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A re-evaluation of the Dynomenidae Ortmann, 1892 (Crustacea, Decapoda, Brachyura, Podotremata), with the recognition of four subfamilies

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Abstract

A re-evaluation of the Dynomenidae Ortmann, 1892, on the basis of morphological characters, allows four subfamilies to be recognised, viz. Acanthodromiinae **n. subfam.**, Dynomeninae Ortmann, 1892, Metadynomeninae **n. subfam.**, and Paradynomeninae **n. subfam.** Sequences of character states for each homologous character (morphocline) show a similar polarity. The Acanthodromiinae **n. subfam**. exhibits a plesiomorphic condition, both in body shape and fronto-orbital disposition as well as in the condition of the thoracic sternum, abdominal holding mechanism and gill structure. Both the Metadynomeninae **n. subfam.** and Dynomeninae are more advanced, the latter being more "carcinized" and the most derived. The Paradynomeninae **n. subfam.** evolved a specialised frontal and buccal region, by forming a projecting "face". The family Dynomenidae, which presently comprises merely five extant genera and 21 species, but with a worldwide distribution, is amongst the most ancestral brachyuran families, with a good fossil record from the Late Jurassic onwards. A few fossil genera such as *Kromtitis* Müller, 1984, and *Kierionopsis* Davidson, 1966, appear to conform to the Paradynomeninae **n. subfam.** A key to the subfamilies of extant Dynomenidae is provided.

Key words: Crustacea, Decapoda, Brachyura, Dynomenidae, podotremes, fossil Brachyura, new subfamilies

Introduction

The family Dynomenidae Ortmann, 1892, has enjoyed a fairly stable existence, with only three extant genera described over the years: the type genus, *Dynomene* Desmarest, 1823, *Acanthodromia* A. Milne-Edwards, 1880, and *Paradynomene* Sakai, 1963. By pointing out that the majority of species had often been assigned often too haphazardly to *Dynomene*, McLay (1999) established two new genera, *Hirsutodynomene* McLay, 1999, and *Metadynomene* McLay, 1999. Our current knowledge of this family owes much to a revision by McLay (1999), in which a number of novel characters were studied. Despite the fact that subsequently two species of *Dynomene* (McLay 2001b), one of *Hirsutodynomene* (McLay & Ng 2005) and five of *Paradynomene* (McLay & Ng 2004) have been named, the Dynomenidae remains a relatively small group, comprising merely five extant genera and 21 species (Table 1), albeit with a worldwide distribution.

The primitive nature of the family Dynomenidae has been recognised ever since its description (Ortmann 1892), having been invariably included in the Dromiacea De Haan, 1833 (Ortmann 1892; Bouvier 1896; Alcock 1900, 1901; Rathbun 1937; Glaessner 1969; Wright & Collins 1972). The Dynomenidae was assigned to the Podotremata Guinot, 1977, in close proximity to the Dromiidae De Haan, 1833, and the Homolodromiidae Alcock, 1900 (Guinot 1978, 1993a; Guinot *et al.* 1994; Scholtz & Richter 1995; Jamieson *et al*. 1993, 1995; McLay 1999; 2001a, 2001b; Guinot & Bouchard 1998; Guinot & Tavares 2001, 2003; Guinot & Quenette 2005; Schweitzer *et al*. 2003; McLay & Ng 2004, 2005; Beschin *et al*. 2007; Ng *et al*. 2008). The Dromiidae and Dynomenidae are generally considered to be sister groups. Based on a cladistic analysis of small

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subunit nuclear ribosomal RNA sequences, Ahyong *et al.* (2007: 582) comment that “reciprocal monophyly of the constituent dromioid families, Dromiidae and Dynomenidae, is less secure” would have benefitted from a consideration of the subfamilial categories in the Dromiidae defined by Guinot & Tavares (2003) and of the wide morphological diversity exhibited by the Dynomenidae. This necessitates the present reappraisal of their systematics.

TABLE 1. List of extant genera and species currently placed in the family Dynomenidae Ortmann, 1892 (after Ng *et al.* 2008: 37) . Generic names in square parentheses are the genera in which the species were originally described

Subfamily Acanthodromiinae **n. subfam.**
Acanthodromia A. Milne-Edwards, 1880 (type genus; type species: *Acanthodromia erinacea* A. Milne-Edwards, 1880, by monotypy; gender feminine)
Acanthodromia erinacea A. Milne-Edwards, 1880
Acanthodromia margarita (Alcock, 1899) [*Dynomene*]

Subfamily Dynomeninae Ortmann, 1892
Dynomene Desmarest, 1823 (type genus; type species: *Cancer hispida* Latreille, *in* Milbert 1812, by subsequent designation of H. Milne Edwards, 1837; gender feminine) [junior synonym: *Maxillothrix* Stebbing, 1921 (type species *Maxillothrix actaeiformis* Stebbing, 1921, by monotypy; gender feminine)]
Dynomene filholi Bouvier, 1894
Dynomene guamensis McLay, 2001 (McLay, 2001b)
Dynomene hispida (Latreille, *in* Milbert 1812) [*Cancer*] [junior synonyms: *Dynomena latreillii* Eydoux & Souleyet, 1842, and *Dynomene granulobata* Dai, Yang & Lan, 1981]
Dynomene kroppi McLay, 2001
Dynomene pilumnoides Alcock, 1900 [junior synonym: *Maxillothrix actaeiformis* Stebbing, 1921]
Dynomene praedator A. Milne-Edwards, 1879 [junior synonyms: *Dynomene sinensis* Chen, 1979; *Dynomene tenuilobata* Dai, Yang & Lan, 1981; *Dynomene huangluensis* Dai, Cai & Yang, 1996]
Dynomene pugnatrix De Man, 1889 [junior synonym: *Dynomene pugnatrix brevimana* Rathbun, 1911]

Hirsutodynomene McLay, 1999 (type species: *Dynomene spinosa* Rathbun, 1911, by original designation; gender feminine)
Hirsutodynomene spinosa (Rathbun, 1911) [*Dynomene*]
Hirsutodynomene ursula (Stimpson, 1860) [*Dynomene*]
Hirsutodynomene vespertilio McLay & Ng, 2005

Subfamily Metadynomeninae **n. subfam.**
Metadynomene McLay, 1999 (type genus; type species: *Dynomene devaneyi* Takeda, 1977, by original designation; gender feminine)
Metadynomene devaneyi (Takeda, 1977) [*Dynomene*]
Metadynomene tanensis (Yokoya, 1933) [*Dynomene*]
Metadynomene crosnieri McLay, 1999

Subfamily Paradynomeninae **n. subfam.**
Paradynomene Sakai, 1963 (type genus; type species: *Paradynomene tuberculata* Sakai, 1963, by monotypy; gender feminine)
Paradynomene demon McLay & Ng, 2004
Paradynomene diablo McLay & Ng, 2004
Paradynomene quasimodo McLay & Ng, 2004
Paradynomene rotunda McLay & Ng, 2004
Paradynomene teufel McLay & Ng, 2004
Paradynomene tuberculata Sakai, 1963

A subdivision of the Dynomenidae has never been attempted, the Dynomeninae of A. Milne-Edwards & Bouvier (1899, 1902) simply corresponding to a taxonomic category composed of Dynomene and Acanthodromia as opposed to the Dromiinae, Homolodromiinae and Homolinae. While the monophyly of the Dynomenidae is not in doubt, a re-evaluation of the family is needed in view of the wide range of variation in morphological characters, and the unequal systematic status of its five extant genera. McLay (1999: 543) realised that too many and diverse species had been assigned to *Dynomene* and that *Acanthodromia* and *Paradynomene* were "radically different from the type genus of the family (*Dynomene*)." New genera were established by McLay (1999), and a reappraisal of the infrafamilial relationships within the Dynomenidae is clearly the next logical step. This diversity, which is expressed at several evolutionary levels, becomes even more impressive when fossil taxa are taken into account, which are much more numerous than extant representatives.

Based on an examination of almost all modern dynomenid taxa and on a preliminary palaeontological study, the family Dynomenidae is here subdivided into four subfamilies, namely Acanthodromiinae **n. subfam.**, Dynomeninae Ortmann, 1892, Metadynomeninae **n. subfam.**, and Paradynomeninae **n. subfam.** All are monotypic, except for the Dynomeninae. Although there are problems surrounding the creation of monotypic groupings, the number of outstanding distinctive subfamilial characters necessitates such a subdivision.

The fact that extant representatives are mere relicts of an ancestral brachyuran group may explain this extreme diversification. The Dynomenidae has an extensive fossil record going back to the Late Jurassic (Glaessner 1960, 1969), although only a limited set of characters, mostly only carapace, was used in assigning these taxa. Placement of some fossil genera either in the Dynomenidae or in the Dromiidae has been widely discussed, often lacking support either way in the absence of clear distinctions between these two families, in particular when more primitive extant representatives are considered. Guinot & Tavares (2003), who recently revised the Dromiidae, hypothesised on apparent relationships amongst basal podotremes (Dromiidae, Dynomenidae, and Homolodromiidae) and provided a key for the Dromiacea.

Similar problems have been encountered by neontologists when trying to assign some species either to the Dynomenidae or to the Dromiidae, or otherwise (McLay 1999: 433). *Acanthodromia* was originally placed in the Dromiidae (A. Milne-Edwards 1880; Alcock 1899), also regarded as a possible prosopid (Prosopidae von Meyer, 1860; see Wright & Collins 1972), and finally assigned to the Dynomenidae by A. Milne-Edwards & Bouvier (1902). In contrast, *Dynomene platyarthrodes* Stebbing, 1905, was transferred to the family Dromiidae, as *Speodromia platyarthrodes* (Stebbing) (McLay 1993, 1999). *Maxillothrix actaeiformis* Stebbing, 1921, was originally placed in the Xanthidae prior to being synonymised with *Dynomene pilumnoides* Alcock, 1900. It is likely that some fossil taxa now included in the Prosopidae or Homolodromioidea in fact may prove to be dynomenids. Similarly, some fossils assigned to the Dynomenidae may belong to the Sphaerodromiinae Guinot & Tavares, 2003 (Dromiidae), on account of comparable plesiomorphic features, notably in the shape of the front and orbits.

This study attempts to assist palaeontologists in reassessing primitive fossil taxa by providing clear definitions in order to facilitate assignment of extant podotreme crabs to families and subfamilies. The nature, development and path of carapace grooves in modern dynomenids are significant characters which help distinguish the subfamilial groups erected here as monophyletic units. The subfamilial diagnoses given below, which are based on extant dynomenids and actually follow detailed generic descriptions by McLay (1999) and McLay & Ng (2004, 2005), will likely need modifications to allow for inclusion of fossil taxa.

Methods

This study is based on the extensive collections of Brachyura deposited at the Muséum national d'Histoire naturelle, Paris (MNHN), which is essential for a sound and comprehensive analysis. The terminology basically follows that of McLay (1999). A character ignored by all previous carcinologists and previously referred to as “sterno-coxal depressions” by Guinot (1995) and Guinot & Bouchard (1998) must be added to the morphological features defined by McLay (1999). At the level of P2 to P4, or only P2 and P3, the thoracic sternum is laterally hollowed by depressions, inside of which the coxae of the pereopods may slide in their movements to hold the abdomen against the ventral surface, probably also for walking (Figure 4A). Sterno-coxal depressions characterise basal podotremes, virtually all of which have abdominal holding by the appendages (Dromiacea, Homolidae De Haan, 1839, Poupiniidae Guinot, 1991). They are well developed and deep in the Dynomenidae, even in genera in which the abdomen is loosely held.

Some characters of the Acanthodromiinae **n. subfam.** (e.g. the degree of fusion of the abdominal somites) are difficult to determine due to the numerous spines which conceal the sutures and to the scarcity of available material.

The articles of the pereopds have two articular structures, the knob and its corresponding cavity. The knob, named “condyle” (from the Greek *kondulos*: articulation), fits into a small cavity or socket, named “gynglyme” (from the Greek *gyn*: female). The coxa of each pereopod has two condyles; the coxo-sternal condyle articulates with the thoracic sternum by a gynglyme located on the lateral part of each sternite (episternite) (Figure 4A). The gynglymes on the sternum are important features because they allow locate the sternites. This terminology was explained for brachyuran crabs by H. Milne Edwards (1851: 52), and the mechanical action described in some detail by Herrick (1911). Bourne (1922: 33, footnote) used two new names for these structures (“strophidium” for the condyle, “strophingium” for the socket) in his study of the Raninoidea De Haan, 1839. The terminology of H. Milne Edwards (1851: 52; see Guinot 1979: 72) is used here.

The penis is defined as the external extension of the vas deferens which enters the first gonopod (Duvernoy 1850; 1853; Brocchi 1875; Guinot & Tavares 2003; Figure 4 A, C-F) and not as an intromittent organ for insemination as defined by Moore & McCormick (1969: R99).

Abbreviations used: mxp1–mxp3 (first to third maxillipeds), P1–P5, first to fifth pereopods (P1 as cheliped), 1–8, thoracic sternites 1 to 8; 1/2–7/8, thoracic sternal sutures 1/2 to 7/8. Measurements of carapace length x carapace width are given in millimetres (mm).

Specimens examined are deposited at the Muséum national d'Histoire naturelle, Paris (MNHN), National Museum of Natural History, Smithsonian Institution, Washington D.C. (USNM), and in the Zoological Reference Collection, Raffles Museum of Biodiversity Research, National University of Singapore (ZRC).

Systematics

Family Dynomenidae Ortmann, 1892

Dynomenidae Ortmann, 1892: 541; Alcock 1900: 127, 133; 1901: 34; Rathbun 1937: 51; Glaessner 1960: 46, fig. 22; 1969: R487; 1980: 190, fig. 22; Wright & Wright 1950: 26, fig. 13; Wright & Collins 1972: 48; Jamieson *et al*. 1993: 311–322, fig. 3; 1995: 274; Guinot 1978: 231; 1993a: 1226; 1995: 186; Guinot *et al*. 1994: fig. 7; 1998: 78, 92, 93, fig. 8; Guinot & Bouchard 1998: 629, 674, 681; Collins *et al*. 1995: 177; Ng 1998: 1065; McLay 1999: 427–569; 2001b: 809; McLay & Ng 2004: 1–24; McLay & Ng 2005: 15; Martin & Davis 2001: 74; Davie 2002: 167; Schweitzer *et al*. 2003: 18; Schweitzer & Feldmann 2005: 21, 22, tables 1, 4; Guinot & Tavares 2001: 525, 529, 531; 2003: 112, 115, 120; Guinot & Quenette 2005: 282; Poore 2004: 308; Števčić 2005: 18; De Angeli & Garassino 2006: 29; Beschin *et al*. 2007: 20; Ng *et al*. 2008: 37.

Dynomeninae A. Milne-Edwards & Bouvier 1902 *pro parte*: 22.

Remarks. McLay’s (1999) diagnosis of the family is accurate in most points. However, some aspects need modification or elaboration, and new characters described in this study should be added. For instance, the abdomen, instead of being “folded loosely under the thorax” (McLay 1999: 468), is actually firmly held in

Acanthodromia by coxal structures on mxp3 and P1–P3. In *Acanthodromia*, the abdominal somites are not "freely movable" (McLay 1999: 536), but there is fusion of somites 3–6. Admittedly, it is difficult to determine the degree of abdominal fusion. Although traces of sutures are still visible in places, they are concealed by numerous spines. In any case, somites are functionally ankylosed in the specimens examined so far. To this effect, I follow Ng *et al.* (2008: 14) in that "we here regard fusion as segments which are immobile and cannot articulate with each other, regardless of whether the sutures are visible" at varying degrees.

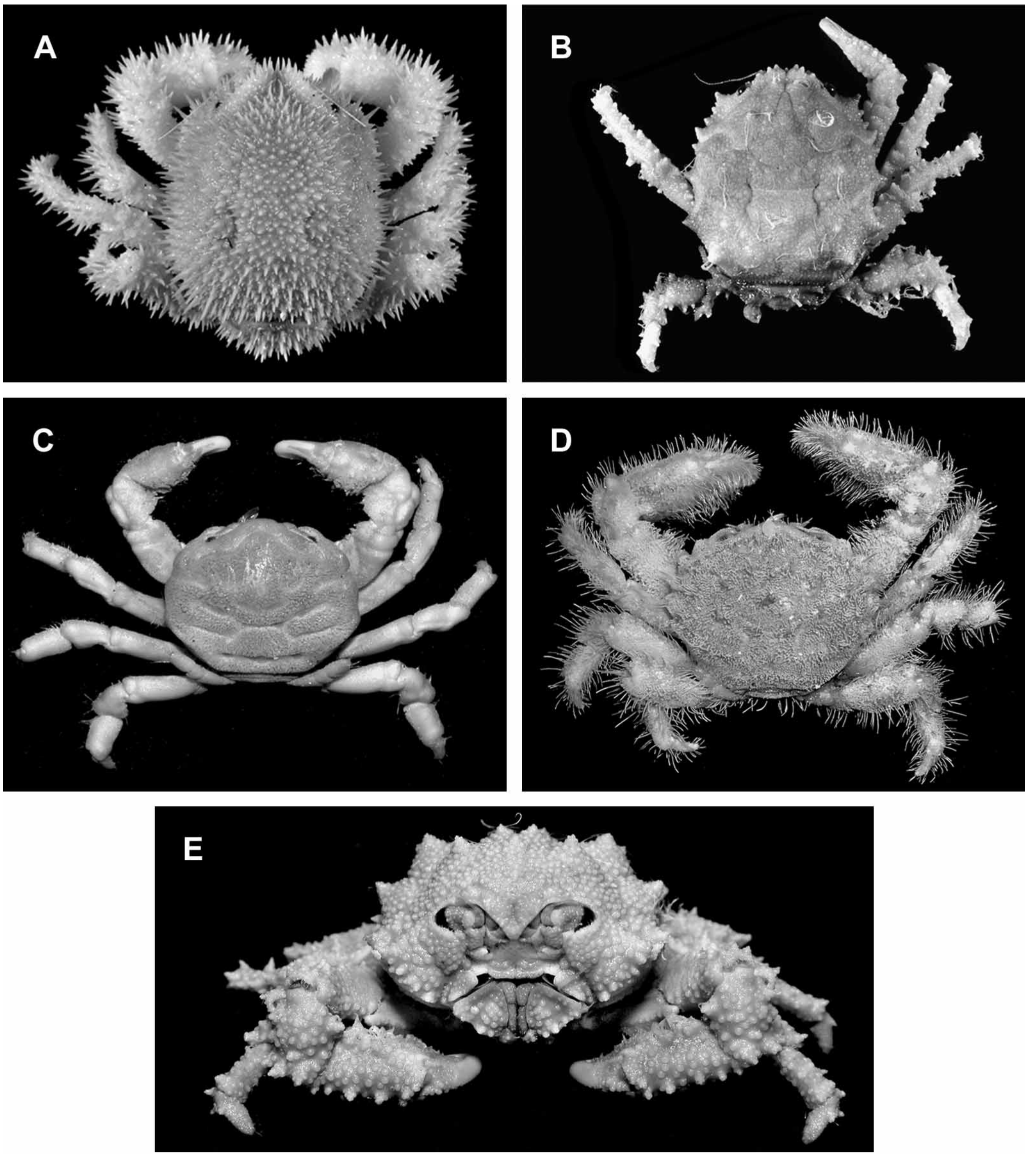

FIGURE 1. Representative species of the four subfamilies of Dynomenidae, overall view. **A**, Acanthodromiinae **n. subfam.**: *Acanthodromia margarita* (Alcock, 1899), Balicasag Island, Panglao, Bohol, Visayas, Philippines (ZRC) (see McLay & Ng 2005: 18); **B**, Paradynomeninae **n. subfam.**: *Paradynomene tuberculata* Sakai, 1963, Balicasag Island, Panglao, Bohol, Visayas, Philippines (ZRC) (see McLay & Ng 2004: 4); **C**, Metadynomeninae **n. subfam.**: *Metadynomene tanensis* (Yokoya, 1933) with its undulating tomentum, Balicasag Island, Panglao, Bohol, Visayas, Philippines (ZRC) (see McLay & Ng 2005: 25); **D**, Dynomeninae Ortmann, 1892: *Hirsutodynomene vespertilio* McLay & Ng, 2005, Balicasag Island, Panglao, Bohol, Visayas, Philippines (ZRC) (see McLay & Ng 2005: 21). **E**, *Paradynomene tuberculata* Sakai, 1963, New Caledonia, frontal view showing the characteristic "face" (ZRC). (All photographs courtesy of P.K.L. Ng).

Some characters are redefined and added.

Orbits either elongate, deep, obliquely arranged or shorter, shallower, more transversal. Frontal margin variously projecting. Posterior margin of carapace rather concave. Mxp3 more or less opercular; basis and ischium of endopod fused but suture distinct, either complete or not. Narrow shield formed by sternites 1 and 2 or 1–3; following thoracic sternites either completely included between coxae of pereopods or with narrow lateral portion intercalated between abdomen and pereopods; sternum forms a plate that regularly declines posteriorly; sternite 8 tilted, located in another plane than preceding ones. Anterior sternites 1, 2 small, fused into a narrow shield, either pentagonal, onion-shaped or, more rarely, triangular; stacking up of anterior sternites may be recognised by location of gynglymes for articulation of mxp1–mxp3 along thick margin of shield (Figure 4A). Sternite 3 either clearly distinct, visible (plesiomorphy), or represented at base of shield by short band, of about same width as sternite 4 in its anterior part (apomorphy); suture 3/4 indicated by change of level, straight or convex, or marked by denticulate crest. Sternites 4–7 (except episternites) fused into undivided plate, with parallel margins, medially forming flat area, varying from moderately wide to wide. Sternal sutures 4/5–6/7 hardly visible, hidden by borders of sterno-coxal depressions; suture 4/5 may be medially replaced by convex line; suture 7/8 present, even in males, relatively short in both sexes. Sterno-abdominal depression deep, completely covered by male abdomen over entire length and width, or shallow, not well defined, always with medial flat floor. Deep sterno-coxal depressions present at level of P2–P4 (Figures 2A, B, 4A). Male abdomen either long, narrow, completely accommodated in sterno-abdominal depression, or shorter, relatively broad even in males, flexible; telson reaching base of mxp3 or level of mid-sternite 4; lateral margins of abdomen (uropod margin included) may be slightly modified (Acanthodromiinae **n. subfam.**, Paradynomeninae **n. subfam.**), and not modified in the two other subfamilies. Abdomen with somites 1–6 free or with somites 3–6 fused in both sexes (at least in *Acanthodromia margarita*), sutures still partially visible. Abdominal holding either firm in both sexes and involving coxae of mxp3 and P1–P3 (Acanthodromiinae **n. subfam.**), or less so but still fairly tight (Paradynomeninae **n. subfam.**), or loose and performed by a structure which is either coxal (Metaynomeninae **n. subfam.**) or sternal (Dynomeninae). Sexual dimorphism of abdominal somite 6 correlated with sexual dimorphism of uropod. Vestigial pleopods present on male somites 3–5, biramous (two rami either equal or, more often, unequal, exopodite being longer than endopodite); exceptionally (*Dynomene praedator* A. Milne-Edwards, 1879), pleopods 3–5 uniramous; thus pleopodal formula complete (Figure 3B). Uropods as dorsal plates (Figure 5), varying from small, slightly mobile to well developed, immobile (even at so great extent that penultimate abdominal somite excluded from reaching abdominal lateral margin), usually not prominent in males (slightly prominent in Paradynomeninae **n. subfam.**), may be sexually dimorphic (larger in females). Apertures of spermathecae ending well apart from each other, slightly behind female gonopore on P3 coxa. Chelipeds usually equal, may be unequal at least in males, and homomorphic, slightly dimorphic sexually (however with marked growth and modifications in large males of *Dynomene praedator*). P5 strongly reduced, not movable, directed obliquely between posterolateral margin of carapace and P4; basis-ischium free or fused to merus; subchelate mechanism involving dactylus opposed to distal extension of propodus, sexually dimorphic, more developed, more spinous in females. P5 coxa modified in males, extended in long projection enclosing most of penis (Figure 4C–F). Endophragmal skeleton with junction between phragmae formed by fusion; skeletal parts variously layered (cf. Secretan 2002). Gills (cf. McLay 1999) usually 19 (including 6 podobranchs) + 7 epipods, with basically phyllobranchiate structure, but plates very variable in shape and number of epibranchial lobes.

Acanthodromiinae n. subfam.

(Figures 1A, 2, 5O–P)

Dynomeninae A. Milne-Edwards & Bouvier 1899 *pro parte*: 9; Alcock, 1900 *pro parte*: 127, 133; 1901 *pro parte*: 34, 74; A. Milne-Edwards & Bouvier 1902 *pro parte*: 22.

Type genus. *Acanthodromia* A. Milne-Edwards, 1880 (type species by monotypy: *A. erinacea* A. Milne-Edwards, 1880).

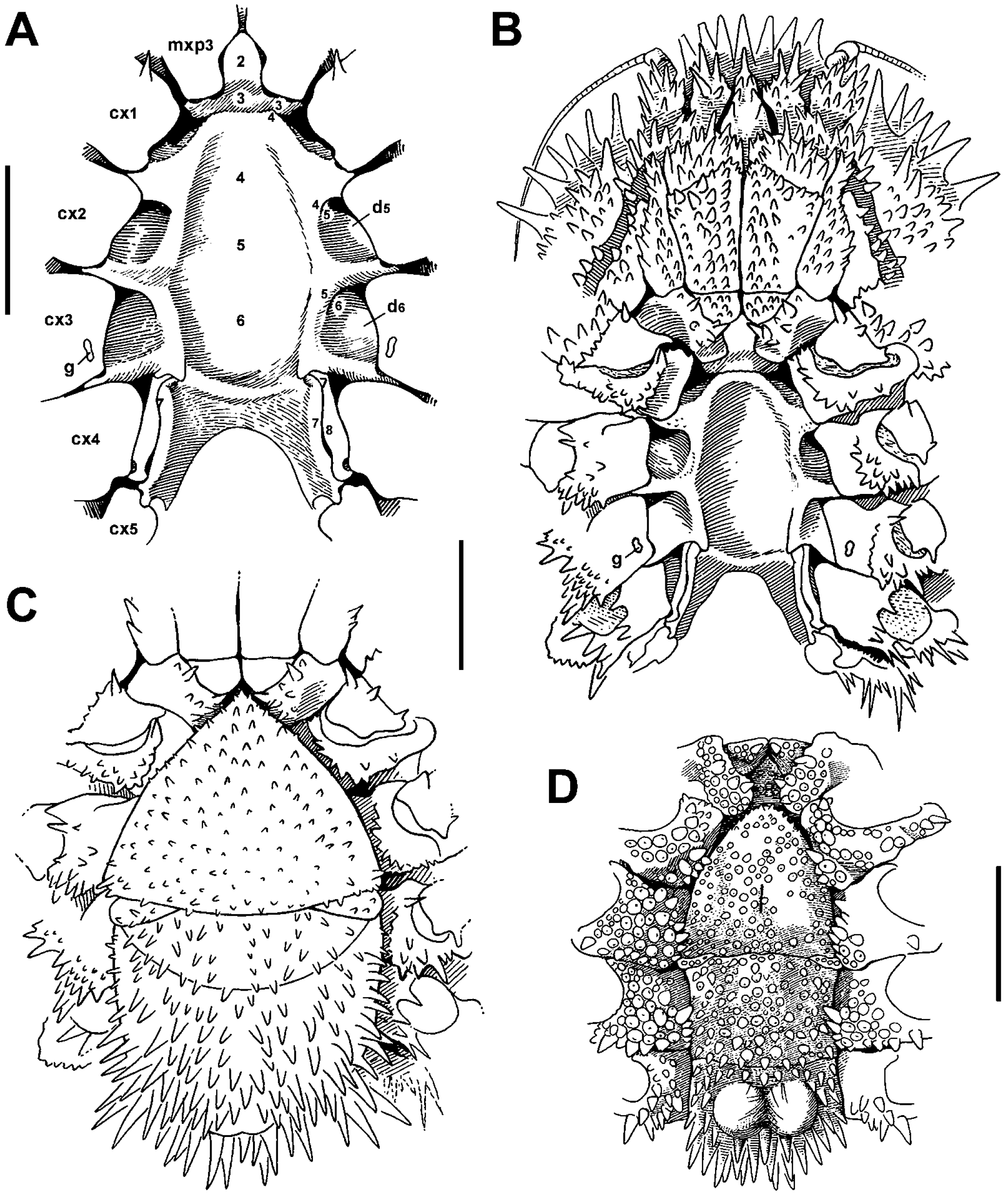

FIGURE 2. *Acanthodromia* A. Milne-Edwards, 1880 (Acanthodromiinae **n. subfam.**). **A–C**, *Acanthodromia erinacea* A. Milne-Edwards, 1880, ovigerous female, 14.7 x 12 mm, west of Puerto Rico (USNM 124263). **A**, thoracic sternum; **B**, ventral surface without abdomen; **C**, abdomen. **D**, *Acanthodromia margarita* (Alcock, 1899), male, 11.6 x 12.8 mm, Balicasag Island, Panglao, Bohol, Visayas, Philippines, McLay & Ng det. (MNHN-B28812) [The abdominal sutures are erroneously too much pronouced in these figures since there is a fusion of abdominal somites 3–6]. cx1–cx5, coxae of P1–P5; d5–d6, sterno-coxal depressions 5 and 6; g, female gonopore; 2–6, sternites 2–6 (1 and 2 fused into shield; 3, individualised thoracic sternite 3; 3/4, limit between thoracic sternites 3 and 4; 4/5–5/6, thoracic sternal sutures 4/5–5/6 (indistinct); 7/8, distinct thoracic sternal suture 7/8. Scale bars: 2.5 mm.

Diagnosis. Carapace longer than wide, oblong; dorsal surface convex, ornamented with close-set spines. Cervical, branchial grooves not well visible, branchiocardiac groove crescent- shaped. Anterolateral margins poorly defined, joining corners of buccal cavity, obscured by numerous spines. Posterior margin markedly concave. Frontal margin forming narrow projection; supraorbital margin oblique, continuous above orbits, eave-like, rimmed, not notched, spinous, prolonged in straight groove delineating subhepatic region; infraorbital margin concave, ornamented with spines. Orbits obliquely located, elongated, clearly visible from dorsal view; eyestalks short. Antenna with urinal article extended transversely, not medially beaked; second article with firmly fixed exopod. Proepistome short. Epistome narrow. Anteroventrally, front, inflated subhepatic pterygostomial portion forming together with merus of mxp3 a weak “face”. Anterior border of endostome forming raised wall, laterally notched by exhalant orifices. Mxp3 operculiform, angled; basis separated from ischium by nearly complete suture; ischium narrow at base, merus not extended laterally, narrow. Pleural line as wide, decalcified zone; branchiostegite of normal texture. Thoracic sternum extremely narrow, entirely (apart from sternites 1, 2) covered by male abdomen, abdominal margins close to P2, P3 coxae. Sternites 1, 2 fused into small, narrow shield, inserted between bases of mxp3; sternite 3 distinct but short, expanded laterally, delimited posteriorly by convex crest, corresponding to suture 3/4; sternites 3–8 not exposed laterally when abdomen closed; sternite 8 tilted. Sterno-coxal depressions very deep. Female sutures 7/8 ending well apart, along internal border of P3 sterno-coxal depression; spermathecal aperture small, slightly behind level of female gonopore. Sterno-abdominal depression narrow, deep, with steep sides, medially a flat floor. Abdomen broad, curved, extending over entire sternum (sternites 3–8) and reaching mxp3; first somite dorsal, with same concave curvature as posterior margin of carapace in which it is inserted; subsequent somites narrow, subequal in width; telson long, broadly triangular, slightly wider at base; somite 4 with a prominent, pearl-shaped double tubercule. Abdominal somites 3–6 fused in males, probably also in females; sutures obscured by spines, only partially visible; suture between somites 5, 6 absent in males, more clearly visible in females (at least in *Acanthodromia margarita*); in females somites 3–5 each with lateral portions produced as flanges overlapping following somites; flange of somite 6 more pronounced, raised. Male uropod small, showing as narrow transverse plate, slightly mobile. Abdomen tightly locked in both sexes by mechanism involving coxae of 4 thoracopods: coxa of mxp3 with spinules overhanging posterior part of telson; coxae of P1–P3 with several spinules or granules overhanging telson at P1, P2 levels, somite 6 with uropods, and somite 5 at P3 level (in *Acanthodromia margarita* all spinules better developed in females than in males). Chelipeds equal, more robust than P2; dactylus strongly curved downwards; fixed finger almost straight; both fingers spoon-tipped. P2–P4 ornamented with spines; dactyli curved, bearing numerous spines; 4 or 5 spines on inferior margin. P5 conspicuously reduced, sexually dimorphic; basis-ischium fused to merus, basis-ischium-merus proportionally thicker than distal articles; dactylus rudimentary ending in subchelate mechanism, obsolete in males, more noticeable in females. P5 coxa of males modified, extended to enclose penis. Pl1 vestigial in females. Vestigial pleopods on somites 3–5 in males. Gonopod 1 stout, forming half-rolled tube. G2 needle-like, with row of small distal spines.

Remarks. The subfamily is monotypic, and *Acanthodromia* comprises only two species (Table 1). The morphology is masked by the spines which cover the whole body, so the precise outline and the grooves on the dorsal surface of carapace are not evident, which implies that potentially related fossil taxa are not easily assigned to this subfamily. The initial assignment of *Acanthodromia* to the Dromiidae (A. Milne-Edwards 1880; Alcock 1899) and subsequent transfer to the Prosopidae, subfamily Pithonotinae Glaessner, 1933 (Wright & Collins 1972), illustrates well the “curious mixture” (McLay 1999: 534) of characters, already pointed out by A. Milne-Edwards & Bouvier (1902). The present study has shown that there is strong support for the interpretation that the Recent *Acanthodromia* retains ancestral characters and is the most primitive of all extant dynomenids.

Dynomeninae Ortmann, 1892

(Figures 1D, 3C, D, 4A–C, E, 5A–H)

Type genus. *Dynomene* Desmarest, 1823 (*Cancer hispida* Latreille, 1812: type species by monotypy by subsequent designation of H. Milne Edwards, 1837: 180; ICZN 1999, Art. 67.2.2).

The authorship of *Dynomene hispida*, usually credited to Guérin or Guérin-Méneville (1832), is incorrect, the first author to describe this species was actually Latreille (*in* Milbert 1812) (see Cleva *et al.* 2007: 246, fig. 14C; Ng *et al.* 2008: 37).

Other genus included. *Hirsutodynomene* McLay, 1999 (type species by original designation: *Dynomene spinosa* Rathbun, 1917).

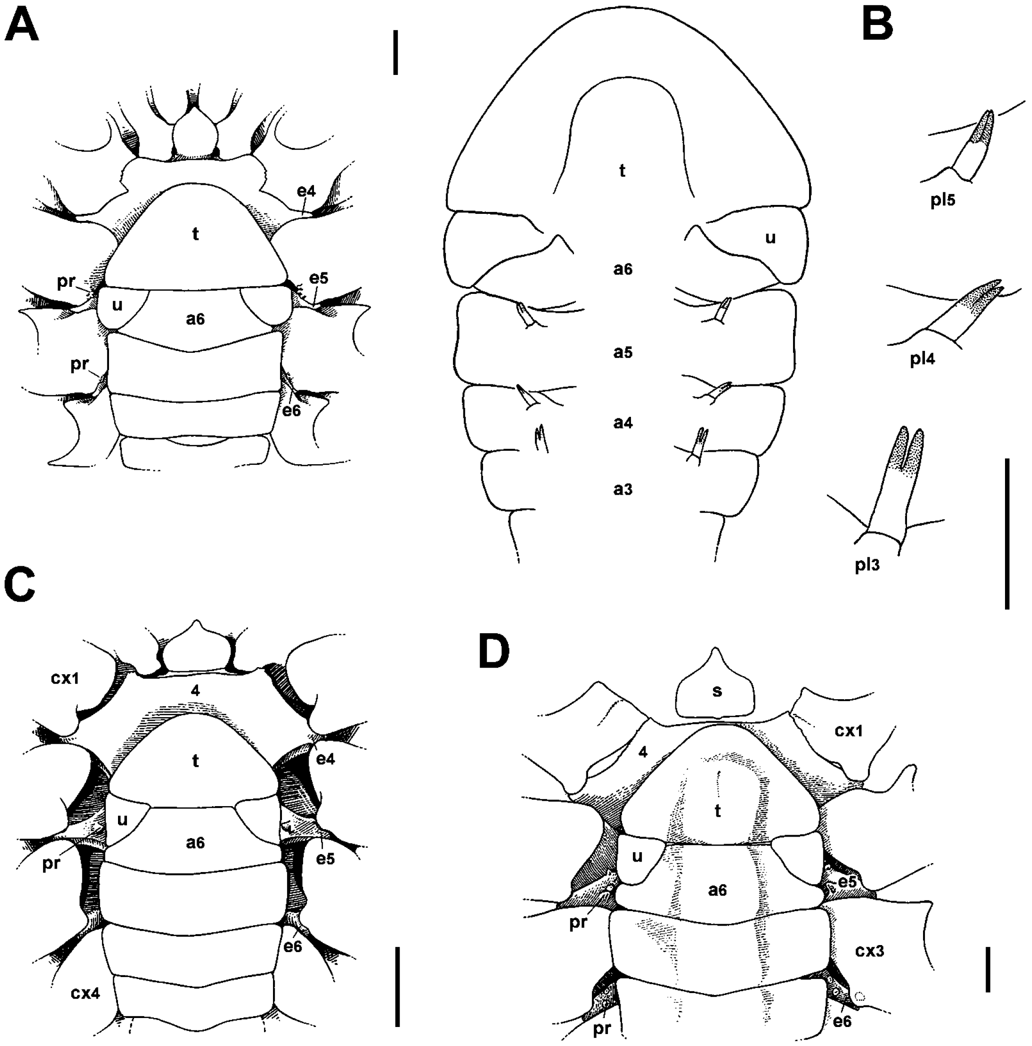

FIGURE 3. Metadynomeninae **n. subfam.** (A, B) and Dynomeninae Ortmann (C, D), views of thoracic sternum and abdomen (A, C, D) and ventral surface of abdomen (B). **A**, *Metadynomene tanensis* (Yokoya, 1933), male 12,5 x 13,5 mm, New Caledonia, SMIB 2 (MNHN-B25583): abdominal holding by P2 coxa; **B**, *Metadynomene crosnieri* McLay, 1999, holotype, male, 23.2 x 22.7 mm, western Indian Ocean, îles Glorieuses, Benthedi Exp. (MNHN-B22510): biramous vestigial pleopods 3–5; detail at right; **C**, *Dynomene hispida* (Latreille, *in* Milbert 1812), male 6.9 x 8.8 mm, New Caledonia (MNHN-B22091): abdominal holding mechanism by sternal structure; **D**, *Hirsutodynomene spinosa* (Rathbun, 1911), male, 14.3 x 16.4 mm, western Indian Ocean, îles Glorieuses (MNHN-B6899): abdominal holding mechanism by sternal structure (see Bouchard 2000: fig. 24A). a3–a6, abdominal somites 3–6; cx1–cx4, coxae of P1–P4; e4–e6, episternites 4–6; pl3–pl5, vestigial pleopods on abdominal somites 3–5; pr, coxal projection; s, shield; t, telson; u, uropod; 4, sternite 4. Scale bars: 1 mm.

Diagnosis. Carapace wider or much wider than long, broadly rounded in outline, with "xanthoid" facies; dorsal surface moderately convex, may be areolate, smooth or granulate, may be laterally spiny, sparsely covered with short or long setae. Cervical groove as broad V, usually pronounced, never reaching, thus not forming notch with lateral carapace margin, interrupted between elongated gastric pits, or not interrupted; branchial groove faint, generally indistinct laterally or, rarely, joining lateral border of carapace; branchiocardiac variously marked. Anterolateral margin beginning slightly below infraorbital border, well defined, armed with distinct teeth, rarely by granules only. Posterior margin concave. Frontal margin broadly triangular, continuous above orbit; supraorbital margin gently oblique, may be notched, usually ornamented; infraorbital margin usually irregular, may be toothed, granular, notched. Orbits well defined, directed more or less obliquely; eyestalks rather short. Antenna with narrow urinal article beaked medially; second article with exopod firmly fixed. Proepistome very narrow. Anterior border of endostome not prominently raised. Mxp3 not firmly operculiform; basis separated from ischium by incomplete suture. Branchiostegite decalcified. Thoracic sternum slightly tilted posteriorly, wide, not entirely covered laterally by abdomen at level of P2–P3 coxae, a small portion of episternites 5, 6 remaining exposed when male abdomen folded. Sternites 1, 2 fused as pentagonal shield, variously pointed at anterior end; sternite 3 represented by narrow band at base of shield, delimited posteriorly by change in level (Figure 3C, 4A); suture 4/5 indistinct but limit between sternites 4, 5 marked transversely by setiferous, convex, line, may be salient, ornamented; sternites 4–8 mostly fused into single wide plate. Sterno-coxal depressions deep. Female sutures 7/8 ending well apart, inserted in ridged groove along internal border of sterno-coxal depression for P3; spermathecal aperture slightly posterior to coxal female gonopore, tiny, below prominence. Sterno-abdominal depression wide, shallow. Male abdomen with all somites free, wide, not entirely filling sterno-abdominal depression, leaving exposed thoracic sternites 1–3, mostly (Figure 3C) or totally (Figure 3D) sternite 4, and episternites 5, 6; first abdominal somite dorsally visible, narrow, slightly wider than somite 2. Somites 3–5 of males with vestigial, rudimentary pleopods, biramous, rarely uniramous. Pl1 vestigial in females. Uropods sexually dimorphic, immobile, rather large, occupying variable length of abdominal somite 6, not filling whole length of somite 6 in males and females (Figure 5A, C–H) in contrast to females in some species (Figure 5B). Abdominal holding structure sternal (but only restricting lateral movements of abdomen); in males a small tubercle on episternite 5 facing either uropod margin or abdomen margin (location dependent on size of uropod and its extension along somite 6); tubercle lost in mature females. Chelipeds equal, either stout or slender; fingers largely gaping at base, dactylus strongly curved. P2–P4 conspicuously ornamented with spines or granules; dactyli with 4–6 spines on inferior margin. P5 sexually dimorphic, reduced; basis and ischium free, not fused to merus; dactylus rudimentary, with obsolete subchelate mechanism. Coxa of P5 modified in males, extended to enclose penis. Gonopod 1 stout, forming half-rolled tube, with apical plate. G2 needle-like, with varying number of subterminal spines.

Remarks. The subfamily comprises only two genera: *Dynomene*, with McLay (2001b) recently describing two new species from Guam, and *Hirsutodynomene*, with McLay & Ng (2005) adding one new species from the Philippines (Table 1).

Metadynomeninae n. subfam.

(Figures 1C, 3A, B, 4F, 5I–L)

Type genus. *Metadynomene* McLay, 1999 (type species by original designation: *Dynomene devaney*i Takeda, 1977).

Diagnosis. Carapace as wide as long, or only slightly wider than long, subcircular, rather thick; dorsal surface convex, densely covered by short tomentum giving surface uneven undulating appearance with transverse troughs. Cervical groove well defined, complete (sulcus, however, interrupted between rounded gastric pits), crossing whole carapace, forming notch with lateral carapace margin; branchial groove absent medially, but well developed laterally, parallel to cervical groove, prolonging onto ventral side; branchiocardiac groove well marked. Anterolateral margin long, beginning at postorbital angle, well defined, notched or armed with few teeth. Posterior margin concave. Frontal margin broadly triangular, V-shaped, continuous above orbit; proepistome wide, moderately long, may be short; supraorbital margin oblique, smooth, not notched, not ornamented; infraorbital margin not toothed or notched, projecting, shelf-like, clearly visible from dorsal view. Orbits deep, long, oblique, clearly exposed dorsally; eyestalks well protected. Antenna with urinal article long, relatively narrow, suboval transversely, beaked medially; second article with exopod firmly fixed. Anterior border of endostome not markedly raised. Mxp3 not strongly operculiform; basis separated from ischium by incomplete suture. Branchiostegite may be decalcified. Thoracic sternum tilted posteriorly, rather wide, filled laterally by male abdomen when folded; episternites 5, 6 not visible dorsally, except for small external extensions inserted between P2–P3 and P3–P4 coxae. Sternites 1, 2 fused into pentagonal, narrow shield, which may be slightly pointed; sternite 3 as short band, of same width as sternite 4 in anterior portion, delimited posteriorly by deep depression (Figure 3A); most portions of sternites 4–8 fused into single wide plate; limit between sternites 4, 5 marked by transverse convex setiferous line (more salient, serrated in males); limit between sternites 5–6 indicated by membranous, translucent band across sternum. Sterno-coxal depressions very deep. Female sutures 7/8 in shallow groove, below prominent ridge; spermathecal aperture slightly posterior to level of female gonopore on P3 coxa, small but clearly visible. Sterno-abdominal depression slightly excavated, either shallow or with more oblique external sides. Male abdomen with all somites free, not entirely filling sterno-abdominal depression when folded, wide, in contact with P3–P5 coxae, leaving exposed thoracic sternites 1–3, major portion of sternite 4, and very small lateral portions of episternites 5 and 6; first somite dorsally visible, extended laterally, much wider than narrow somite 2. Male abdominal somites 3–5 with biramous (two equal rami) vestigial pleopods. Pl1 vestigial in females. Uropods not sexually dimorphic, being very large in both sexes, immobile; in males and females, uropod filling entire length of abdominal somite 6, excluding it from reaching lateral margin of abdomen. Abdominal holding by coxal structures in males, one developed on P2 coxa close to the uropod margin or base of telson, a smaller one on P3 coxa; these coxal structures only restrict lateral movements of abdomen in males, are absent in females. Chelipeds unequal (at least in males), stouter than P2–P4; with a small gap between fingers, prehensile borders of fingers touching for most of their length, dactylus barely curved. P2–P4 without spines, weakly ornamented with granules; dactyli with 2–4 spines on inferior margin. P5 sexually dimorphic, reduced; basis-ischium free, not fused to merus; dactylus rudimentary. P5 coxa modified in males, extended to enclose penis. Gonopod 1 stout, forming semi-rolled tube, with apical plate. G2 needle-like, row of curved spines on anterior surface.

Remarks. The subfamily is monotypic. *Metadynomene*, which contains only three extant species, forms a remarkably homogeneous group (Table 1). That the Metadynomeninae **n. subfam.** and the Sphaerodromiinae (see McLay & Crosnier 1991) appear related is due to a number of comparable plesiomorphic features, as has already been noted by McLay (1991: 465, table 1), who illustrated the similarities between *M. devaneyi* and the species of *Sphaerodromia* (see also discussion and key in Guinot & Tavares 2003).

Paradynomeninae n. subfam.

(Figures 1B, E, 4D, 5M, N)

Type genus. *Paradynomene* Sakai, 1963 (type species by monotypy: *P. tuberculata* Sakai, 1963).

Diagnosis. Body thick, uniformly covered with tubercles, granules and/or spines. Carapace longer than wide or as long as wide, sometimes slightly wider than long, subquadrangular, may be suboval; dorsal surface convex, distinctly areolated, often with swellings or bosses, usually densely ornamented. Cervical groove entire, not reaching lateral carapace margin; frontal, cervical, branchial, branchiocardiac grooves pronounced. Anterolateral margins subparallel or slightly convex, distinctly joining corners of buccal cavity, armed with 4–6 irregular salient teeth or prominences. Posterolateral margin with produced and elongated subdistal tooth; a tooth present posteriorly, variously salient. Posterior region of carapace recessed; posterior margin strongly concave. Frontal margin usually distinctly projecting, tridentate, rarely bidentate; supraorbital margin with small tubercles, notch; infraorbital margin with granules, teeth, notches. Orbits oblique, clearly visible from dorsal view; eyestalks short. Antenna with suboval urinal article, beaked medially; second article with firmly

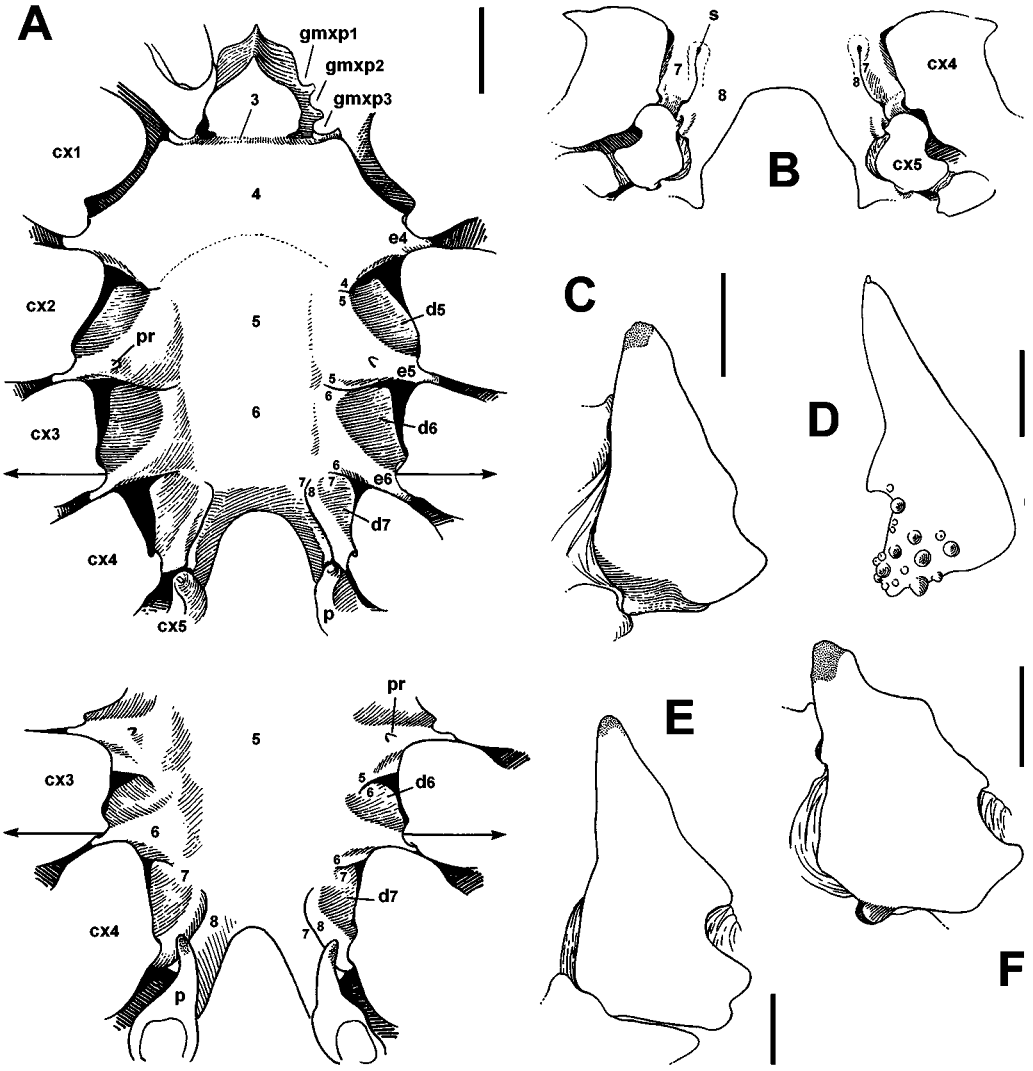

FIGURE 4. A–B, *Dynomene hispida* (Latreille, *in* Milbert 1812), A, male, 8.8 x 11.5 mm, New Caledonia (MNHN-B22091): **A**, thoracic sternum, two views (arrow indicates difference in level); **B**, female, 8.3 x 10 mm, New Caledonia (MNHN-B22091): posterior view showing sutures 7/8 and spermathecal apertures. **C–F**, P5 coxa, enclosing penis for its most part. **C**, *Dynomene hispida* (Latreille, *in* Milbert 1812), male, 8.8 x 11.5 mm, New Caledonia (MNHN-B22091). **D**, *Paradynomene* sp., male, 11 mm width, New Caledonia (MNHN-B24780); E, *Hirsutodynomene ursula* (Stimpson, 1860), male, 9.6 x 11.7 mm, Galápagos Is. (MNHN-B27637); **F**, *Metadynomene tanensis* (Yokoya, 1933), male, 12.5 x 13.5 mm, New Caledonia, SMIB 2 (MNHN-B25583). cx1–cx4, coxae of P1–P4; d5–d7, sterno-coxal depressions on sternites 5, 6 and 7; e4–e6, episternites 4–6; gmxp1–gmxp3, gynglymes of mxp1–mxp3; p, penis; pr, projection; s, spermatheca; 3–8, sternites 3–8; 4/5–6/7, thoracic sternal sutures 4/5–6/7 (indistinct); 7/8, distinct thoracic sternal suture 7/8. Scale bars: 1 mm (A, B, D); 0.5 mm (C, E, F).

fixed exopod. Proepistome wide. Presence of a produced ventral anterior area, forming "face" with projecting front, inflated subhepatic, pterygostomial portions and merus of mxp3; when retracted, chelipeds with fingers resting next to mxp3 exopod and flat portion of pterygostomial region. Anterior border of endostome forming raised wall, laterally notched by exhalant orifices. Mxp3 operculiform, sharply angled; basis long, separated from ischium by incomplete suture; ischium, merus almost at right angles, ischium narrow basally, merus trigonal, laterally extended. Pleural line partially indistinct; branchiostegite of normal texture. Thoracic sternum narrow, completely covered laterally by abdomen, except for external portion of episternite 5 and small extension of episternite 6 which remain exposed when abdomen closed; external margin of abdomen close to P2, P3 coxae. Sternites 1 and 2 fused into triangular or cordiform shield; sternite 3 represented by short, narrow band at base of shield, delimited posteriorly by change in level and denticulate crest; no other marks on successive sternites. Most part of sternites 4–8 fused into single wide plate; sternite 8 tilted. Sterno-coxal depressions deep. Female sutures 7/8 ending well apart, mostly hidden by internal border of P3 sterno-coxal depression; spermathecal aperture extremely small, opening slightly behind level of coxal female gonopore. Sterno-abdominal depression moderately excavated, with oblique slopes in males, and with flat median floor. Male abdomen with all somites free, wide, long, extending onto sternum up to base of anterior shield; first somite dorsal, in prolongation of carapace, proximal portion inserted into concave posterior margin of carapace; somite 2 slightly narrower, other abdominal somites wider, increasing in width; telson broadly triangular. In males rudimentary biramous pleopods on somites 3–5. Male uropod moderately developed, occupying about half length of lateral margin of abdominal somite 6, slightly mobile. Movements of abdomen restricted in both sexes because of sets of granules on P2, to a lesser extent on P3 coxae. Chelipeds equal, more robust than P2–P4; fingers closed for about half or to most of their length, dactylus not curved or moderately curved; fixed finger almost straight. P2 to P4 relatively stout, ornamented with prominences, blunt teeth or spines; dactyli with 4 or 5 spines on lower margins. P5 reduced, sexually dimorphic; basis-ischium fused to merus, forming a single article; rudimentary ending (dactylus as long as propodal extension) forming a subchelate mechanism in females only. Coxa of P5 modified in males to enclose penis, extension narrow, elongated. Pl1 vestigial in females. Gonopod 1 stout, forming semi-rolled tube, with apical oval lobe surrounded by dense fringe of long setae. G2 needle-like, with linear row of tiny distal spines.

Remarks. The. subfamily is monotypic. *Paradynomene*, which until recently was monospecific, now comprises six extant species (McLay & Ng 2004; Table 1).

Discussion

The major morphological features of the four dynomenid subfamilies, as recognised here, are compared as follows.

Carapace. Carapace outline varies in the Dynomenidae from elongated and oblong (Acanthodromiinae **n. subfam.**; Figure 1A), subquadrangular (Paradynomeninae **n. subfam.**; Figure 1B, E), to ovoid (Metadynomeninae **n. subfam.**; Figure 1C) or subcircular and with "xanthoid" facies (Dynomeninae, Figure 1D). In the Paradynomeninae **n. subfam.**, the carapace lateral margins are subparallel, and there are two posterolateral teeth, one marking each posterior corner. The body is very thick, offering a characteristic frontal "face" (Figure 1E); the thickness of the body and the "face" are much less distinct in the Acanthodromiinae **n. subfam.** Both the Acanthodromiinae **n. subfam.** and Paradynomeninae **n. subfam.** have very ornamented bodies (Cleva *et al*. 2007: fig. 16A). The "face" is absent in the weakly ornamented Metadynomeninae **n. subfam.** and Dynomeninae, the latter having a fairly flat carapace, usually armed with anterolateral spines (Cleva *et al*. 2007: figs. 14, 15A–C). The three known metadynomenine species are characterised by dense, short tomentum which gives the surface an uneven undulating appearance with transverse troughs. In all subfamilies the posterior margin is a conspicuous concavity, which varies in degree. In Acanthodromiinae **n. subfam.** and Paradynomeninae **n. subfam.** the concavity is very conspicuous, accommodating the abdomen, with an arched first somite; the concavity is less marked in the Metadynomeninae **n. subfam.** and Dynomeninae, the latter having a nearly straight first abdominal somite.

Carapace grooves are well distinct in the Metadynomeninae **n. subfam.** (Figure 1C), with cervical (complete, deep) and branchial (incomplete, absent medially, only lateral) grooves distinct, subparallel and forming notches with the lateral margins (Cleva *et al*. 2007: fig. 15D). Additional grooves delineate a completely areolated dorsal surface in the extant Paradynomeninae **n. subfam.** (Figure 1B). In the Dynomeninae (Figure

1D), the grooves are weak, the cervical groove being conspicuous medially but never reaching the lateral margin of the carapace; the branchial groove is faint, rarely reaching the lateral margin of the carapace. The grooves are obscured by dense spiny ornaments in the Acanthodromiinae **n. subfam.** (Figure 1A).

In the Dynomenidae the gastric pits, called "submedial pits" by McLay (1999: fig 1), are small slits, rounded or elongated, always placed just on the cervical groove.

Front and orbit. The front varies from a narrow projection (Acanthodromiinae **n. subfam.**) to a more or less broad, triangular or rounded extension (Metadynomeninae **n. subfam.**, Dynomeninae); the projection may be tridentate, more rarely bidentate in the Paradynomeninae **n. subfam**. The orbit is well developed and varies from strongly oblique and long (Acanthodromiinae **n. subfam.**) to less inclined, occasionally being directed transversely, in other subfamilies. The orbital eave is variously marked, and the eyestalk is positioned more or less obliquely.

Thoracic sternum. A. Milne-Edwards (1879) and A. Milne-Edwards & Bouvier (1902) well described and illustrated the thoracic sternum in *Dynomene praedator* A. Milne-Edwards, 1879, and *Acanthodromia erinacea*, respectively, but this feature remained unstudied until recently. The dynomenid thoracic sternum appears to be in about the same plane: sternites 1–7 are visible dorsally, only a posterior declivity at level of sternite 8, which is tilted. Sternites 1 and 2 are fused into a characteristic short, narrow shield, either pentagonal, cordiform, onion-shaped (Acanthodromiinae **n. subfam.**, Metadynomeninae **n. subfam.**, Dynomeninae, Paradynomeninae **n. subfam.**, *pro parte*) or triangular (Paradynomeninae **n. subfam.**, *pro parte*). Dissection reveals the thickness of the shield (Figure 4A). The location of the gynglymes for mxp1 to mxp3 spaced out along the shield’s height proves that sternites 1–3 are partially stacked (instead of being arranged forwards to backwards), suggesting evidence of a distinct cephalic curvature. Sternite 3 is clearly displayed only in the Acanthodromiinae **n. subfam.**, whereas it shows as a short band at the base of the shield in the other three subfamilies. Suture 3/4 is marked by a change of level, line, and/or crest, always complete. Sternites 4–7 are fused into an undivided plate, with straight margins (apart from the episternites), forming medially a flat area and varying from moderately wide in Acanthodromiinae **n. subfam.** to wide in the Metadynomeninae **n. subfam.** and Dynomeninae. According to McLay (1999: 455) “most sternal sutures are absent in dynomenids”. Sutures 4/5, 5/6, and 6/7 are indeed located laterally, probably recessed, so they are hardly visible from the border of the sterno-coxal depressions. In the Dynomenidae the limit between sternites 4 and 5 is indicated by a convex line across the sternum. In the Metadynomeninae **n. subfam.** suture 5/6 is indicated by a complete, membranous band. In the Dynomenidae, suture 7/8 is visible, fairly long, even in males.

The dynomenid thoracic sternum shows a general configuration similar to that of the Dromiidae (Guinot & Tavares 2003) or the Homolodromiidae (Guinot 1995) but differs by its faint sutures 4/5 to 6/7. The dynomenid sternum is also characterised by having the whole plate in about the same plane, a more or less developed flat and undivided surface, and by the narrow anterior shield which is never found in the Homolodromiidae and Dromiidae. The homoloid sternum is distinguished from the dromiacean one by being wider, having a complete suture 6/7 and always bearing a “button” on sternite 4 (corresponding to a socket on abdominal somite 6, taking the place of the dromiacean uropod in the form of a ventral lobe or a dorsal plate). In the Dynomenidae episternites 4–6 are well produced, and their extremities are hollowed by depressions corresponding to the gynglymes of the P1–P3. A median line is always absent in the Dynomenidae as in the Dromiidae and Homolodromiidae, while it is often present posteriorly in the Homoloidea De Haan, 1839.

The pentagonal or triangular shield formed by the anterior sternites, which characterises the Dynomenidae, is roughly similar in shape to that found in the Raninoidea De Haan, 1839 (Guinot 1993b: figs. 1–6) where it is termed a “crown” by palaeontologists. Such a shield is never encountered in any other Recent Brachyura.

The advanced Dynomenidae (Dynomeninae) are characterised by a shortening of the cephalothoracic axis and by broadening of the thoracic sternum, which are combined with a widening of the sterno-abdominal depression. Instead of being narrow, long and completely inserted between the appendages and firmly tightened (as in Acanthodromiinae **n. subfam.**), the male abdomen forms a flexible plate in the Metadynomeninae **n. subfam.** and the Dynomeninae.

In all dynomenids there are deep sterno-coxal depressions excavated above the episternal extremities on the outer edges of the sternum at level of P2, P3 and even P4 (sterno-coxal depressions 5, 6 and 7) (Figures 2A, B, 3A, C, D, 4A). In podotreme crabs whose abdominal holding is by the coxae, these depressions, into which fit the inner edges of the coxae of the pereopods, allow the coxae to slip easily on to the sternum (Guinot & Bouchard 1998). Being very deep in the Acanthodromiinae **n. subfam.**, where the P1–P3 coxae are involved in abdominal holding, the sterno-coxal depressions are similarly well developed in the Metadynomeninae **n. subfam.** and the Dynomeninae, where the abdomen is not firmly held.

The absence of sterno-coxal depressions in all Eubrachyura is clearly linked to the complete loss of abdominal holding mechanism by the appendages and thus to the insertion of a sternal portion between the pereopods and the abdomen. It would be interesting to determine the role of these sterno-coxal depressions in the locomotion of podotreme crabs, which all (except the Cyclodorippoidea and Raninoidea) show such a condition.

Male sterno-abdominal depression and abdomen. The male sterno-abdominal depression is narrow, deep and with steep slopes in the Acanthodromiinae **n. subfam.** (Figure 2), slightly wider and with more or less oblique sides in the Paradynomeninae **n. subfam.**, broad and shallow in the Metadynomeninae **n. subfam.** (Figure 3A) and Dynomeninae (Figures 3C, D, 4A). The male abdomen follows the pattern of the depression, being extremely narrow and extended over the entire length and width of sternum in the Acanthodromiinae **n. subfam.**; it is wider in the other subfamilies, being however narrower and longer in the Paradynomeninae **n. subfam.** than in the Metadynomeninae **n. subfam.** and Dynomeninae. Either all the abdominal somites are free (Paradynomeninae **n. subfam.**, Metadynomeninae **n. subfam.** and Dynomeninae) or somites 3–6 are fused in both sexes, but with partially visible sutures that are obscured by spines (Acanthodromiinae **n. subfam.**). The first abdominal somites are dorsal, at least the first two ones in the Acanthodromiinae **n. subfam.** and Paradynomeninae **n. subfam.**, the first somite being strongly arched and fitting perfectly into the concave posterior carapace margin. The folding of the abdomen is well developed in the Metadynomeninae **n. subfam.** and Dynomeninae. The telson is well developed in all four subfamilies. A. Milne-Edwards (1879: 4) had suggested that the dynomenid abdomen could be used for swimming. Observation of live *Dynomene praedator* (Dynomeninae) has shown that the flexible abdomen often makes flicking movements, similar to those made by porcellanids (McLay 1999: 456). Observation of live *D. praedator* in Hawaii has shown, however, that, even when the crab was disturbed, the flexing of the abdomen was never as strong or as prolonged as in porcellanids, and it could not be used for swimming as in porcellanids (P.K.L. Ng, pers. com.).

Uropods. McLay (1999) studied the uropods in the Dynomenidae in some detail. They always take the form of dorsal plates, often well developed, never prominent in males except for the Paradynomeninae **n. subfam.** (Figure 5M, N) where they are slightly salient; in the Acanthodromiinae **n. subfam.** (Figure 5O, P) the uropods are visible as narrow plates, transversely elongated, and obscured by spines. Dynomenid uropods are usually smaller in males, although their involvement in the holding of the abdomen is very limited, consisting only of a coaptation by simple juxtaposition. The small structure, either appendicular on the P2 coxa or on sternite 5, only restricts lateral movements of the abdomen.

The Dynomenidae exemplifies two main patterns of male dorsal uropod. It shows either as well-developed, triangular and immobile plate, occupying the entire length of lateral margin of abdominal somite 6 in both sexes (Metadynomeninae **n. subfam.**, Figure 5I–L), or as a smaller plate occupying only partially the length of somite 6 (other subfamilies). The uropods are either similar in both sexes (Metadynomeninae **n. subfam.**) or sexually dimorphic as in the Dynomeninae. In the Metadynomeninae **n. subfam.** the outline at the level of abdominal somite 6 is exclusively uropodial in both sexes (Figure 5I–L). In *Dynomene hispida* the male uropod is small (Guinot & Bouchard 1998: fig. 7D; Figure 4A), in contrast to the female one (Figure 4B) which occupies, as in species of *Metadynomene*, the entire length of abdominal somite 6 (McLay 1999: fig. 18g). The Dynomenidae are characterised by the small size of abdominal somite 6, especially in the mature female, in which a large uropod encroaches on somite 6.

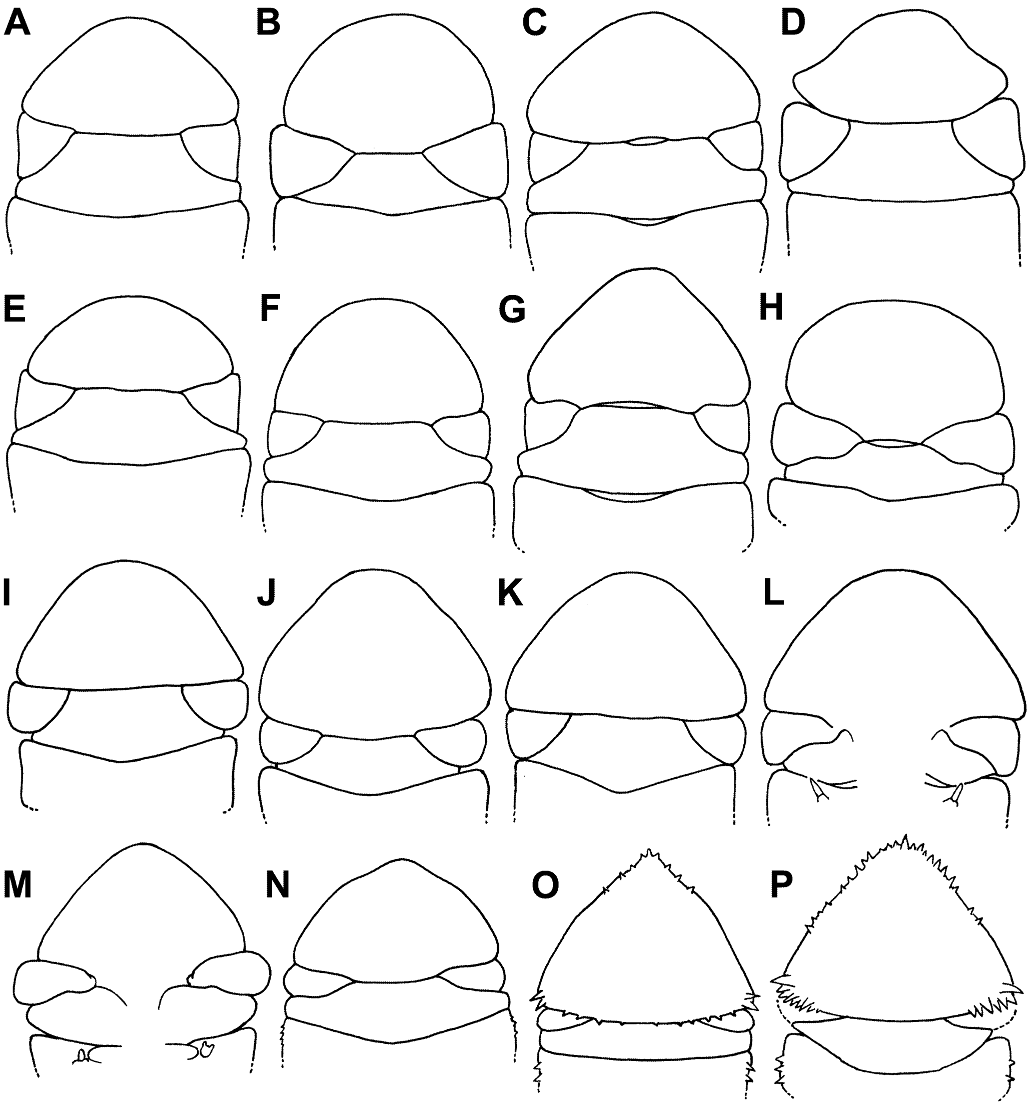

FIGURE 5. Uropods in the four dynomenid subfamilies (dorsal surface, unless mentioned otherwise). A–H, Dynomeninae Ortmann, 1892; I–L, Metadynomeninae **n. subfam.**; M–N, Paradynomeninae **n. subfam.**; O–P, Acanthodromiinae **n. subfam.** **A–B**, *Dynomene hispida* (Latreille, *in* Milbert 1812): **A**, male, New Caledonia (MNHN-B22091); **B**, female (After McLay 1999: fig. 18g). **C**, *Dynomene pilumnoides* Alcock, 1900, female (After McLay 1999: fig. 21g). **D**, *Dynomene praedator* A. Milne-Edwards, 1879, male (After McLay 1999: fig. 19g). **E**, *Dynomene pugnatrix* De Man, 1889, male (After McLay 1999: fig. 22g). **F**, *Dynomene filholi* Bouvier, 1894, male (After McLay 1999: fig. 20g). **G**, *Hirsutodynomene spinosa* (Rathbun, 1911), male (After McLay 1999: fig. 23g). **H**, *Hirsutodynomene ursula* (Stimpson, 1860), female (After McLay 1999: fig. 24g). **I–J**, *Metadynomene tanensis* (Yokoya, 1933): **I**, male, New Caledonia, dorsal surface (MNHN-B25583); **J**, female, ventral surface (After McLay 1999: fig. 27g). **K–L**, *Metadynomene crosnieri* McLay, 1999, male, holotype, western Indian Ocean, îles Glorieuses (MNHN-B22510): dorsal (K) and ventral (L) surfaces; **M–N**, *Paradynomene* sp., New Caledonia (MNHN-B 24779); **M**, male: ventral surface; **N**, female: dorsal surface (After McLay 1999: fig. 32g). **O**, *Acanthodromia erinacea* A. Milne-Edwards, 1880, female, Puerto Rico (USNM 124263); **P**, *Acanthodromia margarita* (Alcock, 1899), female (After McLay 1999: fig. 31f).

Large uropods are present in the Metadynomeninae **n. subfam.** in both sexes (Figure 5I–L) (no other podotreme exhibits such large dorsal plates) and, to a lesser extent, in the Dynomeninae.

The Dynomenidae is distinguished from the Dromiidae, in which mobile, smaller but usually salient dorsal uropods are effectively involved in the holding of the abdomen and exhibit a strong sexual dimorphism. The Homolodromiidae has uropods as ventral lobes (Guinot 1995), as in some Dromiidae. All Podotremata which have vestigial uropods (dorsal plates or ventral lobes) are devoid of sockets. These podotreme crabs devoid of sockets form the Dromiacea (Dromiidae, Dynomenidae, and Homolodromiidae). This is evidence that the Dromiacea and Homolidea should not be referred to the same taxonomic category and therefore not be grouped under the name "Dromiacea". All (or nearly all) brachyuran crabs that lack uropods (regardless of their condition) possess sockets.

Within the Brachyura, a complete pleopodal formula is encountered only in the podotremes, and exclusively in the basal clades, i.e. in the Dromiacea (Guinot & Bouchard 1998: table 3; Guinot & Tavares 2003: table 1). Vestigial, usually biramous, pleopods on somites 3–5 are found in male Dynomenidae. Somites 3–5 may bear vestigial pleopods (usually uniramous) in the Homolodromiidae, a character that is rare in the Dromiidae.

The Homoloidea has a socket on abdominal somite 6 while the Cyclodorippoidea does not show any structure on somite 6, and both groups have lost pleopods on abdominal somites 3–5 in males. In the Homoloidea (sternal "homolid button" located on sternite 4) and in the Lyreidinae Guinot, 1993 (1993b) (sternal projection arising from sternite 5), the sternal structure articulates with a socket on abdominal somite 6. Such a combination is not inconsistent with the idea that sockets on somite 6 (in Homoloidea, Lyreidinae and Eubrachyura) are evolved from the decapod biramous uropods.

Abdominal holding. The Dynomenidae exemplifies several patterns of abdominal holding mechanism. Guinot & Bouchard (1998) is followed here, and thus is inversed the polarity defined by McLay (1999: 456) who noted that "There is a gradation from abdomen maintaining mechanisms as found in *Dynomene* + *Hirsutodynomene* where sternal tubercles are used, through *Metadynomene*, using coxal ridges or spines on the second and third pereopods, and *Paradynomene* using coxal granules, to the abdominal locking mechanism found in *Acanthodromia*." An effective locking mechanism characterises the Acanthodromiinae **n. subfam.** (Figure 2) where the abdomen entirely fills the narrow sterno-abdominal depression and is in contact with the coxae of the appendages; the long abdomen is firmly locked, with the involvement of four thoracopods (mxp3, P1–P3). In the Acanthodromiinae **n. subfam.** the abdominal margin is weakly modified, and the narrow uropods do not play any role. The mechanism is as efficient in mature females as it is in males. It is, however, less complete in males than in females, in which the spinules are more numerous and acute (at least in *Acanthodromia margarita*). In the Paradynomeninae **n. subfam.** the male uropods are slightly salient, and the male abdomen is loosely held by granulated P2 and P3 coxal prominences (Guinot 1993a: 1227; Guinot & Bouchard 1998: 632); a similar organisation occurs in females. In the Metadynomeninae **n. subfam.** and Dynomeninae the wider male abdomen is not closely held on the sternum, the coxal structures (absent in the females) being not really efficient and only restricting lateral movements of the abdomen. These structures are coxal in the Metadynomeninae **n. subfam.** (Figure 3A) (plesiomorphy), but sternal in the Dynomeninae (Figure 3C, D) (apomorphy). In the Dynomeninae the sternal press button on sternite 5 (more precisely on episternite 5) is not accompanied by a socket (Guinot & Bouchard 1998). In brief, the dynomenid abdomen is either locked by coxal structures of mxp3 and P1–P3 (Acanthodromiinae **n. subfam.**), or less firmly held (Paradynomeninae **n. subfam.**), or only loosely applied on the sternum and restricted in its sideways movements (Metadynomeninae **n. subfam.** and Dynomeninae).

Among the Dromioidea, the Dynomenidae is the only family to display a sternal innovation (in the subfamily Dynomeninae), all other dromioids having structures dependent on the appendages. In the Dromiidae, the abdominal and/or uropodial border is strongly ventrally or laterally modified, and the uropod is often markedly involved in a strong holding mechanism. In contrast, in the Dynomenidae the uropod is slightly salient in one subfamily (Paradynomeninae), never in the other subfamilies. The abdominal (uropod included) margin is only slightly modified in the Acanthodromiinae **n. subfam.** and Paradynomeninae **n. subfam.**, but not modified in the two other subfamilies. In the poorly known Acanthodromiinae **n. subfam.**, where the available material is limited, and in the Paradynomeninae **n. subfam.**, the uropod is mobile, to an extent that it is difficult to appreciate. The uropods are immobile in the Dynomeninae and the Metadynomeninae **n. subfam.**, where they are developed as large to very large dorsal plates, respectively.

In the Dynomeninae, members of which possess a small sternal press button, the uropod which lies beside is not transformed into a socket. Modification of coxal structures (Acanthodromiinae **n. subfam.**, Metadynomeninae **n. subfam.**, and Paradynomeninae **n. subfam.**) into sternal structures (Dynomeninae) is a consequence of the broadening of the thoracic sternum, i.e. of carcinization. The Dynomeninae are carcinized podotremes, an idea that is consistent with the wider and flat carapace and other advanced characters found in this subfamily.

The sternal structure of the Dynomeninae is quite different from the typical press button of the Eubrachyura. Moreover, the involvement of the abdomen appears to be quite different: the abdomen is only loosely applied on the sternum and restricted in its lateral movements. In the dynomenines, a press button system is lacking and the uropod is not transformed into a socket. In the Homoloidea (sternal “homolid button”, located on sternite 4) and in the raninoid Lyreidinae Guinot, 1993 (hook-shaped sternal projection arising from sternite 5) the sternal structure articulates with a socket on abdominal somite 6. Such a combination is not inconsistent with the idea that sockets on somite 6 (in Homoloidea, Lyreidinae and Eubrachyura) are derived from biramous decapod uropods.

Spermathecae. The female sutures 7/8 end well apart from each other and are short in the four subfamilies. The spermathecal apertures at the extremities of sutures 7/8 open slightly behind the female gonopore on P3 coxa (Figure 4B). The aperture is small in the Metadynomeninae **n. subfam.**, Paradynomeninae **n. subfam.** and Dynomeninae. In the single female *Acanthodromia* examined, suture 7/8 was hidden laterally and the aperture was not visible.

P5. The P5 of the Dynomenidae, extensively studied by McLay (1999), is reduced, very rudimentary, straight and positioned obliquely, and not mobile. The dynomenid P5 is a unique structure among the Brachyura, being the most distinctive character when contrasted to the subcheliform and mobile last leg(s) of the Homolodromiidae (only P5 modified for carrying behaviour) and Dromiidae (both P4 and P5 modified for carrying behaviour). In extant Acanthodromiinae **n. subfam**. and Paradynomeninae **n. subfam.** the basis-ischium is fused to the merus (Guinot 1993a: fig. 1), in contrast to the Metadynomeninae **n. subfam.** and Dynomeninae which have a free basis-ischium. This fusion, resulting in a single article, the basis-ischium-merus, is indicative of the ancestry of the two subfamilies (Acanthodromiinae **n. subfam.** and Paradynomeninae **n. subfam.**), as is the fusion of abdominal somites 3–6 in the Acanthodromiinae **n. subfam.**

The obsolete and sexually dimorphic subchelate ending presents different patterns in the Dynomenidae, but the four subfamilies were not systematically studied. McLay (1999) described and figured the subchela, which is better developed in females than in males for most species. In male dynomenids the P5 coxa is strongly modified, the extension enclosing the penis being apparently longer and narrower in the Acanthodromiinae **n. subfam.** and probably in the Paradynomeninae **n. subfam.** (Figure 4D) than in the Metadynomeninae **n. subfam.** (Figure 4F) and Dynomeninae (Figure 4C, E).

Gonopods 1 and 2. These were well described by McLay (1999). The long, needle-like G2 bears an exopod on the basal article (plesiomorphy); its distal part has spines to propel the spermatophores into the G1 (McLay 1999: 459). This spinulation, which varies amongst species, is typical of the Dynomenidae.

Endophragmal skeleton. A. Milne-Edwards (1879: fig. 26) presented an excellent illustration of the axial skeleton in *Dynomene praedator.* In the Dynomenidae, as well as in the Dromiidae, junctions between the phragmae of the skeleton occur by fusion, instead of junction by interdigitation as in the Homolodromiidae (and Homoloidea). A sella turcica is absent, as in other Dromiacea (and all podotreme crabs). The intertagmal phragma skirts the last endosternite to join the median mass from below (Secretan 1998). The skeletal system shows three distinct patterns within the family, and is in concordance with the different character states encountered in the subfamilies erected herein, although species of *Acanthodromia* could not be dissected. A primitive pattern is present in the Paradynomeninae **n. subfam.**, where the skeletal parts are layered, the median fusion is longitudinally extended into a rather long portion (Secretan 1998: figs. 7, 8, *Paradynomene* sp.). The transversal bridge is longer and narrower in the Metadynomeninae **n. subfam.** than in the Dynomeninae, where it is very thick (see A. Milne-Edwards 1879: fig. 26, *Dynomene praedator*; Guinot & Quenette 2005: fig. 4D, *Dynomene pilumnoides* Alcock, 1900; Guinot & Quenette 2005, fig. 4B, *Metadynomene tanensis* (Yokoya, 1933)).

The monophyly of the Dynomenidae is supported by examining the graded series of character states: the sequences of character states (morphocline) for each homologous character show a similar polarity. The Acanthodromiinae **n. subfam.** exhibits the most plesiomorphic condition as well in body shape, the fronto-orbital disposition and in the condition of the thoracic sternum, the abdominal holding and gill structure. The Paradynomeninae appears as more specialised. The Metadynomeninae **n. subfam.** is more primitive that the Dynomeninae, which is more carcinized and probably the most derived subfamily. The fusion of abdominal somites 3–6 in *Acanthodromia* and fusion of articles of P5 (basis-ischium fused with merus) in both Acanthodromiinae **n. subfam.** and Paradynomeninae **n. subfam.** is linked to a long evolutionary process.

Within the Dromiacea, the Dynomenidae have several features in common with the Sphaerodromiinae, the most primitive dromiid subfamily, all of which are plesiomorphic: vestigial male pleopods (usually biramous) on somites 3–5, short female sutures 7/8, apertures of the spermathecae lying not far from the female gonopores on P3 coxae, G2 with exopod, and a P5 coxa prolonged to form a hardened process enclosing most of the penis. Some dynomenids may be confused with sphaerodromiines as both have similar projecting fronts and orbits. But in the extant sphaerodromiines the deep orbit is surrounded by the supraorbital margin which forms a high eave, visible from dorsal view; furthermore, the carapace is globose and suboval, the cervical and branchial grooves are obsolete or faint, there is only a branchiocardiac groove, and the long anterolateral border is either divided by lobes or entire, always marked posteriorly by a strong notch (see McLay 1991: table 1). In the Sphaerodromiinae a weak abdominal holding mechanism is assumed, at least in the rare specimens that were examined, by a prominence on the P2 coxa that acts on the telson, without any involvement of the small dorsal uropod. The sphaerodromiine thoracic sternum does not possess the peculiar anterior shield characteristic of the Dynomenidae. The Sphaerodromiinae is a component of the Dromiidae, notably due to both P4 and P5 which are reduced, dorsal and subchelate, presumably allowing individuals to carry large pieces of sponge for camouflage.

The function of the reduced, obliquely directed P5 of the Dynomenidae, with a small, sexually dimorphic subchela (more pronounced in females) and an articulation that allows only restricted movement, is a vexing question. Apart from its role in reproduction (coxa bearing the male gonopore and extended to enclose the penis), the function of the vestigial dynomenid P5 is unknown. A cleaning or grooming role was not suspected (McLay 1999: 454). The P5 appears to be incapable of being held over the carapace as in other podotreme crabs, and the function in extant species is not to assist in securing a sponge for camouflage. Observation of live *Metadynomene tanensis* and *Dynomene praedator* has shown that the P5 could turn and move, which does not exclude a function in cleaning, gripping the substrate or otherwise, holding objects, or flexing under the carapace as do porcellanids (P.K.L. Ng, pers. com.). The condition of P5 in fossils may yield some information, but this is a challenge since hind walking legs are often missing in fossils and thus it is highly unlikely to expect that this small appendage would be preserved.

The characteristic “face” found in the Paradynomeninae **n. subfam.** (Figure 1E) (only faintly developed in the Acanthodromiinae **n. subfam.**) is related to their habit of burying into surface coral fragments, as evidenced by the presence of specialised exhalant openings anterior to the operculiform maxillipeds and by the coaptation of the chelipeds with the carapace to fit compactly against the body (see McLay 1999 on *Paradynomene*).

The geographical distribution of the family Dynomenidae can be regarded as representative of a very ancient group, with a relatively limited number of extant species showing a worldwide distribution. Only two subfamilies, representing three genera, are known from the Western Hemisphere: the Acanthodromiinae **n. subfam.** from the western Atlantic, with the insular species *Acanthodromia erinacea* restricted to the Caribbean area, and the Dynomeninae, with two species in two genera, the insular species *Dynomene filholi* Bouvier, 1894, restricted to the South Atlantic, and *Hirsutodynomene ursula* (Stimpson, 1860) confined to the Pacific coast of Central America. Only one species of Dynomeninae, *Dynomene pugnatrix* De Man 1889, is present in the eastern Atlantic, being also insular. In the Metadynomeninae **n. subfam.** two species (*M. devaneyi* and *M. crosnieri* McLay, 1999) are rare, while *M. tanensis* is more common. *Metadynomene tanensis* and *Dynomene pilumnoides* are now known from New Zealand (C.L. McLay, pers. com.). The small size of most dynomenids and their frequent association with dead and live coral make it more than likely that new species could be discovered, as illustrated by the recent description of five new species of *Paradynomene* by McLay & Ng (2004).

The ancestral origin of the Acanthodromiinae **n. subfam.** is demonstrated by the distribution of its two representatives, *Acanthodromia erinacea* in the Atlantic and *A. margarita* in the Indo-West Pacific but with no major morphological divergence to warrant generic separation (McLay 1999: 539, 552). The origin of the Acanthodromiinae **n. subfam.** from a Tethyan ancestor, perhaps as early as the Late Jurassic, has been hypothesised (McLay 1999).

The cladistic analyses of Brösing *et al.* (2007) and Brösing (2008) on the basis of several foregut characters in two species of *Dynomene* and one of *Paradynomene*, did not support the monophyly of the dynomenid genera. Such a conclusion does not embrace the various generic dynomenid taxa, which clearly show a multitude of differences, obscuring phylogenetic relationships. Consequently, any reappraisal of the family first needs to use a number of different morphological characters and secondly to take into account all five genera, as well as several species.

In the present reassessment, the monophyly of the Dynomenidae is supported by the peculiar condition of the P5, which constitutes the strongest synapomorphy of the family. Despite the various states of characters, the family forms a cohesive clade, with a similar polarity for all characters. The relative width of the abdomen in males (not pronounced, however, in the Acanthodromiinae **n. subfam.**), the long telson, the thoracic sternum devoid of distinct sutures 4/5 to 6/7, and the flat and undivided medial surface of the sterno–abdominal depression are characteristic of the Dynomenidae.

Fossil Dynomenidae (preliminary remarks)

Ancestral dynomenids are believed to have been Tethyan crabs (McLay 1999). Extant dynomenids are survivors from the Jurassic, having endured Cretaceous/Paleogene perturbations (Wright & Wright 1950; Schweitzer & Feldmann 2005). It is evident that the diversity of their morphological features, exhibiting different states of transformation, is linked to early diversification and a long evolutionary history. Ten fossil dynomenid genera were listed by McLay (1999: 434), who suggested that extinct species traditionally assigned to *Dynomene* could in fact belong to other genera. Schweitzer *et al*. (2003: 20, 21) recognised 13 fossil dynomenid genera. The assignment of some fossil genera to the Dynomenidae needs to be corroborated, however. Fortunately, dorsal carapace features tentatively suffice to assign dynomenid species to a particular subfamily. The Acanthodromiinae **n. subfam.** perhaps is an exception because of its spinose ornament which masks the grooves and sutures.

Diaulax Bell, 1863 (type species: *D. carteriana* Bell, 1863, Lower Cretaceous), alternatively considered to be a prosopid (Wright & Wright 1950: 24) or a dynomenid (Glaessner 1969: R488), is now the type genus of the Diaulacidae Wright & Collins, 1972 (see Bishop 1983: 45; 1986: 133), and thus affiliated to the Podotremata (Guinot & Tavares 2001). The Diaulacidae was synonymised with the Dynomenidae by Schweitzer *et al.* (2003). Bell (1863: 7, pl. 1, figs. 14–16) described the basal portions of the pereopods preserved in *D. car-*

teriana and indicated that "the last pair are placed on a much higher level than the others". Wright & Collins (1972: 58, pl. 9, figs. 6–8, pl. 10, fig. 1a, b) described the sternum as twice as long as wide, anteriorly with "an acute point", the abdominal somites as "short, flat and rectangular", and the telson as "bluntly triangular, wider than long (in a supposed male)". According to Bell's original and subsequent descriptions of the type material (Carter 1898: 19; Wright & Wright 1950: 24, pl. 1, fig. 9a, b; Wright & Collins 1972: 57), there are two parallel transversal grooves that cross the dorsal carapace. The cervical one is continuous, with "a slight interruption on the middle line, on either side of which is a small pit" [i.e., herein gastric pit] (Wright & Collins 1972: 57), and probably notches the lateral margin; the branchial one is not so pronounced. In the absence of any significant illustration, it is difficult to assign *Diaulax carteriana* with certainty. This observation is of importance because the Diaulacinae could admittedly constitute a senior synonym of one of the subfamilies erected herein. Synonymy with the Acanthodromiinae **n. subfam.** or the Paradynomeninae **n. subfam.** may be reasonably excluded as they are so different morphologically. A possible relationship with the Metadynomeninae **n. subfam.** is also questionable. According to Glaessner (1931: 4; 1969: R488), *Diaulax* originated during the Late Jurassic (see also Wright & Wright 1950: fig. 13; Wright & Collins 1972: 56; Fraaye 1996: fig. 3), and this could imply (in the case of a genuinely close relationship between *Diaulax* and the Metadynomeninae **n. subfam.**) an early appearance of the metadynomenine lineage, together with the diaulacine one.

Some fossil genera appear to conform to the new diagnostic subfamilial definitions and may be more easily assigned. A good example is the Paleocene *Kierionopsis* Davidson, 1966 (type species. *K. nodosa* Davidson, 1966: 211–213, figs. 1, 2), which was originally (Davidson, 1966: 211) and subsequently (Schweitzer & Feldmann 2008: 122) attributed to the Dromiidae, as possibly related to *Dromilites americana* Rathbun, 1935, or regarded as "enigmatic" (Schweitzer *et al*. 2002: 41, fig. 29, table 4) within the Dynomenidae (Schweitzer *et al*. 2003: 21; Schweitzer & Feldmann 2005: 22), and clearly belongs to the Paradynomeninae **n. subfam**. as defined here. In *K. nodosa*, the carapace is subrectangular, the dorsal surface is ornamented by 12 elevated granular bosses, the posterolateral border bears an elongated subdistal tooth, the intestinal region is recessed, and there is an orbital eave, all characters found in the extant Paradynomeninae **n. subfam.** Apart from the front, slightly bidentate in *K. nodosa*, distinctly bidentate or tridentate in extant *Paradynomene*, the resemblance is amazing.

The Paleocene *Dromilites americana* Rathbun not only "differs significantly from the type of the genus" *Dromilites* H. Milne Edwards, 1837, *D. bucklandii* (H. Milne Edwards, 1837) (see Schweitzer *et al*. 2003: 21) but, moreover, the thoracic sternum figured by Rathbun (1935: pl. 17, fig. 2) does not correspond to that of a dromiacean crab and probably does not represent a podotreme condition. Consequently, the assignment of *Dromilites americana* to *Dromilites* and its attribution to the Dynomenidae, with a possible link to *Kierionopsis*, are not recognised here. *Dromilites* should be assigned to the Dromiinae (Dromiidae).

Similar to *Kierionopsis*, *Kromtitis* Müller, 1984 (type species: *Dromilites koberi* Bachmayer & Tollmann, 1953), assigned to the Dromiidae (Müller 1984: 64, pl. 31, figs. 1–4; Müller & Collins 1991: 63, fig. 3e, pl. 3, figs. 4, 5, 8; Portell & Collins 2004: 111; Beschin *et al*. 2002: 12; Donovan *et al.* 2003: 106) or to the Dynomenidae in close proximity of *Paradynomene* (Beschin *et al*. 2007: 26, 27; see also Beschin *et al*. 2004), can be confidently included in the Paradynomeninae **n. subfam.** In *Kromtitis,* as in *Kierionopsis*, the subrectangular carapace, the pronounced subdistal posterolateral teeth, the lobate and ornamented dorsal surface closely matches those of species of *Paradynomene* species recently described by McLay & Ng (2004). At least, in dorsal carapace features, there has scarcely been any divergence between these fossil genera and extant Paradynomeninae **n. subfam.** All species of *Kromtitis*, from the Eocene to the Miocene, are coral associates (Beschin *et al*. 2007: 27), as are extant species of *Paradynomene*. Modern Paradynomeninae **n. subfam.** clearly are barely modified relicts.

A number of fossils, known solely from their dorsal carapaces and which conform to the general pattern of the Dynomenidae, appear as possible metadynomenines. Such is the case, for instance, of species of *Dromi-*

opsis Reuss, 1859 (type species: *Brachyurites rugosus* von Schlotheim, 1820) as *D. elegans* Reuss, 1859, with a rounded carapace, complete and deep cervical groove and lateral branchial groove, both grooves reaching and forming notches with the lateral border of the carapace. However, the genus *Dromiopsis*, supposed to be a dynomenid genus, is probably not monophyletic.

It is premature and beyond the scope of the present paper to assign podotreme fossils to a dynomenid subfamily, the preliminary task being to attempt to include extinct genera in their appropriate family, i.e., either in the Dromiidae (and possibly in its constituent subfamilies) or Homolodromiidae or Dynomenidae, without excluding extinct families such as the Diaulacidae and also the Prosopidae which are the ancestors of the Homolodromioidea. Any affiliation based on the carapace shows only similarities and thus remains speculative at best. The nature of fossil dromiacean genera, even those that are known from a number of characters, remains questionable. For example the familial status of *Basinotopus* M'Coy, 1849 (type species: *Inachus lamarckii* Desmarest, 1822), traditionally assigned to the Dromiidae (P4 and P5 reduced and dorsal), is puzzling, despite the availability of both male and female abdomens with their uropods (M'Coy 1849; Bell 1858; see Guinot & Tavares 2001). Recent discoveries of more complete specimens of the Eocene *Basinotopus tricornis* Collins & Jakobsen, 2004, which in particular reveal sternal characters (Collins & Jakobsen 2004: 69, fig. 3, pl. 2, figs. 1–7), require a new interpretation based on all known data in accordance with phylogeny.

Key to the subfamilies of extant Dynomenidae

1. Carapace longer than wide or as long as wide (exceptionally slightly wider than long); dorsal surface much ornamented. Male abdomen long, entirely filling sterno-abdominal depression in length and width. Uropods relatively small...2

\- Carapace wider than long, may be as wide as long; dorsal surface weakly ornamented; cervical and branchial grooves well visible. Male abdomen not completely filling entire length of sterno-abdominal depression, leaving exposed anterior portion of sternite 4. Uropods large to very large. 3

2. Carapace elongated, oblong, covered by dense spines, obscuring cervical and branchial grooves, as well as areolation. Carapace lateral margins poorly defined, obscured. Sternites 1 and 2 fused into small, extremely narrow shield; sternite 3 distinct, albeit short, expanded laterally. Male abdomen reaching base of mxp3 and tightly locked in deep, narrow sterno-abdominal depression by ornaments on mxp3, and P1, P2 and P3. Uropods as narrow plates. ....Acanthodromiinae **n. subfam.**

\- Carapace subquadrangular; areolation, cervical and branchial grooves clearly visible. Carapace lateral margins subparallel; 2 posterolateral teeth, one marking each posterior corner. Ventral anterior area, produced, forming a "face" with projecting front, inflated subhepatic and pterygostomial portions, and merus of mxp3. Sternites 1 and 2 fused into triangular or cordiform shield. Male abdomen extending on thoracic sternum until base of anterior shield, movements restricted in both sexes due to sets of granules on P2 and, to a lesser extent, of P3 coxae. Uropods as moderately developed dorsal plates, occupying about half length of lateral margin of abdominal somite 6...Paradynomeninae **n. subfam.**

3. Carapace ovoid, densely covered by short tomentum giving to surface an uneven undulating appearance with transverse troughs; dorsal surface smooth. Cervical groove complete, deep, branchial groove absent medially but well developed laterally, both grooves subparallel, forming notches with lateral margins. Sternites 1 and 2 fused into pentagonal, narrow shield, which may be slightly pointed. Male abdomen filling laterally entire width of sterno-abdominal depression. A tubercle on P2 coxa, only restricting lateral movements of abdomen. Uropods showing as large dorsal plates occupying all length of lateral margin of abdominal somite 6 in both sexes...Metadynomeninae **n. subfam.**

\- Carapace broadly rounded, with "xanthoid" facies; dorsal surface areolate or not, smooth or granulate, may be laterally spiny, more or less sparsely covered with short or long setae; anterolateral margin armed with teeth, rarely by granules only. Cervical groove present, broad, V-shaped, incomplete, not forming notch with lateral margin of carapace. Branchial groove faint, either indistinct laterally or, more rarely, joining lateral margin of carapace. Sternites 1 and 2 fused into pentagonal shield, more or less pointed at tip. Male abdomen leaving thoracic sternum laterally exposed. A small sternal tubercle (on episternite 5) facing either uropodial margin or abdominal margin, only restricting lateral movements of abdomen. Uropods showing as dorsal plates occupying variable length of abdominal somite 6, never filling whole length of somite 6, at least in males. ....Dynomeninae Ortmann, 1892

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