized that *B. rugosus* was distinct from *"Dromilite" bucklandi*.

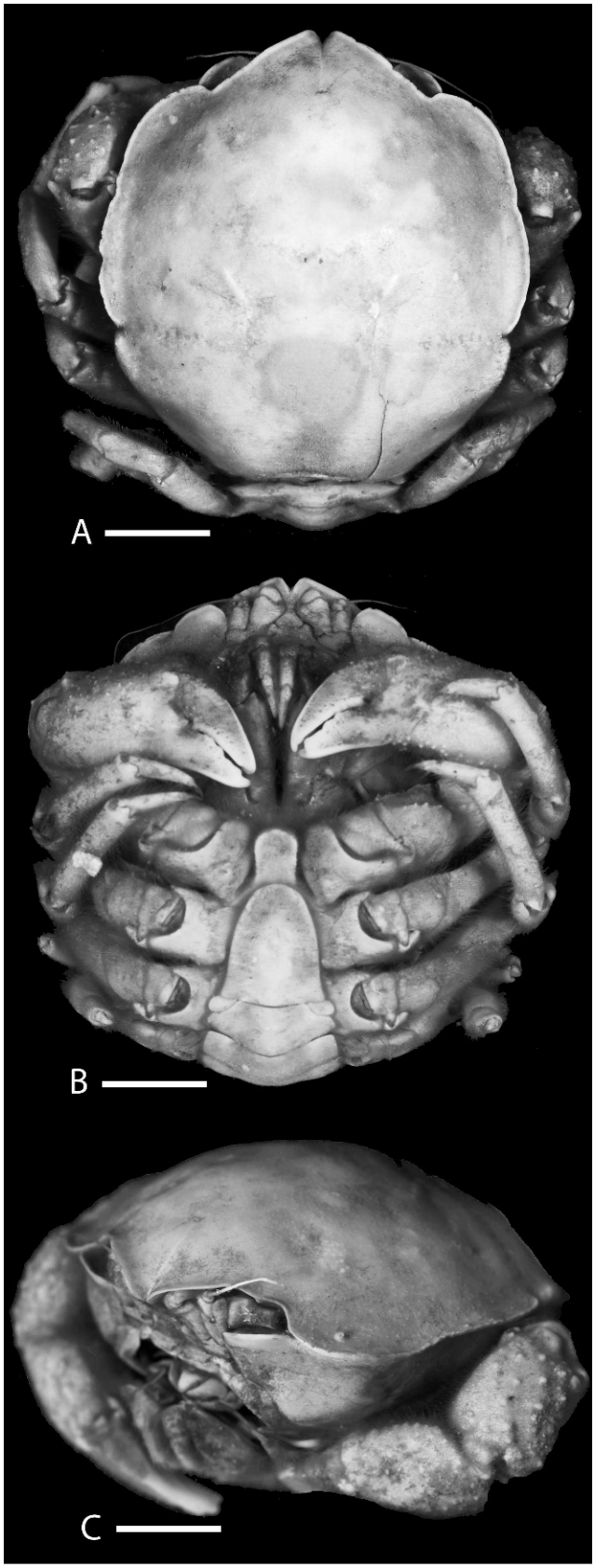

Fig. 1. *Sphaerodromia lamellata* Crosnier, 1994, USNM 266782. A, dorsal carapace showing crispate lateral margins; B, ventral surface with male abdomen and long extension of sternite 4; C, oblique frontal view showing inflated subhepatic region and merging of crispate lateral ridge with outer corner of orbit. Scale bars = 1 cm.

Subsequent usage of the name has been as *Dromilites* in the sense of Bell (1858), who illustrated specimens of *Dromilites bucklandi* and spelled the name with an "s." A type species for *Dromilites* does not seem to have been officially designated by H. Milne Edwards. Interestingly, Glaessner (1929, 1969) considered *D. bucklandi* to be the type species by original designation; thus, there was some feeling that H. Milne Edwards intended that it be the type. Quayle and Collins (1981) noted the considerable confusion over the name and indicated that an application was being made to the ICZN to stabilize the name, but that seems not to have happened.

Thus, we suggest the following. Under Article 67.2.2 of the International Code of Zoological Nomenclature, *Dromilites bucklandi* should be the type species as it has been recognized for nearly 200 years. Under Article 32.2, we suggest that Bell (1858) was the First Reviser and that the spelling *Dromilites* be maintained, especially because it has been in common usage for nearly 150 years. In addition, we note that, by applying the same criteria stated in Article 23.9.1.2.for reversing precedence, *Dromilites* has been used in at least 25 works, by at least 10 authors, over a 150 year period. Thus, the name is well established, and changes to its usage or rendering it a nomen nudum would threaten stability.

Remarks.—*Dromilites* has historically been placed within Dromiidae (Glaessner, 1969; Schweitzer et al., 2009). A better placement for it is Sphaerodromiidae based upon its possession of a long telson, visible uropodal plates, triangular epimeres on the sixth pleonites, rectangular terminations on the remaining pleonites, a long anterior process of sternite 4, posteriorly placed spermatheca, both pereiopods 4 and 5 reduced in size and five carried subdorsally, a bilobed front, and crispate lateral margins. These features are remarkably similar to extant *Sphaerodromia* spp. (Fig. 1). The only features of *Dromilites* that differ significantly from extant sphaerodromiids are the nature of the grooves; in *Dromilites*, the cervical, postcervical, and branchiocardiac grooves are all well defined. In extant sphaerodromiids, only the branchiocardiac groove is moderately defined; the others are very weak.

Dromilites has been expanded over the nearly two centuries since it was named to embrace a broad range of taxa. In fact, there are only a few species that are referable to the genus. *Dromilites bucklandi* is a morphologically well-known taxon, with well-preserved male and female individuals (Fig. 2). Thus, it is possible to erect a detailed diagnosis for the genus and to eliminate most other species from it. *Dromilites pastoris* and *D. vicensis*, both from the middle Eocene (Lutetian) of Spain (Vía, 1959; Barnolas Cortinas, 1973) remain within the genus with reservations (Figs. 3A, B). Both species appear to be about as long as wide, based upon the holotype specimens, although illustrations show *D. pastoris* to be longer than wide (Vía, 1959, fig. 6), differing from *D. bucklandi*. In addition, *Dromilites pastoris* seems to be more granular than is *D.*

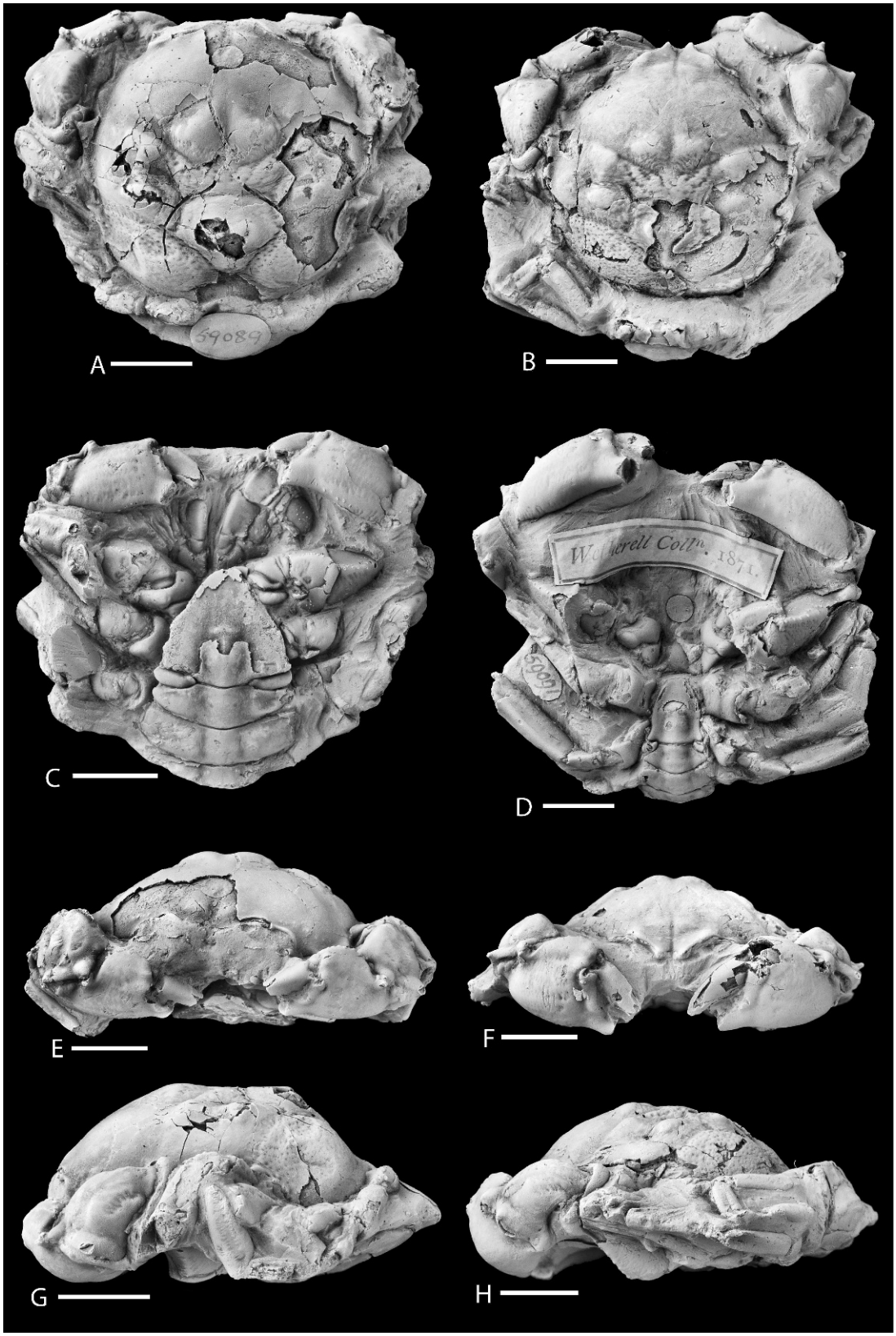

Fig. 2. *Dromilites bucklandi* H. Milne Edwards, 1837 [in 1834-1840]. A, C, E, G: female, (BMNH) 59089, dorsal carapace (A), ventral surface showing uropods, telson, and somites 4-6 (C), anterior view (E), and left lateral view (G); B, D, F, H: male, (BMNH) 59091, dorsal surface (B), ventral surface showing uropods, telson, somites 4-6, and anterior extension of sternite 4 (D), frontal view showing bifid rostrum (F), and left lateral view (H). Scale bars = 1 cm. Photos copyrighted by The Natural History Museum, London, UK, and photographed by Mr. P. Crabb.

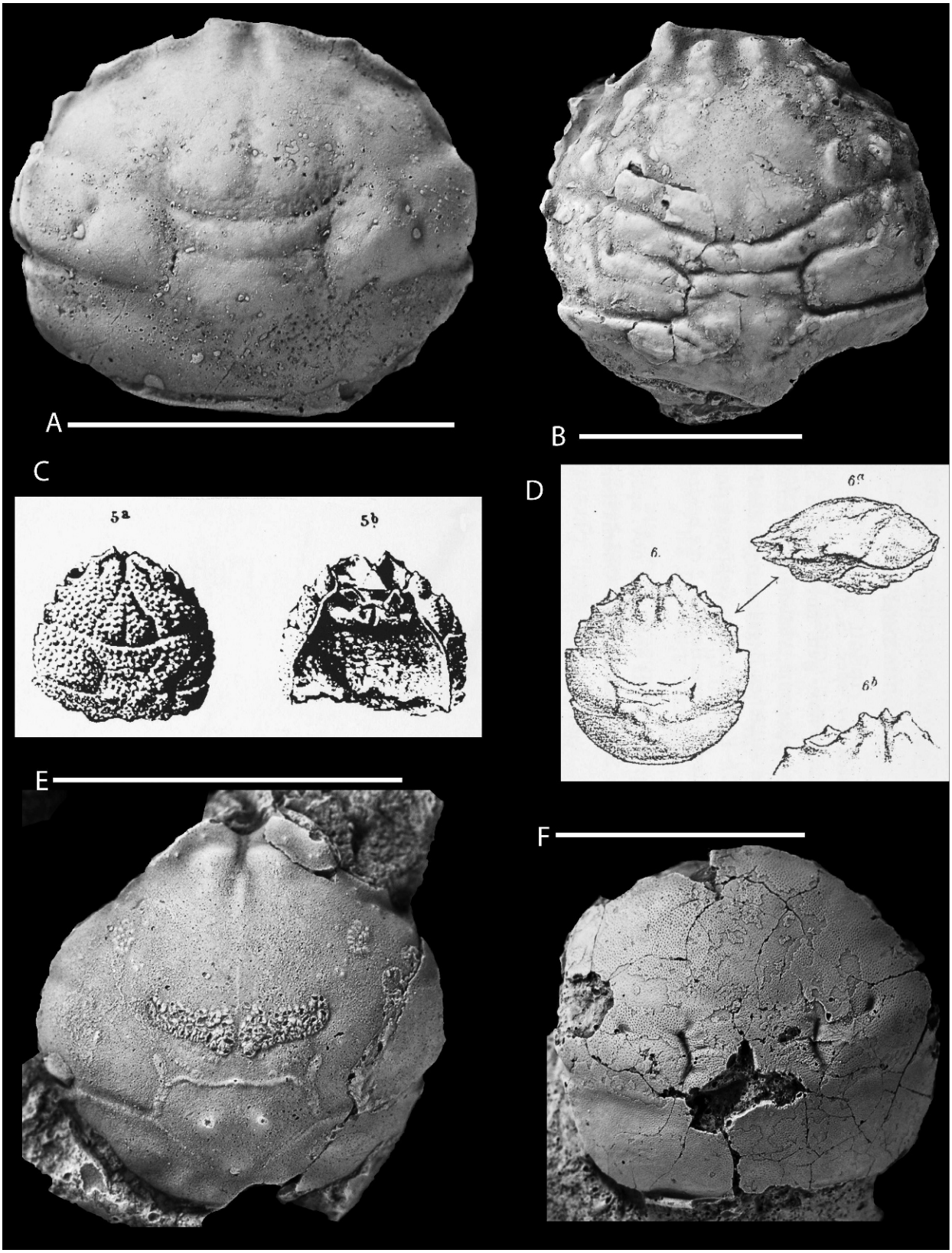

Fig. 3. Dromioidea. A, cast of holotype of *Dromilites vicensis* Barnolas Cortinas, 1973, MGSB 23888; B, cast of holotype of *Dromilites pastoris* Vía, 1959, MGSB15955; C, *Pseudodromilites hilarionis* (Bittner, 1883), digital image from Bittner (1883, pl. 1, fig. 5); D, *Dromia corvini* Bittner, 1893, digital image from Bittner (1893, pl. 2, fig. 6); E, cast of holotype of *Dromilites subglobosa* Müller and Collins, 1991, M91-127; F, cast of paratype of *Dromilites simplex* Quayle and Collins, 1981, (BMNH) In. 61700. Scale bars = 1 cm.

bucklandi and is ornamented with tubercles, whereas *D. bucklandi* is not. However, both species possess deep grooves, crispate lateral margins drawn into spines; inflated epibranchial regions; and swellings on the protogastric regions, similar to features seen in *D. bucklandi*. Thus, *D. pastoris* and *D. vicensis* remain within the genus until more complete specimens can be found to confirm their placement.

Dromilites lothi Förster and Mundlos, 1982, and *D. alpina* Glaessner, 1929a, are each better placed within *Kromtitis* Müller, 1984. Each of these species is known from incomplete specimens, and each is characterized by deep grooves; very well-defined carapace regions with large swellings; and strongly projected anterolateral margins with large, triangular spines. These are diagnostic features for *Kromtitis*, well known from the Eocene through Miocene of Europe (Beschin et al., 2007).

Dromilites subglobosa Müller and Collins, 1991, is best placed within *Dromia* (Fig. 3E). *Dromilites fossata* Müller and Collins, 1991, may well be a juvenile of *D. subglobosa*. The type specimen of *D. subglobosa* lacks detail but suggests the overall shape, broadly bifid rostrum, deep branchiocardiac groove, and weaker cervical groove typical of dromiids. *Dromilites fossata* is much smaller in size and is known from the same formation as *D. subglobosa* and has similar features. The smooth carapace, weak cervical and postcervical grooves, lack of carapace swellings, crispate margins, and equant carapace exclude these species from *Dromilites*. For now, we place them in *Dromia* sensu lato until type specimens can be examined or more material can be collected.

Bittner (1883, 1893) named two species of *Dromia*, *D. hilarionis* Bittner, 1883, and *D. corvini* Bittner, 1893, respectively (Figs. 3C, D). Beurlen (1928) erected *Pseudodromilites* to accommodate *D. hilarionis*, and later, Lőrenthey (in Lőrenthey and Beurlen, 1929) named *Pseudodromilites pentagonalis* Lőrenthey (in Lőrenthey and Beurlen, 1929). Glaessner (1929b) synonymized *Pseudodromilites* with *Dromilites*. Note that in the original paper, *Pseudodromilites* was misspelled in the generic heading as "*Pseudodromilitis*" (Beurlen, 1928, p. 167), and this is how it appears in Nomenclator Zoologicus. It is clear that Beurlen intended the spelling to be "*Pseudodromilites*," as he used that spelling throughout the rest of the work at least six times, including on the first page of the article (Beurlen, 1928, p. 144). Lőrenthey and Beurlen (1929) and Glaessner (1929b) as the first revisers used the spelling *Pseudodromilites*; thus, that is the spelling we use here. Illustrations of these latter two species indicate that they do not belong within *Dromilites* and are best left as a discrete genus, *Pseudodromilites*. They are characterized by a granular carapace overall, an apparently broadly bifid rostrum, anterolateral margins with triangular spines, and deep grooves. The two species lack large swellings on the carapace regions, and they do not appear to possess the crispate anterolateral margins seen in *Dromilites*. Thus, we recognize *Pseudodromilites* and two constituent species, *P. pentagonalis* and *P. hilarionis*. *Dromia corvini* (Fig. 3D) lacks the granulations on the dorsal carapace and instead was described as being covered with punctae. For now, we retain it in *Dromia* sensu lato based upon its deep branchiocardiac groove, trifid front, weak cervical and postcervical grooves, and spined lateral margins.

Dromilites americana Rathbun, 1935, poses problems. The nature of the sternum, which is broad and ovate (Rathbun, 1935, pl. 17, fig. 2), clearly eliminates it from the Dromiacea. It seems to have affinities with members of the Palaeoxanthopsidae Schweitzer, 2003, or Tumidocarcinidae Schweitzer, 2005; investigation of that species is ongoing. Armstrong et al. (2009) placed it within *Tehuacana*, but their illustrations of the species contain more than one taxon. Thus, further investigation of the species is required.

Dromilites humerosus Quayle and Collins, 1981, was originally named as a subspecies of *Dromilites lamarckii* (now *Basinotopus lamarckii*) but was raised to species level by Collins (2002). He noted that there was no basis for comparing the subspecies to *Basinotopus lamarckii* but retained the species in *Dromilites*. The description and illustrations of *D. humerosus* suggest that it is a member of the Majoidea Samouelle, 1819. Specimens of the species broaden posteriorly, have well-developed carapace regions, and lack a branchiocardiac groove. Thus, we place it within the Majoidea incertae sedis until the holotype can be examined closely to determine its affinities.

Thus, the range of *Dromilites* sensu stricto has been severely restricted (Table 2). It is known only from the Eocene of Britain and Spain.

Dromilites bucklandi (H. Milne Edwards, 1837 [*in* 1834-1840])
Fig. 2

Dromia bucklandi H. Milne Edwards, 1837 [*in* 1834-1840], p. 178.
Dromilites bucklandi H. Milne Edwards, 1837. Bell, 1858, p. 31, pl. 6, figs. 1-11; Carter, 1898, p. 18; Schröder, 1906, 7; Gripp, 1925, p. 129; Beurlen, 1928, p. 164; Glaessner, 1929b, p. 139; Glaessner, 1969, p. R487, fig. 297.3; Förster and Mundlos, 1982, p. 155; Schweitzer et al., 2009, p. 64.

Diagnosis.—Carapace about equi-dimensional; with crispate, spinose lateral margins; grooves well developed; regions well ornamented with large swellings; manus with spine on upper proximal margin.

Description.—Carapace about as long as wide, ovate, reaching maximum width at about half the distance posteriorly on carapace; strongly vaulted longitudinally and transversely; carapace regions moderately defined.

Rostrum projected moderately beyond orbits, bilobed, axially notched; orbits poorly known, rimmed, directed forward. Lateral margins convex, crispate, with at least one spine anterior to intersection with cervical groove; notched at intersection with cervical groove; two spines between notched intersection with cervical and branchiocardiac grooves; one spine just posterior to intersection with branchiocardiac groove; posterolateral portion of lateral margin rounding into posterior margin; posterior margin concave axially.

Epigastric regions weakly inflated, rectangular; mesogastric region triangular, best defined posteriorly by pair of swellings anterior to cervical groove. Protogastric and hepatic regions confluent; metagastric region wide, exhib-

Table 2. Species previously assigned to *Dromilites* and their current placement (references in text).

Species	Current placement	Occurrence
Dromilites bucklandi (type)	*Dromilites*	Eocene (UK, Germany)
D. simplex	*Dromilites*	Eocene (UK)
D. pastoris	*Dromilites*	Eocene (Spain)
D. vicensis	*Dromilites*	Eocene (Spain)
D. lothi	*Kromtitis*	Late Eocene-early Oligocene (northern Germany)
D. alpina	*Kromtitis*	Middle Eocene (Austria)
D. subglobosa	*Dromia*	Eocene (Hungary)
D. fossata	*Dromia*	Eocene (Hungary)
D. hilarionis	*Pseudodromilites*	Middle Eocene (Italy)
D. corvini	*Dromia* sensu lato	Middle Eocene (Italy)
D. americana	Carpilioidea?	Eocene (Alabama, Texas)
D. humerosus	Majoidea incertae sedis	Eocene (UK)

iting well-developed reniform muscle scars; urogastric region very short; cardiac region triangular, with apex directed posteriorly, inflated centrally; intestinal region depressed well below level of cardiac region. Epibranchial region long, with three swellings, one just posterior to cervical groove, two arranged posteriorly anterior to branchiocardiac groove; remainder of branchial region undifferentiated, short.

Cervical groove moderately deep, arcing convex forward from anterolateral margin, then curving concave forward around base of mesogastric region. Postcervical groove continuous across axis; lateral aspects curving in convex forward arcs onto epibranchial regions. Branchiocardiac groove approximately parallel to cervical groove; extending across carapace, defining posterolateral margins of cardiac region.

Third maxillipeds long, pediform. Chelipeds weakly heterochelous, proximal articles short; outer surface of manus smooth, spine on proximal upper surface; fixed finger with teeth on occlusal surface, scoop-shaped; movable finger edentulous. Pereiopods 2 and 3 of moderate size, pereiopod 4 somewhat smaller than 4; pereiopod 5 smallest, carried subdorsally.

Male sternum narrow. Male pleon narrow; pleonites 4 and 5 short, wide; pleonite 6 with triangular epimeres, uropods visible, nested between pleonite 6 and telson, telson much longer than wide, reaching base of coxae of chelipeds. Female pleon moderately wide, pleonite 5 rectangular; pleonite 6 with triangular tips; uropods large, triangular, visible, nested between pleonite 6 and telson, telson longer than wide, reaching anterior end of coxae of chelipeds.

Material Examined.—(BMNH) 59091 (male), (BMNH) 59089 (female), (BMNH) 59096, (BMNH) In. 48213 (female).

Occurrence.—The examined specimens were collected from the Eocene London Clay (Bell, 1858). Other occurrences are noted from the early Eocene of northern Germany (Glaessner, 1929b).

Remarks.—*Dromilites bucklandi* is one of the best preserved, extinct brachyuran species we know of. It retains sterna and pleons of both males and females, so that detailed comparison to extant families is possible. The scoop-like terminations on the fixed fingers suggest that this species may have been adapted for eating algae (Warner, 1977).

Dromilites simplex Quayle and Collins, 1981
Figs. 4, 5

Dromilites simplex Quayle and Collins, 1981, p. 736, pl. 104, figs. 1, 2, 3, 10. Müller and Collins, 1991, p. 62; Schweitzer et al., 2009, p. 64.

Diagnosis.—Carapace rectangular, longer than wide; front bifid; orbits deeply bilobed, fronto-orbital width about two-thirds maximum carapace width; lateral margins straight, crispate; cervical and branchiocardiac grooves strong, postcervical groove weak; upper margin of manus of cheliped smooth.

Description.—Carapace rectangular, longer than wide, width about 90% maximum length, position of maximum width about 60% the distance posteriorly on carapace; moderately vaulted transversely; strongly vaulted longitudinally.

Rostrum bifid, projected moderately beyond orbits, axially sulcate, margins rimmed, about 17% maximum carapace width. Orbits with two round lobes, lobes small, deep, directed forward, with small protuberance on upper-orbital margin separating lobes from one another; lower orbital margin extending farther anteriorly than upper margin, visible in dorsal view, small; forward directed spine on outer orbital margin; fronto-orbital width about two-thirds maximum carapace width. Outer-orbital spine followed by short concave segment, then small, forward-directed spine completing anterior margin of carapace. Lateral margins more or less straight and parallel to one another, crispate; two spines including spine at anterior corner anterior to intersection of cervical groove with lateral margin, second spine just anterior to notch marking intersection; elongate crispate projection between notches of intersections of cervical and branchiocardiac grooves with margin; posterolateral portion entire.

Epigastric regions weakly inflated; mesogastric region poorly defined, best defined anteriorly and posteriorly, weakly inflated posteriorly, axially divided posteriorly by weak longitudinal groove; protogastric and hepatic regions confluent; metagastric region wide; urogastric region short; cardiac region triangular, apex directed posteriorly; intestinal region depressed well below level of cardiac region, apparently with scabrous ornamentation. Epibranchial region long, flattened laterally, inflated axially; remainder of branchial regions undifferentiated.

Cervical groove weakly convex-forward, then arcing concave forward around base of mesogastric region; postcervical groove weak, barely visible across axis, terminating in weak arcuate pits at lateral margin; branchiocardiac groove approximately parallel to cervical groove, then arcing posteriorly around posterolateral margin of cervical groove.

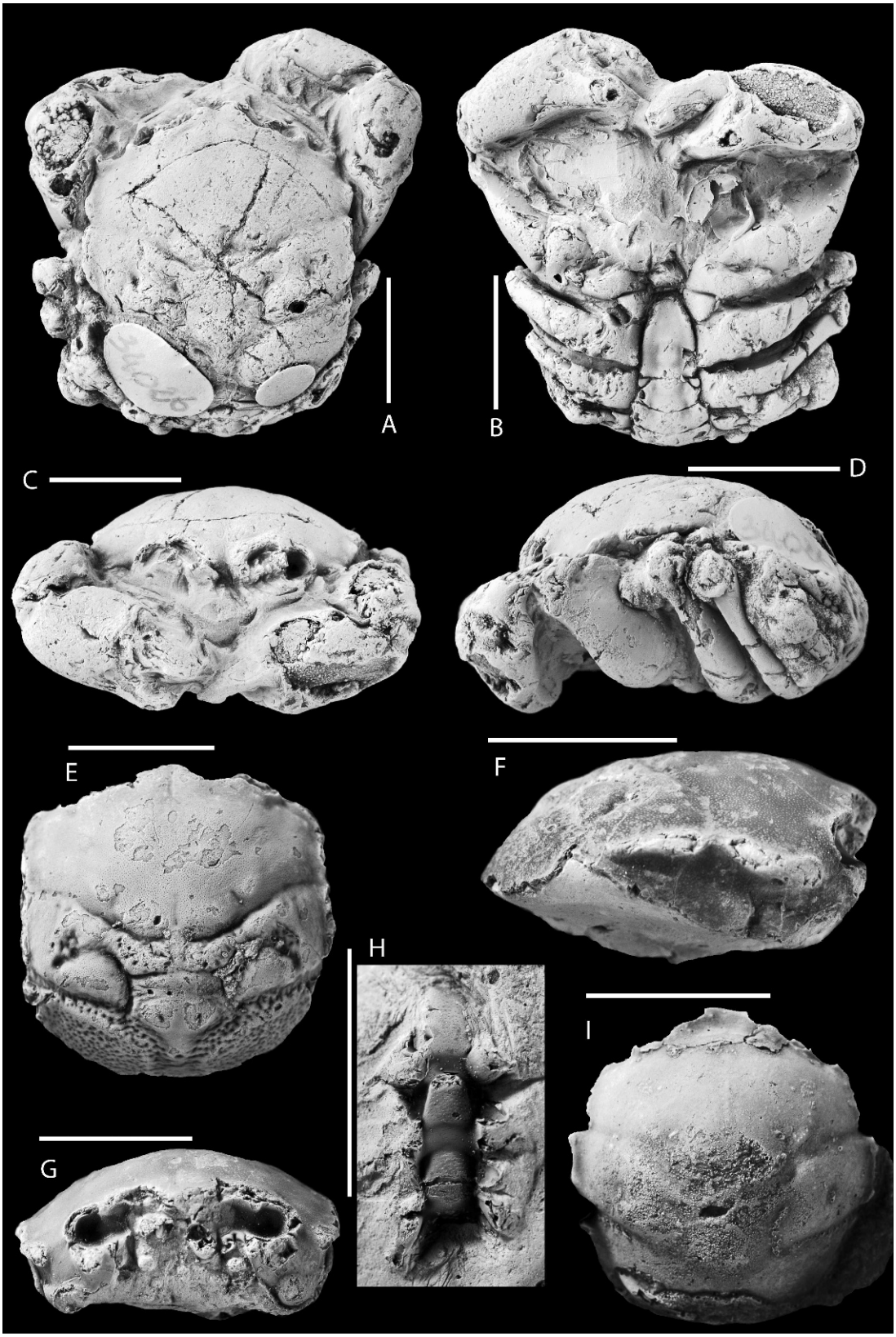

Fig. 4. *Dromilites simplex* Quayle and Collins, 1981. A-D, (BMNH) 34026, holotype, male, dorsal surface (A), ventral surface showing ventral surface, uropods, long triangular telson, somites 4-6, and anterior extension of sternite 4 (B), anterior view (C), and left lateral view showing reduced pereiopods 4 and 5 (D); E-H, (BMNH) NHM IC 548 specimen, female, dorsal surface (E), right lateral view showing inflated subhepatic region (F), anterior view (G), and female sternum showing long anterior projection on sternite 4 (H); I, cast of (BMNH) In. 28173, paratype, showing well-developed lateral ridges. Scale bars = 1 cm. Photos A-D copyrighted by The Natural History Museum, London, UK, and photographed by Mr. P. Crabb.

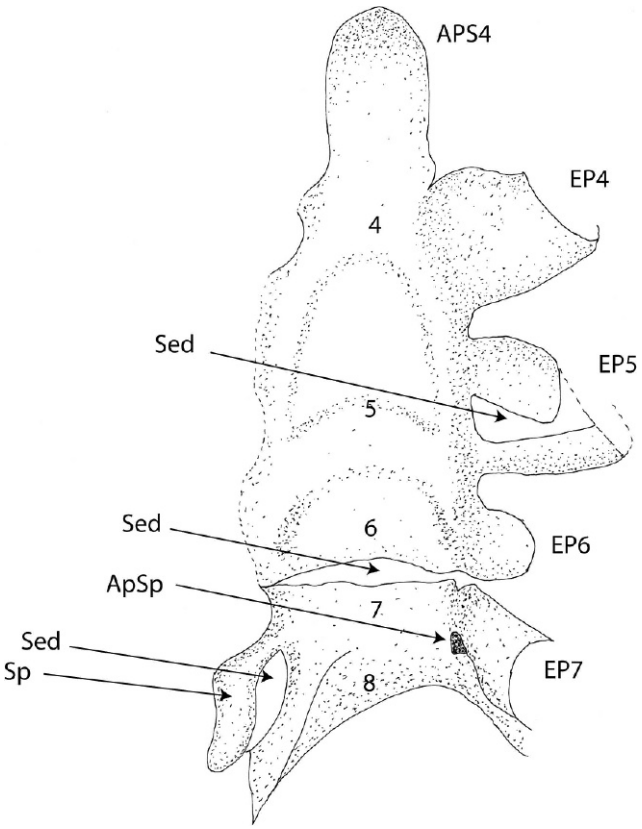

Fig. 5. *Dromilites simplex*. Line drawing of female sternum of (BMNH) NHM IC 548 (Fig. 4H). Numbers 4-8 indicate sternite number; APS4, anterior projection of sternite 4; EP4, episternite 4; EP5, episternite 5, EP6, episternite 6; EP7, episternite 7; Sed, indicates places obscured by sediment; ApSp, aperture of spermatheca; Sp, spermatheca in cross section.

Subhepatic swelling strongly inflated. Flanks oriented perpendicular to dorsal carapace, high anteriorly, becoming shorter posteriorly. Cervical groove extending onto flank obliquely anteriorly, bounding anterior margin of subhepatic swelling; posterior to cervical groove lies a subepibranchial swelling. Branchiocardiac groove extending in very oblique path onto flank, joining ventral extension of cervical groove just ventral to subepibranchial swelling.

Pereiopods weakly heterochelous; outer surface of manus smooth. Pereiopods 2 and 3 moderate in size, coxae of pereiopods 2 with small knob-like swelling at base; pereiopod 4 smaller than 3; pereiopod 5 smallest, carried subdorsally.

Female sternum narrow. Sternite 4 very long, downturned anteriorly; with long, slightly anterolaterally directed episternal projections oriented at about 60° to long axis of sternum; arcuate, raised central swelling between sternites 4 and 5. Sternite 5 with long, straight-sided segment anterior to episternal projections which are laterally directed. Sternite 6 raised axially, shorter than 4 and 5, with weakly posterolaterally directed episternal projections oriented at about 105° to long axis of sternum. Sternite 7 longer than 6, possibly separated from 6 by complete suture, with posteriorly widening, posterolaterally directed episternite oriented at about 120° to long axis of sternum. Sternite 8 directed strongly posterolaterally oriented at about 130° to long axis of sternum. Spermatheca situated just at termination between episternites 7 and 8, opening rather large, circular; opening connected with a tube directed moderately posterolaterally oriented at about 120° to long axis of sternum, then strongly posterolaterally oriented at about 150° to long axis of sternum.

Male pleonites 4 and 5 rectangular, wider than long; pleonite 6 with triangular epimeres, uropods small, visible, nested between pleonite 6 and telson, telson much longer than wide, reaching anterior ends of coxae of chelipeds.

Material Examined.—BMNH In. 34026, holotype (male); (BMNH) In. 28173, paratype; (BMNH) NHM IC 548 (female). (BMNH) In. 61700, paratype, appears not to be a member of the same taxon.

Occurrence.—All of the confirmed members of the species were collected from the Eocene London Clay (Quayle and Collins, 1981).

Remarks.—*Dromilites simplex* is remarkably well preserved, with a beautifully presented female sternum (Figs. 4H, 5). Such preservation is rare among fossil brachyurans. This sternum is one of the key features indicating referral of *Dromilites* to Sphaerodromiidae. It possesses a long anterior process, posteriorly placed spermatheca, a short suture between sternite 7/8, and in general form, is remarkably similar to the sternum of *Sphaerodromia ducoussoi* McLay, 1991, illustrated by Guinot and Tavares (2003, fig. 21) despite an age difference of approximately 40 million years. Even the arcuate central raised areas on the central part of the sternum are similar between these two species.

One of the paratypes, (BMNH) In. 61700, does not belong to the species (Fig. 3F). Its carapace is pentagonal, with a short branchial region. *Dromilites simplex* is longer than wide and rectangular, and has a moderately long branchial region. This paratype is best referred to *Dromia* sp. until better specimens and a more complete study of the material can be made.

Ferricorda n. gen.

Type Species.—*Dromiopsis kimberleyae* Bishop, 1987, by monotypy.

Diagnosis.—Carapace ovate, narrowing anteriorly, flattened transversely, weakly vaulted longitudinally; rostrum triangular; orbits deep, lower margin extending beyond upper orbital margin, visible in dorsal view; lateral margins rimmed, rim extending to outer-orbital corner; cervical, postcervical, and branchiocardiac grooves well-developed; subhepatic and omega? region inflated; female abdominal somites wide, rectangular.

Description.—As for species.

Etymology.—The genus name is derived from the Latin words *ferrum*, meaning iron, and *cordis*, meaning heart, in reference to the Heart Tail Ranch, on which the specimens were collected, and the Gammon Ferruginous Members of the Pierre Shale, in which the specimens occur.

Discussion.—Bishop's (1987) original placements of *Dromiopsis kimberleyae* in *Dromiopsis* Reuss, 1858 [imprint 1857] cannot be retained. The type species of *Dromiopsis*, *D. rugosus* (Schlotheim, 1820), is characterized by a carapace that is hexagonal and widest in the anterior one-third; spinose anterolateral margins; a narrow fronto-orbital width to width ratio; and a marked gap between the orbit and the anterolateral margin, such that the fronto-orbital width does not occupy the entire frontal margin of the carapace, as seen in *D. kimberleyae*. *Dromiopsis kimberleyae* is ovate and widest about two-thirds the distance posteriorly on the carapace; has a rimmed anterolateral margin; a fronto-orbital width that occupies nearly 60% the maximum carapace width; and lateral ridges that merge with the outer orbital margin. Thus, *D. kimberleyae* is not a member of *Dromiopsis*.

Dromiopsis kimberleyae is well represented by numerous specimens, some of which have the sternum and portions of the pleon preserved (Fig. 6). The morphological similarity of the dorsal carapace of *D. kimberleyae* to *Dromilites bucklandi*, in addition to the similarities between the sterna and pleon of the specimens of *Dromilites* sensu stricto and *Dromiopsis kimberleyae*, indicates that they are referable to the same family (Figs. 2B and 6D especially). *Dromiopsis kimberleyae* and species of *Dromilites* share a longer than wide carapace; rostrum projecting beyond orbits; an orbital area composed of two contiguous circular depressions; an inflated subhepatic region; all grooves well defined; similar ornamentation of the dorsal carapace, and similar sterna. Dorsal carapace features including the singular rostrum in *Dromiopsis kimberleyae* and the less crispate lateral margins in that species suggest that it is referable to a distinct genus within the same family as *Dromilites*. Thus, we refer *Dromiopsis kimberleyae* to a new genus herein erected to accommodate it, referable to Sphaerodromiidae, based upon dorsal carapace and ventral characteristics.

Ferricorda kimberlyae (Bishop, 1987) new combination
Fig. 6

Dromiopsis kimberleyae Bishop, 1987, p. 35, figs. 1, 2. Schweitzer et al., 2003, p. 21; Beschin et al., 2007, p. 24; Schweitzer et al., 2009, p. 65.

Diagnosis.—as for genus.

Description.—Carapace as wide as long, ovate, widest in anterior portion of branchial region about 70% the distance posteriorly on carapace; flattened transversely, weakly vaulted longitudinally. Rostrum triangular, downturned, weakly sulcate axially. Orbits forward directed, ovate, rimmed; lower margin extending beyond upper orbital margin, visible in dorsal view; fronto-orbital width 57% maximum carapace width.

Anterolateral and posterolateral margins confluent, convex, margin anterior to intersection with cervical groove with thick rim; deep notch at intersection with cervical groove; weaker ridge on margin between cervical and branchiocardiac groove, weakening posteriorly; margin deeply notched at intersection with branchiocardiac groove; margin posterior to branchiocardiac groove entire. Posterior margin weakly concave, rimmed.

Epigastric regions equant, inflated. Mesogastric region with long anterior process, triangular overall, with inflated scabrous patches posteriorly; posteriorly longitudinally divided into by short groove. Protogastric and hepatic regions confluent; protogastric area more inflated than hepatic area. Metagastric region short, wide; urogastric region very short, with spherical swellings at distal ends; cardiac region small, triangular; intestinal region long, poorly defined.

Cervical groove deep, broadly concave anteriorly; postcervical groove well developed, extending from axis about half the distance to lateral margins on each side. Branchiocardiac groove deep, curving weakly concave forward, then arcing posteriorly around lateral margins of cardiac region.

Epibranchial region moderately inflated, partially transversely bisected by postcervical groove. Remainder of branchial regions broadly inflated.

Flanks steep, at about 70° angle to dorsal carapace; subhepatic region strongly inflated, bounded posteriorly by ventral extension of cervical groove. Branchiocardiac groove extending onto flank, extending obliquely forward, then curving to parallel lower margin of carapace to intersect cervical groove; area above branchiocardiac groove and posterior to cervical groove inflated (omega?); flank becoming less high posteriorly.

Male? sternite 4 with long, parallel sided portion anterior to episternal projections, which are narrow and taper distally. Sternite 5 with narrow episternal projections. Sternite 6 poorly known. Sternites 7 and 8 directed posteriorly. Female pleonites wide.

Types and Occurrence.—The holotype SDSM 10184, paratype SDSM 10185, and three other specimens, SDSM I 3996-3998, were collected from the Heart Tail Ranch, north of Belle Fourche, in western South Dakota. The rocks are from the early Campanian Gammon Ferruginous Member of the Pierre Shale (Bishop, 1987).

Remarks.—*Ferricorda kimberleyae* is a reasonably well preserved member of the decapod fauna of the Heart Tail Ranch fauna. It is not nearly as common as other taxa described by Bishop (1985) from the locality, but the specimens are well enough preserved to be ascribed to Sphaerodromiidae based upon the carapace, sterna and abdomina. Its Campanian occurrence makes it the oldest member of this extant family.

Discussion

Referral of *Dromilites* and *Ferricorda* to Sphaerodromiidae firmly places Dromioidea within the Late Cretaceous with confidence. Examination of other genera referred to Dromiidae and Dynomenidae is ongoing and should determine their appropriate family placement and therefore the time of origin of the respective families. As has been noted previously, upwards of 80% of decapod families, and possibly more, that were present during the Cretaceous survived the K/T event(s) (Schweitzer and Feldmann, 2005). Investigation of the conservative nature of the Decapoda is ongoing.

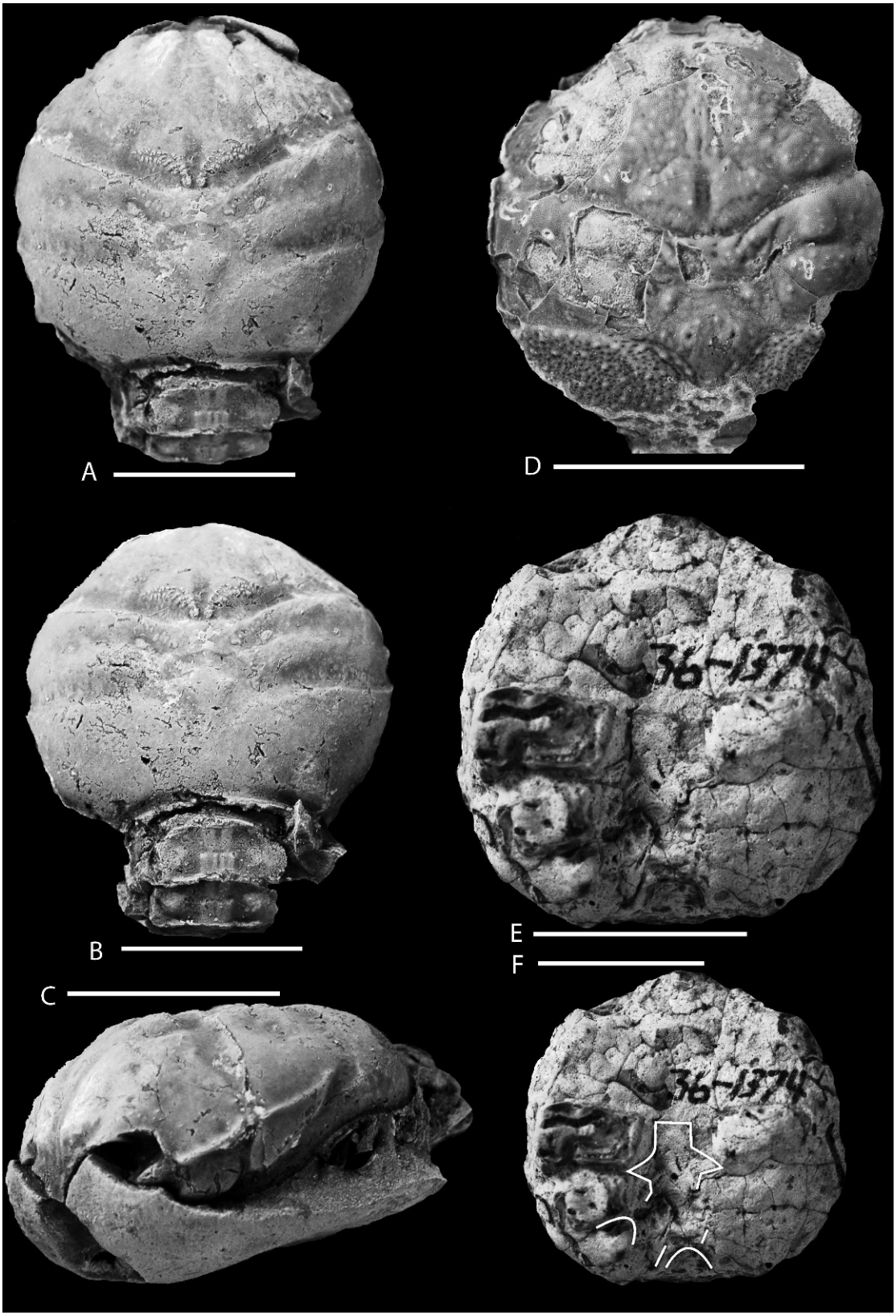

Fig. 6. *Ferricorda kimberleyae* (Bishop, 1987). A-C, SDSM 10184, holotype, female, dorsal view (A), oblique posterior view showing abdominal somites (B), oblique left lateral view showing inflated subhepatic and omega? region and lateral ridge; D, SDSM I 3997, dorsal carapace showing ornamentation; E-F, SDSM I 3996, ventral surface showing sternum (E) and sternum with outline drawn (F). Scale bars = 1 cm.

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