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# A NEW EARLY OLIGOCENE CRAB (DECAPODA, BRACHYURA, DROMIACEA) FROM NORTHWEST BELGIUM, WITH COMMENTS ON ITS PALAEOBIOLOGY

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(3 figures, 1 table)

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**ABSTRACT.** A new genus and species of dromiacean crab, *Lucanthonisia praemium*, is recorded from the basal Belsele-Waas Clay Member (Boom Clay Formation; Rupelian, lower Oligocene) as formerly exposed at the Scheerders van Kerchove (SVK) clay pit near Sint-Niklaas, province of Oost-Vlaanderen (northwest Belgium). Extant dromioid crabs either carry foreign objects for camouflage (Dromiidae, Homolodromiidae) or are associated with corals (Dynomenidae). Although having been collected from the basal portion of the Belsele-Waas Clay Member which is rich in phosphatic nodules, preservation of the new form is such that long-term transport is unlikely. Therefore, the species is assumed to have lived hidden amongst and below such nodules, but it cannot be ruled out that it also carried sponges for defence. To our knowledge, representatives of such biota have not yet been recorded from the Boom Clay Formation. *Dromilites eotvoesi* from middle Miocene ('upper Badenian', Serravallian) strata in the Budapest area (central Hungary) is transferred to the new genus, *Lucanthonisia*. *Lucanthonisia eotvoesi* n. comb. differs from *L. praemium*, the type species, in having shorter, more anteriorly directed lateral spines, more closely spaced and less divergent rostral horns, better-developed epigastric nodes and a less convex carapace longitudinally. Preservation of a partial thoracic sternum in *L. praemium* gen. nov., sp. nov. allows comparison with dromioid families and tentative placement of the new genus, as well as the allied *Basinotopus*, in the Dynomenidae.

**KEYWORDS:** Crustacea, Decapoda, Dromioidea, Dynomenidae, Oligocene, Belgium, new taxa, palaeobiology.

## 1. Introduction

Dromiaceans often hide in crevices or carry foreign objects or organisms such as sponges, shells, ascidians, and rarely sea anemones to prevent being detected by potential predators (Guinot et al., 1995; Müller, 2004). In the Dromiidae diverse objects or organisms are grasped by modified posterior legs, placed on the carapace and held there. Some sponge species and most sea anemones taken by dromioids are toxic and thus provide additional protection against predators. In the fossil record, dromioid diversity (i.e., members of the families Dromiidae de Haan, 1833 and Dynomenidae Ortmann, 1892) increased following Cretaceous-Paleogene (K/Pg) boundary perturbations (Table 1). However, in comparison to other brachyurans, dromiacean crabs constitute only a minor percentage of fossil decapod crustacean faunas (Bell, 1858; Bachmayer & Tollmann, 1953; Quayle & Collins, 1981; Busulini et al., 1983; Solé & Via, 1989; Beschin et al., 1994, 2001, 2002, 2005, 2007a, b; De Angeli, 1995; Blow & Manning, 1996; Kato & Karasawa, 1998; De Angeli & Beschin, 2001; Karasawa, 2001; Fraaije, 2003; Müller, 2004; Schweitzer & Feldmann, 2005), which is comparable to extant faunas (Ng et al., 2008).

In Europe, decapod crustaceans are fairly common in strata of Eocene and Miocene age, but are much rarer in Oligocene deposits. Not only are such strata less well exposed, they also represent mainly siliciclastic, slightly cold-water platform settings, in which sandy and/or clay-rich, volcaniclastic sediments were laid down (Vandenberghe, 1978; Zimmerle, 1994). Notable exceptions are the rich faunas recorded from the lower Oligocene of northern Germany (Förster & Mundlos, 1982) and Piemonte, northern Italy (Allasinaz, 1987). Carbonate nearshore or reefal settings are uncommon during this time interval (compare Müller, 2004), which may explain the rarity of dromioid crabs.

Predominantly clayey Rupelian strata are well known and widely distributed in northwest Belgium, in particular in the Boom area (Fig. 1). Formerly, these clays were excavated on a large scale for local brickworks. In these strata, van Bakel et al. (2006) recognised one species each of macrurans and anomurans, plus four brachyuran taxa, inclusive of the new genus and species described below, to which they referred as 'dromiid n. gen., n. sp.'. The sole crab species of Rupelian age recorded so far from Belgium was *Coeloma* (*Paracoeloma*) *rupeliense*

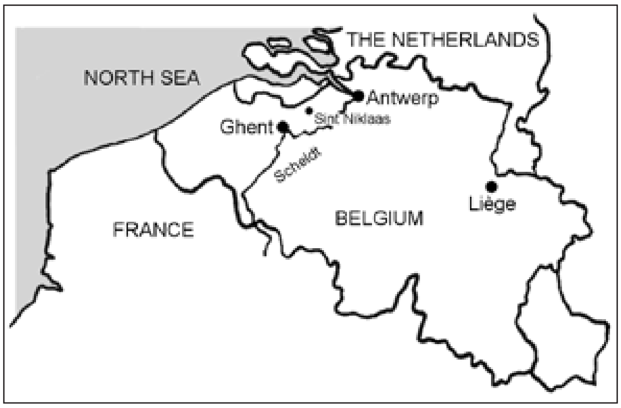

**Figure 1.** Map of Belgium, indicating the location of the former Scheerders van Kerchove (SVK) clay pit near Sint-Niklaas (province of Oost-Vlaanderen).

Stainier, 1887, of which hundreds of nodule-preserved specimens are housed in various museum collections (Van Straelen, 1921; Feldmann & Dhondt, 1991). Verheyden (2002) described collections held at the Institut royal des Sciences naturelles de Belgique (IRScNB, Brussels) in detail, correctly interpreted *Portunus nodosus* Van Beneden, 1883 to be a *nomen nudum* and showed *Coeloma rupeliense* to be the valid name of this taxon. In addition, he illustrated large cheliped remains of a giant macruran, *Homarus percyi* Van Beneden, 1872. Both *Coeloma* (*Paracoeloma*) *rupeliense* and *Homarus percyi* have subsequently also been recorded from nodules reworked into the base of the Pliocene sequence at Kallo, near Antwerp (van Bakel et al., 2006).

In recent years, Rupelian strata at the Scheerders van Kerchove (SVK) clay pit (Fig. 2) have yielded a rich crustacean fauna, the composition of which differs from assemblages known from adjacent outcrops. A diogenid hermit crab with stridulatory apparatus, *Ciliopagurus obesus*, was described by van Bakel et al. (2003). Of *Coeloma* (*Coeloma*) sp. only fragmentary specimens are known, and a cirolanid isopod and stomatopod remains are currently being studied by us. In the present paper, we describe a new genus and species of dromiacean, which could have been derived from the genus *Basinotopus* M'Coy, 1849 (type species: *Inachus lamarckii* Desmarest, 1822). Both genera may be related to the extant genus *Paradynomene* Sakai, 1963 (type species: *P. tuberculata* Sakai, 1963).

## 2. Systematic palaeontology

Classification and terminology follow Guinot & Bouchard (1998), Martin & Davis (2001), Guinot & Tavares (2003), Ahyong et al. (2007) and Ng et al. (2008). Commonly used morphological terms are the following: episternite – lateral extension of the sternite, in the form of a more or less pointed projection which bears the gynglyme receiving the condyle of the corresponding appendage

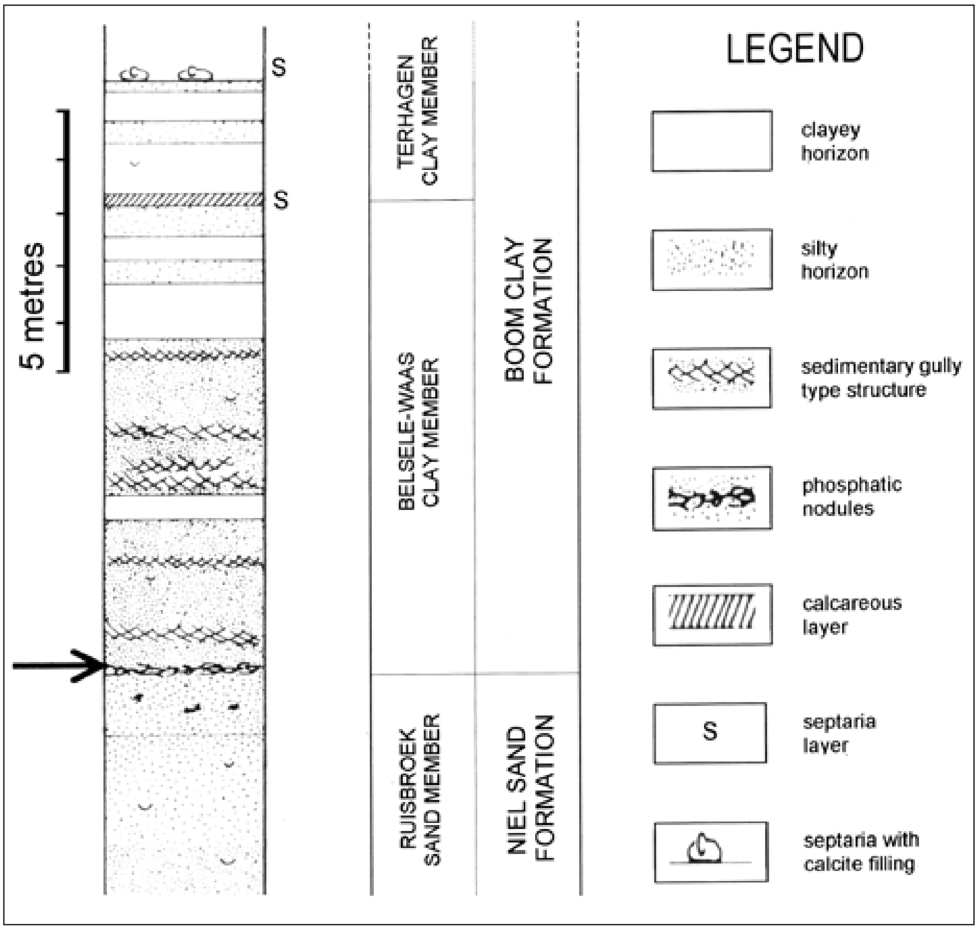

**Figure 2.** Stratigraphy of the section formerly exposed at the Scheerders van Kerchove (SVK) clay pit (modified from Mollen, 2007), with arrow marking provenance of the type specimen of *Lucanthonisia praemium* gen. nov., sp. nov.

(see Guinot & Tavares, 2003: 47); sternocoxal depressions – deeply excavated depressions at the lateral sides of the thoracic sternum in which the coxae of the pereiopods can move, as defined by Guinot et al. (1995) and Guinot & Bouchard (1998). Sternites and episternites are indicated by number 1 to 8, as are the pereiopods 1 to 5 (e.g., P1 for chelipeds, P2-P5 for walking pereiopods). We follow Ng et al. (2008) in assigning authorship of the taxon Brachyura to Linnaeus (1758) rather than to Latreille (1802).

To denote the repositories of specimens referred to in the text, the following abbreviations are used: MAB – Oertijdmuseum De Groene Poort, Boxtel, the Netherlands; MGUH – Geological Museum, Copenhagen University, Copenhagen, Denmark; MNM – Magyar Nemzeti Múzeum, Őslénytár, Hungary.

Infraorder Brachyura Linnaeus, 1758
Section Dromiacea de Haan, 1833
Superfamily Dromioidea de Haan, 1833
Family ?Dynomenidae Ortmann, 1892
Genus *Lucanthonisia* gen. nov.

*Derivation of name*. In honour of Mr Luc Anthonis (Bouwel, Belgium), who collected and donated the type and sole specimen known to date.

*Type species*. *Lucanthonisia praemium* sp. nov.

*Diagnosis*. Carapace subovate with a wide posterior margin; length slightly exceeding width, convex in longitudinal and transverse cross sections; rostrum produced, tridentate with thorn-shaped spines; lateral margins with four equal-sized, slender spines; carapace surface with numerous pits, areolation weak; cardiac region broad, cervical groove does not reach the lateral carapace margin, but the branchial groove does. Orbitofrontal margin more than half the carapace width (excluding lateral spines); orbits deep, ovate, with a small notch below the outer orbital angle, suborbital area with two tubercles. Sternal plate flat, with fused elements 4-7, which are constant in width, except for the episternites which are purely laterally directed; sternite 4 broad.

*Discussion*. As a complement to the extensive revision by McLay (1993), Guinot & Tavares (2003: 44) proposed a

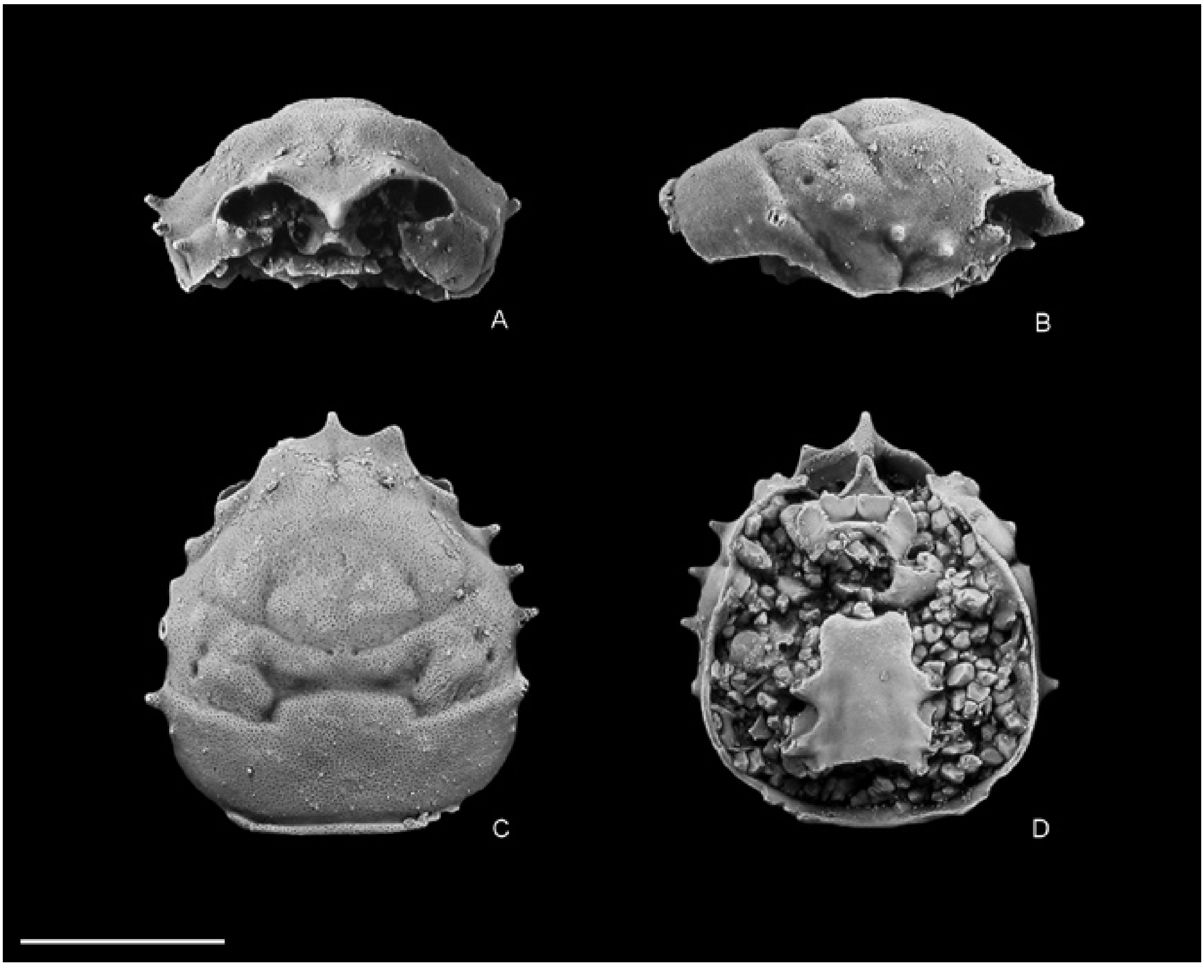

**Figure 3.** *Lucanthonisia praemium* gen. nov., sp. nov., MAB k.2448 (holotype), basal portion of the Belsele-Waas Clay Member, Boom Clay Formation (Rupelian, lower Oligocene), SVK clay pit, Sint-Niklaas (province of Oost-Vlaanderen, Belgium), in orbital (A), right lateral (B), dorsal (C) and ventral (D) views. Specimen coated with ammonium chloride prior to photography. Scale bar equals 3 mm.

new subfamilial arrangement of the Dromiidae and recognised thirty-eight genera, primarily based on, 'the morphology of the thoracic sternum, spermathecae at the extremity of sternal sutures 7/8, uropods, vestigial male pleopods on abdominal somites 3-5, coxa of the fifth pereopod and the penis'. The same characters were primarily used in a key to dromiacean families by Guinot & Tavares (2003: 120). When dealing with fossil material, where mostly only dorsal carapaces are available, proxy characters can be used for classification (Schweitzer, 2003).

### ***Lucanthonisia praemium*** **sp. nov.**

*Derivation of name*. From Latin, *praemium*, reward or recompense, alluding to the enormous amount of sieving residue processed to find the specimen.

*Type*. Holotype, of indeterminate sex, is MAB k.2448 (leg. L. Anthonis). Carapace length (including rostrum) is 6,3 mm, carapace width (including lateral spines) is 5,7 mm; it is interpreted as a juvenile.

*Diagnosis*. Carapace subovate in outline, slightly longer than wide; rostrum produced, wide; tridentate through robust inner orbital spines; lateral margins spinose, posterior margin broad; only central carapace regions well defined.

*Locality and stratigraphy*. Collected from sieve residues of samples taken in 2005 from the basal portion of the Belsele-Waas Clay Member (Boom Clay Formation; see Fig. 2), dated early to middle Rupelian (Oligocene) on the basis of calcareous nannofossils (Steurbaut, 1986, 1992; Laga et al., 2002), typical of calcareous nannoplankton zone NP 23 (sensu Martini, 1971), as exposed at the Scheerders van Kerchove's Verenigde Fabrieken (SVK) clay pit, southwest of Sint-Niklaas, province of Oost-Vlaanderen (Belgium), now no longer worked. For more detailed data on this locality and the section formerly exposed, reference is made to Vandenberghe (1978), Vandenberghe et al. (2002) and Mollen (2007).

*Description*. Carapace subovate, slightly longer than wide, greatest carapace width a third from posterior margin, convex in longitudinal and transverse cross sections; orbitofrontal margin 64 % of maximum carapace width, marginal spines included. Front produced, broad, occupying more than half of orbitofrontal width; inner orbital spines stout and divergent, at slightly lower (vertical) level than sharp, thorn-shaped rostrum; rostrum downturned, but with its tip directed anteriorly; orbits deep, broadly ovate, with weakly raised and entire orbital margin leading to a distinct outer orbital corner. A small notch is situated just below the outer orbital corner; the suborbital margin with two tubercles, the outer slightly larger than the inner. Anterolateral margin long, bearing four upwardly directed, equal-sized conical spines; first three spines slightly anteriorly directed and evenly spaced, separated by broadly U-shaped notches; posterior lateral spine more widely separated from anterior ones, directed perpendicularly to carapace axis. Posterolateral margin short, strongly curved towards posterior margin. Posterior margin equals in width the orbitofrontal margin and is bounded by a distinct rim and a rather deep groove.

Epigastric elevations hardly noticeable, bounding the weakly defined, narrowly triangular, anterior mesogastric process. Posterior mesogastric process more strongly elevated, broadly triangular and subdivided by obscure median sulcus. The large and gently raised protogastric regions barely separated from the narrow hepatic strip; urogastric lobe low, anterior margin concave, posterior margin straight and more clearly defined; lateral margins strongly divergent. Cardiac region large, shield shaped, posteriorly indistinctly bounded. Meso- and metabranchial regions obliquely directed, raised axially, paired by cervical and branchiocardiac grooves, and only basally separated by anterior branch of branchiocardiac groove; only a rim of pterygostomian region is preserved. Cervical groove faint laterally, interrupted axially between clearly visible gastric pits. The cervical groove does not notch the lateral margin, but is replaced by a Y-shaped groove which extends downwards on the subhepatic area, starting at the two anteriormost lateral spines. The branchial groove runs through uninterrupted and makes a notch laterally on margin; it is prolonged ventrally.

Proepistome and epistome preserved : proepistome triangular with apex directed forwards, the lateral sides being concave; epistome wide, with typical wing-shaped lateral projections; mandibular sternite attached to epistome, anteriorly defined by a triangular fossa.

Thoracic sternum well preserved, interpreted to be formed at least by sternites 4-6, broken just posterior to sternite 6. Sternal plate undivided and relatively wide, its width being constant along sternites 4-6 (except for extended episternites). Sternites 1-3 not preserved, the small triangle visible in Fig. 3D is formed by sediment only. Sutures not visible. Sternites 4 and 6 easily recognised on account of the landmarks represented by well-developed gynglymes; sternite 4 quadrate with a concave anterior margin and with a markedly projected episternite. Sternite 6 short; sternites 5 and 6 with a very weak median depression. Posterior sternites not preserved. Episternites 4 and 5 (corresponding to P1 and P2, respectively) elongated, triangular, directed outwardly, their anterior side being hollowed in deep sternocoxal depressions.

Carapace surface with numerous small, evenly distributed pits.

*Discussion*. *Lucanthonisia* gen. nov. is included in the Dromiacea and may be placed either in the Dromiidae (see McLay, 1991, 1993) or Dynomenidae (see McLay, 1999). Since we assume the new genus to be related to *Basinotopus*, the existence of dorsal uropods in *B. lamarckii* (see Bell, 1858: pl. 5, figs. 1, 7-9) eliminates the family Homolodromiidae Alcock, 1900 (see Guinot & Richer de Forges, 1995) in which the uropods always show as ventral lobes and in which the abdominal somites have lateral pleurae.

*Lucanthonisia* might be assigned to the Dromiidae. With respect to the thoracic sternum, the following can be stated. If the holotype of *Lucanthonisia praemium* gen. nov., sp. nov. represents a female specimen, it cannot be referred to the Dromiinae de Haan, 1833, a subfamily in which the female sternal sutures 7 and 8 move forwards, and thus are very long, the apertures of the spermathecae opening far beyond the level of P3 coxa (see Guinot & Tavares, 2003: 49, 121; Guinot & Quenette, 2005: 272, fig. 1). Only the atypical dromiine *Stebbingdromia* Guinot & Tavares, 2003 has short sutures 7 and 8 in females, but the carapace is more rounded, the rostrum is bifid and the anterolateral margin has only two flat teeth. If the type of *L. praemium* gen. nov., sp. nov. represents a male (i.e., in males, the sternal plate is not modified by suture 7/8; see Guinot & Quenette, 2005: 272), it may be a dromiine (compare e.g. the sternum in *Platydromia* Brocchi, 1877 in Guinot & Tavares, 2003: fig. 16, and that of *Exodromidia* Stebbing, 1905 in Guinot & Bouchard, 1998: fig. 5). However, many dromiines have a narrower sternite 4 (compare e.g. *Austrodromidia australis* (Rathbun, 1923) as illustrated by Guinot & Tavares, 2003: fig. 1A) and generally have the anterior termination of sternite 4 as a single apex (as in *Stebbingdromia* Guinot & Tavares, 2003; see Guinot & Tavares, 2003: fig. 17A, C). In extant *Dromidiopsis* Borradaile, 1900, the carapace is more circular, the median rostral tooth does not project beyond the adjacent pair, and the posterior corners are pronounced rather than rounded (see Cleva et al., 2007: fig. 9C). Sternite 4 is very narrow in *Dromidiopsis*, and the episternites not much extended (see Guinot & Tavares, 2003: fig. 6A), which differs significantly from *Lucanthonisia* gen. nov.

If *Lucanthonisia* gen. nov. is not a dromiine, it might belong to the subfamily Sphaerodromiinae Guinot & Tavares, 2003, a group in which the female sternal suture 7/8 is very short, only posterior and located laterally, the apertures of spermathecae being posterior to the level of the P3 coxal gonopore. The carapace outline in sphaerodromiines is ovoid as in *Lucanthonisia* gen. nov., but with a narrower posterior margin.

The atypical dromiacean genus, *Frodromia* McLay, 1993 (see McLay, 1993: figs 6, 17D; considered to be of uncertain status by Guinot & Tavares, 2003; now in the tribe Frodromiini Števčić, 2005, within the Sphaerodromiinae) also has short sutures 7/8 in females. In *Lucanthonisia* gen. nov., sternite 4 is wider than that in *Frodromia* (compare Guinot & Tavares 2003: fig. 25b).

In the genus *Basinotopus*, the broadest portion of the cardiac region typically equals a third of total carapace width, measured from the bases of the lateral spines. Collins (2003) and Collins & Jakobsen (2004) distinguished *Dromilites* H. Milne Edwards, 1837 (type species: *D. bucklandii* H. Milne Edwards, 1837) from *Basinotopus* by noting that *Dromilites* has a bifid rostrum (in dorsal view), while *Basinotopus* differs markedly in showing a produced rostrum between inner orbital horns, i.e. has a tridentate front. Adopting the definition of *Basinotopus* by Collins (2003) and Collins & Jakobsen (2004), *Dromilites eotvoesi* Müller, 1975 (p. 508, pl. 1, fig. 5; pl. 2, figs. 1, 4; holotype is MNM MF 11; see for a better illustration Müller, 1976: 150, pl. 2, figs. 1-3), which was transferred to the genus *Dromia* Weber, 1795 (Müller, 1984: 63, pl. 29, figs. 8, 9; pl. 30, figs. 1-7), could be assigned to *Basinotopus*. However, *Dromilites eotvoesi* cannot be accommodated in *Basinotopus* because, although carapace outline, frontal structure and division of carapace regions are roughly similar, *Dromilites eotvoesi* has a smooth carapace with numerous setal pits. This morphology indicates a hairy appearance in life. In addition, the lateral spines are smaller and more slender. The morphology of *Dromilites eotvoesi* suggests it hid and lived in crevices. The new species from the lower Oligocene of Belgium is closely similar, and both it and *Dromilites eotvoesi* are placed in a new genus, *Lucanthonisia* gen. nov.

*Lucanthonisia eotvoesi* n. comb. was originally described from middle Miocene ('lower upper Badenian', equivalent of lower Serravallian; see Harzhauser et al., 2002) of the Budapest area in central Hungary. It has shorter, more anteriorly directed lateral spines than *L. praemium* sp. nov., its rostral horns are more closely spaced and less divergent, it has better-developed epigastric nodes, while the branchiocardiac groove in *L. praemium* sp. nov. divides the carapace surface more distinctly in the centre. The posterior margin is more clearly rimmed and lined by a deeper groove in *L. praemium*, and the carapace is more convex in longitudinal cross section. Müller (1984: 63) noted that *D. eotvoesi* was known only from 'lower upper Badenian' levels, generally co-occurring with the calappid *Calappa heberti* Brocchi, 1883, and absent from reefal structures.

Of *Basinotopus tricornis* Collins & Jakobsen, 2004 (holotype is MGUH 26778) a number of well-preserved specimens are known from the Lillebælt Clay Formation of Jylland (northern Denmark) of early Lutetian (middle Eocene) age (see Janssen et al., 2007). These specimens show details of abdomen, pereiopods, mouthparts and thoracic sternum (Collins & Jakobsen, 2004: text-fig. 3; pl. 2, figs. 1-7). Whereas only a 'possible male abdomen' is mentioned in their description, one specimen (MGUH 26776; see their pl. 2, fig. 1b) is in fact a female with an obvious gonopore on the (right) P3 coxa. The spermathecae are diminutive, at about the same vertical level as the gonopore, or slightly lower; therefore, sternal suture 7/8 is relatively short. In *B. tricornis* the anterior axial portions of sternite 7 are raised. Sternite 4 is narrower than that in *Lucanthonisia* gen. nov., the episternites are hollowed by sternocoxal depressions as in the new genus. The inclined sulcus between sternites 4 and 5 is absent in *Lucanthonisia praemium* gen. nov., sp. nov. *Basinotopus tricornis* appears closely related to the type species, *B. lamarckii*, from the lower Eocene (Ypresian) of England and the middle Eocene of northern Italy (see Quayle & Collins, 1981; Busulini et al., 1983; Collins, 2003; Beschin et al., 2005), as well as to *B. alpina*

(Glaessner, 1929) from the middle Eocene (Lutetian) of St Pankraz near Salzburg (Austria) and the lower Eocene of Spain (pers. obs.). *Dromilites lothi* Förster & Mundlos, 1982, from the upper Eocene-lower Oligocene of Handorf (north-east Germany), has a tridentate front, and the carapace areolation is utterly different. The delicate nature of the front could have been misinterpreted on account of the poor preservation in the type specimen; in any case, the inner orbital horns are weakly developed. The carapace outline, with its wide posterior margin, and broad sternite 4, makes placement of *Lucanthonisia* gen. nov. and *Basinotopus* in the subfamily Sphaerodromiinae unlikely.

The new genus could belong to the Dynomenidae, a family with a good fossil record (see e.g., Wright & Collins, 1972: fig. 9). In this group, the female sternal suture 7/8 is short, as in males. The thoracic sternum of *Lucanthonisia* shows about the same organisation as that of a dynomenid (compare Guinot & Bouchard, 1998: fig. 7A, C, D): sternites 4-7 fused in an undivided plate of constant width, thus the anterior side of sternite 4 broad, a flat medial area, and the episternites directed purely laterally. The carapace shape in *Lucanthonisia* gen. nov. is more elongate than in most extant dynomenids, but it should be remarked that at least in one dynomenid genus, the most primitive one, *Acanthodromia* A. Milne-Edwards, 1879, the carapace is long as well. *Paradynomene* Sakai, 1963 resembles *Basinotopus* (e.g., *B. lamarckii* and *B. tricornis*) in several respects (see McLay, 1999; McLay & Ng, 2004), although in the former the rostrum is shorter and stouter, the grooves and the branchial ones in particular, are steeper, and the ornament is different.

The combination of carapace ornament, the slender nature of the lateral spines, oval carapace outline and rostral structure, distinguishes the new form from other dromioid genera. Due to its size, which is smaller than average for a dromiacean, the holotype might be considered to represent a juvenile. Carapace size in the family Dynomenidae, to which *Lucanthonisia* gen. nov. and *Basinotopus* could possibly belong (see discussion below), is generally small (see McLay, 1999) but rarely as small as the specimen described here. A detailed comparison with numerous specimens of the related *Basinotopus alpina* from the Ilerdian (= lower Ypresian) of northeast Spain and of *B. lamarckii* from the Ypresian of southeast England, has revealed no indications of changes in carapace ornament or morphology during ontogeny, which is why we exclude the possibility that the type of *L. praemium* gen. nov., sp. nov. is an immature individual of *Basinotopus*.

*Noetlingia* Beurlen, 1928 has an elongate carapace, with only diminutive lateral nodes. Its type species, *Dromia claudiopolitana* Bittner, 1893, has a length/width ratio of 1.35 *vs* 1.13 in *L. praemium* gen. nov., sp. nov. The length measured includes the rostrum, the width is inclusive of the lateral spines. In addition, in *Noetlingia* the branchial and cardiac grooves are not clearly distinguished.

In conclusion, we tentatively assign *Lucanthonisia* gen. nov. to the Dynomenidae, as based on combined thoracic and carapace features shared with primitive dynomenid genera such as *Acanthodromia* and *Paradynomene*. However, this conclusion remains tentative, because we have not been able to examine male and female uropods, abdominal holding structures, spermathecae, or the condition of pereiopods 4 and 5; diagnostic of familial and subfamilial assignments within Dromiacea.

## 3. Palaeobiology

Carapace ornament is highly functional in dromiacean crabs, setal pits being indicative of a hairy surface, and whenever this occurs, it extends to the pereiopods, which all together give the crab a woolly appearance. A comparable morphology is seen in e.g. porcellanids and majids. In the homoloid *Poupinia hirsuta* Guinot, 1991, the last pair of legs are extremely mobile and covered with long setae, and can be bent over the carapace to camouflage it (Guinot et al., 1995). A different way for dromiids to camouflage their bodies is to hold an object with their modified posterior pereiopods (P4 and P5) (see e.g., Lewinsohn, 1984; McLay, 1991, 1993, 2001; McLay & Crosnier, 1991; Guinot & Bouchard, 1998).

The Eocene *Basinotopus* is characterised by a scabrous posterior carapace surface, distinctly differentiated regions with crests, and strong lateral spines of considerable length. Representatives of this genus were likely covered by epizoobionts (*sensu* Taylor & Wilson, 2002) such as ascidians, and even after being noted by a predator would not be considered a palatable choice. Such epizoobiont cover could be referred to as a symbiosis, it being an ecological relationship between organisms of two different species that live together in direct contact (Zann, 1980; Campbell et al., 1999). In extant Dromiidae and Homolodromiidae, permanently with a camouflaging host carried on by P4 and P5, it is an obligatory relationship, from which in particular the crab benefits; thus, it is better referred to as commensalism.

Long and stout lateral spines, a thick shell, and sharp spines on the dorsal surface would complicate consumption and thus protect the crab's soft parts; however, it also means severe restrictions for the crab to enter small crevices and cavities. A carapace surface roughened by tubercles and with well-differentiated regions would facilitate achorage of epizoobionts such as sponges, sea anemones and seagrasses. Subdorsal, mobile and subchelate posterior pereiopods could place these foreign objects onto the carapace, or even carry them. Elevation of carapace regions is a constant and distinctive character throughout dromioid evolution. McLay (1993) was of the opinion that dromiids were evolving towards a loss of carrying behaviour, coupled with a tendency to develop a strongly ornamented carapace and with a loss of modified P4 and P5.

Having been collected from the basal portion of the Belsele-Waas Clay Member, which is rich in phosphatic nodules, the holotype of *Lucanthonisia praemium* gen.

nov., sp. nov. is remarkably well preserved. This makes long-term transport highly unlikely, and suggests the species lived hidden amongst or under such nodules. However, it cannot be ruled out that it also carried foreign objects such as sponges, but these have not been documented so far from the Boom Clay Formation. Strata correlative with the Boom Clay Formation (Stover & Hardenbol, 1994) elsewhere in Europe (see e.g., von Daniels et al., 1994; Gaemers, 1994) may be expected to yield similar decapod crustacean faunas, possibly inclusive of dromioids.

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**Table 1:** Overview of Paleogene and Neogene dromiid and dynomenid (dromioid) crabs described to date, arranged alphabetically, indicating provenance, stratigraphic level and pertinent references.

***Ameridromia hyneorum*** Blow & Manning, 1996

South Carolina, USA; middle Eocene (Blow & Manning, 1996)

***Basinotopus alpina*** (Glaessner, 1929)

Spain; lower Eocene. Austria; middle Eocene (Glaessner, 1929; Vogeltanz, 1968; this paper)

***Basinotopus lamarckii*** (Desmarest, 1822)

England; lower Eocene. Veneto and Sicily, Italy; middle Eocene (De Angeli & Beschin, 2001; Collins, 2003; Beschin et al., 2005; De Angeli & Garassino, 2006)

***Basinotopus tricornis*** Collins & Jakobsen, 2004

Denmark; middle Eocene (Collins & Jakobsen, 2004; Janssen et al., 2007)

***Cyamocarcinus angustifrons*** Bittner, 1883

Veneto and Sicily, Italy; Hungary, Austria; lower-upper Eocene (Wank, 1968; De Angeli & Beschin, 2001; De Angeli & Garassino, 2006; Beschin et al., 2007b)

***Cryptodromia*** aff. ***fallax*** (Lamarck, 1819)

Japan; Plio-Pleistocene (Karasawa, 2001)

***Dromia neogenica*** Müller, 1979a

Hungary; middle Miocene (Müller, 1979a, 1984)

***Dromia personata*** (Linnaeus, 1758)

Sicily, Italy; upper Pleistocene (De Angeli & Garassino, 2006, as *D. vulgaris* H. Milne Edwards, 1837)

***Dromidia bedetteae*** Blow & Manning, 1996

South Carolina, USA; middle Eocene (Blow & Manning, 1996)

Dromiidae gen. et sp. indet. 1

Japan; Pleistocene (Kato & Karasawa, 1998)

Dromiidae gen. et sp. indet. 2

Japan; Pleistocene (Kato & Karasawa, 1998)

Dromiidae sp.

France; Miocene (Artal & Gilles, 2007)

***Dromilites bucklandii*** H. Milne Edwards, 1837

England; lower Eocene (Collins, 2003)

***Dromilites corvini*** (Bittner, 1893)

Hungary; upper Eocene. Vicenza, Italy; upper Eocene-lower Oligocene (Beschin et al., 2001; De Angeli & Beschin, 2001; De Angeli & Garassino, 2006)

***Dromilites fossata*** Müller & Collins, 1991

Hungary; upper Eocene (Müller & Collins, 1991)

***Dromilites hilarionis*** (Bittner, 1883)

Vicenza, Italy; Spain; middle-upper Eocene (Busulini et al., 1983; De Angeli, 1995; De Angeli & Beschin, 2001; Beschin et al., 2005; De Angeli & Garassino, 2006)

***Dromilites humerosus*** Quayle & Collins, 1981

England; middle-upper Eocene (Quayle & Collins, 1981; Collins, 2003)

***Dromilites lothi*** Förster & Mundlos, 1982

Germany; upper Eocene-lower Oligocene (Förster & Mundlos, 1982)

***Dromilites pastoris*** Via Boada, 1959

Vicenza, Italy; Spain; middle Eocene (Beschin et al., 1994; De Angeli & Beschin, 2001; Beschin et al., 2005; De Angeli & Garassino, 2006)

***Dromilites simplex*** Quayle & Collins, 1981

England; middle-upper Eocene (Quayle & Collins, 1981)

***Dromilites subglobosa*** Müller & Collins, 1991

Hungary; upper Eocene (Müller & Collins, 1991)

***Dromilites vicensis*** Barnolas, 1973

Spain; Eocene (Solé & Via, 1989)

***Dromiopsis americana*** Roberts, 1956

New Jersey, USA; Paleocene (Roberts, 1956; Collins & Wienberg Rasmussen, 1992)

***Dromiopsis elegans*** Reuss, 1859

Denmark; lower Paleocene (Collins & Jakobsen, 1995)

***Dromiopsis granulata*** Collins & Wienberg Rasmussen, 1992

West Greenland; Maastrichtian (Collins & Wienberg Rasmussen, 1992)

***Dromiopsis laevior*** Reuss, 1859

Denmark; lower Paleocene (Collins & Jakobsen, 1995)

***Dromiopsis minor*** von Fischer-Benzon, 1866

Denmark; lower Paleocene (Collins & Jakobsen, 1995)

***Dromiopsis paucigranosa*** Beschin, Busulini, De Angeli & Tessier, 2007

Vicenza, Italy; lower Eocene (Beschin et al., 2007b)

***Dromiopsis rugosa*** (von Schlottheim, 1820)

Denmark, southern Sweden; lower Paleocene (Jakobsen & Collins, 1997; Collins & Jakobsen, 2005)

***Dynomene emiliae*** Müller, 1979b

Austria, Bulgaria, Poland, Hungary; middle Miocene (Müller, 1979b, 1984; Friebe, 1987)

***Dynomene hispida*** (Latreille in Milbert, 1812)

Japan; Plio-Pleistocene (Karasawa, 2001, as *D. hispida* Guérin-Méneville, 1832) (see for synonymy: Ng et al., 2008: 38)

***Dynomene lessinea*** Beschin, De Angeli & Checchi, 2001

Vicenza, Italy; lower Oligocene (Beschin et al., 2001; De Angeli & Beschin, 2001; De Angeli & Garassino, 2006)

***Dynomene*** aff. ***praedator*** A. Milne-Edwards, 1879

Japan; Plio-Pleistocene (Karasawa, 2001)

***Dynomene variabilis*** Portell & Collins, 2004

Jamaica; lower Miocene (Portell & Collins, 2004)

***Eotrachynotocarcinus airaghii*** Beschin, Busulini, De Angeli & Tessier, 2007

Vicenza, Italy; lower Eocene (Beschin et al., 2007b)

***Epigodromia areolata*** (Ihle, 1913)

Japan; Plio-Pleistocene (Karasawa, 2001)

***Gemmellarocarcinus loerentheyi*** Checchia-Rispoli, 1905

Sicily, Italy; middle Eocene. Hungary; upper Eocene (De Angeli & Garassino, 2006)

***Kierionopsis nodosa*** Davidson, 1966

Texas, USA; Paleocene (Davidson, 1966)

***Kromtitis koberi*** (Bachmayer & Tollmann, 1953)

Austria; upper Miocene (Bachmayer & Tollmann, 1953; Müller, 1984)

***Kromtitis koberiformis*** Beschin, Busulini, De Angeli & Tessier, 2007

Vicenza, Italy; lower Eocene (Beschin et al., 2007b)

***Kromtitis levigatus*** Beschin, Busulini, De Angeli & Tessier, 2007

Vicenza, Italy; lower Eocene (Beschin et al., 2007b)

***Kromtitis subovatus*** Beschin, Busulini, De Angeli & Tessier, 2007

Vicenza, Italy; lower Eocene (Beschin et al., 2007b)

***Kromtitis pentagonalis*** Müller & Collins, 1991

Hungary; upper Eocene (Müller & Collins, 1991)

***Kromtitis spinulata*** Portell & Collins, 2004

Jamaica; lower Miocene (Portell & Collins, 2004)

***Kromtitis tetratuberculatus*** Beschin, Busulini, De Angeli & Tessier, 2002

Vicenza, Italy; middle Eocene (Beschin et al., 2002; De Angeli & Garassino, 2006)

***Kromtitis*** sp.

Vicenza, Italy; middle-upper Eocene (Beschin et al., 2007a)

***Lucanthonisia eotvoesi*** (Müller, 1975)

Hungary; middle Miocene (Müller, 1975, 1984; this paper)

***Lucanthonisia praemium*** sp. nov.

Belgium; lower Oligocene (this paper)

***Noetlingia claudiopolitana*** (Bittner, 1893)

Hungary; upper Eocene. Veneto, Italy; middle Eocene (Beschin et al., 1994; De Angeli & Beschin, 2001; De Angeli & Garassino, 2006)

***Noetlingia succini*** (Noetling, 1885)

Samland Peninsula, Kaliningrad, Russia; middle Eocene (Noetling, 1885; Jagt et al., 2006)

***Noetlingia veronensis*** (Bittner, 1886)

Veneto, Italy; middle/upper Eocene (De Angeli & Garassino, 2006)

***Trechmannius circularis*** Collins & Donovan, 2007

Jamaica; lower Paleocene (Collins & Donovan, 2007)