A new subfamilial arrangement for the Dromiidae de Haan, 1833, with diagnoses and descriptions of new genera and species (Crustacea, Decapoda, Brachyura)

Danièle GUINOT
Département Milieux et Peuplements aquatiques,
Muséum national d'Histoire naturelle,
61 rue Buffon, F-75231 Paris cedex 05 (France)
guinot@mnhn.fr

Marcos TAVARES
Universidade Santa Úrsula,
Instituto de Ciências Biológicas e Ambientais,
Rio de Janeiro, 22231-040 (Brazil)
mtavares@alternex.com.br

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ABSTRACT

A review of the morphology among members of the Dromiacea (and among other members of the Podotremata) revealed that the present classification of the Dromiidae does not reflect the wide variation of morphological patterns within the family. The Dromiidae are for the first time subdivided into three subfamilies: Dromiinae de Haan, 1833 n. status (type genus: *Dromia* Weber, 1795); Hypoconchinae n. subfam. (type genus: *Hypoconcha* Guérin-Méneville, 1854); and Sphaerodromiinae n. subfam. (type genus: *Sphaerodromia* Alcock, 1899). Thirty-eight dromiid genera are recognized herein: 34 in the Dromiinae n. status, five of which are new: *Lamarckdromia* n. gen. (type species: *Dromia globosa* Lamarck, 1818), *Lewindromia* n. gen. (type species: *Cryptodromiopsis unidentata* Rüppell, 1830), *Mclaydromia* n. gen. (type species: *Mclaydromia colini* n. gen., n. sp.), *Moreiradromia* n. gen. (type species: *Dromidia antillensis* Stimpson, 1858), and *Stebbingdromia* n. gen. (type species: *Dromidiopsis plumosa* Lewinsohn, 1984); one in the Hypoconchinae n. subfam. (*Hypoconcha* Guérin-Méneville, 1854); and two in the Sphaerodromiinae n. subfam. (*Sphaerodromia*, *Eodromia* McLay, 1993). The diagnoses of the following four dromiine genera are emended: *Austrodromidia* McLay, 1993; *Cryptodromiopsis* Borradaile, 1903; *Dromidia* Stimpson, 1858; and *Dromidiopsis* Borradaile, 1900. The monotypic

KEY WORDS
Crustacea,
Podotremata,
Dromiidae,
Dromiinae n. status,
Hypoconchinae n. subfam.,
Sphaerodromiinae n. subfam.,
uropod,
thoracic sternum,
spermathecae,
new subfamilies,
new genera,
new species,
phylogeny.

Platydromia Brocchi, 1877 (type species: *Dromia spongiosa* Stimpson, 1858) is resurrected. Seven dromiine genera are discussed in detail: *Conchoecetes* Stimpson, 1858; *Desmodromia* McLay, 2001; *Epipedodromia* André, 1932; *Fultodromia* McLay, 1993; *Hemisphaerodromia* Barnard, 1954; *Homalodromia* Miers, 1884; and *Pseudodromia* Stimpson, 1858. *Sphaerodromia*, *Eodromia*, *Hypoconcha* and the enigmatic *Frodromia* are analyzed in detail. Special reference is made to 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. A key to the families of the Dromiacea and the subfamilies of the Dromiidae is provided.

RÉSUMÉ

Nouvel arrangement subfamilial pour les Dromiidae de Haan, 1833, avec diagnoses et descriptions de nouveaux genres et espèces (Crustacea, Decapoda, Brachyura).

Une revue de diverses dispositions morphologiques chez les Dromiacea (et plus largement chez les Podotremata) a révélé que la classification actuelle des Dromiidae ne reflètait pas la richesse des patterns morphologiques dans cette famille. La famille des Dromiidae est ici, pour la première fois, subdivisée en trois sous-familles : Dromiinae de Haan, 1833 n. status (genre type : *Dromia* Weber, 1795) ; Hypoconchinae n. subfam. (genre type : *Hypoconcha* Guérin-Méneville, 1854) ; et Sphaerodromiinae n. subfam. (genre type : *Sphaerodromia* Alcock, 1899). Trente-huit genres de Dromiidae sont reconnus : 34 genres de Dromiinae n. status, dont cinq nouveaux : *Lamarckdromia* n. gen. (espèce type : *Dromia globosa* Lamarck, 1818), *Lewindromia* n. gen. (espèce type : *Cryptodromiopsis unidentata* Rüppell, 1830), *Mclaydromia* n. gen. (espèce type : *Mclaydromia colini* n. gen., n. sp.), *Moreiradromia* n. gen. (espèce type : *Dromidia antillensis* Stimpson, 1858) ; et *Stebbingdromia* n. gen. (espèce type : *Dromidiopsis plumosa* Lewinsohn, 1984) ; un genre d'Hypoconchinae n. subfam. (*Hypoconcha* Guérin-Méneville, 1854) ; et deux genres de Sphaerodromiinae n. subfam. (*Sphaerodromia* et *Eodromia* McLay, 1993). La diagnose de quatre genres de Dromiinae n. status (*Austrodromidia* McLay, 1993, *Cryptodromiopsis* Borradaile, 1903, *Dromidia* Stimpson, 1858 et *Dromidiopsis* Borradaile, 1900) est émendée. *Platydromia* Brocchi, 1877 (espèce type : *Dromia spongiosa* Stimpson, 1858), monotypique, est réhabilité. Sept genres dromiens sont traités de façon détaillée : *Conchoecetes* Stimpson, 1858, *Desmodromia* McLay, 2001, *Epipedodromia* André, 1932, *Fultodromia* McLay, 1993, *Hemisphaerodromia* Barnard, 1954, *Homalodromia* Miers, 1884 et *Pseudodromia* Stimpson, 1858. Sont étudiés en détail les genres *Hypoconcha*, *Sphaerodromia*, *Eodromia* et l'énigmatique genre *Frodromia*. Nous avons privilégié les caractères suivants : organisation du sternum thoracique, morphologie de la spermathèque à l'extrémité de la suture sternale 7/8, de l'uropode, des pléopodes mâles vestigiaux sur les somites abdominaux 3-5, de la coxa du cinquième péréiopode et du pénis. Une clé des familles de Dromiacea et des sous-familles de Dromiidae est fournie.

MOTS CLÉS
Crustacea,
Podotremata,
Dromiidae,
Dromiinae n. status,
Hypoconchinae n. subfam.,
Sphaerodromiinae n. subfam.,
uropode,
sternum thoracique,
spermathèque,
nouvelles sous-familles,
nouveaux genres,
nouvelle espèce,
phylogénie.

INTRODUCTION

With more than 100 species, the Dromiidae de Haan, 1833, or sponge crabs, is the largest family of primitive brachyuran crabs. Dromiids occur in tropical and warm temperate waters worldwide. Five new genera are described, bringing to 38 the total number of dromiid genera recognized in the current paper.

The Dromiidae is currently regarded as part of the monophyletic Brachyura Latreille, 1802. Two major clades are recognized within the Brachyura: 1) the Podotremata Guinot, 1977, containing all crabs with paired spermatheca (Tavares & Secretan 1993; Guinot & Tavares 2001); and 2) the assemblage Heterotremata Guinot, 1977-Thoracotremata (Eubrachyura de Saint Laurent, 1980), which includes all crabs with paired vulvae (Guinot 1977, 1978, 1979a). We consider here the section Podotremata as containing three subsections: the subsection Dromiacea de Haan, 1833, which consists in two superfamilies: Homolodromioidea Alcock, 1900 (one family: Homolodromiidae Alcock, 1900) and Dromioidea de Haan, 1833 (two families: Dromiidae de Haan, 1833 and Dynomenidae Ortmann, 1892); the subsection Homolidea de Haan, 1839 (one superfamily Homoloidea, with three families: Homolidae de Haan, 1839, Latreilliidae Stimpson, 1858, and Poupiniidae Guinot, 1991); the subsection Archaeobrachyura Guinot, 1977 (three families: Cyclodorippidae Ortmann, 1892, Phyllotymolinidae Tavares, 1998, Cymonomidae Bouvier, 1897; and the superfamily Raninoidea de Haan, 1839).

HISTORICAL ACCOUNT

Before the formal establishment of the Brachyura by Latreille (1802), the genus *Dromia* Weber, 1795 (type genus of the Dromiidae; type species: *Cancer personatus* Linnaeus, 1758 by subsequent designation by Holthuis 1962) had appeared in a list along with a number of other crab genera (Weber 1795: 92). When Latreille (1802: 20, 22; 1803: 155, 188, 382; see Dupuis 1986) established the Brachyura, he formally placed *Dromia* within that group. Even when Latreille (1817a: 27) coined the vernacular term "Anomaux" (latinized into Anomalia by Latreille [1817b: 358]; see McLaughlin & Holthuis 1985) to separate the Hippidae Latreille, 1825, Paguridae Latreille, 1802, and Galatheidae Samouelle, 1819 from the Macrura Latreille, 1802, he retained *Dromia* as a part of the Brachyura. Until H. Milne Edwards (1832), the position of the Dromiidae as part of the Brachyura remained unchallenged (e.g., Latreille 1802, 1806, 1817a, b, 1825, 1829; Desmarest 1825; Guérin-Méneville 1832; de Haan 1833). However, H. Milne Edwards (1832: 313, 317, 320, 323, 324) transferred the "dromies" (*Dromia*) to the "Anomoures", and subsequently maintained this same view (H. Milne Edwards 1834-1837). H. Milne Edwards' viewpoint was followed by influential authors such as Lamarck (1838), Dana (1852, 1853), Stimpson (1858), and Henderson (1888), although not by Lucas (1840, 1850). Boas (1880) transferred the Dromiidae back to the Brachyura, and his arguments were adopted by Ortmann (1892), Alcock (1900), Borradaile (1903a, b), Ihle (1913), and Bouvier (1896, 1940), and have since been followed by many carcinologists. For some time, the dromiids and related crabs were named "Brachyura Anomala", as opposed to the "Brachyura genuina" (Alcock 1899; Stebbing 1910).

It should be noted that, in a poorly known paper, H. Milne Edwards (1832) was the first to recognize the basic types of female genital orifices in the Decapoda: 1) gonopore on the coxa of the third pereopod; and 2) gonopore on the thoracic sternite 6, already named "vulve" by Desmarest (1825: 62, 63, pl. 2, fig. 13) (see Latreille 1829: 29; H. Milne Edwards 1832: 304; 1837: 168). Because the Dromiidae and related families share with the Macrura and Anomura the female gonopore on the coxa of the third pereopod, H. Milne Edwards (1832: 304, 305) decided to remove them from the Brachyura where the female gonopore opens on the thoracic sternite 6: "La position des vulves éloigne encore tous les Anomoures, ainsi que les Macroures, du groupe des Brachyures, et ce caractère est si facile à constater, même sur les individus desséchés et conservés dans les collections, qu'il est étonnant que jusqu'ici on y ait fait si peu d'attention". H. Milne Edwards (1832: 327, 331) recognized a "famille naturelle" containing the genera "Ranine, Homole, Dromie et Dynomene". He was the first to give a good definition and key for these genera as forming a coherent group but left it unnamed. This large group corresponds to the Dromiacea, the "Decapodum Brachygnathorum Familia Tertia" of de Haan (1833: ix, x; 1839: 102). The "tribu des Dromiens" of H. Milne Edwards (1837: 168) was restricted to the genera *Dromia* Weber, 1795 and *Dynomene* Guérin-Méneville, 1832, clearly distinct from the "tribu des Homoliens" and "tribu des Raniniens".

H. Milne Edwards (1837: 167) divided the Anomura into two groups: the "Ptérygures" (abdomen with paired mobile uropods) and the "Apterures" (abdomen without biramous uropods). The true anomurans were placed in the Ptérygures, whereas the Dromiidae and their relatives were arranged in the Apterures. Fransen *et al.* (1997: 159) rightly credited the name Anomura to H. Milne Edwards, 1832, and not to MacLeay (1838: 54) who first latinized "Anomoures" into "Anomura". The position of the Dromiidae within the Brachyura has been recently challenged by studies based on molecular data (Spears *et al.* 1992; Spears & Abele 1996; see Martin 2001; Martin & Davis 2001). However, the debate on the relationships of the sponge crabs suffers from the lack of accurate understanding of dromiid morphology, and from insufficient molecular data. Despite being the largest and most diverse family of podotreme crabs, no subfamilial divisions have yet been attempted for the Dromiidae (Borradaile 1903a, b; Ihle 1913; Forest 1974; Lewinsohn 1977, 1979, 1984; McLay 1993, 1998, 2001a, b; McLay *et al.* 2001).

McLay's (1993) recent revision of sponge crabs was a major step towards a comprehensive picture of morphology and systematics of the Dromiidae. Because many genera and species had been poorly defined, McLay's work focused primarily on dromiid diversity. Emphasis on the nature of female sternal sutures 7/8 was abandoned (McLay 1993: 111) and more attention devoted to characters such as carapace ornamentation, arrangement of spines on the legs, specially on the two last pairs, number of abdominal segments, and uropod plates. Altough these criteria are of good use in defining a number of dromiid genera, a comprehensive view of morphology and systematics of the group should include a detailed study of the thoracic sternum. A new view of the Dromiidae will likely emerge when a clear understanding of the dromiid thoracic sternum is achieved.

PRELIMINARY MORPHOLOGICAL CONSIDERATIONS

The female thoracic sternum changes dramatically during ontogeny (Gordon 1950: fig. 23), and the most drastic change refers to the development of the female sternal sutures 7/8 (the "sternal grooves" or "sternal furrows" of earlier authors). Just because a character or a character complex changes during ontogeny is not, in itself, an argument for not using it to define genera (Manning & Holthuis 1981: 15-17; McLay 1993: 122, 150; 2001a: 86); it is evident that morphological comparisons should only be made between fully developed individuals. The generic condition of female sternal sutures 7/8 does not detract their usefulness in the arrangement and reveals to be a way as fruitful as "overall appearance and camouflage-carrying equipment" (McLay 2001a: 86). As a result of the extension of sutures 7/8, the thoracic sternum of adult females appears very much distorted, the sternites 7 and 8 occupying much of the ventral surface of the cephalothorax (Tavares 1994: fig. 37C, D). In many dromiids, the female sternal surface also becomes more complex, owing to the fact that, often, the apertures of spermathecae end apart on (or beneath) two more or less prominent tubercules, or more or less together on (or beneath) a unique tubercle. In many mature females a sperm plug, fixed to a more or less large part of the sternum, has been observed. The presence of a sperm plug, however, does not imply that the second gonopod of the male has not entered the aperture of spermatheca to penetrate for a more internal insemination. When surrounding the spermathecal apertures, the plaque of hardened secretions was sometimes pierced by an opening, probably leaving a passageway to the spermathecae. The displacement of female sutures 7/8 and their terminal apertures to the anterior part of thoracic sternum (see Gordon 1950: 244-247, fig. 23) is not exclusive to the Dromiidae (see Key to families of Dromiacea and subfamilies of Dromiidae, included in this study). A similar forward movement of sutures 7/8 is also encountered in the more advanced podotreme families (Cyclodorippidae Ortmann, 1892, specially in *Neocorycodus* Tavares, 1993, see Tavares 1996: fig. 23D; Cymonomidae Bouvier, 1897, and Phyllotymolinidae Tavares, 1998, see Tavares 1994), but the apertures of spermathecae on the anterior part of sternum correspond to a somewhat different pattern.

In conclusion, all Podotremata are characterized by the presence of paired spermathecae that open independently on the line of sutures 7/8, and the podotreme female thoracic sternum is markedly modified for a sexual function (for the special condition of spermathecal apertures in the Raninoidea, see Hartnoll 1979).

Besides a rather similar podotreme groundplan (with the thoracic sternum essentially exposed by its somites 4-8), diverse patterns are encountered in the Dromiidae. Particular attention has been paid during this study to arrangement of the anterior thoracic sternites. Because sternites 1-3 are extremely narrow, and located at lower plane, they are often concealed. Nevertheless, in some dromiids sternites 1 and 2 are discernible, or, at least in males, only sternite 3 may be exposed and clearly visible dorsally. Sternite 4 shows an array of variations in both sexes. When male abdomen is flexed against ventral surface, either the thoracic sternum is entirely covered by the abdomen, or the thoracic sternum is left partly uncovered anteriorly. In neither case, a part of thoracic sternum between the abdominal margin and the coxae of the pereopods is exposed at level of sternites 5 to 8 (episternite 5 excepted) (Guinot & Tavares 2001). Only some anterior sternal parts, especially sternite 4, including its episternite (episternite 4), remain uncovered, and, in a few cases, also the small episternite 5.

The correct identification of the sternites may be difficult in the Podotremata since the sternal sutures are located only laterally. Because the appendages are articulated on the sternum by their condyles, thoracic sternites are usually located by finding the corresponding appendages. Sometimes it is easier to locate the gynglymes (H. Milne Edwards 1851: 52). The gynglyme (from the Greek, *gyn*: female) is a type of socket hollowed on the sternal surface, more precisely on the episternite, which receives one of the articular condyles (sternal condyle) of the pereopod (Fig. 16); the other condyle (pleural condyle) is articulated on the pleurite of the same metamere.

Ongoing studies on the primitive brachyuran crabs have necessitated a review of the morphological patterns within the Dromiacea (Homolodromiidae, Dynomenidae, and Dromiidae). As far as the Dromiidae are concerned, it was found that the current classification does not reflect the wealth of morphological patterns found within the family. In the literature the dromiacean uropod, for example, is always described by the simplistic expression of "vestigial", without taking into account whether the uropod shows as a ventral plate (Homolodromiidae, Dromiidae *pro parte*), a dorsal plate (Dynomenidae, Dromiidae *pro parte*) (see Guinot & Tavares 2001: fig. 15), or, rarely, is lost. Because the dromiid uropod is so diverse, emphasis is here given to its character states (see Patterns of uropods and vestigial male pleopods 3-5, and Table 1), all the more since the dorsal plate is very often used to hold the immature female and male abdomens, while the ventral plate does not fill any apparent function.

The study of the coxa of the fifth pereopod in the male, with its gonopore and penis, generally overlooked in the Decapoda, have received particular attention here and led to the recognition of two main dromiid patterns (see Patterns of P5 coxa and penis). The condition of the female gonopore on the coxa of third pereopod has not been specified. It may show as occluded or perforated, probably in relation to the moult which seems usual before mating in the female dromiids (see Gordon 1950: 245; Hartnoll 1975: 669).

NEW PROPOSALS

A preliminary subfamilial division for the Dromiidae is proposed herein. Three subfamilies are recognized: Dromiinae de Haan, 1833 n. status, Hypoconchinae n. subfam., and Sphaerodromiinae n. subfam. The new subfamilial system is largely based upon the organization of the thoracic sternum, the male abdomen, the morphological relationship between thoracic sternum and abdomen, the uropods and their role in holding of abdomen, the male coxa of P5 and penis, the female thoracic sternal sutures 7/8, the apertures of spermathecae, and the condition (if known) of all the abdominal appendages including vestigial male pleopods and uropods. All descriptions, generic comparisons, and illustrations concentrate on the ventral surface of the body. The tomentum has not been described nor figured, and, by stating "thoracic sternite 4 visible dorsally", we do not refer to its possible concealment by setae.

The reappraisal of several species has necessitated a strict delineation of a number of genera (they are indicated "sensu nobis" in the present paper), and the establishment of five new ones:

1) *Dromidia* Stimpson, 1858 and *Cryptodromiopsis* Borradaile, 1903 are redefined on the basis of their type species, *D. hirsutissima* (Lamarck, 1818) and *Cryptodromiopsis tridens* Borradaile, 1903, respectively. As a result, several species formerly described in or transferred to *Dromidia* or *Cryptodromiopsis*, are removed from *Dromidia* sensu nobis and from *Cryptodromiopsis* sensu nobis. They are as follows:

– *Dromidia spongiosa* Stimpson, 1858 is assigned to *Platydromia* Brocchi, 1877, which is resurrected to accomodate it.

– *Dromidia antillensis* Stimpson, 1858 and *D. sarraburei* Rathbun, 1910 are transferred to *Moreiradromia* n. gen.

– *Dromia unidentata* Rüppell, 1830, transferred by Kossmann (1880) to *Dromidia* and later by McLay (1993) to *Cryptodromiopsis*, becomes the type species of *Lewindromia* n. gen.

2) *Dromidiopsis* Borradaile, 1900 is redefined on the basis of its type species, *D. australiensis* (Haswell, 1882).

– *Dromidiopsis globosa* (Lamarck, 1818), previously *Dromia globosa* Lamarck, 1818, becomes the type species of *Lamarckdromia* n. gen.

– *Dromidiopsis dubia* Lewinsohn, 1984 is herein placed in *Mclaydromia* n. gen. A new species, *M. colini* n. gen., n. sp., is described.

– *Dromidiopsis plumosa* Lewinsohn, 1984, originally placed questionably in *Dromidiopsis* and later transferred by McLay (1991) to *Dromidia*, and then by McLay (1993, 2001a) to *Cryptodromiopsis*, becomes the type species of *Stebbingdromia* n. gen.

In adopting the same way than McLay (1993) the generic names are formed by combining the name of a person with *Dromia*.

The examination of extensive material, generally including the type species, was necessary to clear up a number of systematic uncertainties. This has allowed a redefinition of other genera, as follows: *Austrodromidia* McLay, 1993; *Conchoecetes* Stimpson, 1858; *Eodromia* McLay, 1993; *Epipedodromia* André, 1932; *Frodromia* McLay, 1993; *Fultodromia* McLay, 1993; *Hemisphaerodromia* Barnard, 1954; *Homalodromia* Miers, 1884; *Hypoconcha* Guérin-Méneville, 1854; *Pseudodromia* Stimpson, 1858; and *Sphaerodromia* Alcock, 1899. A few genera and species are in need of review, for example the large and heterogeneous *Dromia* Weber, 1795, and some poorly known monotypic, endemic genera to southern Australia and southern Africa. Some synonymies are restricted. A key to separate the families of the Dromiacea and subfamilies of the Dromiidae is provided.

ABBREVIATIONS

G1	first male pleopod or gonopod;
G2	second male pleopod or gonopod;
mxp3	third maxilliped;
P1-P5	first to fifth pereopods;
Pl3-Pl5	third to fifth pleopods;
AM	Australian Museum, Sydney;
BM	The Natural History Museum (ex British Museum [Natural History]), London;
EMU	Estación Mazatlán, Universidad Nacional Autónoma, México;
MNHN	Muséum national d'Histoire naturelle, Paris;
QM	Queensland Museum, Brisbane;
RMNH	Nationaal Natuurhistorisch Museum, Leiden;
ZRC	National University of Singapore, Raffles Museum, Zoological Reference Collection.

Descriptive terminology essentially follows that of McLay (1993). Measurements of carapace length × carapace width are given in millimeters (mm). Most material used in this study is deposited at the MNHN. Other specimens came from various institutions.

SYSTEMATICS

Section PODOTREMATA Guinot, 1977
Subsection DROMIACEA de Haan, 1833
Superfamily DROMIOIDEA de Haan, 1833
Family DROMIIDAE de Haan, 1833

Subfamily DROMIINAE de Haan, 1833 n. status

Dromies H. Milne Edwards, 1832: 302, *sq.*

Dromiacea de Haan, 1833 *pro parte*: ix, x; 1839 *pro parte*: 102.

Dromiens – H. Milne Edwards 1837 *pro parte*: 167, 168.

Dromites – Lucas 1840 *pro parte*: 112.

Dromiidae – Ortmann 1892: 541, 543. — Barnard 1950: 306. — Holthuis 1962: 56. — Manning & Holthuis 1981: 11 [Name 356 on Official List]. — McLay 1993 *pro parte*: 111-251. — Guinot *et al.* 1994: 255, fig. 7. — Hendrickx 1995 *pro parte*: 127. — Ng 1998: 1056, 1063, 1085. — Ng *et al.* 2000 *pro parte*: 156; 2001 *pro parte*: 5. — Melo & Campos 1999 *pro parte*: 274. — Martin & Davis 2001 *pro parte*: 49, 74. — Chen & Haibao 2002 *pro parte*: 73, 541.

TYPE GENUS. — *Dromia* Weber, 1795 (type species: *Cancer personatus* Linnaeus, 1758 by subsequent designation under the Plenary Powers of the International Commission on Zoological Nomenclature, Opinion 688, see Holthuis 1962). Name 1568 on Official List.

GENERA INCLUDED. — *Ascidiophilus* Richters, 1880; *Alainodromia* McLay, 1998; *Austrodromidia* McLay, 1993; *Barnardromia* McLay, 1993; *Conchoecetes* Stimpson, 1858; *Cryptodromia* Stimpson, 1858; *Cryptodromiopsis* Borradaile, 1903; *Desmodromia* McLay, 2001; *Dromia* Weber, 1795; *Dromidia* Stimpson, 1858; *Dromidiopsis* Borradaile, 1900; *Epigodromia* McLay, 1993; *Epipedodromia* André, 1932; *Eudromidia* Barnard, 1947; *Exodromidia* Stebbing, 1905; *Fultodromia* McLay, 1993; *Haledromia* McLay, 1993; *Hemisphaerodromia* Barnard, 1954; *Homalodromia* Miers, 1884; *Lamarckdromia* n. gen.; *Lauridromia* McLay, 1993; *Lewindromia* n. gen.; *Mclaydromia* n. gen.; *Moreiradromia* n. gen.; *Paradromia* Balss, 1921; *Petalomera* Stimpson, 1858; *Platydromia* Brocchi, 1877; *Pseudodromia* Stimpson, 1858; *Speodromia* Barnard, 1947; *Stebbingdromia* n. gen. (uncertain status); *Sternodromia* Forest, 1974; *Stimdromia* McLay, 1993; *Takedromia* McLay, 1993; *Tunedromia* McLay, 1993.

DESCRIPTION

Carapace varying from longer than wide, as wide as long to much wider than long; convex, clearly subdivided into anterior and posterior portions; dorsal regions rather well-defined and variously ornamented; lateral margins usually rounded. Front variously shaped, often with median rostrum and two pseudorostral teeth, one at each side of rostrum. Supra- and infraorbital margins usually toothed and separated from each other by deep notch. Orbits small, rather circular, oriented more or less horizontally. Ocular stalk rather short, more or less thick, diversely shaped. Thoracic sternum narrow. Gynglymes of thoracic sternites 1-3 largely spaced from each other, situated at lower plane. Sternite 4 forming plate in contact with bases of the mxp3 or separated from mxp3 by sternite 3 when exposed. Episternites 4 and 5 more or less narrow, with gynglymes of P1 and P2 in almost terminal location. Female sternal sutures 7/8 long (except *Stebbingdromia* n. gen.), and apertures of spermathecae opening into thoracic sternum far beyond level of coxa of P3 (except *Stebbingdromia* n. gen.), apart or together, on two tubercules or on central prominence; apertures usually showing as minute pores at extremities of sutures 7/8, exceptionally as slits (*Sternodromia*). Anterior part of thoracic sternite 4 and episternites 4 and 5 either completely covered or left diversely uncovered by male abdomen when folded. Deep sterno-coxal depressions usually present. Male abdomen length variable, when flexed attaining the coxa of mxp3 or diverse levels of the P1 coxa. Male abdomen generally narrow, often without pleural parts recognizable, or sometimes broader; all segments free (exceptionally segment 5 and 6 more or less fused), segment 6 not noticeably extended laterally. Male Pl3-Pl5 usually absent, but sometimes vestigial. In males and immature females, uropods showing as salient calcified dorsal plates, often playing role in abdominal holding, or as ventral plates or lobes (see Patterns of uropods and vestigial male pleopods 3-5). Mature female uropods generally more horizontal, not so salient. Male telson usually short, variously shaped. Holding of male and immature female abdomens variable, usually efficient, a variable number of pereopods being involved. Chelipeds with or without epipod; podobranch absent. P2 and P3 often lobed or nodose; propodus short, lacking distal propodal spine (except *Stebbingdromia* n. gen.); dactylus curved and armed with spines on inner border. P4 and P5 reduced, similar in size and shape (rare exception: *Conchoecetes*), shorter than preceding ones, oriented subdorsally (P4) or dorsally (P5), prehensile; subcheliform apparatus present on propodus and dactylus and formed by variable number of spines, varying from multiple to only one, sometimes without opposing propodal spines. Male P5 coxa unmodified; penis emerging as long and mobile calcified tube ("penial tube") (see Patterns of P5 coxa and penis). G2 long, with long, styliform and needle-like flagellum (except *Stebbingdromia* n. gen.), without exopod.

Carrying behaviour

Sponges, compound or solitary ascidians, soft coral or actinians occasionally, bivalve shells rarely (see discussion under Shell-carrying behaviour), fragments of weed. Some dromiine members (*Epigodromia*, *Takedromia*), with small last pereopods, are not known to carry any camouflage (Wicksten 1986a: 364; McLay 1993: 213, 216, 219, 224; 2001b: 7; Guinot *et al.* 1995: 385, 401; Ng *et al.* 2000: 157).

REMARKS

The following four dromiid genera have not been included in the Dromiinae n. status: *Hypoconcha* Guérin-Méneville, 1854 referred to Hypoconchinae n. subfam. (see Hypoconchinae n. subfam.); and *Eodromia* McLay, 1993 and *Sphaerodromia* Alcock, 1899, referred to Sphaerodromiinae n. subfam. (see Sphaerodromiinae n. subfam.); the subfamilial status of *Frodromia* McLay, 1993 needs a re-appreciation.

A total of 34 genera are herein included in the subfamily Dromiinae. The present list of dromiid genera should be regarded as provisional, and further adjustements and emendations might be necessary. For example, the large genus *Dromia*, as currently defined (McLay 1993: 149, table 2), appears to be composite, and we regard it as *Dromia* s.l. We consider *Sternodromia* valid.

Genus *Austrodromidia* McLay, 1993 sensu nobis
(Figs 1; 2)

Dromia – Haswell 1882a *pro parte*: 755; 1882b *pro parte*: 139, 140. (Non *Dromia* Weber, 1795).

Dromidiopsis – Ihle 1913 *pro parte*: 25. (Non *Dromidiopsis* Borradaile, 1900).

Dromidia – Rathbun 1923a: 147. — Griffin 1972: 52. (Non *Dromidia* Stimpson, 1858).

Cryptodromia – Rathbun 1923a: 151. — Hale 1925: 406; 1927: 107. — Griffin 1972: 53. (Non *Cryptodromia* Stimpson, 1858).

Austrodromidia McLay, 1993 ?*pro parte*: 125, 185, 186, table 6. — McLay *et al.* 2001 *pro parte*: 733, 740, 743, table 2.

TYPE SPECIES. — *Dromidia australis* Rathbun, 1923 by original designation (McLay 1993: 185). Gender: feminine.

SPECIES INCLUDED. — *Dromidia australis* Rathbun, 1923; *Dromia octodentata* Haswell, 1882.
Cryptodromia incisa Henderson, 1888, from Australia and Japan, and *Dromidia insignis* Rathbun, 1923, from Australia, assigned to *Austrodromidia* by McLay (1993: 185), were not available for study. Whether or not they belong to *Austrodromidia* deserves further investigation.

DISTRIBUTION. — Australia.

DESCRIPTION

Carapace slightly wider than long, convex; dorsal surface with regions not well-defined; branchial groove marked. Anterolateral margin beginning at orbital level, armed with several teeth; posterolateral margins toothed, not markedly convergent posteriorly. Front narrow, appearing tridentate, rostral tooth deflexed, two pseudorostral teeth; supraorbital, suborbital and exorbital teeth well-developed. Exopod of antennal basal article thickly developed, directed downwards, internal corner strongly produced. Mxp3: coxae with

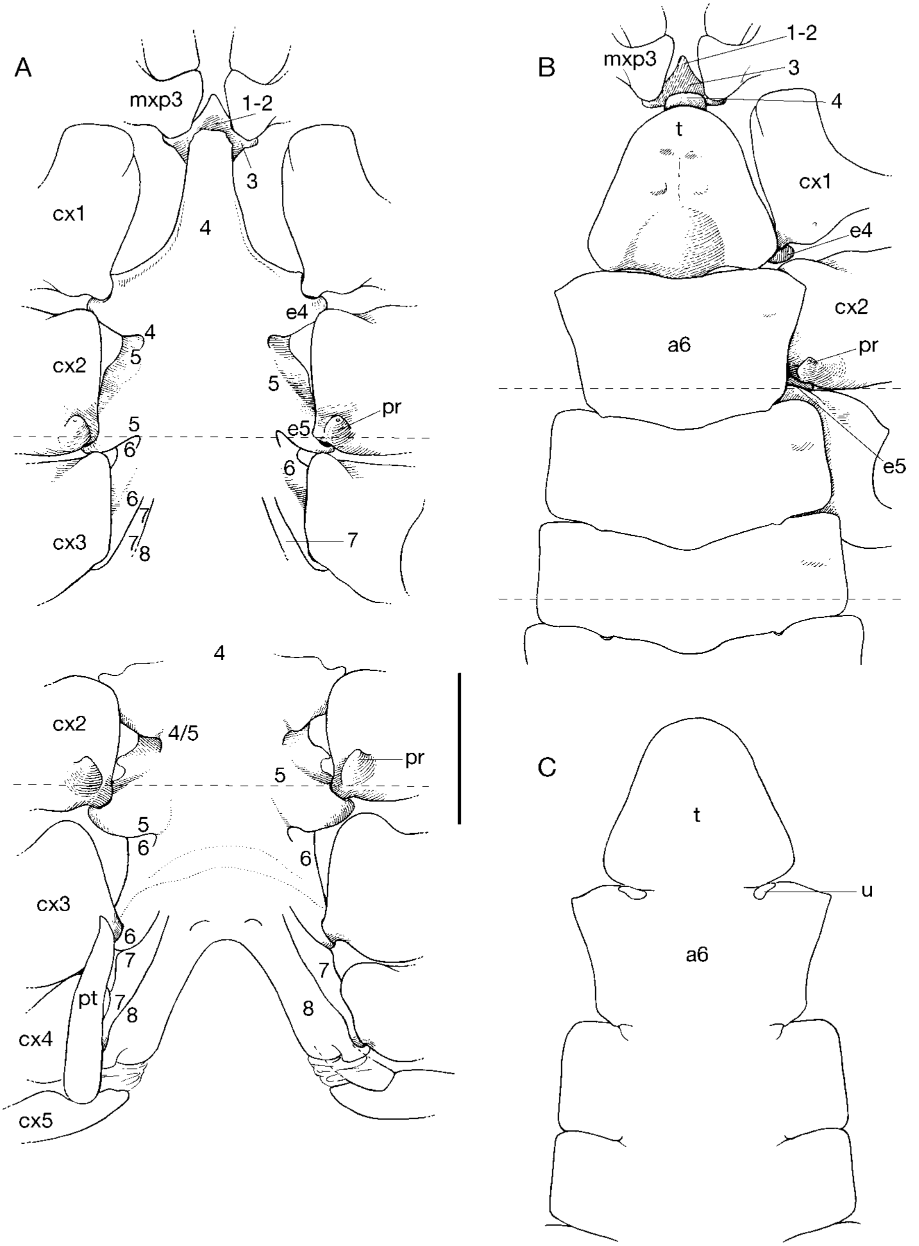

FIG. 1. — *Austrodromidia australis* (Rathbun, 1923), New South Wales, off Eden, *Goonambee*, 1922, ♂ 29.5 × 33 mm (AM P5777); **A**, thoracic sternum, two front views; **B**, abdomen, dorsal view; **C**, abdomen, ventral view; note uropods showing as very narrow ventral plates. Abbreviations: **a6**, abdominal segment 6; **cx1-cx5**, coxae of P1-P5; **e4**, **e5**, épisternites 4, 5; **mxp3**, external maxilliped; **pr**, holding prominence; **pt**, penial tube; **t**, telson; **u**, uropod; **1-2**, sternites 1-2; **3-8**, sternites 3-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bar: 5 mm.

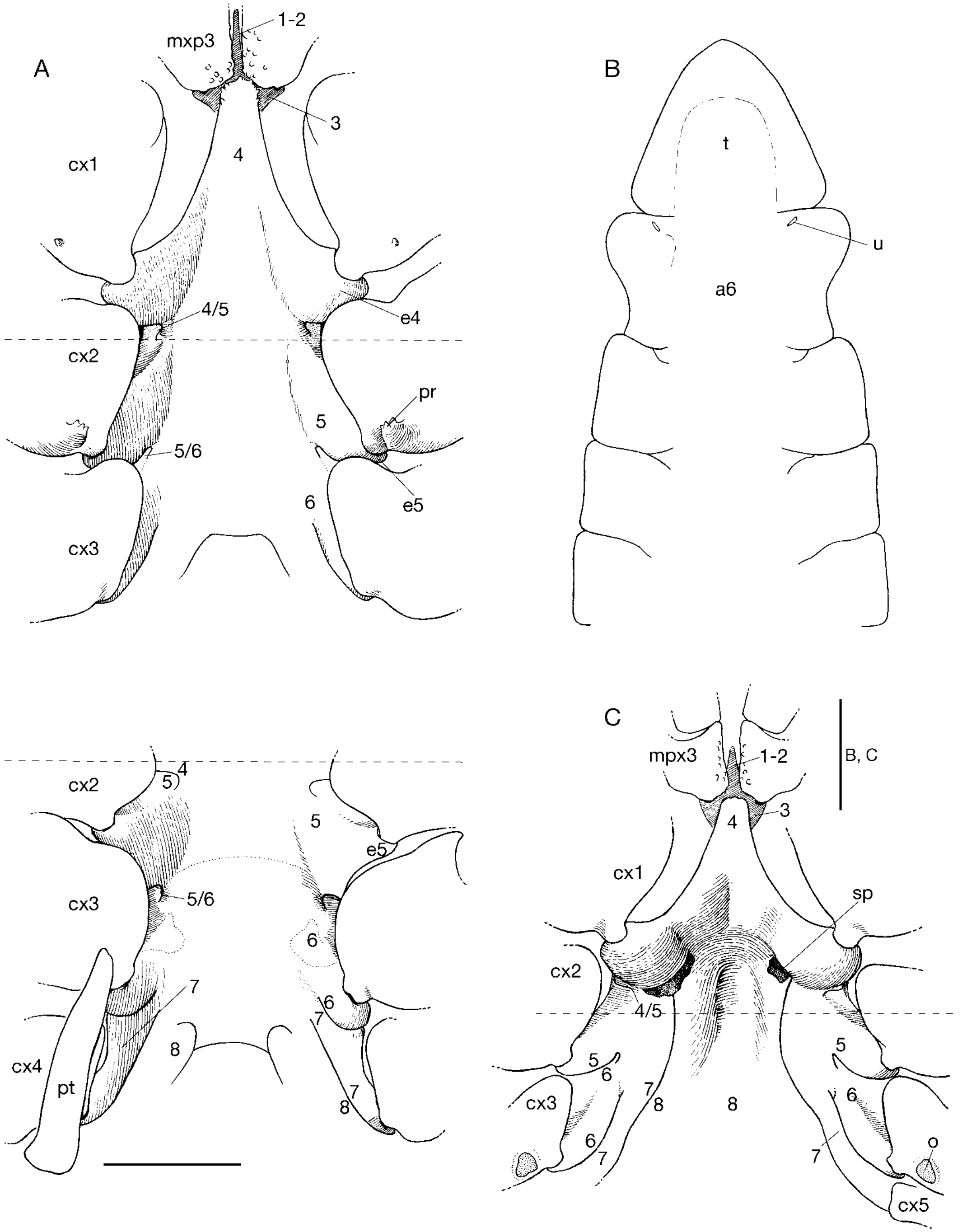

FIG. 2. — *Austrodromidia octodentata* (Haswell, 1882), South Australia, Kangaroo Island, *Endeavour*, Rathbun det. *Cryptodromia octodentata*; **A**, **B**, ♂ 39 × 42 mm (AM E. 801); **A**, thoracic sternum, two front views; **B**, abdomen, ventral view; note uropods reduced to nearly obsolete buds; **C**, ♀ 44 × 46 mm (AM P. P2311), thoracic sternum and apertures of spermathecae, covered with spermatic plug. Abbreviations: **a6**, abdominal segment 6; **cx1**-**cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **mxp3**, external maxilliped; **o**, female gonopore; **pr**, holding prominence; **pt**, penial tube; **sp**, spermatic plug; **t**, telson; **u**, uropod; **1-2**, sternites 1-2; **3-8**, sternites 3-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 5 mm.

(*A. australis*) or without (*A. octodentata*) narrow gap between them.

Thoracic sternites 1-3 clearly (*A. australis*, Fig. 1A, B) or weakly (*A. octodentata*, Fig. 2A, C) visible. Male thoracic sternite 4 markedly narrowing anteriorly, with anterior margin truncate. Female sternal sutures 7/8 rather long, ending at level of P2; apertures of spermathecae wide apart between P2, beneath very prominent episternites 4 (Fig. 2C). Sternite 3 remaining exposed when male abdomen is applied against ventral surface; sternite 4 almost completely covered; episternite 4 and episternite 5 exposed.

Male abdomen with all segments free, completely covering most of sterno-abdominal depression; telson bluntly triangular or rounded, almost reaching mxp3, its base enlarged; pleural parts visible. Male segment 6 with external borders deeply hollowed (but not thickened) in anterior part, and broadly expanded in posterior part. Males without vestigial pleopods. Male uropods as ventral lobes, small and narrow (*A. australis*), or inconspicuous, or nearly obsolete (*A. octodentata*). Uropods not involved in holding of abdomen. Abdomen hold folded by sharp or cristiform prominence on P2 coxa. Female uropods indistinct.

Chelipeds without epipod. P2 and P3 short, not knobbed; propodus without distal spine; inner margin of dactylus armed with spines. P4 and P5 reduced; P5 longer and slender, propodus short and broad; P4 carrying terminal apparatus formed by two distal propodal spines opposing curved dactylus; P5 terminal apparatus formed by one distal propodal spine opposing dactylus; a long spine on outer margin of dactylus.

Male P5 coxa with mobile penial tube (Figs 1A; 2A).

Carrying behaviour

Sponges, ascidians, "marine growths, including two species of plants", "fragments of weed or large shell" (Hale 1925: 406, pl. 40A; 1927: 108, 109); see discussion under Discussion, Shell-carrying behaviour.

REMARKS

In *Austrodromidia* the uropods have been reported as "reduced and concealed or absent" and the female sternal sutures 7/8 as ending together between P2 (McLay 1993: 185, 186, table 6). These structures, however, have not been previously described or figured in detail, even in the type species *A. australis* (Rathbun 1923a: 147) (see Hale 1927: 106; Griffin 1972: 52 as *Dromidia australis*). The examination of a male of *A. australis* (AM P. 5777) revealed two very small but distinct ventral plates hidden under the setae that cover the foliaceous posterior part of ventral surface of segment 6, and not visible dorsally (Fig. 1B, C). In *A. octodentata* (Fig. 2B, C) the male uropods are even more rudimentary, reduced to nearly obsolete buds. These buds are easily overlooked and have been interpreted as "absent" (McLay 1993). In *A. octodentata*, however, the bud is found exactly in the same location where an uropod should be. In *A. australis* the uropods are reduced to small plates. The uropods are indistinct in the females of *A. octodentata*. We had no access to females of *A. australis* and therefore its uropod condition remains unconfirmed. Rathbun's (1923a: 148) descriptions of the sternal sutures 7/8 of *A. australis* (as *Dromidia australis*) are also not accurate. We suspect that *A. australis* and *A. octodentata* (Fig. 2C) share a similar condition in this regard, i.e. sutures 7/8 end apart instead of ending together.

Austrodromidia octodentata, one of the largest Australian sponge crabs, is known to have direct development and brood its young, the abdomen forming a pouch for the young crabs (Hale 1927: 109, figs 104, 105). A colour photograph of a specimen from South Australia carrying a colourful colonial ascidian is given by Debelius (1999: 249 as *Cryptodromia octodentata*).

The status of *Cancer aegagropila* Fabricius, 1787, described supposedly from Australia and synonym of *Dromia australiasae* Weber, 1795 (*nomen nudum*) (see Holthuis 1962), needs further investigation.

Genus *Conchoecetes* Stimpson, 1858
(Fig. 3)

Dromia – Fabricius 1798 *pro parte*: 360. — Haswell 1882b *pro parte*: 141. (Non *Dromia* Weber, 1795).

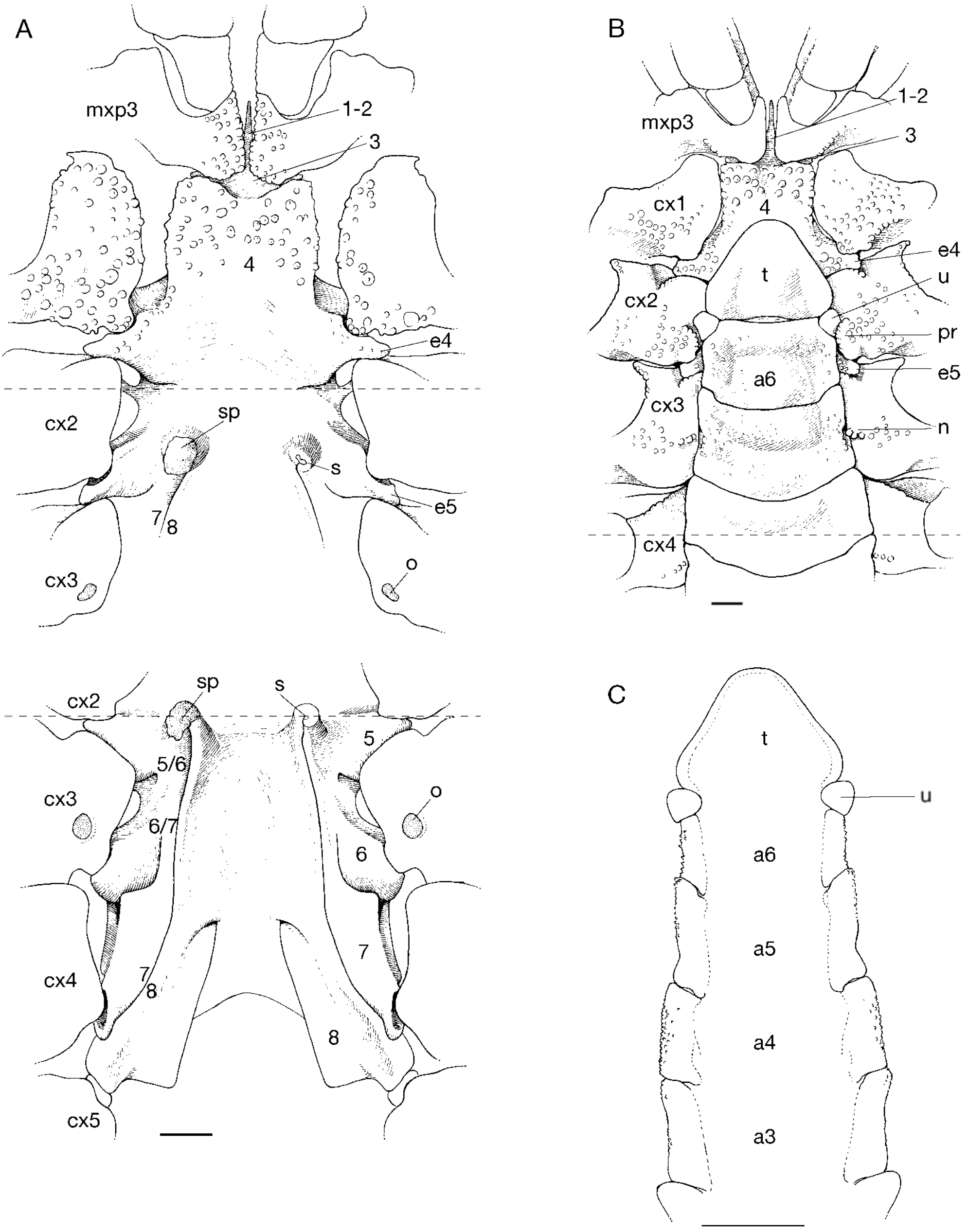

FIG. 3. — **A**, *Conchoecetes artificiosus* (Fabricius, 1798), Madagascar, Nosy-Bé, ♀ 23 × 22 mm (MNHN-B 6890), thoracic sternum, two front views, and spermathecae; **B**, **C**, *Conchoecetes intermedius* Lewinsohn, 1984; **B**, Madagascar, ♂ 16 × 17 mm, holotype (MNHN-B 6891), thoracic sternum with abdomen; **C**, Moluccas, ♂ 9 × 9 mm (MNHN-B 15890), abdomen, ventral view; note absence of vestigial pleopods. Abbreviations: **a3**-**a6**, abdominal segments 3-6; **cx1**-**cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **mxp3**, external maxilliped (coxae separated for clarity); **n**, notch on margin of abdominal segment 5; **o**, female gonopore; **pr**, holding prominence; **s**, aperture of spermatheca; **sp**, sperm plug; **t**, telson; **u**, uropod; **1**-**2**, sternites 1-2 (normally covered by mxp3 coxae, closely approximated); **3**-**8**, sternites 3-8; **4/5**-**7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 1 mm.

Conchoecetes Stimpson, 1858: 266; 1907: 180. — Henderson 1893: 407. — Alcock 1900: 150; 1901: 40. — Borradaile 1903a: 301. — Ihle 1913: 50. — Chopra 1934: 478. — T. Sakai 1936: 41; 1976: 26. — Barnard 1950: 308. — Lewinsohn 1984: 119. — Dai & Yang 1991: 30. — Tirmizi & Kazmi 1991: 14. — McLay 1993: 123, 174, table 5; 2001b: 8. — Guinot & Bouchard 1998: 621, 622. — Guinot & Tavares 2000: 301. — Ng *et al.* 2000: 156-159. — McLay *et al.* 2001: 743, table 2. — Chen & Haibao 2002: 73, 97, 540.

Conchoedromia Chopra, 1934: 477 (type species: *Conchoedromia alcocki* Chopra, 1934 by original designation; gender: feminine).

TYPE SPECIES. — *Dromia artificiosa* Fabricius, 1798 by monotypy. Gender: masculine.

SPECIES INCLUDED. — *Conchoecetes andamanicus* Alcock, 1900; *Dromia artificiosa* Fabricius, 1798; *Conchoecetes intermedius* Lewinsohn, 1984.
Conchoecetes canaliculatus Yang & Dai, 1994 was regarded as a probable junior synonym of *C. intermedius* by Ng *et al.* (2000).

DISTRIBUTION. — Indo-West Pacific.

DESCRIPTION

Carapace as long as wide or slightly wider than long, subpentagonal. Dorsal surface flattened, sometimes partly membranous, with some regions defined; cervical and branchial grooves distinct. Anterolateral margin long, unarmed or with small teeth only; posterolateral margins with or without tooth, straight or convergent posteriorly. Front narrow, with three subequal teeth, the deflexed rostral tooth and two pseudorostral teeth; supraorbital tooth small; suborbital and exorbital teeth not marked. Antenna: urinal article relatively narrow, widening towards beak-like part; anterior part of beak narrow, acute, posterior part rounded; exopod of basal article well-developed, with internal corner acutely produced and curved. Orbits rounded; ocular stalks short, eyes large. Mxp3: coxae closely approximated.

Thoracic sternite 3 partly visible dorsally in both sexes (sternites 1-2 concealed) (Fig. 3A, B). Thoracic sternite 4 broad, with anterior margin truncate. Female sternal sutures 7/8 separated wide apart; apertures of spermathecae ending apart on two raised tubercles placed between P2 (Fig. 3A). In males, sternite 4 and episternites 4 and 5 remaining exposed when male abdomen applied against ventral surface. Posterior sternites tilted backwards.

Male abdomen with all segments free, not completely covering sterno-abdominal depression; telson rounded at tip. Male segment 6 with subparallel external borders. Vestigial pleopods absent in males (papillae on segment 3 may be present, to be verified) (Fig. 3C). Uropods (Fig. 3B, C) showing as salient dorsal plates, involved in holding of abdomen, and acting together with strong and ornamented prominence on P2 coxa; episternite 5 with some granules; P3 coxa with rounded tubercle matching notch on lateral margin of abdominal segment 5; granule on P4 coxae similar to that on P3, perhaps too small to be efficient.

Chelipeds with epipod; P1-P3 with some nodosities or tubercles. Propodus of P2 and P3 without distal spine. P4 and P5 very dissimilar in position, size and shape, and with grasping system to hold bivalve shell. P4 noticeably heavy, ending in thick propodus and in long curved dactylus; posterior border of propodus bearing hollow, socket-like projection, with mobile process. P5 small and ending in simple, upturned dactylus.

Male P5 coxa with mobile penial tube.

Carrying behaviour

Exclusively involving bivalve shells (Nishimura 1987: pl. M4; Ng *et al.* 2000: fig. 1b). See under Discussion, Shell-carrying behaviour.

REMARKS

The case of *Cancer mutus* Linnaeus, 1758 (p. 625), described with a smooth and anteriorly truncated carapace and with a brown anterior border, and for which the indication "? Mediterranea" could be erroneous, is interesting. The type specimen(s) is (are) no longer extant. The name was subsequently used by Herbst (1783: 116), who listed the species, but without any figure. The species was then forgotten until the name was used again by K. Sakai (1999), this time for a dromiid. Sakai (1999: pl. 4, fig. F) figured a specimen found in the Berlin Museum which had been identified and labelled by Herbst as "*Conchoecetes mutus* Linnaeus, 1758". The specimen figured by Sakai corresponds to a

Conchoecetes species (*C. intermedius*), whereas the characters noted by Linnaeus are that of a trapeziid crab, probably *Tetralia* Dana, 1851 (or *Tetraloides* Galil, 1986) (P. Castro and P. K. L. Ng pers. comm.).

McLay (1993, 2001b) and McLay *et al.* (2001) argued for the close relationships between *Conchoecetes* and *Hypoconcha*, mostly based on the special condition of P4 and P5, the obligate shell-carrying behaviour, and the similarities in larval and postlarval development. For a comparison of the specialized morphological features that allow the two genera to grasp a shell, see Guinot & Tavares (2000: figs 4, 5). The systematic position of *Conchoecetes* is discussed under Hypoconchinae n. subfam.

The precise condition of the vestigial pleopods, suspected to be absent, needs to be verified.

The development of *Conchoecetes* only includes two zoeal stages and the megalopa (Sankolli & Shenoy 1968; see McLay *et al.* 2001: 740, 744, table 1).

Genus *Cryptodromiopsis* Borradaile, 1903 sensu nobis
(Fig. 4)

Cryptodromiopsis Borradaile, 1903a: 299, 302; 1903b: 578. — Tweedie 1950: 106. — McLay 1991 *pro parte*: 467, 469; 1993 *pro parte*: 187, table 6; 2001a *pro parte*: 84.

Dromidia – Lewinsohn 1979 *pro parte*: 3. (Non *Dromidia* Stimpson, 1858).

TYPE SPECIES. — *Cryptodromiopsis tridens* Borradaile, 1903 by monotypy (senior synonym of *Dromidia fenestrata* Lewinsohn, 1979). Gender: feminine.

SPECIES INCLUDED. — *Cryptodromiopsis tridens* Borradaile, 1903.

DISTRIBUTION. — Indo-West Pacific.

DESCRIPTION

Carapace distinctly wider than long, convex; dorsal surface with regions not well-defined; branchial groove quite distinct. Anterolateral margin toothed; posterolateral margins without tooth, and not markedly convergent posteriorly. Front narrow, appearing tridentate, rostral tooth long and deflexed, two pseudorostral teeth weaker; border joining rostrum and supraorbital tooth, which is wide apart, uninterrupted, eave-like; suborbital and exorbital teeth well-developed. Proepistome developed, raised. Subhepatic area convex, prominent dorsally. Antenna: urinal article upturned, with urinal opening placed above axis of urinal article, and very narrow, widening towards beak-like part; basal article much enlarged and touching front on both corners; exopod very developed and with internal corner so produced that article 4 is completely or almost included. Mxp3: coxae separated by gap.

Thoracic sternite 1-2 discernible; sternite 3 visible dorsally as a short triangular plate. Male thoracic sternite 4 with external borders oblique. Female sternal sutures 7/8 long, separated wide apart proximally, but abruptly joined at level of P2; apertures of spermathecae ending together on slight tubercle between chelipeds. When male abdomen applied against ventral surface, sternites 1-3 and extreme anterior part of sternite 4 (with episternite 4) remaining visible.

Male abdomen with all segments free, not completely covering sterno-abdominal depression; no pleural parts discernible; telson broadly triangular. Male segment 6 with external borders subparallel on anterior half. No vestigial pleopods in males. Uropods showing as salient dorsal plates, obliquely oriented, very mobile. Abdominal holding by granulous crest on P2 coxae, far from uropods (Fig. 4A, B).

Chelipeds without epipod, and of moderate size, knobbed; fingers gaping, prehensile margin of fixed finger markedly concave; both cutting margins without proximal teeth, only armed with interlocking distal teeth. P2 and P3 short, knobbed; propodus without distal spine; inner margin of dactylus armed with spines. P4 and P5 reduced, P5 longer and more slender. P4 and P5 carrying terminal apparatus formed mostly by one distal propodal spine opposing curved dactylus which ends in horny spine; a stout outer propodal spine. P5 dactylus with spine on outer margin.

G1 with setose apex, armed with sharp tubercle. G2 with thin, needle-like, long flagellum, not overreaching sterno-abdominal depression.

Male P5 coxa with mobile penial tube (Fig. 4B).

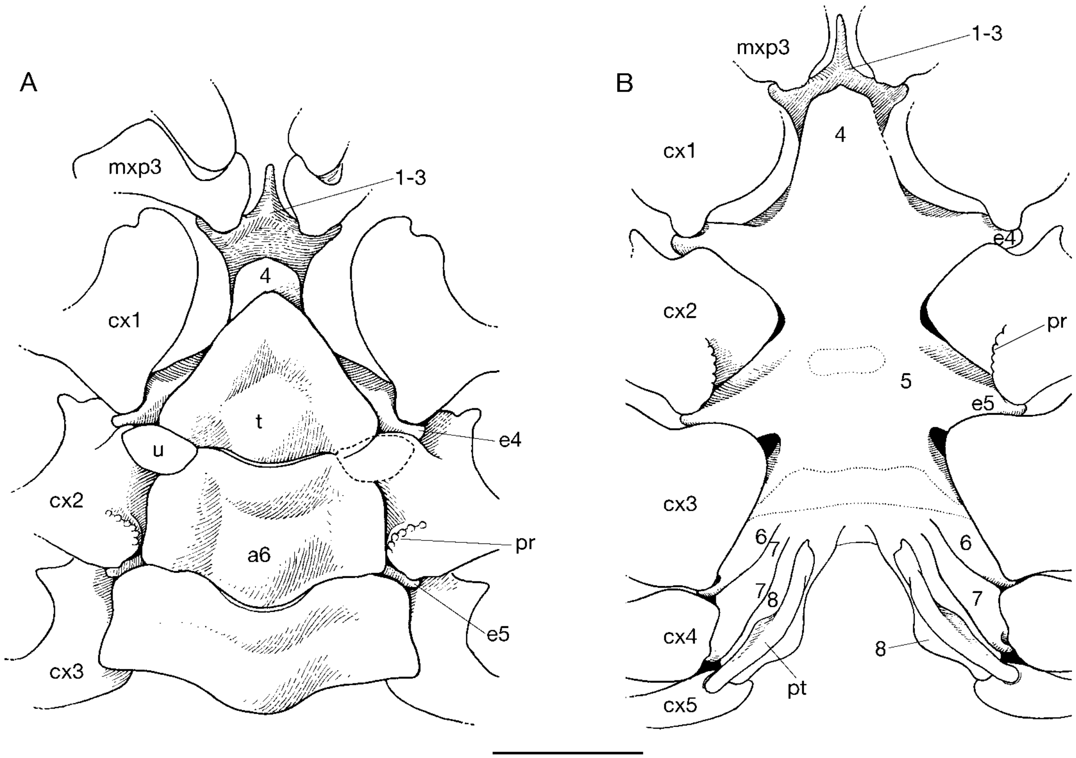

FIG. 4. — *Cryptodromiopsis tridens* Borradaile, 1903, Polynesia, Moorea, 1979, C. Bouchon coll., ♂ 6.2 × 7.5 mm (MNHN-B 22579); thoracic sternum with (**A**) and without (**B**) abdomen. Abbreviations: **a6**, abdominal segment 6; **cx1-cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **mxp3**, external maxilliped; **pr**, holding prominence; **pt**, penial tube; **t**, telson; **u**, uropod; **1-3**, sternites 1-3; **4-8**, sternites 4-8; **6/7-7/8**, thoracic sternal sutures 6/7-7/8. Scale bar: 1 mm.

Carrying behaviour

Sponges, compound ascidians.

REMARKS

Borradaile (1903a: 299, 302; see 1903b: 578) erected *Cryptodromiopsis* mostly to separate from *Cryptodromia* Stimpson, 1858 (type species: *C. coronata* Stimpson, 1858 by original designation) those species with female sternal sutures 7/8 ending together (i.e. converging), in contrast to wide apart in *Cryptodromia.*

While studying specimens of *Cryptodromiopsis tridens* from French Polynesia, McLay (1991: 467-470, fig. 5) remarked that at that time the species included in *Cryptodromiopsis* did "not make a natural group, having very little in common with each other". More recently, however, McLay (2001a: 84) maintained that "the genus contains six species for certain", which is the number of species included in his (McLay 1993: 187, table 6) previous definition of *Cryptodromiopsis.*

The examination of several species presently included in *Cryptodromiopsis* led to the conclusion that the genus is indeed a composite one. The following species are now being removed from *Cryptodromiopsis* sensu nobis: 1) *C. unidentata* (Rüppell, 1830) transferred to *Lewindromia* n. gen.; 2) *C. antillensis* (Stimpson, 1858) and *C. sarraburei* (Rathbun, 1910) transferred to *Moreiradromia* n. gen.; and 3) *C. plumosa* (Lewinsohn, 1984) transferred to *Stebbingdromia* n. gen.

For the time being, *Dromia* (*Cryptodromia*) *bullifera* Alcock, 1900 is perhaps better placed in *Cryptodromia.*

The two Chinese species *Cryptodromiopsis dubia* Dai, Yang, Song & Chen, 1981 and *C. planaria* Dai, Yang, Song & Chen, 1981 were not examined. Their status was suggested as doubtful by McLay (1993: 187). The male abdomen of *C. dubia* figured by Chen & Haibao (2002: fig. 42.4) seems rather similar to that of *C. tridens* (Fig. 4A).

Thus, *Cryptodromiopsis* is herein reduced to the type species, *C. tridens*. Because of similarities between *C. tridens* and *C. coronata* Stimpson, 1858, the type species of *Cryptodromia*, McLay (1991: 470; 1993: 188) argued that *Cryptodromiopsis* is perhaps no longer necessary. *Cryptodromiopsis tridens* has been well illustrated by Lewinsohn (1979: fig. 1, as *Dromidia fenestrata*) and by McLay (1991: fig. 5). Its main resemblances with *Cryptodromia coronata* are as follows: 1) thoracic sternite 3 visible (Fig. 4); 2) episternite 4 uncovered when male abdomen is folded; 3) general shape of male abdomen and similar holding of abdomen; 4) G2 needle-like but not much longer than G1; and 5) similar shape of urinal article of antenna.

The differences that enable to distinguish *Cryptodromiopsis* from *Cryptodromia* include: 1) apertures of spermathecae approximated on a median tubercle (wide apart in *Cryptodromia*); 2) front narrow, with weak pseudorostral teeth, and presence of a frontal eave (pseudorostral teeth developed and no eave in *Cryptodromia*); 3) antennal basal article broad and long, reaching front (not so developed in *Cryptodromia*); and 4) male thoracic sternite 4 with external borders oblique and anterior border somewhat triangular (external borders subparallel and anterior border squarely truncate in *Cryptodromia*).

Even if these differences will in the future prove to be within the range of variation of the large genus *Cryptodromia*, one will have to consider that *Cryptodromia* s.l., as currently defined with some 20 species, is an heterogeneous assemblage. *Cryptodromiopsis tridens* is distinguished from all other dromiids by presence of two conspicuous smooth, naked areas at posterior angles of carapace (see Lewinsohn 1979: fig. 1A, as *Dromidia fenestrata*).

Genus *Desmodromia* McLay, 2001

Desmodromia McLay, 2001b: 1-8.

TYPE SPECIES. — *Desmodromia griffini* McLay, 2001 by original designation. Gender: feminine.

SPECIES INCLUDED. — *Desmodromia griffini* McLay, 2001; *D. tranterae* McLay, 2001.

DISTRIBUTION. — Australia.

DESCRIPTION

See McLay 2001b: 1-8, figs 1-3, table 1.

REMARKS

The inclusion in the Dromiinae n. status of the presumably shell-carrying species of the genus *Desmodromia* (regarded as an "unusual dromiid crab" by McLay 2001b: 1) is puzzling. The males of both species are unknown and the description of the females is incomplete. Important information on the two small *Desmodromia* species (not available during this study) is missing, such as: 1) organization of thoracic sternum; 2) shape of male abdomen; 3) male uropods (showing as well-developed dorsal plates in an immature female of *D. tranterae*); 4) complete male pleopodal formula; and 5) morphology of male P5 coxa (presence or not of a differentiated mobile penial tube). Besides, it remains unclear whether the last legs are really dissimilar in size and shape (also their terminal grasping apparatus have not been figured in detail) and whether the female thoracic sternites 7 and 8 are tilted. The female sternal sutures 7/8 ending apart between P2 (McLay 2001b: 2) are typically dromiine.

Despite some resemblance of the short and upturned dactyli of P4 and P5 to that of the shell-carrying *Hypoconcha*, McLay (2001b: 8) separated *Desmodromia* in his key from the couplet *Conchoecetes*/*Hypoconcha*.

As far as we can tell, *Desmodromia* and *Conchoecetes* (Fig. 3) share the following characters: 1) female sternal sutures 7/8 ending between P2; and 2) abdomen hold folded by dorsal uropods and, mostly, by a structure on P2 coxae. Besides their different carapaces, *Desmodromia* and *Conchoecetes* differ from each other in: 1) epipod absent on P1 in *Desmodromia* (present in *Conchoecetes*); 2) P4 and P5 more or less similar, with same dactylus which is simply upturned and without opposing propodal spines (P4 and P5 markedly dissimilar in size and shape in *Conchoecetes*, with P4 very stout and specialized subcheliform apparatus, P5 filiform and ending in small upturned dactylus; see Guinot & Tavares 2000: fig. 4); and 3) abdominal holding by structure on P2 coxa only (additional efficient structure on P3 coxae and inefficient structure on P4 coxae in *Conchoecetes*, Fig. 3B; see Guinot & Bouchard 1998: 622, fig. 4A).

The carapace of *Desmodromia*, although not membranous on posterior half as in *Hypoconcha*, may be poorly calcified and flattened, and the eaves overhang eyes. The differences between *Desmodromia* and *Hypoconcha* consist of: 1) epipod absent on P1 in *Desmodromia* (present in *Hypoconcha*); 2) uropods as dorsal plates (as minute ventral plates in *Hypoconcha*, Fig. 19B, C); 3) female sternal sutures 7/8 ending between P2 (more posteriorly in *Hypoconcha*, Fig. 19A); 4) P2 coxae and uropods functioning in abdominal holding (in *Hypoconcha* either a differentiation on P1 coxa without involvement of uropods or only provided by strong natural flexion of abdomen, see Guinot & Bouchard 1998: fig. 1C, D); and 5) P4 and P5 simply ending in upturned dactylus (with diverse specialized features in *Hypoconcha*, see under Hypoconchinae n. subfam., and Guinot & Tavares 2000: fig. 5).

For a comparison of *Desmodromia* with *Epipedodromia* (Fig. 7A) and *Homalodromia* (Fig. 9), in which the eyes and cephalic appendages are also ventrally located, see discussion of *Homalodromia*.

Carrying behaviour

Unknown, but supposedly bivalve shells (McLay 2001b: 7, 8). For comments on shell-carrying in Dromiidae, see under Discussion, Shell-carrying behaviour.

Genus *Dromidia* Stimpson, 1858 sensu nobis
(Fig. 5)

Dromia – Lamarck 1818 *pro parte*: 264. — Lucas 1840 *pro parte*: 113. (Non *Dromia* Weber, 1795).

Dromidia Stimpson, 1858 *pro parte*: 225; 1907 *pro parte*: 170. — Borradaile 1903a *pro parte*: 299. — Stebbing 1910 *pro parte*: 342. — Barnard 1950 *pro parte*: 319. — Tirmizi & Kazmi 1991 *pro parte*: 27. — McLay 1993 *pro parte*: 125, 183, table 5. — McLay *et al.* 2001 *pro parte*: 740, table 3.

Non *Platydromia* Brocchi, 1877: 54 (type species: *P. depressa* Brocchi, 1877 by monotypy).

Non *Parasphaerodromia* Spiridonov, 1992: 69 (type species: *P. subglobosa* Spiridonov, 1992 by original designation).

TYPE SPECIES. — *Dromia hirsutissima* Lamarck, 1818 by original designation (Stimpson 1858: 225). Gender: feminine.

Lamarck (1818: 264) stated that his *Dromia hirsutissima* came from Cape of Good Hope ("Cap de Bonne-Espérance") and that it was deposited in the Paris Museum. H. Milne Edwards (1837: 176 as *Dromia hirtissima*, *sic*) seems to have examined the same material and also mentioned that it was housed in the Paris Museum. The only specimen of *Dromidia hirsutissima* (Lamarck, 1818) in the MNHN collections is a male (26.6 × 31 mm) labeled "Cap de Bonne-Espérance" (MNHN-B 22034), and without details on the label. This specimen, presently preserved in alcohol (at one time dry, and perhaps rehydrated), is presumed to be the type of *Dromia hirsutissima* and is selected here as the lectotype of the species.

SPECIES INCLUDED. — *Dromia hirsutissima* Lamarck, 1818.

Whether *Dromidia aegibotus* Barnard, 1947, *Dromidia dissothrix* Barnard, 1947 and *Dromidiopsis cornuta* Barnard, 1947 belong to *Dromidia*, as stated by McLay (1993), deserves further investigation. *Dromidia spongiosa* Stimpson, 1858 is herein transferred to *Platydromia* Brocchi, 1877.

DISTRIBUTION. — South Africa.

DESCRIPTION

Carapace wider than long, convex; dorsal surface only with low gibbosities; only branchial groove marked. Anterolateral margin long, with one tooth separated from exorbital angle by a deep concavity, and followed by a prominence; a blunt tooth behind branchial groove; posterolateral margins very short, markedly convergent posteriorly. Front inclined, narrow, with median rostral tooth directed downwards, and two pseudorostral teeth; supraorbital, suborbital and exorbital teeth present. Antenna: basal article with exopod more developed than internal angle which is hardly produced. Mxp3: coxae separated by narrow gap.

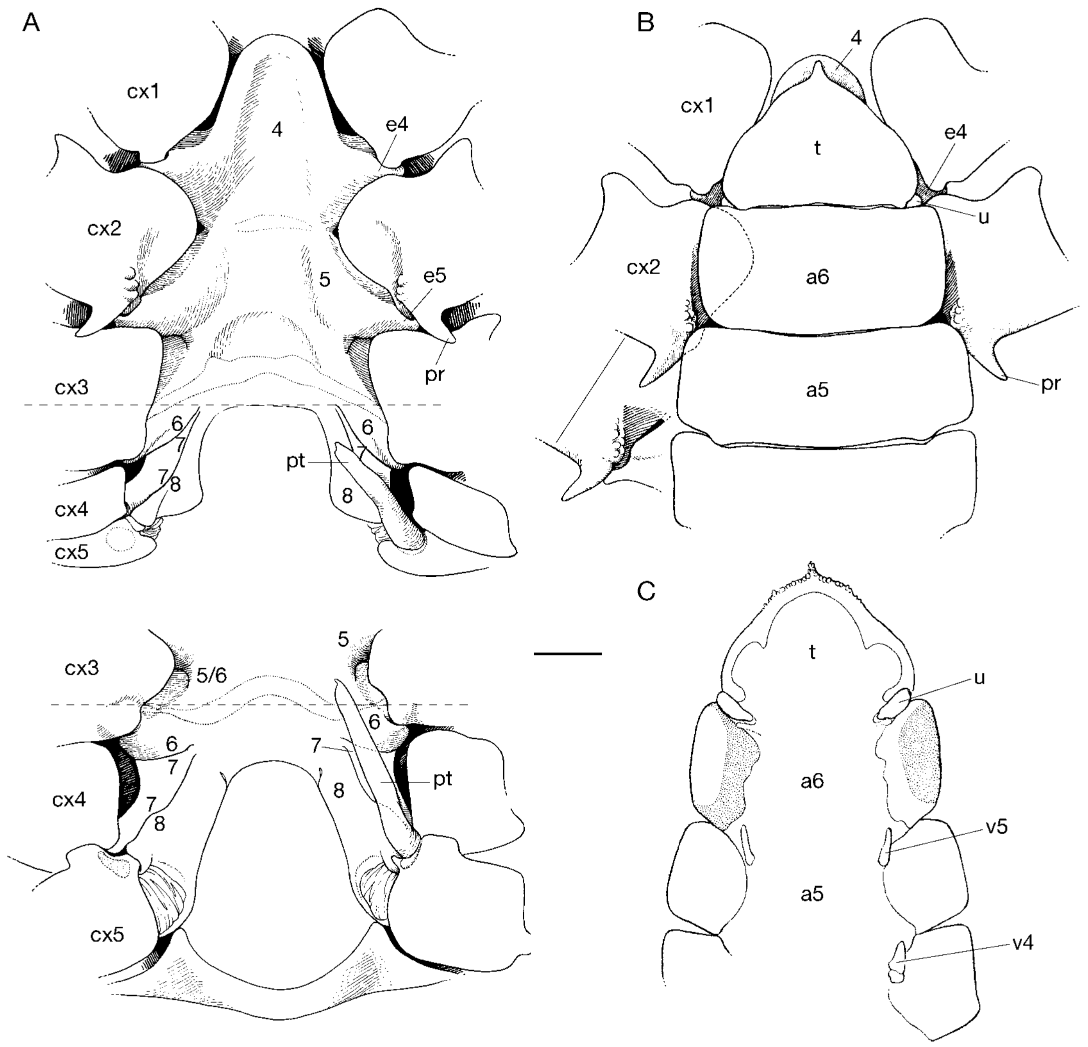

FIG. 5. — *Dromidia hirsutissima* (Lamarck, 1818), "Cap de Bonne-Espérance", ♂ 26.6 × 31 mm, lectotype (MNHN-B 22034); **A**, thoracic sternum, two front views; **B**, **C**, abdomen, dorsal and ventral views; note uropods showing as ventral plates, hardly visible dorsally. Abbreviations: **a5**, **a6**, abdominal segments 5, 6; **cx1**-**cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **pr**, spiniform holding prominence; **pt**, penial tube; **v4**, **v5**, elongated vestigial pleopods 4 and 5 (pleopods present also on segment 3); **t**, telson; **u**, uropod; **4-6**, sternites 4-6; **5/6-7/8**, thoracic sternal sutures 5/6-7/8. Dotted line indicates difference in level. Scale bars: 2 mm.

Thoracic sternite 3 hardly visible dorsally; sternite 4 forming plate weakly hollowed medially, with lateral borders oblique and anterior margin gently rounded (Fig. 5A, B). Female sternal sutures 7/8 long, with apertures of spermathecae ending together on slight prominence between chelipeds. When male abdomen is applied against ventral surface, only a small part of sternite 4 and episternite 4 remaining exposed.

Male abdomen long, wide, with distinct spaced pleural parts, and with all segments free; telson broadly triangular, ending in acute tip (Fig. 5B, C). Male segment 6 with external borders parallel. Vestigial pleopods present in males, as elongated lobes on segments 3-5 (Fig. 5C). Uropods showing as narrow ventral plates, deeply inserted ventrally, oblique, hardly visible dorsally. Uropods not involved in holding of abdomen. On P2 coxa a strong spine, directed backwards, which may maintain abdominal segment 5 only when P2 are moved backwards.

Chelipeds long, without epipod. P1, P2 and P3 thick, not nodose or ridged; propodus of P2 and P3 without distal spine; inner margin of dactylus armed with spines. P4 and P5 reduced, P5 being more slender. Propodus of P4 and P5 with distal spine opposing dactylus, which is very long and ends in horny spine; a spine on external border of P5 propodus.

Male P5 coxa with mobile penial tube (Fig. 5A).

Carrying behaviour

Individuals carry a compound ascidian.

REMARKS

McLay (1993: 183) stressed the confusion regarding the concept of *Dromidia*, for which "no fewer than eight definitions have been published". The present new restricted description is based on the type species of the genus, *D. hirsutissima*, previously poorly known and endemic to South Africa (see Barnard 1950: 320, fig. 61a-c). Stimpson (1858: 225) clearly defined the genus by the female sternal sutures 7/8 ("sulci") ending together between chelipeds, "in tuberculum approximati". For Rathbun (1923b: 67, 68) the Hawaiian *Dromia hirsutissima* of Dana (1852) and Edmondson (1922) belong to *Dromia dormia* (Linnaeus, 1763).

The differences that enable to distinguish *Dromidia* from *Austrodromidia* (Figs 1; 2), both sharing ventral uropods, include: 1) uropods narrow, oblique, deeply inserted but developed and only slightly visible dorsally in *Dromidia* (very small plates, may be indistinct in *Austrodromidia*); 2) vestigial pleopods Pl3-Pl5 present (absent in *Austrodromidia*); 3) apertures of spermathecae ending together on slight prominence between P1 (ending wide apart between P2 in *Austrodromidia*); 4) male segment 6 with external borders parallel (anteriorly concave and posteriorly expanded in *Austrodromidia*); 5) male telson ending in acute tip, leaving exposed anterior part of sternite 4 and episternite 4 (telson bluntly rounded at tip, almost completely recovering sternite 4, but episternites 4 and 5 exposed, in *Austrodromidia*); and 6) abdomen maintained folded by a strong P2 coxal spine, directed backwards (a sharp prominence on P2 coxa in *Austrodromidia*).

The presence of uropods is not mentioned by Barnard (1947, 1950) in *Dromidia aegibotus* and *Dromidiopsis cornuta*, meaning perhaps that they are ventral. In both species, the apertures of spermathecae end on prominence between P1. In *Dromidiopsis aegibotus* telson ends in sharp point and P2 coxa bears a sharp spine directed backwards, as in *Dromidia hirsutissima*. The generic status of these two species and of *D. dissothrix*, only known by a female, remains uncertain.

Genus *Dromidiopsis* Borradaile, 1900 sensu nobis (Fig. 6)

Dromia – H. Milne Edwards 1837 *pro parte*: 178. — Haswell 1882a *pro parte*: 755; 1882b *pro parte*: 139. (Non *Dromia* Weber, 1795).

Dromidiopsis Borradaile, 1900: 572; 1903a: 298; 1903b *pro parte*: 576. — Holthuis 1962: 56. — Lewinsohn 1984 *pro parte*: 95, 97-103. — Forest 1974 *pro parte*: 72, 74, 102, 103. — McLay 1993 *pro parte*: 135-137, table 2; 2001a *pro parte*: 79, 80. — McLay *et al.* 2001 *pro parte*: 733, 742, tables 2, 3. — Chen & Haibao 2002 *?pro parte*: 102, 541.

TYPE SPECIES. — *Dromia australiensis* Haswell, 1882 by monotypy and subsequent designation (see Holthuis 1962: 56; McLay 1993: 135, 136, and below). Gender: feminine.

SPECIES INCLUDED. — *Dromia australiensis* Haswell, 1882; *Dromidiopsis edwardsi* Rathbun, 1919; and *Dromidiopsis tridentata* Borradaile, 1903. Probably also *Sphaerodromia lethrinusae* Takeda & Kurata, 1976 included in *Dromidiopsis* by McLay (1993: 135, 139), see below.

Two species assigned to *Dromidiopsis* by McLay (1993, 2001), *D. globosa* (Lamarck, 1818) and *D. dubia* Lewinsohn, 1984, are herein excluded from *Dromidiopsis* sensu nobis: *D. globosa* becomes the type species of *Lamarckdromia* n. gen., while *D. dubia* is included in *Mclaydromia* n. gen. The generic status of *Dromidiopsis richeri* McLay, 2001 remains doubtful.

DISTRIBUTION. — Indo-West Pacific.

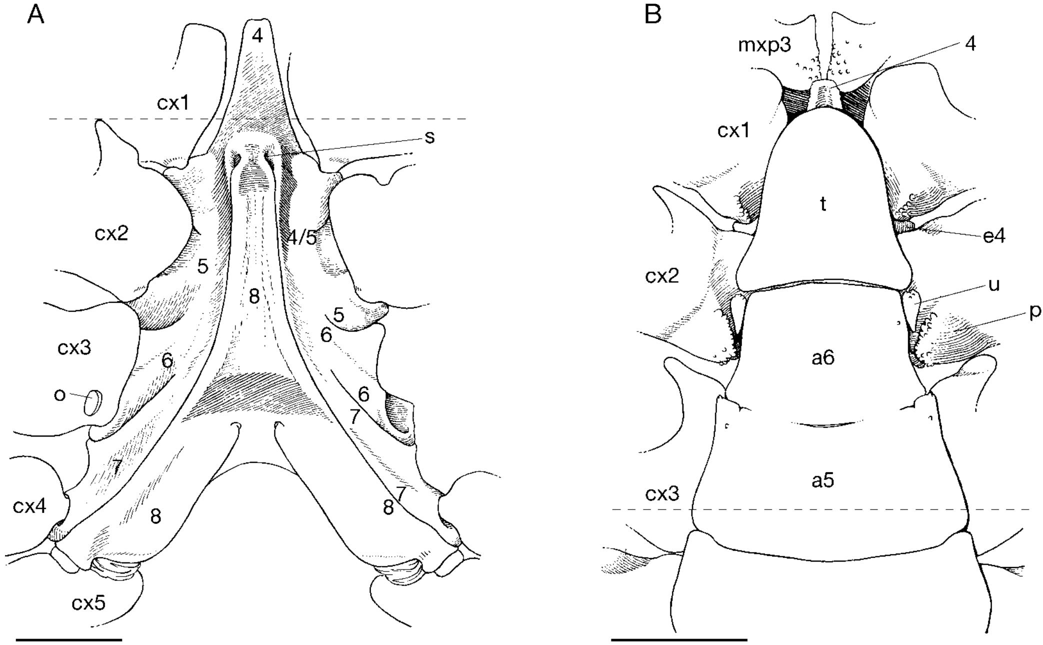

FIG. 6. — **A**, *Dromidiopsis tridentata* Borradaile, 1903, New Caledonia, LAGON, stn DW 554, ovigerous ♀ 12.7 × 12 mm (MNHN-B 22550), thoracic sternum and spermathecae; **B**, *D. australiensis* (Haswell, 1882), Australia, Queensland, Cape Bedford, D. J. G. Griffin det., ♂ 15.4 × 14 mm (AM P16598), thoracic sternum with abdomen. Abbreviations: **a5**, **a6**, abdominal segments 5, 6; **cx1-cx5**, coxae of P1-P5; **e4**, episternite 4; **mxp3**, external maxilliped; **o**, female gonopore; **pr**, holding prominence; **s**, aperture of spermatheca; **t**, telson (setae covering sternite 4 not shown); **u**, uropod; **4-8**, sternites 4-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 2 mm.

DESCRIPTION

Carapace longer than wide, strongly convex; dorsal surface smooth, with regions not defined; branchial groove poorly defined. Anterolateral margin entire or armed with several blunt (variable) teeth; only a small tooth behind branchial groove; posterolateral margin about as long as anterolateral margin. Front appearing almost entire, only bilobed or with two rounded very low pseudorostral teeth; rostrum strongly deflexed, not or hardly visible dorsally; no supraorbital and exorbital teeth; suborbital tooth faintly indicated. Antenna: urinal article thick, slightly wider than long, and with anterior part of beak very narrow; basal article with exopod well-developed and internal corner acutely produced. Mxp3: coxae not completely approximated.

Thoracic sternite 3 very slightly visible. Thoracic sternite 4 narrow, with anterior margin bluntly truncate. Female sternal sutures 7/8 getting progressively close to each other; apertures of spermathecae ending between P1 or just behind them, together on central prominence. When male abdomen is applied against ventral surface, no part or only extreme anterior part of sternite 4, with small episternite 4, remaining visible (setae of telson anteriorly covering sternite 4); episternite 5 not visible.

Male abdomen with segments 5-6 fused (sutures may be partly visible); telson long, ovate and rounded at tip. Male segment 5 with posterior angles expanded; segment 6 with external borders oblique and slightly thickened on edge. No vestigial pleopods in males. Uropods as dorsal plates narrow and oriented vertically in males, as horizontal plates in females. Uropods involved in holding of abdomen, provided by strong dentate crest on coxa of P2; in addition, presence of a granular prominence on P1 coxa, in contact with telson.

Chelipeds with epipod. P2 and P3 short and stout, not knobbed or nodose; propodus of P2 and P3 without distal spine; inner margin of dactylus armed with spines. P4 and P5 reduced, but P5 relatively long and, when extended forward, reaching as far as outer orbital angle. Propodus of P4 only slightly longer than wide. P5 much longer than P4, merus and carpus elongated; propodus, clearly longer than wide, being noticeably longer than that of P4. Subcheliform apparatus formed by one distal spine opposing dactylus; on P5 one outer propodal spine and one outer dactylus spine.

P5 coxa with mobile penial tube.

Male G2 with needle-like flagellum almost reaching anterior margin of sternite 4 and completely covered by abdomen.

Carrying behaviour

Sponges, compound or solitary ascidians.

REMARKS

Dromia australiensis (Haswell, 1882) is the type species of *Dromidiopsis* (Borradaile 1900: 572) by monotypy (Holthuis 1962: 56). However, McLay (1993: 135) indicated *Dromia australiensis* as type species "by present designation". On account of the fact that "most records of *D. australiensis* in the literature are more likely to represent *D. tridentata* than *D. australiensis*", including those of Borradaile (1900) and Lewinsohn (1984: 100), McLay concluded that "the name of the genus [*Dromidiopsis*], definition of the genus, and description of the type species all occured at different times". Borradaile (1903a, b) "gave a definition of *Dromidiopsis* which clearly included *D. tridentata* but not necessarily *Dromia australiensis*" (McLay 1993: 135, 136), hence the necessity to clearly designate here the type species of *Dromidiopsis*.

Dromidiopsis australiensis is a poorly known species, only briefly described and not figured by Haswell (1882a: 755; 1882b: 139). Unfortunately, in recent years not enough attention has been paid to this species (McLay 1993: 136, 137 in key; 2001a: 79, 80 in key). Although Lewinsohn (1984: 99-101, pl. 3, fig. A, pl. 4, figs A, B) compared *D. australiensis* with *D. tridentata* and cleared up the synonymy of these two species, many important morphological characters of *D. australiensis* remained obscure. This situation led McLay (1993: 135, table 2; 2001a: 79) to propose a composite *Dromidiopsis*. According to McLay (2001: 80, key), the following seven species belong to *Dromidiopsis*: *D. australiensis*, *D. dubia*, *D. edwardsi*, *D. globosa*, *D. lethrinusae*, *D. tridentata* and *D. richeri*. *Dromidiopsis* sensu nobis is herein restricted and now includes only *D. australiensis*, *D. edwardsi* and *D. tridentata*, and perhaps *D. lethrinusae*. Its main diagnostic features are as follows: 1) front and orbital border entire or without marked teeth; 2) male abdomen with segments 5-6 fused; 3) telson long; 4) male uropods showing as dorsal plates vertically oriented (Fig. 6B); and 5) female sternal sutures 7/8 long, and apertures of spermathecae ending between P1 or just behind them, together on central prominence (Fig. 6A).

Dromidiopsis edwardsi, a new name given by Rathbun (1919: 197) to the Indo-West Pacific crab identified as "*Dromia caputmortuum*" by H. Milne Edwards (1837: 178, "from Indian Ocean") (non *Cancer caputmortuum* Linnaeus, 1766), remains in *Dromidiopsis* sensu nobis. We examined the material labeled *Dromia caputmortuum* by H. Milne Edwards (1837), two dry specimens without locality and in poor condition (MNHN-B 1 and 2). These specimens constitute the syntypes of *Dromidiopsis edwardsi*. Because a holotype has not been designated, the female specimen MNHN-B 2, with the mention "Exp. de l'*Astrolabe*", is now selected as the lectotype, and the remaining individual is the paralectotype. McLay (1993: 137) remarks that "there is a need to clarify the validity of the records outside Australia" for *D. edwardsi* (see Rathbun 1923a: 145). The records from Indian Ocean and Indonesia may belong to another species, perhaps *D. tridentata*. The sperm of *D. edwardsi* has been described by Jamieson *et al.* (1993).

Sphaerodromia lethrinusae Takeda & Kurata, 1976, described on basis of small specimens, was assigned to *Dromidiopsis* by McLay (1993: 135, 139) but left in *Sphaerodromia* Alcock, 1899 by

Chen & Haibao (2002: 76, fig. 29). The original immature female was shown with incompletely developed sternal sutures 7/8 (Takeda & Kurata 1976: fig. 1.4), but mature females examined by McLay (1993: 140) has long sutures 7/8 which end between chelipeds, and also other characters indicating that *S. lethrinusae* should be placed in *Dromidiopsis*.

Dromidiopsis globosa and *D. dubia* should no longer be referred to *Dromidiopsis* sensu nobis. For *D. globosa* we establish *Lamarckdromia* n. gen. (Fig. 10), whose main characteristics are: 1) all abdominal segments free and presence of pleural parts; 2) uropods showing as completely concealed ventral plates; 3) apertures of spermathecae ending between P2; and 4) uropods not used to maintain the abdomen when folded.

Dromidiopsis dubia, also excluded from *Dromidiopsis* sensu nobis, is herein attributed to *Mclaydromia* n. gen., whose male uropods show as salient dorsal plates that are obliquely oriented (Fig. 12A, *M. colini* n. sp.). A male abdomen with all segments free is another difference between *Mclaydromia* n. gen. and *Dromidiopsis* sensu nobis.

The generic status of *Dromidiopsis richeri* remains uncertain. McLay (2001a: 82, figs 1, 4A) indicated in his key that *D. richeri* belonged to the third couplet, containing *D. globosa*. *Dromidiopsis richeri* is only known from two immature females (perhaps parasitized), in which the apertures of spermathecae lie between P3 (probably more forward in sexually mature females), the uropods (present in the smallest specimen, absent in the largest) show as dorsal plates, vertically oriented, and the abdominal holding is still effective. *D. globosa*, on the other hand, is the type species of *Lamarckdromia* n. gen. (Fig. 10), characterized by uropods showing as ventral plates and by antero-lateral border of carapace having a single tooth. *Dromidiopsis globosa* and *D. richeri* cannot be placed in the same genus.

Dromidiopsis sensu nobis and *Lauridromia* McLay, 1993, which consist of large-sized species, share many features: shape of male abdomen (with segments 5 and 6 partly fused), uropods narrow and vertically oriented, holding prominences on P2 and also on P1 coxae, and sternal sutures 7/8 ending at level of the chelipeds. The differences between *Dromidiopsis* and *Lauridromia* are very few (see McLay 1993: 135, 145, table 2): small size of individuals in *Dromidiopsis* (large size in *Lauridromia*); apertures of spermathecae located together on central prominence (Fig. 6A) (wide apart on long and strong tubercles in typical *Lauridromia*). In *L. indica* (Gray, 1831), however, the female sternal sutures 7/8 end together at summit of two coalescent tubercles; in these respects, *L. indica* seems to be close to *Dromidiopsis*.

Genus *Epipedodromia* André, 1932
(Fig. 7A)

Platydromia Fulton & Grant, 1902a: 57 (pre-occupied by *Platydromia* Brocchi, 1877, type species: *Platydromia depressa* Brocchi, 1877, junior synonym of *Dromidia spongiosa* Stimpson, 1858, see under *Platydromia spongiosa* (Stimpson, 1858)). — Fulton & Grant 1906a: 11; 1906b: 20. — Hale 1925: 412; 1927: 105. — Griffin 1972: 52.

Epipedodromia André, 1932: 180 (replacement name, with same type species: *Epipedodromia thomsoni*). — McLay 1993: 224, 225, table 8; 2001b: 2, 7, table 1. — McLay *et al.* 2001 *pro parte*: 743.

TYPE SPECIES. — *Platydromia thomsoni* Fulton & Grant, 1902 by monotypy. Gender: feminine.

SPECIES INCLUDED. — *Epipedodromia thomsoni* (Fulton & Grant, 1902).

DISTRIBUTION. — Australia.

DESCRIPTION

Males not examined by the authors.

Carapace wider than long, subpentagonal; dorsal surface flattened, not membranous, with regions not defined; branchial groove indistinct, not marked by tooth. Prominent ledge present posterior to front, and limiting anterior margin of carapace, front and cephalic parts at lower plane and showing as "false front", marked by hairy ridge and divided into four parts by deep grooves. When viewed from above, carapace quadrate. Lateral margin formed by anterior part (slightly convex and corresponding to lateral border of "false front"), by straight medial part (anteriorly delimitated by notch), and by concave border

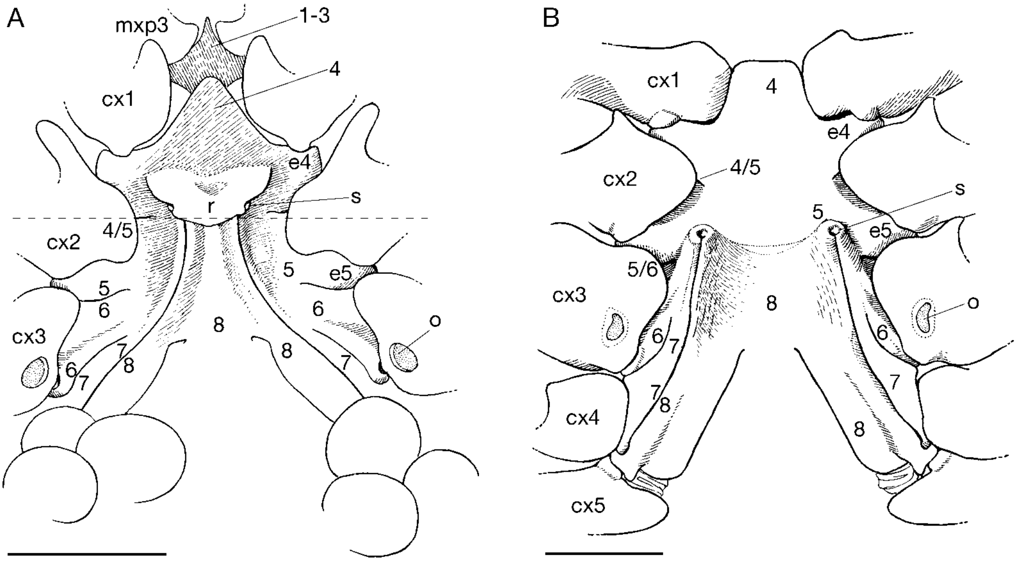

FIG. 7. — **A**, *Epipedodromia thomsoni* (Fulton & Grant, 1902), Australia, Victoria, Port Phillip, ♀ 9 × 11 mm (BM 1884-39), thoracic sternum and spermathecae; **B**, *Hemisphaerodromia monodus* (Stebbing, 1918), Madagascar, Fort-Dauphin, Decary coll., det. *H. abellana* Barnard, 1954, ♀ 16 × 18 mm (MNHN-B 12725), thoracic sternum and spermathecae. Abbreviations: **cx1**-**cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **mxp3**, external maxilliped; **o**, female gonopore; **r**, medial ridge; **s**, aperture of spermatheca; **1**-**3**, sternites 1-3; **4**-**8**, sternites 4-8; **4/5**-**7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 2.5 mm.

corresponding to posterolateral margin. Front partly visible dorsally, entire; rostrum truncate medially; pseudorostral teeth eave-like, turned upwards. Proepistome small but marked by raised ridge. Orbits deep; eyes small. No supra-orbital and exorbital teeth; suborbital tooth forming thickening. Antenna: urinal article with anterior part of beak very narrow and posterior part shorter and rounded; basal article with exopod and internal corner similarly developed and produced. Mxp3: coxae separated by gap. Pterygostomial region soft.

Thoracic sternite 3 distinctly developed and completely visible. Thoracic sternite 4 forming raised piece, with medial part triangular and lateral parts largely expanded. In females, posterior sternites sharply and vertically tilted to form brood chamber; female sternal sutures 7/8 ending apart; apertures of spermathecae between P1 and P2, at level of episternite 4, and beneath raised medial ridge (Fig. 7A).

Male abdomen with all segments free, acutely triangular in shape but telson rounded, obtuse at tip. No vestigial pleopods in males (to be verified). Uropods absent (verified in ovigerous females only). Holding of abdomen by raised knob on P2 coxae. Female abdomen well-developed, first three segments positioned dorsally.

Chelipeds without epipod. P2 and P3 longer than chelipeds, smooth. P4 and P5 reduced; P5 longer, its curved merus almost as long as lateral margin of carapace. Subcheliform apparatus formed by single distal propodal spine opposing dactylus.

Carrying behaviour

"Unknown, but probably sponge" (McLay 2001b: 2, table 1).

REMARKS

Epipedodromia thomsoni has the front and cephalic parts being at lower plane, that provides a somewhat similar appearance than in *Desmodromia* and *Homalodromia* and also in *Hypoconcha*, see under *Homalodromia*.

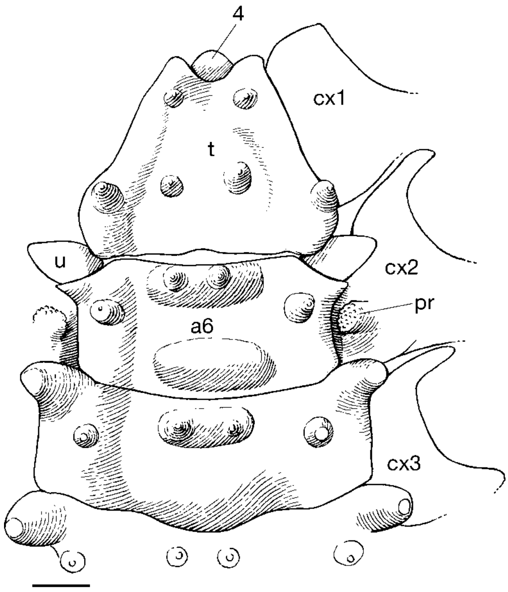

FIG. 8. — *Fultodromia spinifera* (Montgomery, 1931), Moluccas, *Pele*, stn AN 1/1, ♂ 17.5 × 17.5 mm, abdomen (after Bouchard 2000: fig. 18E). Abbreviations: **a6**, abdominal segment 6; **cx1**-**cx3**, coxae of P1-P3; **pr**, holding prominence; **t**, telson; **u**, uropod; **4**, sternite 4. Scale bar: 1 mm.

The examination of male of *Epipedodromia thomsoni* will show whether the uropods are missing (McLay 1993: 225, table 8; 2001b: 2, table 1), or are simply reduced to small ventral plates.

The species is characterized by the development of a brood chamber and by direct development. As Hale (1925: 412), we found very few large eggs in the pouch.

Genus *Fultodromia* McLay, 1993
(Fig. 8)

Dromia – Guérin-Méneville 1832: pl. 14, fig. 1. — H. Milne Edwards 1837 *pro parte*: 170, 177. (Non *Dromia* Weber, 1795).

Cryptodromia – Stimpson 1858 *pro parte*: 255; 1907 *pro parte*: 172. — Baker 1907: 180. — Ihle 1913 *pro parte*: 32. — Montgomery 1931: 413. (Non *Cryptodromia* Stimpson, 1858).

Petalomera – Rathbun 1923a *pro parte*: 154. — Hale 1927 *pro parte*: 111, 112. (Non *Petalomera* Stimpson, 1858).

Dromidiopsis – Balss 1935: 113. (Non *Dromidiopsis* Borradaile, 1900).

Fultodromia McLay, 1993: 124, 162, table 3.

TYPE SPECIES. — *Dromia nodipes* Guérin-Méneville, 1832 by original designation (McLay 1993: 162). (*Dromia nodipes* Lamarck, 1818: 264 is a *nomen nudum*). Gender: feminine.

A specimen of *Dromia nodipes* (female 22.5 × 23 mm, MNHN-B 15, rehydrated and now in alcohol) is regarded as the presumed type and selected here as the lectotype. It is not accompanied by any original label indicating the country of origin. This agrees to the question mark in the caption of the figure by Guérin-Méneville (1832: 11) and in the text of H. Milne Edwards (1837: 170). The mention "Cap de Bonne-Espérance" in the MNHN inventory register most probably results from a mistake of a subsequent transcription: it is perhaps useless to assign the reference for Port Esperance or Esperance Bay in South Australia (McLay 1993: 162). Therefore, the origin of the lectotype remains unknown. However, *Fultodromia nodipes* is most probably an Australian species, where it has been found by Baker (1907: 180, pl. 25, fig. 1, as *Cryptodromia depressa*), Hale (1927: 112, fig. 110, as *Petalomera depressa*) and Rathbun (1923a: 154, as *P. depressa*).

SPECIES INCLUDED. — *Dromia nodipes* Guérin-Méneville, 1832 (senior synonym of *Cryptodromia tumida* Stimpson, 1858; *Petalomera depressa* Baker, 1907, and *Dromidiopsis michaelseni* Balss, 1935); *Cryptodromia tumida* var. *spinifera* Montgomery, 1931.

DISTRIBUTION. — Australia.

DESCRIPTION

Carapace almost as long as wide, convex; dorsal surface with regions not well-defined; branchial groove indistinct but a tooth just behind it. Anterolateral margin joining exorbital angle and armed with several developed blunt teeth; posterolateral margins nearly straight. Front with deflexed rostral tooth and two prominent pseudorostral teeth; supraorbital and exorbital teeth prominent; suborbital tooth may be developed. Antenna: urinal article with anterior part of beak longer and more acute than posterior ones; basal article with exopod very long and thickened and with internal corner produced, both enclosing two following articles. Mxp3: coxae closely approximated.

Thoracic sternite 3 not visible. Male thoracic sternite 4 with anterior margin bluntly triangular; episternites 4 and 5 narrow. Female sternal sutures 7/8 reaching forward to between coxae of

P1; apertures of spermathecae apart, but not separated by wide space. When male abdomen is applied against ventral surface, only a small part of sternite 4 exposed; episternite 4 not visible or only a minute part discernible; episternite 5 not visible.

Male abdomen with all segments free, wide, and with characteristic blunt but developed prominences in latero-posterior angles; telson with base very enlarged and may be markedly concave at tip. Male segment 6 with external borders thickened on anterior half. No vestigial pleopods in males. Male uropods showing as much salient and mobile dorsal plates, with petaloid expansions similar to those of posterior angles of abdominal segments (Fig. 8). Holding of abdomen consisting of a strong serrated prominence on P2 coxa, far from uropods.

Chelipeds with epipod. All pereopods short and thick. P2 and P3 nodular; propodus without distal spine; inner margin of dactylus with spines. P4 and P5 reduced, with terminal apparatus formed by up to two distal propodal spines opposing dactylus; two or three other spines on outer propodal margin.

Male P5 coxa with long mobile penial tube.

Carrying behaviour

Sponges, compound ascidians.

REMARKS

The female sternal sutures 7/8 end wide apart "in a small mound" in *Fultodromia nodipes*, and "in a transverse ridge" in *F. spinifera* (Montgomery 1931: 414, pl. 29, fig. 3a).

Genus *Hemisphaerodromia* Barnard, 1954
(Fig. 7B)

Cryptodromia – Stebbing 1918: 56. — Barnard 1950 *pro parte*: 307, 328. (Non *Cryptodromia* Stimpson, 1858).

Hemisphaerodromia Barnard, 1954: 100. — Lewinsohn 1979: 10; 1984: 117. — McLay 1993: 124, 159, table 3. — Guinot & Bouchard 1998: 624, 628.

Petalomera – Kensley 1970 *pro parte*: 110. (Non *Petalomera* Stimpson, 1858).

TYPE SPECIES. — *Cryptodromia monodus* Stebbing, 1918 by monotypy (senior synonym of *Hemisphaerodromia abellana* Barnard, 1954). Gender: feminine.

SPECIES INCLUDED. — *Hemisphaerodromia monodus* (Stebbing, 1918).

DISTRIBUTION. — Indian Ocean.

DESCRIPTION

Carapace wider than long, rounded/pentagonal, strongly convex; dorsal surface smooth, with regions not well-defined; branchial groove distinct. Anterolateral margin with only blunt small teeth; posterolateral margins straight, with blunt tooth. Front entire and continuous to orbital margin, a small rostral tooth and two eave-like pseudorostral teeth; no suborbital nor exorbital teeth. Antenna: urinal article developed, with only anterior part of beak acute, posterior part being wide; basal article with exopod well developed and internal corner thickly produced, both enclosing two following articles. Mxp3: coxae closely approximated.

Thoracic sternite 3 not visible. Male thoracic sternite 4 with anterior margin truncate. Female sternal sutures 7/8 ending apart behind P2; apertures of spermathecae wide apart on tubercule, at level of episternite 5 (Fig. 7B). When male abdomen is applied against ventral surface, only anterior part of sternite 4 and narrow episternite 4 exposed.

Male abdomen with all segments free, wide; telson with base enlarged and bluntly rounded at tip. Male segment 6 with external borders deeply hollowed and much thickened in anterior part. No vestigial pleopods in males. Male uropods showing as markedly salient and mobile dorsal plates. Uropods involved in holding of abdomen, which is particularly efficient, being provided with whole base of P2 coxa which bears a serrated salient ridge, tightly encircled by depression on border of segment 6. Female uropods visible dorsally.

Chelipeds with an epipod. All pereopods short and stout. P2 and P3 lobed; propodus without distal spine; inner margin of dactylus with few tiny spines. P4 and P5 reduced, with terminal

apparatus formed by one distal propodal spine opposing dactylus; only one another very small spine on outer propodal margin.
Male P5 coxa with long mobile penial tube.

Carrying behaviour
Compound ascidians.

REMARKS

As pointed out by Barnard (1954) and McLay (1993), *Hemisphaerodromia* resembles *Sphaerodromia* only by the shape of carapace, particularly the front. Nevertheless, *Hemisphaerodromia* is a typical dromiine, with salient dorsal uropods, male P5 coxa bearing a long penial tube, female sternal sutures 7/8 ending behind P2 and apertures of spermathecae rather far from female gonopores on P3 (Fig. 7B).
Fultodromia (Fig. 8) and *Hemisphaerodromia* are close and characterized by uropods showing as salient and mobile dorsal plates. The uropod and the coxal prominence on P2 are near each other in *Hemisphaerodromia* (Guinot & Bouchard 1998: fig. 3C, D), not in *Fultodromia* (Bouchard 2000: 82, figs 18E, 20D); the abdominal segment 6 is markedly modified on both. In *Hemisphaerodromia* (Fig. 7B) the apertures of spermathecae are located at level of episternites 5 between P2, while in *Fultodromia* they reach forward between coxae of P1. The terminal carrying apparatus on P4 and P5 also distinguishes the two genera.

Genus *Homalodromia* Miers, 1884
(Fig. 9)

Homalodromia Miers, 1884: 553. — McLay 1993: 125, 225, table 8; 2001b: 2, 7, table 1. — McLay *et al.* 2001 *pro parte*: 740, table 3.

Pseudodromia – Alcock 1900 *pro parte*: 149. (Non *Pseudodromia* Stimpson, 1858).

Lasiodromia Alcock, 1901: 56 (type species: *Homalodromia coppingeri* Miers, 1884). — Ihle 1913: 51.

TYPE SPECIES. — *Homalodromia coppingeri* Miers, 1884 by monotypy.
The replacement name *Lasiodromia* created by Alcock (1901) for *Homalodromia* Miers, 1884, because of the resemblance and possible confusion with *Homolodromia* A. Milne Edwards, 1880 (Homolodromiidae) was unnecessary (ICZN 1999: article 56.2).

SPECIES INCLUDED. — *Homalodromia coppingeri* Miers, 1884, and perhaps another species, *Homalodromia unidentata* (Ihle, 1913) (see Takeda 1977: 73; McLay 1993: 227).

DISTRIBUTION. — Indo-West Pacific.

DESCRIPTION

Carapace longer than wide, whole anterior part strongly deflected; rest of dorsal surface flattened, with regions not defined; branchial groove distinct, may be sometimes marked by tooth. Subhepatic area inflated. Eyes and cephalic appendages not visible dorsally. Anterolateral margin convex, may be sometimes with single small tooth oriented ventrally; posterolateral margins convergent. Front particular, at lower plane and appearing quadridentate in counting pseudorostral and supraorbital teeth; rostrum markedly deflexed, without tooth; each prominent acute pseudorostral tooth fused with similarly shaped supraorbital tooth, together forming broad, concave eave. Suborbital tooth acute, long, visible dorsally; exorbital tooth marked. Proepistome small but marked by raised ridge. Antenna: basal article much longer than wide, with enlarged exopod and internal corner similarly strongly produced; following articles well developed. Mxp3: coxae closely approximated. Pterygostomial region soft.
Thoracic sternite 3 not visible dorsally. Thoracic sternite 4 with anterior margin bluntly truncate, in contact with mxp3 coxae. When male abdomen is applied against ventral surface, anterior part of sternite 4 and epsisternite 4 remaining visible. In females, posterior sternites obliquely tilted; female sternal sutures 7/8 ending apart, just at level of P1; apertures of spermathecae at each extremity of tubular curved prominence forming bridge between P1 coxae (Fig. 9B).
Male abdomen with all segments free, triangular in shape but with telson very long and obtuse at tip. No vestigial pleopods in males. Male uropods as elongated and mobile dorsal plates, vertically

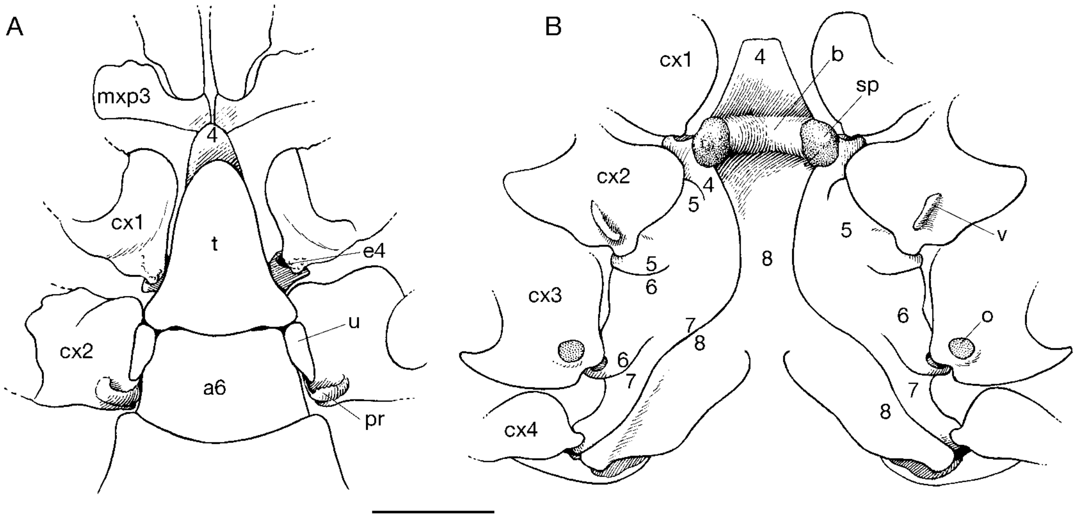

FIG. 9. — **A**, *Homalodromia coppingeri* Miers, 1884, Seychelles, ♂ 5.2 × 5.3 mm (MNHN-B 26130), thoracic sternum with abdomen; **B**, *Homalodromia*? *coppingeri* Miers, 1894, New Caledonia, LAGON, stn 556, ♀ 7.8 × 9 mm (MNHN-B 22528), thoracic sternum and spermathecae; note apertures of spermathecae at level of P1, concealed by sperm plug, and vestigial holding prominence on P2 coxa of female. Abbreviations: **a6**, abdominal segment 6; **b**, tubular bridge between apertures of spermathecae; **cx1**-**cx4**, coxae of P1-P4; **e4**, episternite 4; **mxp3**, external maxilliped; **o**, female gonopore; **pr**, holding prominence; **sp**, sperm plug; **t**, telson; **u**, uropod; **v**, vestige of the holding prominence in the female; **4-8**, sternites 4-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Scale bar: 1 mm.

oriented, involved in holding of abdomen; uropods remaining rather developed in females. Abdominal holding provided by particularly high, cupuliform and denticulated prominence on coxa of P2 (Fig. 9A), which remains as a vestige in mature females (Fig. 9B); on P1 coxa, a small tuberculate prominence.

Chelipeds without epipod, slightly more massive than P2 and P3, none of these verrucose or dilated. P2 and P3 propodus without distal spine, and inner margin of dactylus armed with several small spines. P4 and P5 reduced but unequal; P5 almost as long as P2, merus not so long as lateral margin of carapace, however. Subcheliform apparatus formed by single distal propodal spine opposing the dactylus.

Male P5 coxa with mobile penial tube.

Carrying behaviour

Sponges.

REMARKS

Despite an overall resemblance of the carapace (in particular the front), which permitted the assertion that *Homalodromia* is most closely related to *Epipedodromia* (McLay 1993: 225), several characters of the ventral surface of body separate the two genera, notably: 1) sternite 3 not visible in *Homalodromia* (Fig. 9) (well-developed and completely visible in *Epipedodromia*, Fig. 7A); 2) uropods as elongated dorsal plates vertically oriented, constituting a full-lock system with uropods completely involved in abdominal holding (see Guinot & Bouchard 1998: fig. 3B) (uropods absent, at least in ovigerous females, in *Epipedodromia*; their absence is to be verified in males); 3) apertures of spermathecae apart, each located at the extremity of tubular prominence forming a bridge just behind P1 coxae (Fig. 9B) (apart, beneath raised medial thickening between P1 coxae in *Epipedodromia*, Fig. 7A); and 4) female abdomen normally widened (largely expanded and forming a brood chamber in *Epipedodromia*).

Homalodromia resembles *Dromidiopsis* sensu nobis (Fig. 6) by the shape of their male abdomen, presence of uropods shaped as elongated dorsal plates, that are vertically oriented, and abdominal holding provided by crest on P2 coxae. It differs from it by several features: 1) male abdomen with all segments free (segments 5-6 fused in *Dromidiopsis*); and 2) apertures of spermathecae apart and located at each extremity of tubular bridge just behind P1 coxae (ending between P1, together on central prominence, in *Dromidiopsis*).

Several dromiid genera share with *Homalodromia* the ventral location of eyes and cephalic appendages: *Epipedodromia*, *Desmodromia* and *Hypoconcha*. McLay (2001b: 2, table 1) compared the first three genera, but the morphology of thoracic sternum was not taken into account. Differences include: 1) the anterior sternites 3 and 4 (in *Epipedodromia* large sternite 3 present, sternite 4 raised and triangular, at least in females, Fig. 7A; sternite 3 not exposed and sternite 4 bluntly truncate in *Homalodromia*, Fig. 9); and 2) the shape of uropods (narrow dorsal plates vertically oriented in *Homalodromia*, Fig. 9A, said to be absent in *Epipedodromia*, described as dorsal in immature females of *Desmodromia*). In addition to the features of carapace and last pairs of pereopods, *Hypoconcha* is characterized by a peculiar thoracic sternum (Fig. 19A), the presence of male vestigial pleopods (Fig. 19B), the uropods showing only as minute ventral lobes (Fig. 19B, C), a male abdomen that is short and usually flexed at right angles in the middle, sternal female sutures 7/8 which are relatively short and located on tilted surface of posterior part of sternum (Fig. 19A), and by the presence of an epipod on P1. All of these differences support the inclusion of *Homalodromia*, *Epipedodromia* and *Desmodromia* in the Dromiinae n. status, and the separation of *Hypoconcha* in the Hypoconchinae n. subfam.

Genus *Lamarckdromia* n. gen.
(Fig. 10)

Dromia – Lamarck 1818 *pro parte*: 264. — H. Milne Edwards 1837 *pro parte*: 177. — Haswell 1882b *pro parte*: 140. — Henderson 1888 *pro parte*: 3. — Ihle 1913 *pro parte*: 89. (Non *Dromia* Weber, 1795).

Dromidia – Stimpson 1858 *pro parte*: 225, 239. — Henderson 1888: 5. — de Man 1888 *pro parte*: 396, footnote. — Borradaile 1900: 571. (Non *Dromidia* Stimpson, 1858).

Dromidiopsis – Rathbun 1923a: 146. — Hale 1927: 110; 1941: 281. — Griffin 1972: 53 (*Dromiopsis*, *sic*). — Forest 1974 *pro parte*: 103. — McLay 1993 *pro parte*: 120, 135, 137; 2001a *pro parte*: 79, 80. — McLay *et al.* 2001 *pro parte*: 733, 742. (Non *Dromidiopsis* Borradaile, 1900 sensu nobis).

TYPE SPECIES. — *Dromia globosa* Lamarck, 1818 by present designation.

SPECIES INCLUDED. — *Dromia globosa* Lamarck, 1818 (senior synonym of *Dromidia excavata* Stimpson, 1858).

A damaged, dry specimen of a male, identified as *Dromia globosa* and without locality, deposited in the Historical Reference Collection (MNHN-B 22033), bearing the label "it is probably the material studied by H. Milne Edwards (1837: 177) and sent to M. de Man (1888: 396, footnote, pl. 18, fig. 1)", is to be considered the type of the species and selected here as the lectotype.

ETYMOLOGY. — The genus *Lamarckdromia* n. gen. is dedicated to the eminent French naturalist Jean-Baptiste Pierre de Monet, chevalier de Lamarck (1744-1829), who described several dromiid species. Gender: feminine.

DISTRIBUTION. — Australia.

DESCRIPTION

Carapace about as long as wide, convex; dorsal surface smooth, with regions not defined; subhepatic region hollowed; branchial groove marked and deeply notching external border. Anterolateral margin not joining orbit but reaching middle of pterygostomial border, and armed with only one blunt tooth; no tooth behind level of branchial groove; posterolateral margin short. Front narrow, appearing tridentate, with strongly deflexed rostrum and developed pseudorostral teeth; supraorbital tooth present; no suborbital and exorbital teeth. Orbits deep; eyes small. Antenna: urinal article with anterior part of beak raised; basal article with exopod developed and internal corner produced. Anterior margin of buccal frame formed by raised median wall and two acute lateral teeth. Mxp3: coxae separated by small gap.

Thoracic sternite 3 remaining exposed and visible dorsally, specially in males (sternites 1-2 at lower plane) (Fig. 10A, D). Thoracic sternite 4 narrow,

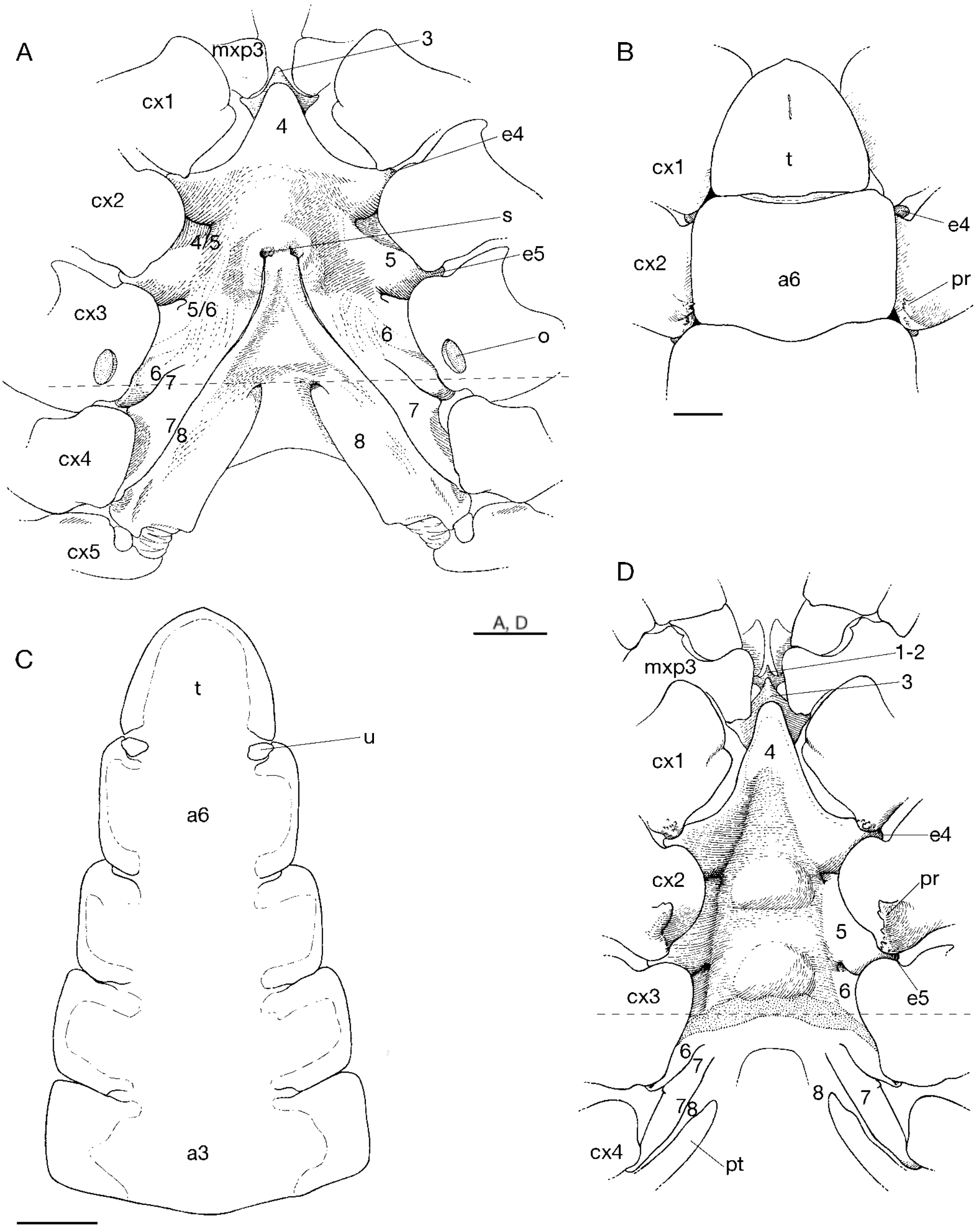

FIG. 10. — *Lamarckdromia globosa* (Lamarck, 1818) n. comb., New South Wales, Port Jackson, det. *Dromidia excavata* Stimpson, McLay redet. *Dromidiopsis globosa* (MNHN-B 22041); **A**, ♀ 25 × 25 mm, thoracic sternum and spermathecae; **B**-**D**, ♂ 24 × 25 mm, extremity of abdomen in dorsal view, abdomen in ventral view, and thoracic sternum without abdomen. Abbreviations: **a3**, **a6**, abdominal segments 3, 6; **cx1**-**cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **mxp3**, external maxilliped; **o**, female gonopore; **pr**, holding prominence; **pt**, penial tube; **s**, aperture of spermatheca; **t**, telson; **u**, uropod; **1**-**2**, sternites 1-2; **3**-**8**, sternites 3-8; **4/5**-**7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 2.5 mm.

with triangular anterior margin. Female sternal sutures 7/8 long, with apertures of spermathecae ending between P2, together on central prominence (Fig. 10A). When male abdomen is applied against ventral surface, extreme anterior part of sternite 4 and small part of episternite 4 remaining visible.

Male abdomen with all segments free; presence of extended pleural parts; telson much broader than long, rounded at tip. Male segment 6 slightly constricted in posterior part and rest of external borders subparallel. Vestigial pleopods absent in males. Uropods showing as ventral rounded/ovate plates, well inserted, relatively developed but completely concealed (Fig. 10B, C). Uropods not involved in holding of abdomen. Abdominal holding provided by very sharp tuberculate prominence on P2 coxa, overhanging base of segment 6 (Fig. 10B, D).

Chelipeds not knobbed. P2 and P3 not knobbed nor nodose; propodus of P2 and P3 without distal spine; inner margin of dactylus armed with spines. P4 and P5 reduced, but P5 much longer than P4 and, when extended forward, reaching as far as the anterolateral tooth; merus and carpus being noticeably much longer than that of P4. P4 very short and stout, propodus wider than long. Subcheliform apparatus of P4 and P5 formed by one distal spine opposing the curved dactylus; three developed and subequal outer propodal spines on P4; on P5, only one long outer propodal spine.

Male P5 coxa with mobile penial tube (Fig. 10D).

Carrying behaviour

Sponges, compound ascidians.

REMARKS

Dromidiopsis globosa (Lamarck, 1818) (see McLay 1993: 135, 137), from Australia, is excluded from *Dromidiopsis* sensu nobis (Fig. 6) since: 1) uropods occur as completely concealed ventral plates (dorsal plates vertically oriented and well visible dorsally in *Dromidiopsis*); 2) females sutures 7/8 only reach bases of P2 (see Forest 1974: pl. 6, fig. 4 as *D. excavata*) (reaching bases of P1 in *Dromidiopsis*); 3) male abdomen has all segments free (segments 5-6 fused in *Dromidiopsis*); 4) male telson is short and wide, bluntly rounded at tip (longer than wide, and more triangular in *Dromidiopsis*); 5) abdominal holding is provided by tuberculate sharp prominence on P2, without involvement of the uropods (presence of a dentate crest on P2 and uropods involved in abdominal holding in *Dromidiopsis*); and 6) there are differences in overall shape of carapace.

Since the uropods show as ventral plates in *Dromidiopsis globosa*, the species is excluded from the existing dromiine genera in which uropods show as dorsal plates (see Table 1). The uropods have been described as "small", "concealed" or "absent" in about 10 dromiine genera. Despite the vagueness and imprecisions in some descriptions, *D. globosa* differs from those 10 genera in the details of the carapace, pereopods, thoracic sternum, and abdomen. Alone, the features of the carapace would be sufficient to place *D. globosa* in its own genus, *Lamarckdromia* n. gen. Additional characters mentioned as follows do not support the inclusion of *D. globosa* in the following genera: 1) *Ascidiophilus* Richters, 1880; 2) *Austrodromidia* McLay, 1993 sensu nobis; 3) *Barnardromia* McLay, 1993; 4) *Dromidia* Stimpson, 1858 sensu nobis; 5) *Epipedodromia* André, 1932; 6) *Eudromidia* Barnard, 1947; 7) *Exodromidia* Stebbing, 1905; 8) *Haledromia* McLay, 1993; 9) *Platydromia* Brocchi, 1877; 10) *Pseudodromia* Stimpson, 1858; 11) *Speodromia* Barnard, 1947; and 12) *Tunedromia* McLay, 1993.

1) *Ascidiophilus* (type species: *Ascidiophilus caphyraeformis* Richters, 1880 by monotypy) and 10) *Pseudodromia* (type species: *Pseudodromia latens* Stimpson, 1858 by original designation). In *Dromidiopsis globosa* (Fig. 10): thoracic sternum "normal" (very narrow, specially sternite 4 showing as small piece in *Ascidiophilus* and *Pseudodromia*); male telson wider than long and rounded at tip (longer than wide and tip pointed in *Ascidiophilus* and *Pseudodromia*); holding of abdomen present, provided by sharp prominence on P2 coxa (absent in *Ascidiophilus* and *Pseudodromia*); when extended forward, P5 reaching anterolateral tooth (reaching as far as

orbital angle in *Ascidiophilus* or even more elongated in *Pseudodromia*); and P4 and P5 propodus with distal spine opposing dactylus (no distal propodal spine opposing dactylus in *Ascidiophilus* and *Pseudodromia*). Another main difference is that the uropods show as ventral plates in *Lamarckdromia* n. gen. such as in *Pseudodromia*, while they are completely absent in both sexes in *Ascidiophilus*.

2) *Austrodromidia* sensu nobis (Figs 1; 2). In *D. globosa*: male abdominal segment 6 with external borders subparallel (deeply hollowed anteriorly and expanded posteriorly in *Austrodromidia*); telson with its base not particularly enlarged (enlarged in *Austrodromidia*); and female sternal sutures 7/8 ending together on central prominence between P2 (ending wide apart at level of P2 in *Austrodromidia*).

3) *Barnardromia* (type species: *Cryptodromia hirsutimana* Kensley & Buxton, 1984 by original designation), in which the sternal parts and abdomen are not figured (Kensley & Buxton 1984: 193, fig. 4). In *D. globosa*: apertures of spermathecae ending together on central prominence between P2 (behind bases of P1 in *Barnardromia*); and P4 and P5 propodus with one distal spine opposing dactylus and three outer propodal spines on P4 and one outer propodal spine on P5 (dactyli of P4 and P5 opposed by single distal propodal spine in *Barnardromia*, in McLay 1993: 180, table 5).

4) *Dromidia* sensu nobis. In *D. globosa*: male uropods showing as ventral plates totally concealed (Fig. 10B, C) (ventral plates slightly visible dorsally in *Dromidia*, Fig. 5B, C); vestigial pleopods absent (Fig. 10C) (Pl3-Pl5 present, in *Dromidia*, Fig. 5C); male telson rounded at tip (Fig. 10B, C) (ending as sharp spine in *Dromidia*, Fig. 5B, C); abdominal holding provided by tuberculate, sharp prominence on P2 coxa (Fig. 10B, D) (a strong spine on P2 coxa, directed backwards and partly overhanging abdomen in *Dromidia*, Fig. 5A, B); and sternite 4 bluntly triangular (Fig. 10A, D) (rounded at tip in *Dromidia*, Fig. 5A, B).

5) *Epipedodromia* André, 1932 (type species: *Platydromia thomsoni* Fulton & Grant, 1902). In *D. globosa*: uropods present, showing as ventral plates in both sexes (absent in ovigerous females in *Epipedodromia*; absence to be verified in males); sternite 3 discernible (Fig. 10A, D) (sternite 3 developed and completely visible in *Epipedodromia*, Fig. 7A); in females, posterior sternites gently tilted (sharply and vertically tilted, with formation of brood chamber in *Epipedodromia*); and apertures of spermathecae between P2, together on central prominence (apart, beneath thick medial bridge just behind P1, in *Epipedodromia*, Fig. 7A).

6) *Eudromidia* (type species: *Eudromia frontalis* Henderson, 1888 by monotypy). In *D. globosa*: apertures of spermathecae ending between P2, together on central prominence (between P1, on a tubercle in *Eudromidia*); and P4 and P5 reduced, but P5 reaching anterolateral tooth (P4 and P5 smaller, P5 being filiform in *Eudromidia*, at least in *E. frontalis*). In *Eudromidia* the uropods, which have not been figured, are poorly known; McLay (1993: 179) refers to the uropods as "very small, concealed".

7) *Exodromidia* (type species: *Dromidia spinosa* Studer, 1883 by monotypy). In *D. globosa*: male telson rounded at tip (ending in spine in *Exodromidia*); vestigial pleopods absent in males (Pl3-Pl5 present in *Exodromidia spinosa* (Studer, 1883), or only Pl5 present in *E. bicornis* (Studer, 1883) and *E. spinosissima* (Kensley, 1977)); thoracic sternite 3 dorsally visible, only by very small part, specially in males (largely exposed in *Exodromidia*); and male sternite 4 not hollowed medially, almost completely covered by abdomen, and with triangular tip (deeply hollowed and remaining always partly visible when abdomen folded, and with truncate tip, in *Exodromidia*). The shape of ventral uropods, partly or totally concealed, also distinguishes the two genera: showing as rounded/ovate plates, not really movable in *Lamarckdromia* n. gen. (Fig. 10B, C), as narrow and elongated plates in *Exodromidia*.

8) *Haledromia* (type species: *Dromia bicavernosa* Zietz, 1887 by monotypy). In *D. globosa*: apertures of spermathecae ending between P2, together on central prominence (Fig. 10A), while

in *Haledromia* the apertures end as far forward as P1, on large tubercle.

9) *Platydromia* (type species: *Dromidia spongiosa* Stimpson, 1858), which has also ventral and concealed uropods. In *D. globosa*: sternite 3 with a small part visible, particularly in males (Fig. 10A, D) (largely exposed in both sexes of *Platydromia*, Figs 15A; 16); sternite 4 triangular (Fig. 10A, D) (wide and with convex lateral margins in both sexes of *Platydromia*); male telson rounded at tip (Fig. 10B, C) (ending in acute tip in *Platydromia*, Fig. 15B, C); and apertures of spermathecae ending together, on central prominence between P2, Fig. 10A (ending together, on slight prominence between chelipeds in *Platydromia*, Fig. 16).

11) *Speodromia* (type species: *Dynomene platyarthrodes* Stebbing, 1905 by monotypy). In *D. globosa*: female uropods not visible dorsally (visible beneath setae in *Speodromia*, after Stebbing 1905: 60, pl. 17, as *Dynomene platyarthrodes*; according to McLay 1993: 182, table 5, the uropods are not visible in both sexes); apertures of spermathecae between P2 (between P1 in *Speodromia*); and P4 and P5 reduced, with P4 short and stout, P5 much longer than P4 and, when extended forward, reaching as far as anterolateral tooth (P4 and P5 dissimilar in size and shape in *Speodromia*: P4 short, thick and three-sided; P5 much more slender, specially last three articles).

12) *Tunedromia* (type species: *Petalomera yamashitai* Takeda & Miyake, 1970, by original designation). *Tunedromia* is now known from females and males (Takeda 2001). In *D. globosa*: uropods showing as ventral plates, relatively developed but completely concealed (absent in both sexes of *Tunedromia*); and P5 propodus with one distal spine opposing the dactylus and one single long outer propodal spine (multiple propodal spines opposing the dactylus and several outer propodal spines in *Tunedromia*).

Lamarckdromia globosa n. comb. has its subhepatic region deeply hollowed, which provided the specific name of *excavata* given by Stimpson (1858: 77, as *Dromidia excavata* Stimpson, 1858, junior synonym of *Dromia globosa* Lamarck, 1818). The body and legs are covered by a dense, shaggy coat of setae, and the deflexed front portion of carapace is concealed by a transverse fringe of longer setae, giving it a unique appearance. *Epipedodromia thomsoni* (Fulton & Grant, 1902) has a similar hairy ridge, forming a ledge that limits the anterior margin of the flattened carapace.

Lamarckdromia globosa n. comb. is only known from Australia. It has direct development and broods its young (Hale 1941: 281, figs 15, 16, as *Dromidiopsis excavata*; McLay *et al.* 2001: 742, as *Dromidiopsis globosa*).

Genus *Lewindromia* n. gen.
(Fig. 11)

Dromia – Rüppell 1830 *pro parte*: 16. — H. Milne Edwards 1837 *pro parte*: 170. — Alcock 1900 *pro parte*: 139. (Non *Dromia* Weber, 1795).

Dromidia – Borradaile 1903a *pro parte*: 299. — Ihle 1913 *pro parte*: 31. — Edmondson 1922: 34. — Barnard 1950 *pro parte*: 319, 323. — Garth 1973: 316. — Lewinsohn 1977: 9; 1979 *pro parte*: 2. — Tirmizi & Kazmi 1991 *pro parte*: 27. (Non *Dromidia* Stimpson, 1858).

Cryptodromiopsis – McLay 1993 *pro parte*: 187, 192; 2001a *pro parte*: 84. — McLay *et al.* 2001 *pro parte*: 740, table 3. — Chen & Haibao 2002 *pro parte*: 102, 541, 542. (Non *Cryptodromiopsis* Borradaile, 1903).

TYPE SPECIES. — *Cryptodromiopsis unidentata* Rüppell, 1830 by present designation. Gender: feminine.

ETYMOLOGY. — The genus *Lewindromia* n. gen. is dedicated to Chanan Lewinsohn (1927-1983) in recognition for his contribution to the knowledge of the Indian Ocean dromiids.

SPECIES INCLUDED. — *Cryptodromiopsis unidentata* Rüppell, 1830.
Dromidia unidentata hawaiiensis Edmondson, 1922 and *Cryptodromia unilobata* Campbell & Stephenson, 1970 were synonymised with *Dromidia unidentata* by McLay (1993: 192, 194).

DISTRIBUTION. — Indo-West Pacific: Red Sea and Indian Ocean, including sea mounts of the western Indian Ocean (see Zarenkov 1994), with a large extension in the Pacific (Australia, Hawaii, Kermadec Islands, Easter Island, see Garth 1973: 316).

DESCRIPTION

Carapace longer than wide, evenly convex; dorsal surface with regions poorly defined; branchial

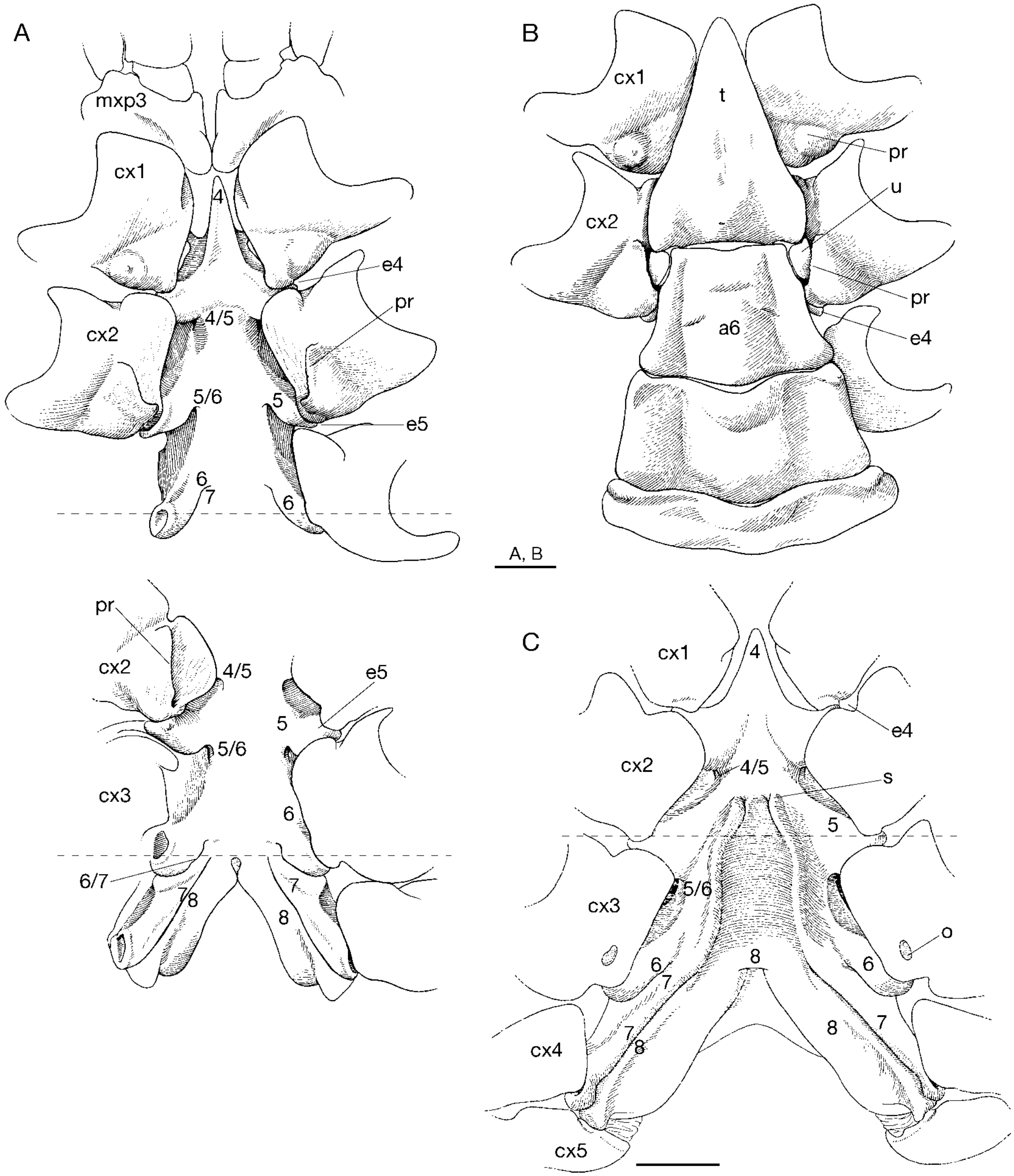

FIG. 11. — *Lewindromia unidentata* (Rüppell, 1830) n. comb.; **A**, **B**, Obock, Lewinsohn det. *Dromidia unidentata*, ♂ about 30 mm width (MNHN B-6930), thoracic sternum, two front views, without abdomen and with abdomen; **C**, Red Sea, Aden and Obock, Nobili det. *D. unidentata*, ♀ 24 × 24 mm (MNHN-B 6940), thoracic sternum and spermathecae. Abbreviations: **a6**, abdominal segment 6; **cx1**-**cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5 (in fact, episternite 4 not so visible when abdomen folded); **mxp3**, external maxilliped; **o**, female gonopore; **pr**, holding prominence: blunt prominence on P1, carina on P2; **s**, aperture of spermatheca; **t**, telson; **u**, uropod; **4-8**, sternites 4-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 2.5 mm.

groove marked, deeply notching external border. Anterolateral margin not joining exorbital angle, long, convex, entire, only with a very blunt tooth behind level of branchial groove; posterolateral margins not noticeably convergent posteriorly. Front narrow, with rostrum very small and blunt, not visible dorsally, and two pseudorostral teeth; supraorbital, suborbital and exorbital teeth present. Antenna: urinal article noticeably developed and rather straight; basal article thick, with exopod strongly developed and internal corner slightly produced, much shorter than exopod; article 4 wide. Mxp3: coxae closely approximated. Thoracic sternite 3 not visible. Sternite 4 very narrow, forming acute plate, ending in sharp tip in both sexes. In females, sternites 7 and 8 tilted, almost perpendicular in relation to precedent ones. Female sternal sutures 7/8 posteriorly wide apart, sharply close to each other at level of P3 where they are marked by thick ridge; apertures of spermathecae ending together on slight prominence between P2 (Fig. 11C). No sternal parts (very small episternite 4 may be discernible) remaining visible when male abdomen applied against ventral surface.

Male abdomen very long, without pleural parts, reaching mxp3, completely covering narrow and deep sterno-abdominal depression, and with all segments free; telson very long, with large base and regularly tapering, pointed at tip. Telson of females semi-ovate. Male segment 6 with external borders oblique and modified on edges. No vestigial pleopods in males. Uropods as dorsal plates, vertically oriented in males (Fig. 11B), well-developed in females. Uropods involved in holding of abdomen. A very efficient abdominal holding provided by long and prominent serrulated carina on P2 coxa; presence of large blunt prominence on P1 coxa.

Chelipeds without epipod. P1, P2 and P3 not knobbed nor nodose; propodus of P2 and P3 without distal spine; inner margin of dactylus armed with spines. P4 and P5 reduced, P5 being much longer than P4 and, when extended forward, reaching about mid-length of anterior margin of carapace. P5 coxa very developed in both sexes. Propodus of P4 and P5 very short and thick, as wide as long, with one distal spine opposing dactylus which is not markedly curved and ends in long horny spine; two smaller outer propodal spines.

Male P5 coxa with mobile penial tube.

Male G2 much longer than G1, thin and long flagellum overreaching sterno-abdominal depression.

Carrying behaviour

Individuals carry a wide range of camouflage material (sponges, soft coral, compound or solitary ascidians, actinians), and the cap is often very large, so that the crab is "deeply embedded" (McLay 2001a: 84). *Lewindromia unidentata* n. comb. looks like "a hairy ball that fits tightly into its piece of camouflage" (McLay 2001a: 84). See also Chen & Haibao 2002: pl. 5, fig. 2.

REMARKS

Dromia unidentata was transferred to *Dromidia* by Kossmann (1880: 67) until McLay (1993: 192) placed it in *Cryptodromiopsis*. The study of *Dromidia* sensu nobis and *Cryptodromiopsis* sensu nobis, which are restricted to their type species, led us to conclude that *D. unidentata* does not belong to neither of these genera and that a new genus should be erected for it. That new genus is named herein *Lewindromia* n. gen.

We found it useful to compare *Lewindromia* n. gen. with the genera below; special reference is made to the features other than those of the carapace.

Lewindromia n. gen. is distinguished from *Austrodromidia* sensu nobis (Figs 1; 2) by the following characters: 1) uropods showing as dorsal plates, vertically oriented (markedly reduced or even obsolete ventral plates in *Austrodromidia*); 2) male segment 6 with external borders oblique (external borders anteriorly hollowed and posteriorly expanded in *Austrodromidia*); and 3) spermathecae ending together on central prominence between P2 (ending wide apart between P2 in *Austrodromidia*).

The differences between *Lewindromia* n. gen. and *Cryptodromia* (type species: *C. coronata* Stimpson, 1858: 226, by original designation) include: 1) apertures of spermathecae closely approximated (situated wide apart in *Cryptodromia*; see the diagnosis by Stimpson 1858: 225: "*Fœminæ sterni sulci remoti, ad segmentum pedum secundi paris tantum producti, terminis in tuberculis*"); 2) male telson much longer than wide (wider than long in *Cryptodromia*); 3) male thoracic sternite 3 not visible (visible dorsally in *Cryptodromia*); 4) male thoracic sternite 4 ending in acute tip (sternite 4 anteriorly truncated in *Cryptodromia*).

Differences between *Lewindromia* n. gen. and *Cryptodromiopsis* sensu nobis (Fig. 4) include: 1) thoracic sternite 1-3 concealed in males (exposed in *Cryptodromiopsis*); 2) coxae of mxp3 placed close together (separated by distinct gap in *Cryptodromiopsis*); 3) thoracic sternite 4 ending in acute tip in males (sternite 4 not pointed in *Cryptodromiopsis*); 4) male telson much longer than wide (wider than long in *Cryptodromiopsis*); and 5) apertures of spermathecae at level of P2 (at level of P1 in *Cryptodromiopsis*).

Lewindromia n. gen. is distinguished from *Dromidia* sensu nobis (Fig. 5) by the following characters: 1) male abdominal segment 6 with external borders oblique and sinuous (external borders subparallel in *Dromidia*); 2) male telson much longer than wide, regularly tapering, and the tip becoming very narrow (telson wider than long, ending by sharp spine in *Dromidia*); 3) male uropods as dorsal plates, vertically oriented, exposed and completely visible dorsally (almost totally concealed ventral plates in *Dromidia*); 4) uropods involved in abdominal holding which consists of uropods fitting in front of serrulated carina on P2 coxae; an additional strong, rounded prominence on P1 coxa (uropods not involved at all in abdominal holding; a strong spine directed backwards, partly overhanging abdomen in *Dromidia*); and 5) thoracic sternite 4 tapering and ending in acute tip (sternite 4 broad, ending in rounded tip in *Dromidia*).

Lewindromia n. gen. and *Dromidiopsis* sensu nobis (Fig. 6), both with uropods oriented vertically, differ from each other as follows: 1) all abdominal segments free (abdominal segments 5 and 6 fused together in *Dromidiopsis*); 2) pseudorostral teeth prominent, so that entire front is strongly produced forward (lateral frontal lobes extremely low so that entire front is produced forward only slightly in *Dromidiopsis*); 3) propodus of P4 and P5 subequal in size (of different size, that of P5 much longer in *Dromidiopsis*); 4) when extended forward, P5 reaching about mid-length of anterior margin of carapace (P5 much long, reaching as far as outer orbital angle in *Dromidiopsis*); 5) female sternal sutures 7/8 sharply close to each other at level of P3 where they are lined by thick ridge (separated wide apart, getting progressively close to each other in *Dromidiopsis*); 6) apertures of spermathecae at level of P2 (at level of P1 or just behind them in *Dromidiopsis*); and 7) thoracic sternite 4 ending in acute tip (sternite 4 truncated distally in *Dromidiopsis*).

Lewindromia n. gen. and *Homalodromia* (Fig. 9), both with uropods vertically oriented, differ from each other, as follows: 1) apertures of spermathecae together on slight prominence between P2 (Fig. 11C) (apertures at each extremity of a tubular prominence forming bridge between P1 coxae in *Homalodromia*); 2) sternite 4 forming acute plate, ending in sharp tip (Fig. 11A, C) (bluntly truncate at tip in *Homalodromia*); and 3) no sternal parts remaining visible when male abdomen applied against ventral surface (Fig. 11B); small episternite 4 hardly dicernible at lower plane or not visible (sternite 4 and episternite 4 remaining visible in *Homalodromia*).

Lewindromia n. gen. and *Lamarckdromia* n. gen. share the thoracic sternite 4 showing as triangular acute plate, but narrower in *Lewindromia* n. gen. The following characters readily distinguish *Lewindromia* n. gen. from *Lamarckdromia* n. gen. (Fig. 10): 1) male abdominal segment 6 with external borders oblique and sinuous (external borders subparallel in *Lewindromia* n. gen.); 2) male telson much longer than wide, regularly tapering, the tip becoming narrow (telson wider than long, rounded at tip, in *Lewindromia* n. gen.); 3) male uropods plates exposed, vertically oriented, involved in abdominal holding (showing as totally concealed ventral plates, not involved, in *Lewindromia*); and 4) thoracic sternite 4 forming acute plate, ending in sharp tip (with anterior margin triangular in *Lewindromia* n. gen.).

Lewindromia n. gen. and *Lauridromia* (McLay 1993: 145, table 2; see Guinot & Bouchard 1998, fig. 2A-C) share several characters: triangular shape of sternite 4, although narrower in *Lewindromia* n. gen.; male abdomen completely covering sterno-abdominal depression; vertically oriented uropods; holding prominences on P2 and P1 coxae. *Lewindromia* n. gen. differs from *Lauridromia* by: 1) all abdominal segments free (segments 5 and 6 fused, at least in some extent, in *Lauridromia*); 2) apertures of spermathecae grouped together on slight prominence between P2 (Fig. 11C) (wide apart, at level of episternites 4, each at summit of tubercle, in *Lauridromia*); 3) epipod on cheliped absent (present in *Lauridromia*); and 4) terminal apparatus of P5 consisting of only one distal propodal spine opposing the dactylus, and two outer propodal spines small (two propodal spines and several others well-developed spines in *Lauridromia*).

Lewindromia n. gen. differs from all the above genera by having an extremely long G2, which overreaches the tip of telson when abdomen is completely folded (G2 shorter, fitted inside sternoabdominal depression in the other genera).

Genus *Mclaydromia* n. gen.
(Figs 12; 13)

?*Dromidiopsis* – Lewinsohn 1984 *pro parte*: 102.

Dromidiopsis – McLay 1993 *pro parte*: 135, 138; 2001a *pro parte*: 79, 80. (Non *Dromidiopsis* Borradaile, 1900 sensu nobis).

TYPE SPECIES. — *Mclaydromia colini* n. gen., n. sp., by present designation.

SPECIES INCLUDED. — *Mclaydromia colini* n. gen., n. sp.; *Dromidiopsis dubia* Lewinsohn, 1984.

ETYMOLOGY. — We dedicate the new genus *Mclaydromia* n. gen. to our colleague Colin L. McLay (University of Canterbury, Christchurch, New Zealand), for greatly improving our view of the Dromiidae. Gender: feminine.

DISTRIBUTION. — New Caledonia and Madagascar.

DESCRIPTION

Carapace distinctly longer than wide, convex. Dorsal surface with regions poorly defined; branchial groove defined and posteriorly marked by blunt tooth. Anterolateral margin of carapace not joining exorbital angle and armed with two or three teeth. Posterolateral margin slightly shorter than anterolateral margin and with blunt tooth just behind branchial groove. Front (Fig. 13) wide, obscurely tridentate: rostrum very small, directed downwards, and not visible dorsally; two pseudorostral teeth, more or less developed, sometimes eave-like. Supraorbital and suborbital teeth not well marked; exorbital angle not produced. Antenna: urinal article broader than long, with anterior part of beak small and downcurved; basal article with well-developed exopod; internal corner about as long as exopod; antennal article 4 long and fitted in between. Mxp3: coxae closely approximated.

Thoracic sternite 3 partly visible at lower plane (sternites 1-2 not exposed); sternite 4 narrow, with subparallel margins, anterior margin truncated (Fig. 12). Female sternal sutures 7/8 long, apertures of spermathecae placed apart, each on a tubercle, between coxae of P2 (Fig. 12B). When male abdomen folded against cephalothorax, sternite 3 (partly) and large part of sternite 4 remaining visible; a minute part of episternite 4 exposed; episternite 5 not visible.

Male abdomen not completely covering sterno-abdominal depression. All abdominal segments free in males and females. Male abdominal segment 6 abruptly constricted, edge markedly thickened. Telson rather long, with enlarged base and rounded anterior margin. No vestigial pleopods in males. Uropods showing as strongly salient dorsal plates in males, that are obliquely oriented. Uropods markedly involved in abdominal holding. Abdominal holding provided by curved, serrate, strong flange on P2 coxa, which is in close contact with uropod and fits into excavation on lateral edge of abdominal segment 6; additionally, on coxa of P1, few tiny tubercles placed closely together, or one more distinctly marked tubercle, without contact with telson.

Chelipeds with an epipod. In both sexes cutting edges of fixed finger and dactylus of two che-

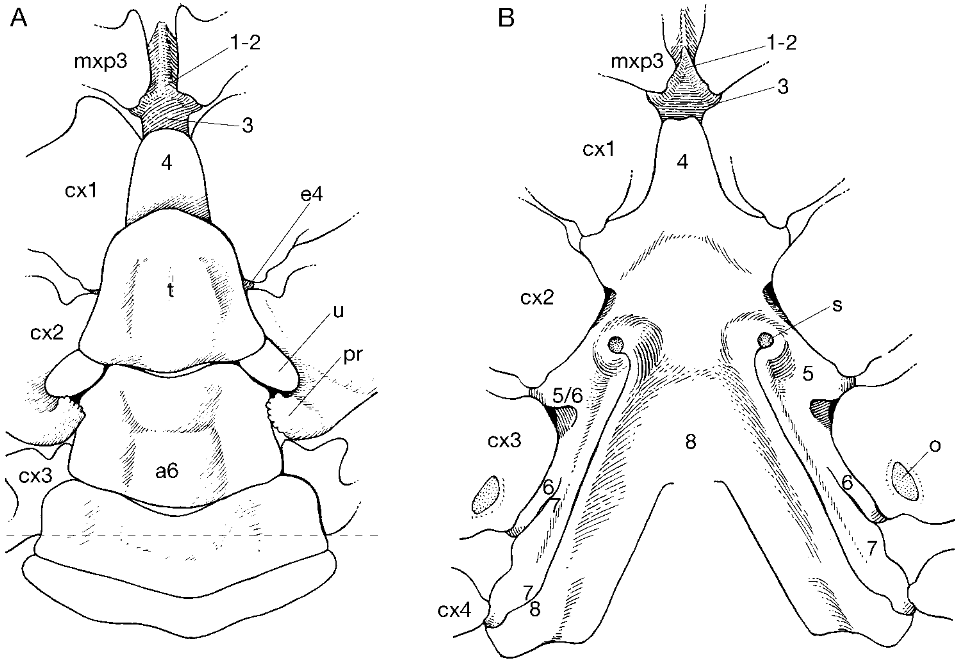

FIG. 12. — *Mclaydromia colini* n. gen., n. sp.; **A**, LAGON, stn 111, 25 m, ♂ 10.4 × 9.1 mm, paratype (MNHN-B 26282), thoracic sternum with abdomen; **B**, LAGON, stn 569, 62 m, ovigerous ♀ 9.4 × 8.6 mm, paratype (MNHN-B 26289), thoracic sternum and spermathecae. Abbreviations: **a6**, abdominal segment 6; **cx1**-**cx4**, coxae of P1-P4; **e4**, episternite 4 (very small); **mxp3**, external maxilliped (coxae separated for clarity); **o**, female gonopore; **pr**, holding prominence; **s**, aperture of spermatheca; **t**, telson; **u**, uropod; **1**-**2** sternites 1-2 (normally not exposed); **3**, sternite 3; **4**-**8**, sternites 4-8; **4/5**-**7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 2.5 mm.

lipeds armed halfway with strong molariform tooth (may be bifid), which is directed backwards and followed by the usual interlocking distal teeth. P2 and P3 short and stout, not knobbed nor nodose; propodus of P2 and P3 without distal spine; inner margin of dactylus armed with spines. P4 and P5 reduced, P5 longer than P4; propodus of P4 and P5 very short, subequal in size. Subcheliform apparatus formed by one small distal spine opposing short and curved dactylus; an outer propodal spine may be present on P5.
Male P5 coxa with mobile penial tube.
Male G2 with a needle-like flagellum, long but completely included in sterno-abdominal depression.

Carrying behaviour
Sponges (McLay 1993: 139, under *Dromidiopsis dubia*).

REMARKS
In assigning with doubt his new species *D. dubia* to *Dromidiopsis*, Lewinsohn (1984: 102, 104, fig. 2b, c) stressed its peculiar features, particularly the fingers and dactyli of chelipeds. The presence of a molariform tooth on two cutting edges in *Mclaydromia* n. gen. appears unique amongst the Dromiidae (which is sometimes present in the Dynomenidae) and may indicate a specialized feeding habit (McLay 1993: 139). A proximal tooth may be present along the cutting edge of dactylus in a few dromiid genera (as in *Epigodromia* McLay, 1993), but the condition of *Mclaydromia* n. gen., with two molariform teeth halfway on prehensile margin of fixed finger and dactylus, is exceptional.
Mclaydromia n. gen. can be readily distinguished from *Dromidiopsis* sensu nobis (Fig. 6) as follows: 1) abdominal segments free (abdominal segments 5 and 6 fused together in *Dromidiopsis*);

2) propodus of P4 and P5 subequal in size (dissimilar, much longer on P5, in *Dromidiopsis*); 3) when extended forward, P5 barely overreaching last lateral tooth of carapace (much long, reaching about outer orbital angle in *Dromidiopsis*); 4) female sutures 7/8 wide apart, oblique, getting progressively close to each other as they run forward over thoracic sternites (getting much closed to each other at level of P3 and subparallel in *Dromidiopsis*); 5) apertures of spermathecae at level of P2 and placed wide apart from each other, on tubercles (at level of P1 or just behind and lying close together, on central prominence, in *Dromidiopsis*); and 6) male uropods showing as dorsal plates that are obliquely oriented (vertically oriented in *Dromidiopsis*).

The following characters readily distinguish *Mclaydromia* n. gen. from *Cryptodromiopsis* sensu nobis (Fig. 4), which also has obliquely oriented dorsal uropods: 1) male segment 6 with external borders deeply hollowed and thickened (subparallel on anterior half in *Cryptodromiopsis*); 2) apertures of spermathecae apart, each on a tubercle, at level of P2 (ending together on slight tubercle between chelipeds in *Cryptodromiopsis*); and 3) P2 and P3 not knobbed (knobbed in *Cryptodromiopsis*).

Mclaydromia n. gen. is very close to *Hemisphaerodromia* on account of similarities on the frontal and orbital regions and of subcheliform nature of the P4 and P5. Additionally, they share a sternite 4 that is anteriorly truncated and with subparallel lateral borders; male abdominal segment 6 broad, and with external borders deeply hollowed and thickened to receive coxal prominence of P2; dorsal uropods salient, that are obliquely oriented and completely involved in abdominal holding (Guinot & Bouchard 1998: fig. 3C, D, *H. monodus*); apertures of spermathecae apart, at about the level of P2 (see Fig. 7B for *H. monodus*, and Fig. 12B for *M. colini* n. gen., n. sp.). The following characters distinguish the two genera: 1) thoracic sternite 3 not exposed in *Hemisphaerodromia* (partly visible at lower plane in *Mclaydromia* n. gen., sternites 1-2 not exposed, however); 2) apertures of spermathecae located at level of episternites 5 in *Hemisphaerodromia* (apertures forward, between P2, in *Mclaydromia* n. gen.); and 3) fingers of chelipeds normally toothed along prehensile margin in *Hemisphaerodromia* (molariform teeth on fixed finger and dactylus in *Mclaydromia* n. gen.).

The following characters readily distinguish *Mclaydromia* n. gen. from *Lewindromia* n. gen. (Fig. 11), with vertically oriented dorsal uropods: 1) sternite 4 with anterior margin truncated (acutely produced in *Lewindromia* n. gen.); 2) male abdominal segment 6 abruptly constricted (with external borders sinuous, oblique, in *Lewindromia* n. gen.); 3) male telson not longer than wide and rounded at tip (very long and pointed in *Lewindromia* n. gen.); and 4) propodus of P4 and P5 not much different in size, a distal spine opposing the curved dactylus, and an outer propodal spine may be present on P5 (P5 much longer than P4 and, when extended forward, reaching about mid-length of anterior margin of carapace, a propodal distal spine opposing the dactylus which is not strongly curved, and two outer propodal spines in *Lewindromia* n. gen.).

Mclaydromia colini n. sp.
(Figs 12; 13)

Dromidiopsis dubia – McLay 1993: 138, fig. 15c. (Non *Dromidiopsis dubia* Lewinsohn, 1984).

TYPE MATERIAL. — **New Caledonia.** LAGON, stn 619, 22°3.2'S, 166°54.2'E, 27-42 m, 06.VIII.1986, holotype ♂ 16.2 × 13.2 mm (MNHN-B 22546); stn 111, 22°24.30'S, 166°47.70'E, 25 m, 22.VIII.1984, paratype ♂ 10.4 × 9.1 mm (MNHN-B 26282); stn 569, 22°48.80'S, 166°58.90'E, 62 m, 17.VII.1985, paratype ovigerous ♀ 9.4 × 8.6 mm (MNHN-B 26289); stn 215, 21°52.90'S, 165°49.90'E, 14 m, 21.IX.1984, paratype ovigerous ♀ 12.0 × 10.3 mm (MNHN-B 26284); stn 303, 22°38'S, 166°49.10'E, 30-35 m, 27.XI.1984, paratype ♂ 11.3 × 9.7 mm (MNHN-B26280); stn 104, 22°26'S, 166°40.40'E, 24 m, 22.VIII.1984, paratype ovigerous ♀ 9.6 × 8.5 mm (MNHN-B 26281).

Although we have examined all the material from New Caledonia referred by McLay (1993), only the specimens selected for the type series are given herein. For the locality details of remaining specimens see McLay (1993: 138).

ETYMOLOGY. — The present species is dedicated to Colin L. McLay (University of Canterbury, Christchurch, New Zealand).

TYPE LOCALITY. — New Caledonia, 22°3.2'S, 166°54.2'E, 27-42 m.

DISTRIBUTION. — Only known from New Caledonia.

DESCRIPTION

Carapace noticeably longer than wide, covered with a fine tomentum. Tomentum more developed on flanks of carapace, chelipeds, and legs. Cardiac region ill defined; branchial groove well recognizable, a blunt small tooth just behind; regions of carapace not defined. Front wide. Median frontal tooth (rostrum) small but well recognizable. Lateral frontal teeth (pseudorostral) prominent, blunt, so that entire front is produced forward. Supraorbital tooth quitely distinct. Exorbital angle without tooth. Orbital fissure very deep. Suborbital margin abruptly interrupted, forming suborbital lobe, and leaving deep and broad hiatus between suborbital lobe and antenna. Two marked but blunt teeth on anterior half of anterolateral margin: first tooth lying about level of orbital fissure; second tooth much larger and placed at higher level than first; a smaller, rounded third anterolateral tooth visible. Subhepatic tubercle strong in adults, low but well recognizable in young.

Carpus of cheliped ornamented with several tubercles on dorsal surface and with strong tubercle on external distal margin; remaining cheliped articles smooth. Cutting edge of dactylus with minute proximal teeth followed by molariform tooth backwards directed, opposed to similar tooth on cutting edge of fixed finger; distally, the usual interlocking teeth. Cheliped with well-developed epipodite.

Rather dense tomentum covering P2 to P5, their margins fringed with closely placed plumose setae. P2 and P3 robust. Upper margin of merus with a rounded tubercle placed distally; upper surface of remaining articles smooth, no obvious tubercles or conspicuous elevations. Dactylus slightly shorter than propodus, inner margin armed with acute spines, claw strong; condyles of P2 and P3 very strong, rounded. P5 longer than P4. Dactylus of P4 curved, opposed by small propodal spine; no spine on outer propodal margin. Dactylus of P5 strongly curved, opposed by single spine propodal, stronger than on P4; a minute spine on distal outer propodal margin.

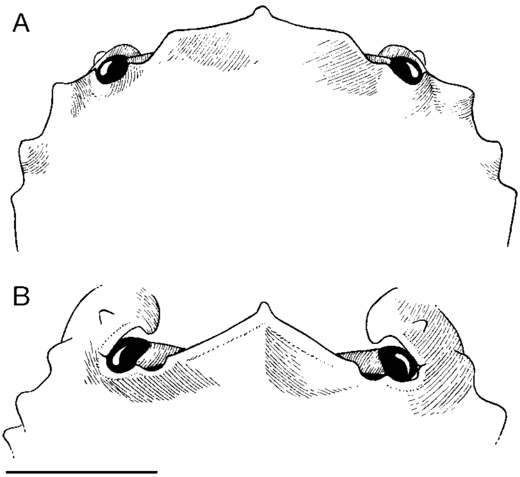

FIG. 13. — *Mclaydromia colini* n. gen., n. sp., LAGON, stn 111, 25 m, ♂ 10.4 × 9.1 mm, paratype (MNHN-B 26282), views of frontal border of carapace; **A**, dorsal view; **B**, anterodorsal view. Scale bar: 2.5 mm.

Abdomen composed of six free segments, plus telson. Male telson about as long as broad, rounded distally. Abdominal segment 2 with wing-like lateral expansion covering base of penial tube issued from P5 coxa. Abdominal segment 6 abruptly constricted, considerably narrower than segment 5. Uropod plates salient, visible dorsally. Abdominal holding consisting of uropod plate fitting in front of curved serrate flange on base of P2 coxa; additionally, on P1 coxa a marked tubercle, may be a group of very small and closely approximated granules, without contact with telson.

REMARKS

Dromidiopsis dubia was described from a single male (the holotype) from Madagascar. The comparison of the holotype and two additional adult males from Madagascar with several individuals from New Caledonia, previously identified as *D. dubia* by McLay (1993: 138), has shown that the New Caledonian specimens should no longer be attributed to *D. dubia*. The material belongs to a new species, named herein *Mclaydromia colini* n. gen., n. sp.

In addition to male holotype (10.5 × 9 mm) of *D. dubia* Lewinsohn, 1984, the following material has been examined:

Madagascar. Near Tany Kely, 13°27'S, 48°10'E, 30 m, 13.VIII.1971, A. Crosnier coll., holotype ♂ 10.5 × 9 mm (MNHN-B 6894). — Near Nosy-Bé, Tany Kely, north-west coast, 23 m, 30.IX.1970, P. Laboute coll., ♂ 12.5 × 11.5 mm (MNHN-B 22592). — 13°40.3'S, 47°48'E, 32 m, 05.XII.1972, A. Crosnier coll., ♂ 15 × 13 mm (MNHN-B 22593).

Mclaydromia colini n. gen., n. sp. and *M. dubia* n. comb. can be differentiated as follows: 1) in *M colini* n. gen., n. sp. the blunt lateral frontal teeth (pseudorostral teeth) are prominent, so that entire front is produced forward, while in *M. dubia* n. comb. the lateral frontal teeth are short and rounded so that entire front is produced only slightly forward; and 2) in *M. colini* n. gen., n. sp. the dorsal face of carpus of cheliped is ornamented with conspicuous tubercles, whereas in *M. dubia* n. comb. the dorsal surface of carpus is smooth.

The above characters are constant throughout the material examined, regardless sex and age of the individuals examined. Full-grown individuals of *Mclaydromia colini* n. gen., n. sp. and *M. dubia* n. comb. can also be separated by the following additional characters: 1) in *Mclaydromia colini* n. gen., n. sp. suborbital margin abruptly interrupted, forming well individualized suborbital lobe and leaving deep and broad hiatus between suborbital lobe and antenna (suborbital margin gently interrupted, leaving only a narrow sinus between suborbital lobe and antenna in *M. dubia* n. comb.); 2) in *M. colini* n. gen., n. sp. a small, rounded but well visible third anterolateral tooth (only a small elevation behind second anterolateral tooth of carapace in *M. dubia* n. comb.); and 3) in *M. colini* n. gen., n. sp. subhepatic tubercle strong (very low in *M. dubia* n. comb.).

The original description of *Dromidiopsis dubia* mentions the absence of subhepatic tubercle on carapace and the smooth cheliped, except two weakly developed tubercles on distal margin of carpus (Lewinsohn 1984: 102). We confirm these features in male holotype (10.5 × 9 mm) but, in a larger male (15 × 13 mm), a subhepatic tubercle is well recognizable although being very low, and the two teeth on carpus of cheliped are absent. The development of carapace teeth varies with age in both species. A colour photograph of a specimen from Maldive Islands is given by Debelius (1999: 249, as *D. dubia*).

Two individuals of *M. colini* n. gen., n. sp. were carrying a sponge cap.

Genus *Moreiradromia* n. gen.

(Figs 14; 28H)

Dromidia – Stimpson 1858 *pro parte*: 225. (Non *Dromidia* Stimpson, 1858, type species: *Dromia hirsutissima* Lamarck, 1818 by original designation).

Dromidia (restricted synonymy) – Henderson 1888 *pro parte*: 12. — Bouvier 1896 *pro parte*: 20 (53). — Borradaile 1903a *pro parte*: 299, 301. — Moreira 1901: 34; 1905: 136. — Rathbun 1937: 32. — Williams 1965: 143; 1984: 255. — Coelho & Ramos 1972: 177. — Coelho & Ramos-Porto 1989: 215. — Forest 1974 *pro parte*: 89, footnote. — Powers 1977: 19. — Manning & Chace 1990: 43.

Evius Moreira, 1912: 322 (type species *Evius ruber* Moreira, 1912 by monotypy. Name pre-occupied by *Evius* Walker, 1855 [type species: *Phalaena hippia* (Stoll, 1790), Lepidoptera]). — Rathbun 1937: 30, footnote. — Franco 1998: 11.

Cryptodromiopsis – McLay 1993 *pro parte*: 187. — Melo 1996: 67. — Hendrickx 1997: 17. — Debelius 1999: 80 (photograph of *C. antillensis*). — Melo & Campos 1999 *pro parte*: 275, 279. — McLay *et al.* 2001 *pro parte*: 733, 743, tables 2, 3. (Non *Cryptodromiopsis* Borradaile, 1903, type species: *Cryptodromiopsis tridens* Borradaile, 1903 by monotypy).

TYPE SPECIES. — *Dromidia antillensis* Stimpson, 1858 by present designation.

SPECIES INCLUDED. — *Dromidia antillensis* Stimpson, 1858; *D. sarraburei* Rathbun, 1910 (not *larraburei*; see Boyko 1998: 234).

ETYMOLOGY. — The present new genus is named after Carlos Moreira (1869-1946) in recognition for his significant contributions to Brazilian carcinology. Gender: feminine.

DISTRIBUTION. — Western Atlantic and Eastern Pacific regions.

DESCRIPTION

Carapace longer than wide or slightly wider than long, convex. Regions weakly defined, except for

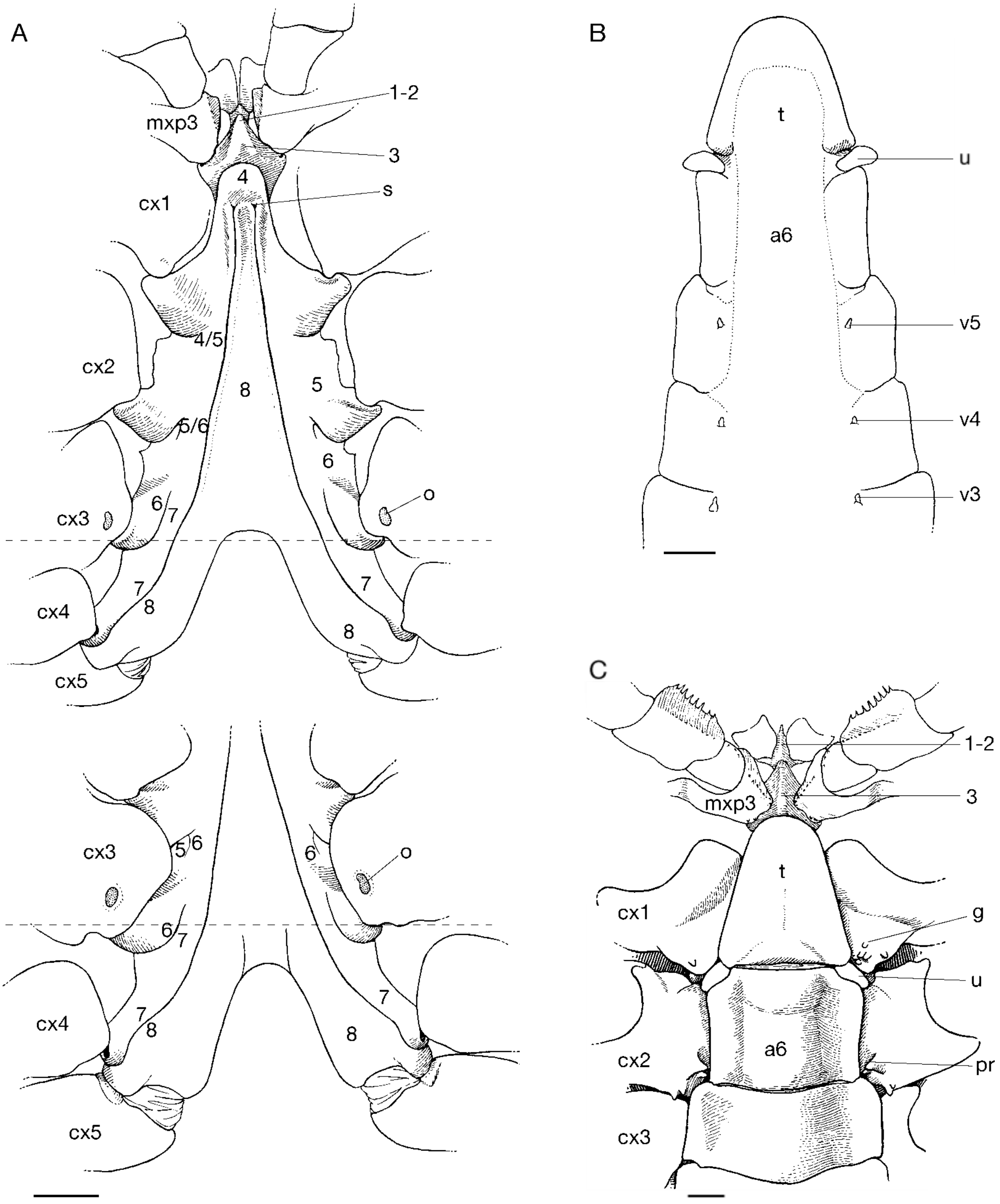

FIG. 14. — **A**, **B**, *Moreiradromia antillensis* (Stimpson, 1858) n. comb.; **A**, South America, *Calypso*, ♀ 14 × 15 mm (MNHN-B 12717), thoracic sternum, two front views, and spermathecae; **B**, Florida, ♂ 16 × 15 mm (MNHN-B 12753), ventral surface of abdomen, with vestigial pleopods on segments 3-5; **C**, *Moreiradromia sarraburei* (Rathbun, 1910) n. comb., San José Island, Diguet coll., McLay det. *Cryptodromiopsis larraburei*, ♂ 18.4 × 19 mm (MNHN-B 12761), thoracic sternum with abdomen (tilted for clarity). Abbreviations: **a6**, abdominal segment 6; **cx1**-**cx5**, coxae of P1-P5; **g**, granules on P1 coxa; **mxp3**, external maxilliped; **o**, female gonopore; **pr**, holding spiniform prominence; **s**, aperture of spermatheca; **t**, telson; **u**, uropod; **v3**-**v5**, vestigial pleopods 3-5; **1-2**, sternites 1-2; **3-8**, sternites 3-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 1 mm.

branchial groove. Front dentate, rostrum directed downward. Anterolateral margin toothed, teeth almost spiniform, a tooth just behind branchial groove. Subhepatic region with tooth, visible dorsally. Supra- and suborbital teeth present, exorbital absent; a deep fissure separating supra- and suborbital margins. Ocular stalk short and stout. Antenna: urinal article rather straight, so urinal opening aligned with horizontal axis of article; basal article with exopod noticeably developed, reaching antennal article 4, and internal angle weakly produced, much shorter than exopod. Mxp3: coxae separated by gap.

Thoracic sternites 1-2 visible at lower plane. Thoracic sternite 3 inserted between mxp3 coxae, exposed but more or less covered by telson (*M. antillensis* n. comb., Fig. 14A; *M. sarraburei* n. comb., Fig. 14C). Sternite 4 narrowing distally, ending in gently rounded/truncate and raised tip (*M. antillensis* n. comb.), slightly concave and not raised (*M. sarraburei* n. comb.), so coxae of P1 close to each other. Female sutures 7/8 extremely long, getting progressively close to each other as they run forward over thoracic sternites; apertures of spermathecae situated together and beyond articular condyle of P1 on anterior part of sternite 4, raised (*M. antillensis* n. comb., Fig. 14A) or not (*M. sarraburei* n. comb.).

Male abdomen long, almost reaching mxp3, leaving no parts of sternite 4 visible; all abdominal segments free. Male abdominal segment 6 long, length as much as three quarters of width; telson longer than wide, rounded and bluntly tipped. Male uropods showing as well-developed dorsal plates, visible in dorsal view of abdomen, obliquely oriented and very movable, not involved in holding of abdomen. Presence of vestigial pleopods in males (Fig. 14B): Pl3-Pl5 showing as vestigial buds, tiny and may be obsolete in larger individuals. Abdominal holding provided by main spine that projects from P2 coxa and overhangs abdominal segment 6; base of P2 coxa may bear other small and not efficient tubercles (*M. sarraburei* n. comb.); on coxae of P1 (*M. sarraburei* n. comb.), P3 and even P4, presence of tubercles or granules, more or less conspicuous; epsiternite 5 with a few granules (*M. sarraburei* n. comb.).

Chelipeds rather short and stout, without epipod. P2 and P3 rather slender, smooth, not nodose; no distal spine on propodus; inner margin of dactylus spinulated. P4 and P5 reduced, P5 much longer than P4, both with a subcheliform apparatus formed by two distal propodal spines opposing dactylus; an outer propodal spine, and one or two spines on margins of P5 dactylus.

Male P5 coxa with mobile penial tube (Fig. 28H). G2 with a styliform, needle like flagellum.

Carrying behaviour

Sponges, zoanthoid polyps, compound ascidians, occasionally sea anemones.

REMARKS

As pointed out by Rathbun (1937), the description as a new genus and species, *Evius ruber* Moreira, 1912, was based on a megalopa stage. Recently Guinot & Tavares (2000) elucidated another case of a dromiid genus based on a megalopa, *Conchoedromia* Chopra, 1934. The description of dromiid genera based on the megalopa stage stems from the fact that the dromiid larvae were poorly known at that time. The only dromiid postlarvae known prior to 1934 were those of *Austrodromidia octodentata* (Haswell, 1882) and *Stimdromia lateralis* (Gray, 1831) (Guinot & Tavares 2000). Had the dromiid megalopa been better documented at that time, someone with Moreira's or Chopra's experience would certainly have recognized his material as a megalopa stage. According to Rathbun (1937: 31, pl. 8, figs 1, 2), *Evius ruber* is the megalopa of *Dromia erythropus* G. Edwards, 1771. A detailed study by Franco (1998) revealed, however, that *E. ruber* was actually described from a megalopa of *Dromidia antillensis*.

Although the availability of the name *Evius* Moreira, 1912 is not affected by the fact that it was applied to a "stage in the life cycle" (ICZN 1999: article 17.3), *Evius* Moreira, 1912 is actually pre-occupied by *Evius* Walker, 1855 (type species: *Phalaena hippia* (Stoll, 1790), Lepidoptera). Consequently, a new name, *Moreira-*

dromia n. gen., is herein established to replace *Evius* Moreira, 1912.

Originally described in *Dromidia*, the position of *D. antillensis* and *D. sarraburei* remained undisputed until McLay (1993: 187, 188) transferred both species to *Cryptodromiopsis*. He provided no morphological information to justify such a decision and limited himself to state that "the Atlantic species formerly known as *Dromidia antillensis* Stimpson, 1858, as well as the closely related *D. larraburei* [*sic*] Rathbun, 1910, from the Pacific, should now be referred to as *Cryptodromiopsis antillensis* (Stimpson, 1858) and *C. larraburei* [*sic*] (Rathbun, 1910)" (McLay 1993: 188). Nevertheless, we agree with McLay that the American species do not belong in *Dromidia* sensu nobis.

A study of species assigned to *Dromidia* and *Cryptodromiopsis* (now restricted to their type species, *Dromidia hirsutissima* and *Cryptodromiopsis tridens*, respectively) showed that a new genus should be created for the American species *antillensis* (Western Atlantic) and *sarraburei* (Eastern Pacific). That new genus is herein referred as *Moreiradromia* n. gen.

Several morphological features support the creation of *Moreiradromia* n. gen. and distinction from *Dromidia* sensu nobis: 1) male uropods showing as movable and well-developed dorsal plates in *Moreiradromia* n. gen. (as ventral plates, almost completely concealed in dorsal view, and almost immovabe in *Dromidia*, Fig. 5); 2) male abdomen narrow (relatively wide in *Dromidia*); 3) male abdomen when folded nearly reaching coxae of mxp3, leaving no parts of sternite 4 visible (anterior portion of sternite 4 and episternite 4 visible in *Dromidia*); 4) male abdominal segment 6 long, with length as much as three quarters of width (short, length half the width, in *Dromidia*); 5) male telson longer than wide, rounded and bluntly tipped (telson much wider than long, ending in spine in *Dromidia*); 6) male Pl3-Pl5 showing as vestigial buds (Fig. 14B), always present but hard to locate due to their tiny size (Pl3-Pl5 longer, easy to locate in *Dromidia*); 7) thoracic sternite 3 present, so a narrow gap between coxae of mxp3 (sternite 3 not visible, coxae of mxp3 closely approximated in *Dromidia*); and 8) P4 and P5 with two distal propodal spines opposing the dactylus (a single distal spine opposing the very long dactylus in *Dromidia*). The abdominal holdings are similar in both genera, being provided on the P2 coxae by spine which overhangs abdomen. In *Moreiradromia* n. gen., however, the coxal spine is much smaller, other tubercles may be present on P2 coxa and episternite 5 (*M. sarraburei* n. comb.), and tubercles or granules exist on P1 coxae (*M. sarraburei* n. comb.), P3 and even P4 coxae (see Guinot & Bouchard 1998: 624, 628, fig. 4C).

The following characters distinguish *Moreiradromia* n. gen. from *Cryptodromiopsis* sensu nobis (Fig. 4): 1) male vestigial Pl3-Pl5 present (absent in *Cryptodromiopsis*); 2) thoracic sternites 1-2 visible dorsally, thoracic sternite 3 exposed, remaining dorsally partly visible or almost completely covered by male abdomen, when folded, in *M. sarraburei* n. comb. (Fig. 14C); sternite 4 always covered (sternites 1-3, anterior portion of sternite 4 and episternites 4 and 5 visible in *Cryptodromiopsis*); 3) holding of abdomen provided mostly by small spine on P2 coxa, overhanging abdominal segment 6, without the involvement of uropods (a serrated granulous prominence on P2 coxa in *Cryptodromiopsis*); 4) female sutures 7/8 getting progressively close to each other as they run forward over thoracic sternites and ending well beyond articular condyle of P1 (separated wide apart, getting close to each other abruptly at level of P2 and ending at level of articular condyle of P1 in *Cryptodromiopsis*); 5) apertures of spermathecae and thoracic sternite 4 placed about at same plane (apertures and sternite 4 placed at different planes; sternite 4 directed downward, in *Cryptodromiopsis*); 6) female thoracic sternite 4 narrowing progressively forward, ending in gently rounded tip, so that P1 coxae get close to each other (wider, noticeably truncated, so that P1 coxae are separated from each other wide apart in *Cryptodromiopsis*); 7) urinal article of antenna rather straight, so that the urinal opening is aligned with horizontal axis of article (upturned urinal article, with opening placed above axis of urinal article in *Cryptodromiopsis*); 8) exopod of basal antennal article noticeably developed, reaching article 4, much longer than internal corner (exopod comparatively poorly developed, much shorter than internal corner which is produced, in *Cryptodromiopsis*); and 9) P4 and P5 with two distal propodal spines opposing the dactylus (only one distal propodal spine in *Cryptodromiopsis*).

The following characters distinguish *Moreiradromia* n. gen. from *Dromidiopsis* sensu nobis: 1) uropods as dorsal plates obliquely oriented in *Moreiradromia* n. gen. (vertically oriented in *Dromidiopsis*, Fig. 6); 2) male abdomen with all segments free (segments 5-6 fused in *Dromidiopsis*); 3) sternite 4 completely covered, when male abdomen folded and reaching coxae of mxp3 (extreme anterior part of sternite 4 and a small epsisternite 4 remaining uncovered in *Dromidiopsis*); 4) apertures of spermathecae on prominence placed well beyond articular condyle of P1 (ending between P1 or just behind them, together on central prominence, in *Dromidiopsis*); 5) P4 and P5 with two distal propodal spines opposing the dactylus (one distal spine opposing the dactylus in *Dromidiopsis*) ; 6) male vestigial Pl3-Pl5 present in *Moreiradromia* n. gen. (absent in *Dromidiopsis*). Other differences between *Moreiradromia* n. gen. and *Dromidiopsis* are the abdominal holdings, provided in *Dromidiopsis* by strong dentate crest on P2 coxae acting with uropods (Fig. 6B), but by a spine on P2 coxa which overhangs abdominal segment 6, without involvement of the uropods, in *Moreiradromia* n. gen. (Fig. 14C).

Carrying behaviour has been reported for both species currently included in *Moreiradromia* n. gen., *M. antillensis* n. comb. and *M. sarraburei* n. comb. Individuals of the two species cover themselves with sponges, zoanthoid polyps, compound ascidians, and occasionally sea anemones (Brusca 1980; Williams 1984; Hendrickx 1997).

Only three dromiid genera are known from the Atlantic and Eastern Pacific: *Dromia* (Dromiinae n. status), *Moreiradromia* n. gen. (Dromiinae n. status), and *Hypoconcha* (Hypoconchinae n. subfam., see Figs 19; 20; 28K). Nevertheless, this rather poor American dromiid fauna, with two endemic genera (*Hypoconcha* and *Moreiradromia* n. gen.), is unique. As currently defined, *Dromia* is composite, and the generic status of a number of species currently assigned to *Dromia* s.s., including the single Western Atlantic species in the genus (*D. erythropus* G. Edwards, 1771), deserves more attention.

A colour photograph of *Moreiradromia antillensis* n. comb. showing a specimen from Dominica is given by Debelius (1999: 80 as *Cryptodromiopsis antillensis*).

Genus *Platydromia* Brocchi, 1877
(Figs 15; 16)

Platydromia Brocchi, 1877: 53, 54. (Non *Platydromia* Fulton & Grant, 1902a: 57, replacement name: *Epipedodromia* André, 1932: 180 footnote, see McLay 1993: 124, 224, table 8, type species: *Platydromia thomsoni* Fulton & Grant, 1902 by monotypy).

Dromien – Vélain 1878: 67, 73.

Platydromia – André 1932: 178, 179.

Dromidia – Stimpson 1858 *pro parte*: 225; 1907: 170. — Henderson 1888: 12. — Bouvier 1896 *pro parte*: 21 (54). — McLay 1993 *pro parte*: 121, 183, 224, 225. (Non *Dromidia* Stimpson, 1858 sensu nobis, type species: *Dromia hirsutissima* Lamarck, 1818 by original designation).

Cryptodromiopsis – Barnard 1947 *pro parte*: 369; 1950: 329. (Non *Cryptodromiopsis* Borradaile, 1903 sensu nobis, type species: *C. tridens* Borradaile, 1903 by monotypy).

?*Parasphaerodromia* Spiridonov, 1992: 69.

Pseudodromia – Macpherson 1988: 61. (Non *Pseudodromia* Stimpson, 1858).

TYPE SPECIES. — *Dromidia spongiosa* Stimpson, 1858 which is a senior synonym of *Platydromia depressa* Brocchi, 1877, type species of *Platydromia* Brocchi, 1877 by monotypy. Gender: feminine.

Several specimens of *Platydromia depressa* Brocchi, 1877, from Saint-Paul Island (M. de l'Isle coll., 600-1876) (MNHN-B 8739), may be considered syntypes. A lectotype, a male 9 × 10 mm, is selected herein (MNHN-B 27934); the remaining specimens are paralectotypes. Other specimens from the same expedition (see Vélain 1878) are labeled "Saint-Paul Island, Vélain coll., 178-1875" (MNHN-B 12724).

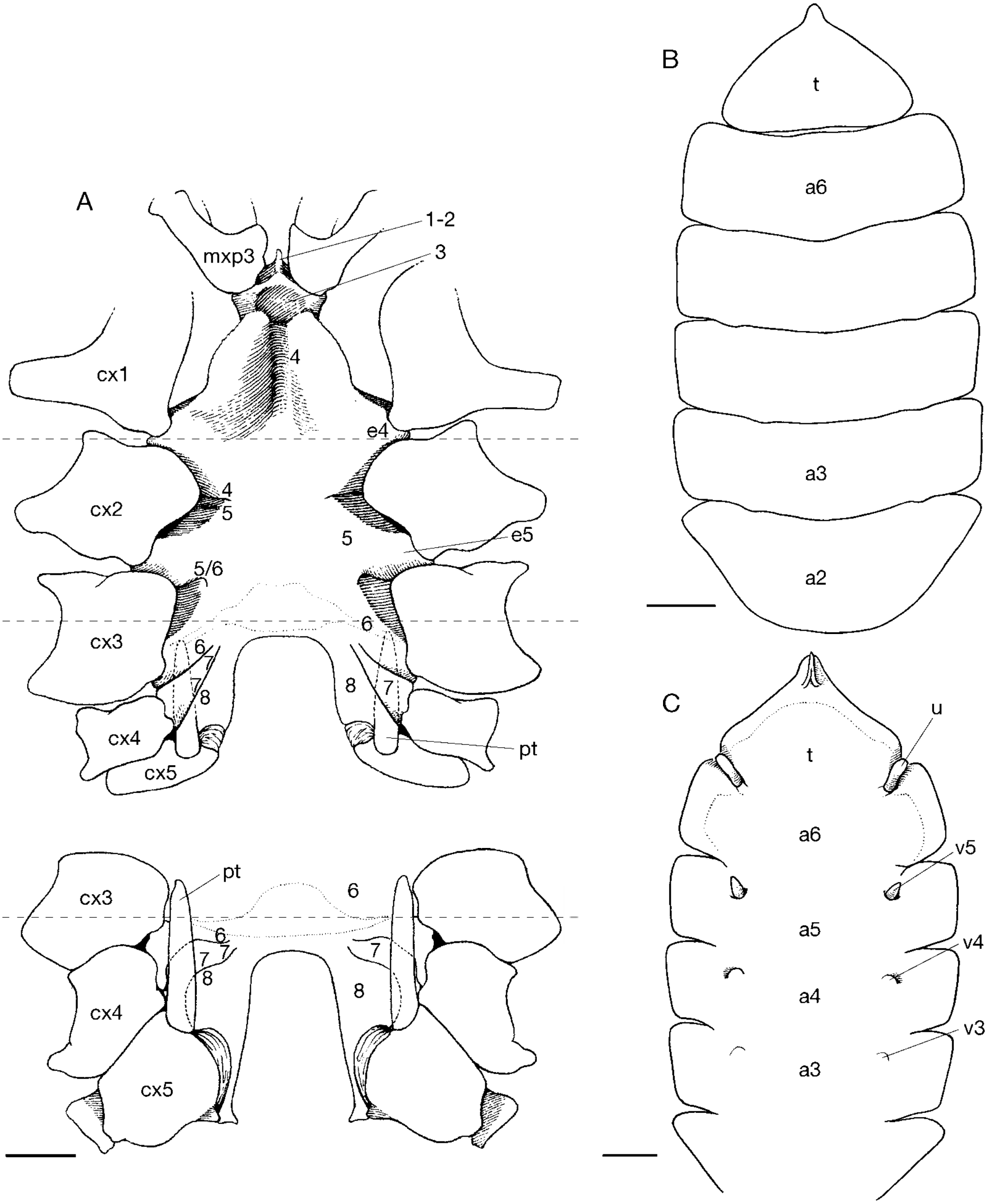

Fig. 15. — *Platydromia spongiosa* (Stimpson, 1858) n. comb.; **A**, **B**, Saint-Paul Island, Brocchi det. *Platydromia depressa* Brocchi, 1877, Vélain coll., 178-1875, ♂ 11 × 14 mm (MNHN-B 12724); **A**, thoracic sternum, two front views, note sternite 4 medially hollowed; **B**, dorsal view of abdomen; **C**, Amsterdam Island, Ams-A4, 11.II.1971, Beurois coll., ♂ 13 × 16 mm (MNHN-B 12728), ventral view of abdomen, note uropods not visible dorsally and oriented forward, and the vestigial pleopods showing only as papillae on segments 3-4. Abbreviations: **a2-a6**, abdominal segments 2-6; **cx1-cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **mxp3**, external maxilliped; **pt**, penial tube; **t**, telson; **u**, uropod; **v3-v5**, vestigial pleopods 3-5; **1-2**, sternites 1-2; **3-8**, sternites 3-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 1 mm.

SPECIES INCLUDED. — *Dromidia spongiosa* Stimpson, 1858.

Whether other species of *Dromidia* or *Cryptodromiopsis* should be transferred to *Platydromia* requires further investigation. For example, the status of *C. lepidota* Barnard, 1947, based on an immature specimen and assigned to *Dromidia* by McLay (1993: 183-185), is uncertain.

DISTRIBUTION. — South Africa and south western Indian Ocean.

DESCRIPTION

Carapace wider than long, convex; dorsal surface with not well-defined regions; branchial groove weakly marked. Anterolateral margin long, strongly convex, entire, only undulated, with only blunt knob behind level of branchial groove; posterolateral margins very short, markedly convergent posteriorly. Front narrow, with rostrum in lower plane and deflexed, and two low pseudorostral lobes; only a slight supraorbital tooth, no suborbital and exorbital teeth. Antenna: urinal article noticeably developed, with anterior part of beak rounded, wider and shorter than posterior ones; basal article very short, with exopod thick; internal angle acutely produced. Mxp3 with coxae not closely approximated.

Thoracic sternites 1 and 2 narrrow and hardly visible; sternite 3 largely visible dorsally, at level not much lower than sternite 4. Thoracic sternite 4 broad, deeply medially hollowed in males, with lateral borders convex and anterior margin medially concave in both sexes (Figs 15A; 16). In males, thoracic sternites 7 and 8 perpendicular in relation to preceding ones; in females, sternites 5-8 perpendicular in relation to sternite 4. Female sternal sutures 7/8 very long, with apertures of spermathecae ending together on slight prominence between chelipeds (Fig. 16). When male abdomen is applied against ventral surface, sternites 1-2 partly discernible, sternite 3 and anterior part of sternite 4 remaining visible, and no episternites exposed.

Male abdomen very broad, with distinct pleural parts, not covering whole sterno-abdominal depression, and with all segments free; telson broadly triangular, ending in sharp tip (Fig. 15B, C); telson of females without acute tip. Segment 6 with external borders parallel. In males, vestigial pleopods present on segments 3-5 (Pl5 as small lobes and Pl4 and Pl3 as short papillae, difficult to see, Fig. 15C). Uropods as ventral plates, not visible dorsally, oriented forward instead laterally; uropods not involved in holding of abdomen. No efficient holding of abdomen: at the more least, a very low prominence on coxa of P2 just in contact with external margin of abdominal segment 6 which is not modified. Female gonopore on P3 coxa relatively large.

Chelipeds without epipod. P1, P2 and P3 very short and stout, not knobbed nor nodose; propodus of P2 and P3 without distal spine; inner margin of dactylus armed with spines. P4 and P5 reduced, P5 being slightly longer and more slender. Propodus of P4 and P5 short and with only one distal spine opposing dactylus which is short and ends in horny spine.

Male P5 coxa with mobile penial tube (Fig. 15A).

Carrying behaviour

Compound ascidians.

REMARKS

Dromidia spongiosa differs substantially from *D. hirsutissima*, type species of *Dromidia* (see above), so that it is necessary to separate it in a different genus. For *D. spongiosa* we rehabilitate the genus *Platydromia* Brocchi, 1877, its type species *P. depressa* being a junior synonym of *Dromidia spongiosa* (McLay 1993: 121, 183).

The species described as *Dromidia spongiosa* by Stimpson has been known under five specific names and placed in at least six genera (McLay 1993: 183). In the present study *D. spongiosa* is excluded from *Dromidia*, its original (Stimpson 1858) and last genus (McLay 1993: 183,184), as well as from *Cryptodromiopsis* where it was placed by Barnard (1947, 1950). It is now *Platydromia spongiosa* (Stimpson, 1858) n. comb.

We agree with McLay (1993: 184) who placed *Pseudodromia inermis* Macpherson, 1988 (p. 61, figs 6, 7) in the synonymy of his *Dromidia spongiosa*. McLay also synonymised with *D. spongiosa* *Parasphaerodromia subglobosa* Spiridonov, 1992

(p. 70, fig. 2a-d), from the South Indian Ocean, indicated with reduced uropods (see below).

Platydromia spongiosa n. comb. differs from *Dromidia* sensu nobis (Fig. 5) in particular by having the frontal, orbital and anterolateral margins without teeth, a thick, sponge-like tomentum, and no spine on P2 coxa. Other characters which distinguish *Platydromia* from *Dromidia* sensu nobis are: 1) front lobate (tridentate in *Dromidia*); 2) sternite 3 visible (not visible dorsally in *Dromidia*); 3) male sternite 4 relatively wide, with convex lateral margins and medially cleft anterior margin (with oblique lateral margins and rounded tip in *Dromidia*); 4) male abdomen that leaves uncovered sternite 3 and part of sternite 4 (Figs 15A; 16) (covering whole abdominal depression with exception of extreme anterior part of sternite 4 in *Dromidia*, Fig. 5A, B); 5) uropods showing as small, totally concealed, ventral plates (Fig. 15B, C) (oblique and intercalary ventral plates, almost entirely concealed in *Dromidia*, Fig. 5B, C); and 6) no efficient abdominal holding (efficient holding by strong coxal spine on P2 in *Dromidia*, Fig. 5B).

Platydromia is easily distinguishable from *Cryptodromiopsis* sensu nobis (Fig. 4) by a number of characters, chiefly: 1) round shape of carapace, longer than wide (distinctly wider than long in *Cryptodromiopsis*); 2) uropods showing as totally concealed ventral plates (salient dorsal plates in *Cryptodromiopsis*); 3) male telson ending in acute tip (triangular tip in *Cryptodromiopsis*); 4) male segment 6 broad (narrower in *Cryptodromiopsis*); 5) male sternite 4 broad, deeply hollowed medially (narrower, not hollowed medially in *Cryptodromiopsis*); and 6) an inconspicuous low prominence on P2 coxa (a serrated prominence, and uropods not involved in *Cryptodromiopsis*).

Platydromia and *Lamarckdromia* n. gen. (type species: *Dromia globosa*), both with ventral and concealed uropods, differ from each other by several features of the carapace and pereopods, and specially by: 1) sternite 3 largely visible in *Platydromia* (only a small part visible in male *Lamarckdromia* n. gen., Fig. 10A, D); 2) sternite

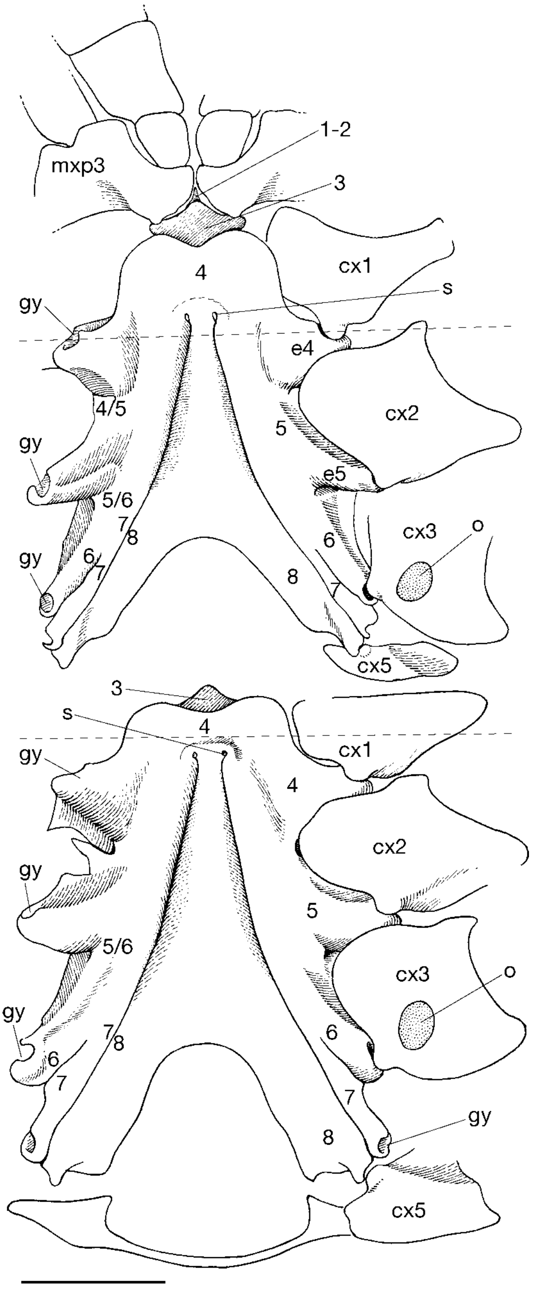

FIG. 16. — *Platydromia spongiosa* (Stimpson, 1858) n. comb., Saint-Paul Island, Vélain coll., 178-1875, Brocchi det. *Platydromia depressa* Brocchi, 1877, ♀ 12 × 16 mm (MNHN-B 12724), thoracic sternum, two front views, and spermathecae. Abbreviations: **cx1-cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **gy**, episternal gynglyme receiving sternal articular condyle of the pereopod; **mxp3**, external maxilliped; **o**, female gonopore; **s**, aperture of spermatheca; **1-2**, sternites 1-2; **3-8**, sternites 3-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bar: 2 mm.

4 wide, with convex lateral margins in both sexes (triangular in *Lamarckdromia* n. gen., Fig. 10A, D); 3) male telson ending in acute tip (rounded at tip in *Lamarckdromia* n. gen., Fig. 10B, C); and 4) apertures of spermathecae ending together on slight prominence between chelipeds (ending together on central prominence between P2 in *Lamarckdromia* n. gen., Fig. 10A).

The carapace and legs of *Platydromia spongiosa* are completely covered with "a dense and firm envelope of pubescence, sponge-like in appearance", "distinctly marked with shallow pits or depressions" (Stimpson 1907: 171, as *Dromidia spongiosa*), or with "a very short close and thick pile" (Barnard 1950: 330, as *Cryptodromiopsis spongiosa*). By comparison, the carapace and legs of *Dromidia hirsutissima* are "covered with short stiff pile, and long dense fibrous and shaggy brown or yellow hairs" (Barnard 1950: 320), hence the name of *hirsutissima* given by Lamarck and the common name of "shaggy sponge crab" (Barnard 1950). The same common name was given to *Cryptodromiopsis plumosa* Lewinsohn, 1984 by Hoover (1998: 266, fig. n. n.; see below under *Stebbingdromia plumosa* n. comb.). In *Lamarckdromia globosa* n. comb. the whole body and legs are covered by a dense shaggy coat of hairs, and the deflexed front portion of carapace is concealed by transverse fringe of longer setae, giving it a characteristic appearance.

The soft and areolated tomentum of *Platydromia spongiosa* n. comb. somewhat resembles that of "*Dromia*" *wilsoni* (Fulton & Grant, 1902b: 61, as *Cryptodromia wilsoni*). The two species may be confused but differ by: 1) shape of carapace, rounded and not toothed laterally in *P. spongiosa* n. comb. (distinctly wider and armed laterally in *D. wilsoni*); 2) uropods, only ventral in *P. spongiosa* n. comb. (very salient dorsal plates in *D. wilsoni*). We agree with McLay in that the generic status of "*Dromia*" *wilsoni* needs a re-appreciation (see McLay 1991: 470, figs 7, 8, as *Petalomera wilsoni*; 2001a: 84, as *Dromia wilsoni*; Ng *et al.* 2000: 160, fig. 2b, as *D. wilsoni*; McLay *et al.* 2001: 742, table 1, as *D. wilsoni*). "*Dromia*" *wilsoni* differs from other *Dromia* species by several morphological features (in particular the abdominal holding with a coaptation by engagement between P2 coxae and the modified edges of abdominal segment 6, and no involvement of uropods, see Bouchard 2000) and larval development (see McLay *et al.* 2001). Its worldwide geographical distribution includes all the three major oceans; it is found as deep as 520 m.

Genus *Pseudodromia* Stimpson, 1858

Pseudodromia Stimpson, 1858: 226. — Henderson 1888: 15. — Alcock 1900 *pro parte*: 149. — Stebbing 1900: 23. — Stimpson 1907: 177. — Barnard 1950 *pro parte*: 315. — Gordon 1950 *pro parte*: 209. — Kensley 1977 *pro parte*: 183; 1978: 257; 1980 *pro parte*: 25. — McLay 1993: 125, 175, table 4. — McLay *et al.* 2001: 741, table 3. — Guinot 1995: 186. — Guinot & Bouchard 1998: 626, table 3. — Stewart *et al.* 2001: 136.

TYPE SPECIES. — *Pseudodromia latens* Stimpson, 1858 by original designation (Stimpson 1858: 226). Gender: feminine.

SPECIES INCLUDED. — *Pseudodromia latens* Stimpson, 1858; *Dromia rotunda* MacLeay, 1838 (see Ng & Ahyong 2001); *Pseudodromia trepidus* Kensley, 1978. *Pseudodromia cacuminis* Kensley, 1980, from the South Atlantic (Vema Seamount), does not belong to *Pseudodromia* (McLay 1993: 176).

DISTRIBUTION. — South Africa.

DESCRIPTION

Carapace more or less longer than wide, extremely narrow anteriorly, convex; dorsal surface smooth, without defined regions; cervical groove not present, branchial groove strongly marked. Anterolateral margin very long, usually without tooth; posterolateral margin short. Front very narrow, tridentate, with rostrum markedly deflexed and hardly or not visible dorsally at all, may be elongated (*P. trepidus*) and with two pseudorostral teeth; supraorbital tooth marked or not; suborbital and exorbital teeth absent. Antenna: urinal article with anterior part of beak much shorter than posterior one and with broad tip; basal article with exopod enlarged and internal angle not elongated. Mxp3 with coxae closely approximated.

Thoracic sternite 3 not visible dorsally. Thoracic sternite 4 very narrow, deeply hollowed medially in males, with lateral borders convex and anterior margin pointed and deflexed. In females, thoracic sternites 7 and 8 very tilted in relation to preceding ones. Female sternal sutures 7/8 long, with apertures of spermathecae ending together on prominence between P2. When male abdomen applied against ventral surface, anterior part of sternite 4 remaining visible and no episternites exposed. Sterno-coxal depressions absent.

Male abdomen completely covering sterno-abdominal depression and with all segments free; male telson relatively long, ending in sharp tip; telson of females without acute tip. Segment 6 becoming more or less narrow posteriorly. No vestigial pleopods present on segments 3-5 in males. Uropods as relatively small but distinct ventral plates, not visible dorsally (*P. latens*, *P. trepidus*) or hardly visible (*P. rotunda*). Absence of any efficient holding of abdomen.

Chelipeds without epipod. P1, P2 and P3 not knobbed nor nodose; propodus of P2 and P3 without distal spine; inner margin of dactylus with spines, longer distally. P4 reduced, P5 distinctly longer than P4 and being about of same size than P2. Propodus of P4 and P5 without spines opposing dactylus; outer propodal spines absent; presence of lateral propodal spines, one on P4 and two on P5; P5 dactylus straight.

Male P5 coxa with mobile and very long penial tube.

Carrying behaviour

Compound ascidians.

REMARKS

Pseudodromia is distinguished by having uropods that show as ventral plates, sometimes partly visible dorsally. This is the major difference from *Ascidiophilus*, since there are no vestigial pleopods in the males of both genera (Guinot 1995: 186). *Pseudodromia* differs from *Austrodromidia* sensu nobis (Figs 1; 2) as follows: 1) sternite 3 not visible dorsally (visible dorsally, clearly or slightly in *Austrodromidia*); 2) sternite 4 very narrow and hollowed medially in males (truncate at tip and not hollowed in *Austrodromidia*); 3) no episternites visible when male abdomen flexed (episternites 4 and 5 visible in *Austrodromidia*); 4) male telson ending in acute tip (bluntly triangular or rounded in *Austrodromidia*); 5) male segment 6 with external borders may be slightly concave (deeply hollowed laterally in *Austrodromidia*); 6) female sternal sutures 7/8 ending together at level of P2 (apart in *Austrodromidia*); and 7) absence of an abdominal holding (abdominal holding by prominence on P2 coxa in *Austrodromidia*).

In *Pseudodromia* (as well in *Ascidiophilus*) the absence of an abdominal holding system seems to be related to the complete protection by a host, the body being almost entirely enclosed by an ascidian (Guinot & Bouchard 1998).

Using DNA sequence data, Stewart *et al.* (2001: 136) questioned the monophyly of *Pseudodromia* but confirmed the specific status of two close species, *P. rotunda* and *P. latens*.

Genus *Stebbingdromia* n. gen.
(Figs 17; 18)

Dromidiopsis – Lewinsohn 1984 *pro parte*: 104, fig. 3. (Non *Dromidiopsis* Borradaile, 1900; type species: *Dromia australiensis* Haswell, 1882).

Cryptodromiopsis – McLay 1993 *pro parte*: 188, 190; 2001a: 85, 86. — Hoover 1998: 266. — ?Chen & Haibao 2002 *pro parte*: 102, 541, 542. (Non *Cryptodromiopsis* Borradaile, 1903, type species: *C. tridens* Borradaile, 1903).

TYPE AND ONLY SPECIES. — *Dromidiopsis plumosa* Lewinsohn, 1984.

ETYMOLOGY. — The new genus is established in honor of Thomas Roscoe Rede Stebbing (1835-1926) for his contributions to carcinology. Gender: feminine.

DISTRIBUTION. — *Stebbingdromia plumosa* n. comb., the only species in the genus, is found from the Seychelles Islands (type locality) to Chesterfield Islands, Guam and Hawaii.

DESCRIPTION

Carapace distinctly wider than long; dorsal surface smooth, with regions not defined. Branchial groove marked and forming laterally very deep notch, but without tooth. Anterolateral margins subparallel except anteriorly, armed with two teeth behind exorbital tooth; posterolateral margin very short. Front projecting beyond orbits; rostrum acute, markedly deflexed but visible dorsally; two acute pseudorostral teeth. Orbital margin eave-like; supraorbital margin notched; supraorbital tooth absent or faintly marked; infraorbital tooth triangular, separated from exorbital angle and from inner infraorbital tooth by deep notches; exorbital tooth dentiform. Proepistome raised, in front of wide epistome.

Orbits directed horizontally, deep. Ocular stalk very long and narrow, curved. Antenna: urinal article wider than long, with posterior part of beak broad; basal article with exopodal scale well-developed, enlarged; internal angle similarly developed and markedly produced, touching front; following article completely included between these two lateral extensions of basal article. Mxp3 with coxae not completely approximated.

Sternite 3 not visible anteriorly but discernible on each side of sternite 4; sternite 4 with triangular anterior part in contact with coxae of mxp3. When male abdomen applied against ventral surface, sternite 4 completely covered except laterally, i.e. episternite 4; episternite 5 remaining exposed. In females, thoracic sternum regularly sloping backwards, posterior part more bent; in males, posterior sternites, i.e. posterior part of sternite 6, and sternites 7 and 8, abruptly tilted, so they are nearly perpendicular to preceding ones. Female sutures 7/8 short, with apertures of spermathecae apart on very slight prominence between P3 (even in mature females, see McLay 2001a: 85, 86), i.e. not far from gonopores on P3; these apertures (hidden beneath sperm plug in the two examined females) completely exposed and perhaps relatively large.

Abdomen long, reaching mxp3, and relatively wide (probably with pleural parts), triangular in shape, with all segments free; telson rather developed, bluntly triangular. Segment 6 much wider than long, with external margins slightly concave. In males, pleopods present on somites 3-5, showing as uniramous vestiges, rather long and dissimilar. In males, uropods showing as elongated dorsal plates, always visible dorsally, deeply inserted medially between segment 6 and telson, horizontally oriented, relatively movable and slightly projecting beyond outline of abdomen. Abdominal holding by distinctly tuberculate crest on P2 coxa; uropods weakly involved in holding; in addition, presence of rounded granular prominence on P1 coxa.

Chelipeds well-developed, with an epipod; sexual dimorphism marked: in males, fingers strongly downcurved, markedly gaping; dactylus with external surface concave and cutting edge armed with small, molariform proximal tooth; cutting edge of fixed finger armed with several pointed teeth (details not visible on the sketch by Lewinsohn 1984: fig. 3c). P2 and P3 neither lobed nor nodose; propodus long and bearing a small distal propodal spine; inner margin of dactylus with several spines. P4 and P5 reduced, very short, practically similar in size, P5 only slightly longer; dactylus strongly curved; subcheliform apparatus formed by multiple spines: three (P4) or two (P5) distal propodal spines opposing dactyli, and two (P4) or three (P5) spines on outer propodal margins; a large spine on outer dactylus margin on P5; namely a total of six spines on P5; P4 and P5 without spines on inner margin of dactylus.

Male P5 coxa with mobile penial tube.

Male G1 without apical plate, only with a setose blunt knob. G2 without exopod, and unusual in the Dromiidae (verified in two males, from Seychelles, MNHN-B 8572 and Chesterfield Islands, MNHN-B 22562): very short, (shorter than G1), stout, regularly tapering to pointed tip, without styliform, needle-like flagellum; third distal part corneous.

Carrying behaviour

Despite the long covering of plumose setae, pieces of sponge are used for camouflage (Hoover 1998: 266).

REMARKS

Because Lewinsohn (1984: 106) was fully aware that the dromiid genera needed to be reviewed, he was uncertain of whether his new species

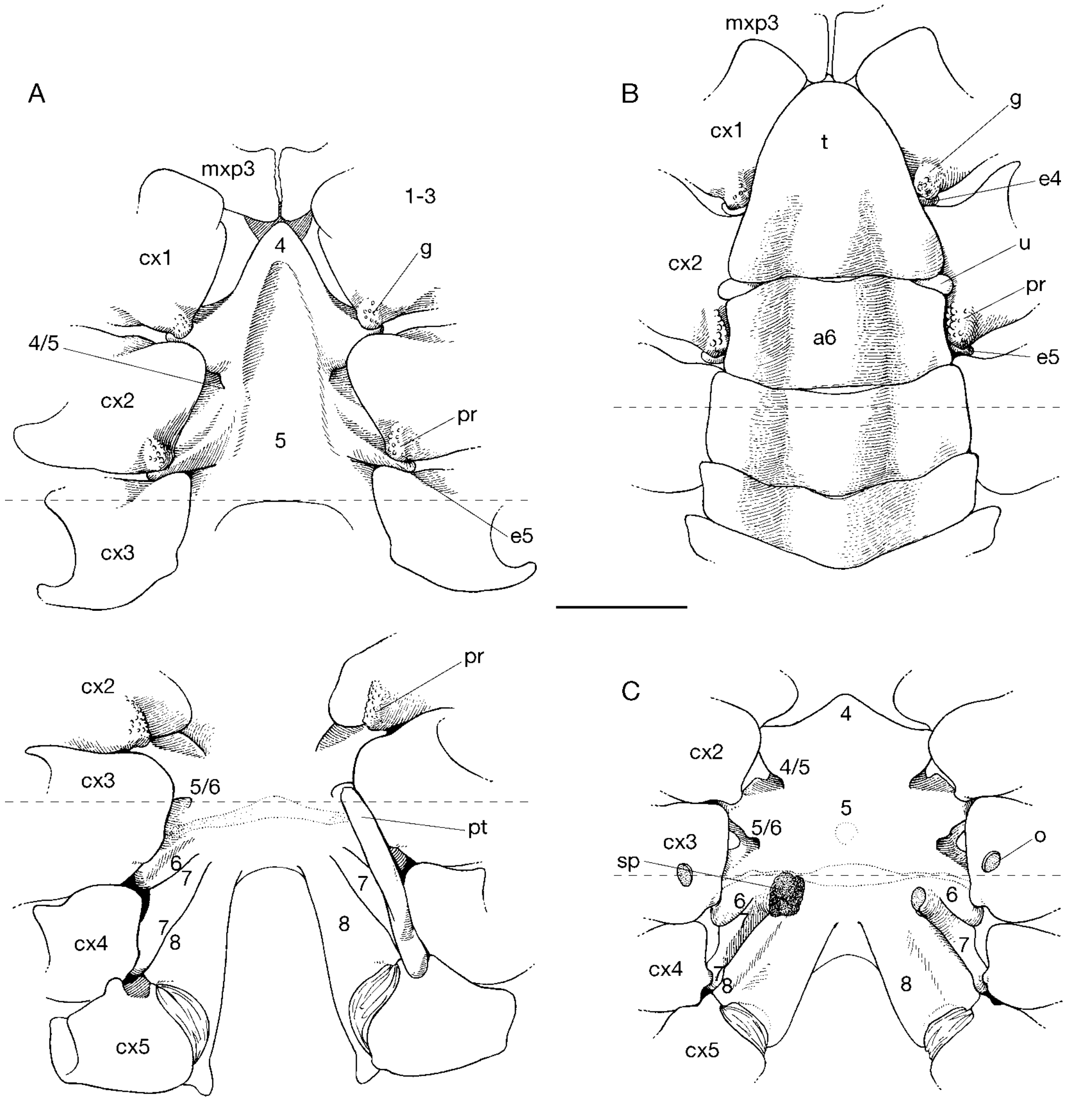

Fig. 17. — *Stebbingdromia plumosa* (Lewinsohn, 1984) n. comb.; **A**, **B**, Chesterfield Islands, CORAIL 2, stn DW 84, McLay det. *Cryptodromiopsis plumosa*, ♂ 11.3 × 13.3 mm (MNHN-B 22562); **A**, thoracic sternum, two front views; **B**, abdomen, dorsal view; **C**, Hawaii, Oahu, McLay det. *C. plumosa*, ovigerous ♀ 9.5 × 10.5 mm (QM W21890), thoracic sternum and spermathecae; note large apertures of spermathecae at level of P3, concealed by sperm plug. Abbreviations: **a6**, abdominal segment 6; **cx1**-**cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **g**, granules on rounded prominence on P1 coxa; **mxp3**, external maxilliped; **o**, female gonopore; **pr**, holding prominence; **pt**, penial tube; **sp**, sperm plug; **t**, telson; **u**, uropod; **1-3**, sternites 1-3; **4-8**, sternites 4-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bar: 2 mm.

Dromidiopsis plumosa ("different from all other known species") should have been placed in *Dromidiopsis*. Lewinsohn's species was eventually transferred by McLay (1991: 470) first to *Dromidia* and later (McLay 1993: 138; 2001a: 85, 86) to *Cryptodromiopsis*. As a result, *D. plumosa* has already been placed in three different genera.

Stebbingdromia plumosa n. comb. is the only dromiid (actually Dromiacea) with a relatively short male G2 (slightly shorter than G1) that is stout and lacks the styliform distal part (Fig. 18B). In all members of Dromiacea the G2 is typically as long as or longer than G1 and ends in neddle-like flagellum (Figs 20B; 23B).

In the description for the first time of a female of *Stebbingdromia plumosa* n. comb., an ovigerous one, McLay (2001a: 86) remarked that female sternal sutures 7/8 "end more posteriorly than in other species of the genus [*Cryptodromiopsis*]. This means that the ends of the sutures [apertures of spermathecae] are just below the female gonopores, only about 1 mm away". This may be regarded as an ancestral condition, such as the arrangement of spines on pereopods (distal propodal spine on P2 and P3; numerous spines on the subcheliform apparatus of P4 and P5).

The apertures of spermathecae are not readily visible in the two available females of *Stebbingdromia plumosa* n. comb. (ovigerous female, 9.5 × 10.5 mm, Hawaii, Oahu, QM W 21890; female 6.8 × 7.2 mm, Guam, Apra Harbour, ZRC 2000.2112), as both individuals still carry sperm plugs (Fig. 17C). We suspect that the spermathecal apertures are relatively large in *Stebbingdromia plumosa* n. comb., and, if confirmed, this will be another distinctive feature of the genus. The apertures of spermathecae show as very minute pores in the Dromiacea, with few exceptions: for example *Sternodromia spinirostris* (Miers, 1881) shows narrow oblique slits (see Forest 1974: fig. 6C, pl. 4, fig. 3). The shapes of G2 (thick) and spermathecal apertures (if large) might be regarded as an indication that both G1 and G2 are involved in the insemination process.

Two characters of *D. plumosa*, female sternal sutures 7/8 ending between P3 (versus ending more anteriorly, as far between or in front of P1, in the other Dromiinae n. status) and male vestigial pleopods combined with intercalary dorsal uropods, make this species so different that none of the existing dromiid genera could accommodate it.

Male vestigial pleopods combined with dorsal uropods are relatively rare in the subfamily Dromiinae n. status (Table 1). This condition occurs only in *Moreiradromia* n. gen. (Fig. 14B, C, may be obsolete in larger individuals) and in *Dromia* pro parte. We observed a long Pl5 and obscure Pl4 and Pl3 in *D. personata* (Linnaeus, 1758) (Fig. 27A), more or less short Pl3-Pl5 in *D. bollorei* Forest, 1974 (Fig. 27B) and *D. marmorea* Forest, 1974, and Pl3-Pl5 showing as short papillae in "*Dromia*" *wilsoni* (Fulton & Grant, 1902). An analogous condition as in *Stebbingdromia* n. gen. is found in the subfamily Sphaerodromiinae n. subfam. (see Fig. 22: but biramous vestigial Pl3-Pl5).

As presently redefined, neither *Dromidiopsis* sensu nobis, *Cryptodromiopsis* sensu nobis, nor *Dromidia* sensu nobis can receive *D. plumosa.*

Stebbingdromia n. gen can be readily distinguished from *Dromidiopsis* sensu nobis (Fig. 6), as follows: 1) abdominal segments free (abdominal segments 5 and 6 fused together in *Dromidiopsis*); 2) when extended forward, P5 reaching about mid-length of lateral margin of carapace (P5 extremely long, reaching about outer orbital angle in *Dromidiopsis*); 3) male G2 short and stout, without styliform flagellum (long and needle-like in *Dromidiopsis*); 4) Pl3-Pl5 as vestiges in males (Pl3-Pl5 absent in *Dromidiopsis*); 5) merus and carpus of P2 and P3 stout, noticeably high; propodus and dactylus long and thin (merus, carpus, propodus, and dactylus looking similar in *Dromidiopsis*); and 6) female sternal sutures 7/8 ending between P3 (between P1 or just behind them, together on central prominence in *Dromidiopsis*). In addition, the fronto-orbital region is dissimilar in the two genera.

Differences between *Stebbingdromia* n. gen. and *Cryptodromiopsis* sensu nobis (Fig. 4) include: 1) thoracic sternite 3 medially concealed in *Stebbingdromia* n. gen. (exposed in *Cryptodromiopsis*); 2) coxae of mxp3 almost approximated (a distinct gap between them in *Cryptodromiopsis*); 3) male thoracic sternite 4 ending in acute tip (truncate in *Cryptodromiopsis*); 4) uropods oriented horizontally and weakly involved in abdominal holding (more salient and oriented obliquely, far from prominence on P2 coxa, in *Cryptodromiopsis*); 5) Pl3-Pl5 as

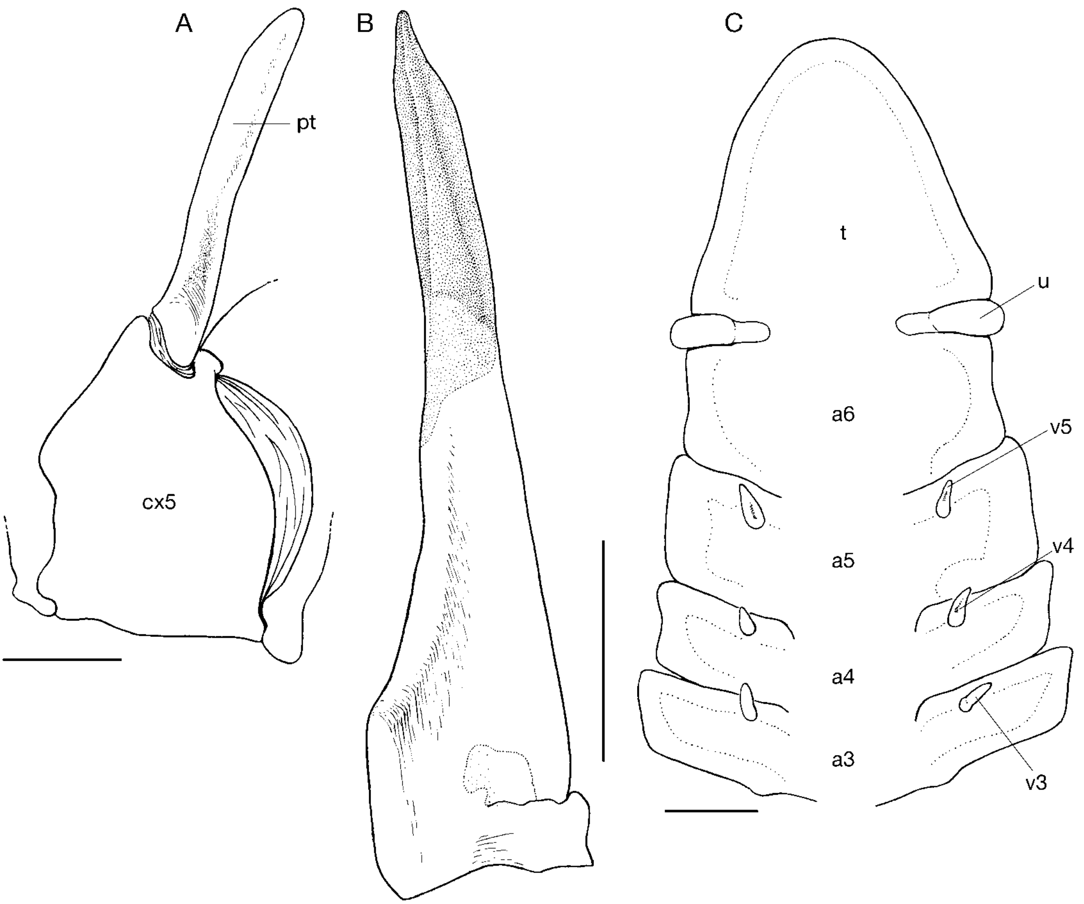

FIG. 18. — *Stebbingdromia plumosa* (Lewinsohn, 1984) n. comb., Chesterfield Islands, CORAIL 2, stn DW 84, McLay det. *Cryptodromiopsis plumosa*, ♂ 11.3 × 13.3 mm (MNHN-B 22562); **A**, coxa of P5, with penis as mobile tube; **B**, G2, without styliform flagellum (corneous part stippled); **C**, abdomen, ventral view. Abbreviations: **a3-a6**, abdominal segments 3-6; **cx5**, coxa of P5; **pt**, penial tube; **t**, telson; **u**, uropod; **v3-v5**, vestigial pleopods 3-5. Scale bars: 1 mm.

vestiges (Pl3-Pl5 absent in *Cryptodromiopsis*); 6) female apertures of spermathecae between P3 (together on slight tubercle between chelipeds in *Cryptodromiopsis*); and 7) male G2 shorter than G1 and without styliform flagellum (long and needle-like in *Cryptodromiopsis*).

Differences, other than the carapace and legs, between *Stebbingdromia* n. gen. and *Dromia* s.s. include: 1) when folded, male abdomen covering whole sternite 4 (anterior part of sternite 4 exposed in *Dromia*); 2) telson longer than wide, triangular (wider than long, rounded/truncate at tip in *Dromia*); 3) dorsal uropods projecting only slightly beyond outline of abdomen (strongly salient and movable in *Dromia*, and with a characteristic small beak overhanging telson, this beak being probably used as stop system for their movement, see Bouchard 2000); 4) apertures of spermathecae apart, between P3 (placed more anteriorly in *Dromia*); and 5) G2 short and stout, not needle-like (with styliform flagellum in *Dromia*).

Differences, other than the carapace and legs, between *Stebbingdromia* n. gen. and *Moreiradromia* n. gen. (Fig. 14) include: 1) thoracic sternite 3 weakly visible dorsally (exposed, may be partly covered by male abdomen, when folded, in *Moreiradromia* n. gen.); 2) sternite 4 anteriorly triangular (truncate in *Moreiradromia* n. gen.); 3) male abdominal segment 6 much wider than long (very long, length as much as three quarters of width in *Moreiradromia* n. gen.); 4) abdominal holding by tuberculate crest on P2 coxa; presence of round prominence on P1 coxa (provided with spine overhanging coxa of P2, which may bear other smaller tubercles, and presence of tubercles or granules on P1, P3 and even P4 coxae in *Moreiradromia* n. gen.); 5) apertures of spermathecae apart, between P3 (together on prominence placed well beyond articular condyle of P1 in *Moreiradromia* n. gen.); and 6) G2 short, not needle-like (long and with a styliform flagellum in *Moreiradromia* n. gen.).

Differences between *Stebbingdromia* n. gen. and *Hemisphaerodromia* (Fig. 7B) include: 1) thoracic sternite 4 ending in acute tip in males and, when abdomen flexed, completely covered, except small episternite 4 (rounded, and anterior and episternal parts exposed in *Hemisphaerodromia*); 2) telson long, in contact with coxae of mxp3 (shorter, remote from mxp3 in *Hemisphaerodromia*); 3) male segment 6 with external margins slightly concave (deeply hollowed in *Hemisphaerodromia*); 4) male pleopods Pl3-Pl5 present as uniramous vestiges, rather long, (absent in *Hemisphaerodromia*); 5) abdominal holding by tuberculate crest on P2 coxa; uropods weakly involved; presence of an additional prominence on P1 coxa (only a serrated prominence on P2 coxa tigthly encircled in the space just behind uropods, markedly involved in abdominal holding, in *Hemisphaerodromia*); 6) female sternal sutures 7/8 ending apart on slight prominence between P3 (ending together on slight tubercle behind P2 in *Hemisphaerodromia*); and 7) male G2 shorter than G1 and without styliform flagellum (long and needle-like in *Hemisphaerodromia*).

It is clear that *Stebbingdromia* n. gen. is quite unique. For instance, in all the families of Dromiacea, i.e. Homolodromiidae, Dynomenidae and Dromiidae (Dromiinae n. status, Hypoconchinae n. subfam., and Sphaerodromiinae n. subfam.), the apertures of spermathecae are minute, a condition that is always connected with a styliform and needle-like G2. *Stebbingdromia* n. gen. is so far the only exception, and it is herein tentatively referred to the Dromiinae n. status. *Stebbingdromia* n. gen. shares (plesiomorphically?) the following features with the Sphaerodromiinae n. subfam.: 1) short female sternal sutures 7/8, ending between P3, so that the apertures of spermathecae lie beside female gonopores (also found in other basal Podotremata, *viz.* the Homolodromiidae and Dynomenidae). In *Stebbingdromia* n. gen., the very visible female sutures 7/8 and the completely exposed apertures of spermathecae (Fig. 17C) actually differ from those found in *Sphaerodromia* (Fig. 21C) and *Eodromia* (Fig. 24C), in which sutures 7/8 and the spermathecae are usually concealed under a lateral heightening of sternite 8; 2) uropods (Figs 17B; 18B) showing as dorsal plates, deeply inserted between abdominal segment 6 and telson, more or less included in outline of abdomen, and not markedly salient. In *Sphaerodromia* (Figs 21A; 22) and *Eodromia* (Fig. 24A, B), however, the uropods are immobile and inserted between telson and segment 6, while in *Stebbingdromia* n. gen. they remain independent and relatively movable. The uropods do not play role in the holding of abdomen in *Sphaerodromia* or *Eodromia* whereas in *Stebbingdromia* n. gen. the role of uropods in the abdominal holding is weak; 3) similar spinulation of walking legs, in particular the long propodi of P2 and P3, which are armed with one distal propodal spine (considered primitive by McLay 1993: 192 in *Stebbingdromia plumosa* n. comb. and *Sphaerodromia* spp.); dactyli of P2 and P3 with numerous spines regularly arranged on inner margin; 4) subcheliform apparatus of P4 and P5, which consists of a large number of propodal spines opposing the dactylus. In *Stebbingdromia* n. gen., however, the absence of spines on inner margin of P4 and P5 dactyli differs from *Sphaerodromia* and *Eodromia*, characterized by the presence of spines; and 5) complete male pleopodal formula (i.e., vestigial Pl3-Pl5 combined with dorsal uropods, Fig. 18C). The only other known Dromiidae with vestigial male pleopods combined with dorsal uropods are the dromiine genera *Moreiradromia* n. gen. (Fig. 14B) and *Dromia* pro parte (see Patterns of uropods and vestigial male pleopods 3-5 Fig. 27; Table 1).

Nevertheless, several features do not permit the assignation of *Stebbingdromia* n. gen. to the Sphaerodromiinae n. subfam. They are as follows: 1) thoracic sternum, in particular the shape of sternite 4; 2) male abdomen, in particular segment 6; 3) G2 shorter than G1 and not needle-like in *Stebbingdromia* n. gen.; 4) coxal structures of the pereopods for abdominal holding, with a tuberculate crest on P2 coxa and a round prominence on P1 coxa, relatively inefficient in *Stebbingdromia* n. gen. (Fig. 17A, B) (versus a prominence on P2 coxae involving telson in anterior part, and an inefficient prominence on P3 coxae covered by abdomen in *Sphaerodromia*, Fig. 21A, B); 5) male coxa of P5 with long, independent penial tube in *Stebbingdromia* n. gen. (Figs 17A; 18A) (male P5 coxa modified into hard process which encloses penis in *Sphaerodromia*, Figs 23A; 28E-G); and 6) mobile uropods (deeply inserted and immobile in *Sphaerodromia*). Other differences refer to orbits and eyes, antennae, front, proepistome, and chelipeds (in particular fingers).

The chelipeds of *Stebbingdromia* n. gen. are peculiar for the Dromiinae n. status. They are markedly sexually dimorphic, with fingers strongly downcurved, very widely gaping, the cutting edge of dactylus concave and armed with several long teeth in males. They do not conform with the chelipeds found in the Hypoconchinae n. subfam. or the Sphaerodromiinae n. subfam. (see below).

The identity of the *Cryptodromidiopsis plumosa* recorded by Chen & Haibao (2002: 102, fig. 41) could not be verified.

Subfamily HYPOCONCHINAE n. subfam.
(Figs 19; 20; 28K)

TYPE GENUS. — *Hypoconcha* Guérin-Méneville, 1854 by present designation. Gender: feminine.

GENUS INCLUDED. — *Hypoconcha* Guérin-Méneville, 1854 (type species: *Cancer parasiticus* Linnaeus, 1763, senior synonym of *Cancer sabulosus* Herbst, 1799, see Holthuis 1962).

DESCRIPTION

Carapace generally rounded, hourglass-shaped; dorsal surface flattened, very thin and partly membranous; on each posterior side, large soft area with special texture; branchiostegal region usually soft and of different texture, perhaps constituting ecdysis area. Cervical groove well marked, on two median gastric pits; cardiac region completely delimitated by well-defined cardiac groove. Branchial groove deep and separating hard part of carapace from soft posterior part. Margin of anterior half of carapace usually hairy, appearing as "ciliated"; posterolateral border often markedly concave. Front and lateral margins greatly expanded, covering all parts of head, except antennal flagella, and displacing eyes in ventral location. Front semicircular or slightly truncate in outline, markedly deflected in large triangular ventral plate connected with proepistome. Eyes, antennules, antennae and mouth parts deeply settled in depressions.

Basal article of antennule well-developed. First article of antenna beak-like; basal article noticeably developed, exopodal scale relatively small and internal angle markedly produced; following article deeply inserted inside basal article; remaining articles very small; flagellum long, setose. Orbits small, concealed beneath body. Mxp3 operculiform; coxa developed and closely approximated; merus subtriangular or trapezoidal; exopod noticeably wide, specially in proximal part; crista dentata (on ischium) with small number of corneous teeth.

Ventral surface and legs solid, sometimes hairy (not in *Hypoconcha parasitica* (Linnaeus, 1763)). Gynglymes of sternites 1-3 largely spaced and stepped at lower plane. Sternite 3 only hardly visible (only represented by a small median hollow) or not visible. Sternite 4 showing as well calcified, narrow and elongated plate, in close contact (except medially) with coxae of mxp3, sometimes appearing fixed to them. Episternites 4 and 5 broad and well calcified. In both sexes, posterior

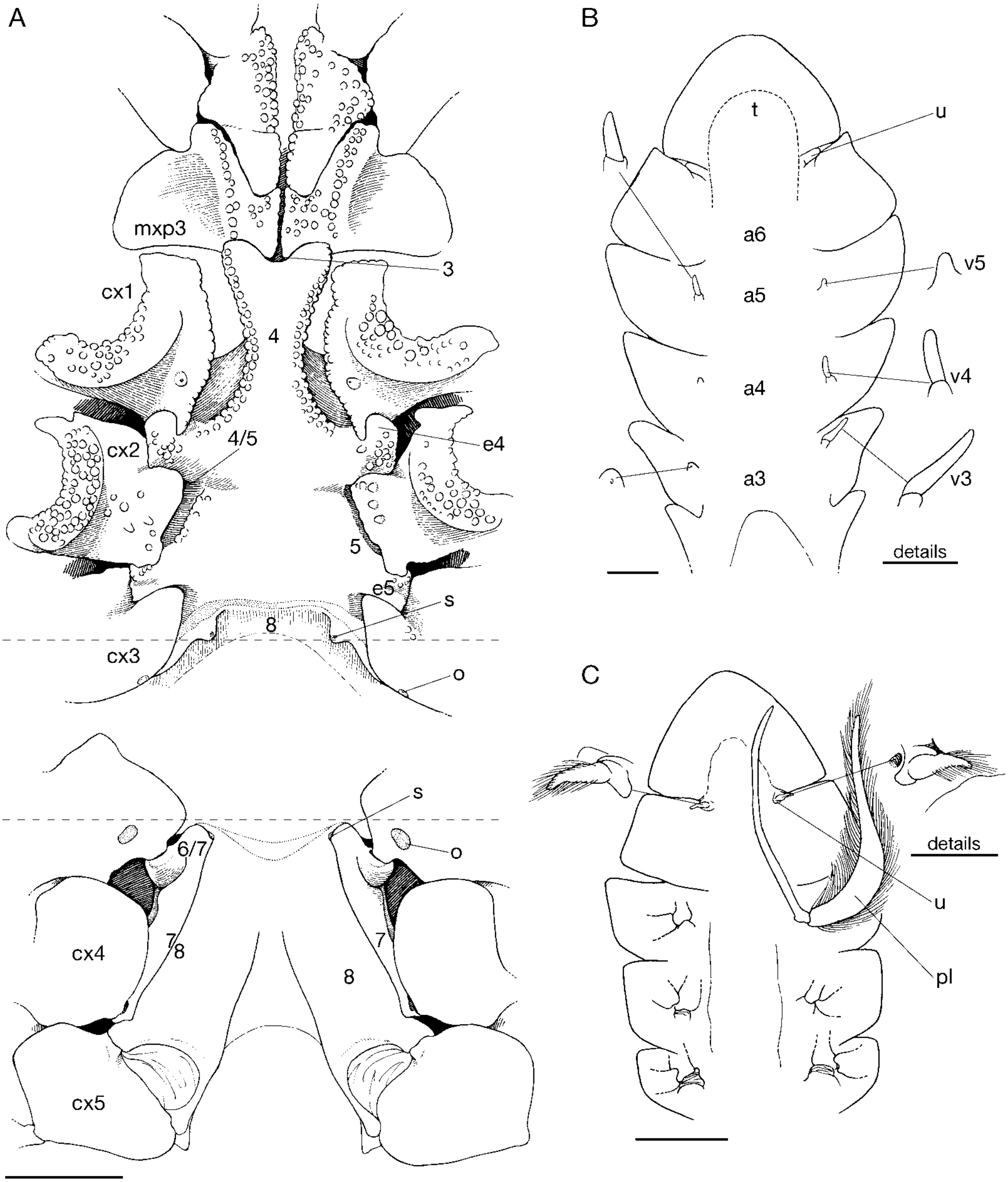

FIG. 19. — **A**, **B**, *Hypoconcha californiensis* Bouvier, 1898, Gulf of California, San José Island (MNHN-B 22066); **A**, ♀ 17 × 18 mm, syntype, thoracic sternum, two front views; note sternites 7 and 8 strongly tilted and perpendicular to preceding ones; **B**, ♂ 20.3 × 19.4 mm, syntype, ventral view of abdomen, with asymmetrical, uniramous vestigial pleopods and uropods showing as ventral plates; **C**, *H. panamensis* Smith, 1869, Lower California, Bouvier det. *H. digueti* Bouvier, 1898, Diguet coll., ♀ about 32 mm width (MNHN-B 22071), abdomen, ventral view; note uropods showing as setiferous ventral lobes. Abbreviations: **a3**-**a6**, abdominal segments 3-6; **cx1**-**cx5**, coxae of P1-P5; **e4**, **e5**, episternites 4, 5; **mxp3**, external maxilliped; **o**, female gonopore; **pl**, female pleopod (setae incompletely figured); **s**, aperture of spermatheca; **t**, telson; **u**, uropod; **v3**-**v5**, vestigial pleopods 3-5; **3**-**8**, sternites 3-8; **4/5**-**7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: A, C, 2.5 mm; B, 1mm.

thoracic sternites 7 and 8 tilted; in females, anterior sternites 4 and 5 forming horizontal plate, sternites 6-8 bent at right angles, so they are perpendicular to preceding ones; sternite 6 small, rejected laterally, its raised anterior part often surrounding apertures of spermathecae. Sternal suture 4/5 horizontal, well-marked laterally, its trace medially discernible; suture 5/6 oblique, clearly visible; sutures 6/7 and 7/8 very oblique. Female sutures 7/8 relatively short, only present on bent surface of posterior sternites, always ending apart. Apertures of spermathecae located only slightly beyond level of condyle of P3, not very far from female gonopores on P3 (Fig. 19A).

Sterno-abdominal depression not noticeably deep and located posteriorly. A large portion of thoracic sternite 4 not concealed by male abdomen, when flexed; episternite 4 greatly exposed. Abdomen with all segments free, usually short (never attaining coxae of mxp3), broad, noticeably widened at level of segments 5 and 6, triangular shaped, and with first segments remaining dorsal, even in males; pleurae may be distinct. In both sexes abdomen bent at right angles about in the middle and disposed into two different planes, so that the posterior part of abdomen lies flat on ventral surface of cephalothorax. This abdominal curvature, less pronounced in males than in females, probably connected with the inclination of two last thoracic sternites, 7 and 8, with regard to preceding ones. Telson triangular, broader than long. Uropods showing as minute ventral plates in both sexes, never visible dorsally, very narrow, rather immovable in males, sexually dimorphic (showing as small and more setiferous lobes in females). Presence of uniramous vestigial male pleopods, varying along the species: Pl3-Pl5 showing as elongated and asymmetrical lobes (*H. californiensis* Bouvier, 1898; Fig. 19B), or only as short papillae (*H. panamensis* Smith, 1869), or indistinct, at least in small specimens (*H. parasitica*, *H. arcuata* Stimpson, 1858). Abdomen holding may be provided by structure on P1 coxa, which bears a series of spinous tubercles, the strongest of which overhangs telson (*H. californiensis*); more often, theses structure are absent (*H. arcuata*, *H. panamensis*); accordingly to its curvature at right angles, abdomen flexed halfway and normally applied to thoracic sternum. Female abdomen becoming expanded in ovigerous specimens, with formation of brood chamber.

Chelipeds stout, epipod present, podobranch lacking. Pereopods capable of being folded compactly against body and partly concealed by carapace, with a perfect complementarity of diverse parts. Fixed finger and dactylus of chelipeds armed on prehensile margin with complementary teeth and close along whole length. P2 and P3 not lobed nor nodose; propodus short, never armed with a distal spine; dactylus not strongly curved, without spines or with only very small spines on inner margin. P4 and P5 both reduced (but not coxae) and oriented in a different way than P2 and P3 i.e. directed subdorsally or dorsally, such as in the Dromiinae n. status, but each markedly dissimilar from the other. P4 subdorsal, noticeably robust, much shorter than preceding legs and P5; merus very stout. P5 completely dorsal, much longer than P4. In both P4 and P5, carpus relatively long; propodus short and stout. Dactylus of P4-P5 with a peculiar dactylus, which is upturned, crescent and lunate, extremely mobile, placed in a deep notch of propodus, and ending in corneous hook.

Male P5 coxa with mobile penial tube (Figs 20A; 28K).

G1 not completely closed, without apical plate. G2 very long, styliform, without exopod (Fig. 20B).

Carrying behaviour

See under Remarks and under Discussion, Shell-carrying behaviour.

REMARKS

This unusual crab has been known for a long time under the name "Faux Bernard l'Hermite", given to *H. parasitica* (Linnaeus, 1763) by Nicolson (1776: 338, pl. 6, fig. 3) (see Rodriguez 1993: 44). Lamarck (1818: 264) considered this species new but did not describe it. The genus *Hypoconcha* was established by Guérin-Méneville (1854: 333-343, pl. 5, as *H. sabulosa*), when he gave a new key for the "Dromiens", already well-defined by H. Milne Edwards (1837). Guérin-Méneville (1854) added *Hypoconcha* to the two other known dromiacean genera, *Dromia* and *Dynomene*. *Hypoconcha* was defined by the flattened carapace, with dorsal surface partly membranous and soft, and by posterior legs ending in crescent-shaped dactylus (carapace more or less inflated and calcified, and P4 and P5 reduced and subcheliform in *Dromia*, and only P5 modified in *Dynomene*). The precise observations and figures of *Hypoconcha* by Guérin-Méneville (1854: pl. 5, fig. 4) referred to the abdomen longer than the carapace and halfway flexed, the uropods as ventral plates, and the crescent and "retractile" dactylus on P4 and P5 to firmly hold the shell.

Members of the subfamily Hypoconchinae n. subfam. are easily recognized by a number of features: 1) carapace generally rounded, hourglass-shaped; dorsal surface flattened, very thin and partly membranous; ecdysis area probably represented by whole branchiostegal region, at least; 2) front and lateral margins greatly expanded, covering all parts of head, except antennal flagella, and displacing eyes in ventral location; front semicircular or slightly truncate in outline; 3) male abdomen widely triangular and flexed at right angles in mid-length; 4) male pleopodal formula complete: Pl3-Pl5 generally as uniramous vestiges in males; 5) uropods showing always as ventral plates; 6) P4 and P5 very dissimilar, with peculiarly contorted and extremely mobile dactyli, which are fitted in deeply notched extremity of propodi (Guinot & Tavares 2000: 306, fig. 5); 7) condyle of propodi of P4 and P5 modified into prop-up plate, noticeably large, not concealed; gynglyme of propodi deeply notched in order to receive propodal condyle; the set prop-up plate/condyle blocking and preventing carpus from completely folding against merus; 8) female thoracic sternites 7 and 8 tilted drastically, perpendicular in relation to preceding thoracic sternites; and 9) obligate carrier of a lamellibranch shell.

In the Hypoconchinae n. subfam. the female sternal sutures are not as extended forward as in the Dromiinae n. status; the apertures of spermathecae are located beyond level of condyle of P3, not very far from female gonopores on P3, however (Fig. 19A).

In the Hypoconchinae n. subfam. the uropods show as ventral plates (not visible dorsally in both males and females) and occur along with vestigial Pl3-Pl5 in males. The male pleopodal formula is complete, such as in the Sphaerodromiinae n. subfam. (intercalary dorsal plates) and in the Dromiinae n. status *pro parte* (see Patterns of uropods and vestigial male pleopods 3-5; Table 1). A combination of characters similar to that found in the Hypoconchinae n. subfam., i.e. vestigial pleopods combined with ventral uropods, occurs (with certainty) in *Dromidia*, *Exodromidia* and *Platydromia*.

In the Hypoconchinae n. subfam. neither the uropod nor any other apparent structure holds the abdomen folded beneath cephalothorax. In *H. californiensis*, however, the P1 coxa bears a series of spiniform tubercules, the strongest one overhanging telson margin. As a result of being disposed onto two planes, the abdomen apparently has its posterior part remaining pressed against thoracic sternum in normal flexion. How the curious keels on P1-P2 coxae of *H. californiensis* (Fig. 19A) play role in holding of abdomen is unknown.

As described in *H. arcuata* by Kircher (1970: figs 2c, 12e) and in *H. parasitica*, by Lang & Young (1980: 860, fig. 8A, D, as *H. sabulosa* (Herbst, 1799)), the megalopa of the Hypoconchinae n. subfam. is the only one in the family Dromiidae with a single, long, terminal setum on dactylus of P5 (versus several feelers in the Dromiinae n. status, even in *Conchoecetes*, see Sankolly & Shenoy 1968; Franco 1998; Guinot & Tavares 2000). The single feeler on dactylus of P5 may well prove to be another diagnostic character of the Hypoconchinae n. subfam.

The larval and postlarval features (plesiomorphies?) shared by *Hypoconcha* and *Conchoecetes* (see McLay *et al.* 2001: 739, 744, table 2) are not exclusive to these genera and could not be regarded here as an indication of close relationship between *Hypoconcha* and *Conchoecetes*. Therefore, the two genera are kept in different subfamilies, Hypoconchinae n. subfam. and Dromiinae n. status, respectively.

Spears *et al.* (1992: 457) obtained interesting results from sequence-divergence estimates and phylogenies inferred by maximum parsymony analyses of 18S rRNA aligned sequences. As far as *Hypoconcha* [*H. arcuata*] is concerned, their results suggested that "it seems unlikely that *Dromidia* [in fact *Moreiradromia antillensis* n. comb., Dromiinae n. status] and *Hypoconcha* [Hypoconchinae n. subfam.], the [only] two dromiid genera used in this study, are as closely related as previously thought".

The uniqueness of *Hypoconcha* led McLay (1993: 229) to question whether it belongs or not to the Dromiidae. McLay (2001b: 8) expressed the opinion that *Hypoconcha* and *Conchoecetes* shared a common ancestor and belonged to the same particular grouping, whereas *Desmodromia* was to be kept amongst the other dromiids. *Hypoconcha* and *Conchoecetes* share a shell-carrying behaviour, but each with a different method of grapsing the shell (see under Shell-carrying behaviour) and (perhaps) some larval features (McLay *et al.* 2001). They also share several characters that is: thin tegument of dorsal carapace (partly membranous in *Hypoconcha*), related to shell-carrying; strongly calcified and anteriorly truncated sternite 4. A closer examination of the morphology of *Hypoconcha* and *Conchoecetes* reveals, however, that overall similarities are probably superficial (Guinot & Tavares 2000) and that there is no reason to include *Conchoecetes* in the subfamily Hypoconchinae n. subfam. The shape of male abdomen, the male uropods (salient dorsal uropods in *Conchoecetes*, Fig. 3B, C, narrow ventral plates in *Hypoconcha*, Fig. 19B) and the condition of sternites 7 and 8 (bent at right angles and bordered laterally by sutures 7/8 in female *Hypoconcha*, Fig. 19A), the sternite 3 visible dorsally in *Conchoecetes* (Fig. 3A, B) (hardly or not visible dorsally in *Hypoconcha*, Fig. 19A), the location of spermathecal apertures (not very far from gonopores on P3 in *Hypoconcha*, Fig. 19A, between P2 in *Conchoecetes*, Fig. 3A) clearly distinguish the two genera. A complete male pleopodal formula is found in *Hypoconcha* (Fig. 19B), but does not seem present in *Conchoecetes* (Fig. 3C). The similarities of thoracic sternum in *Hypoconcha* and *Conchoecetes* are difficult to be appraised: they are probably in close relationship with the shell-carrying behaviour. In male *Hypoconcha* the well calcified, very flat sternite 4 (Fig. 19A) and the short abdomen which only occupies a posterior location (Rathbun 1937: pl.11, fig. 2) are different from the condition of *Conchoecetes* (Fig. 3A, B).

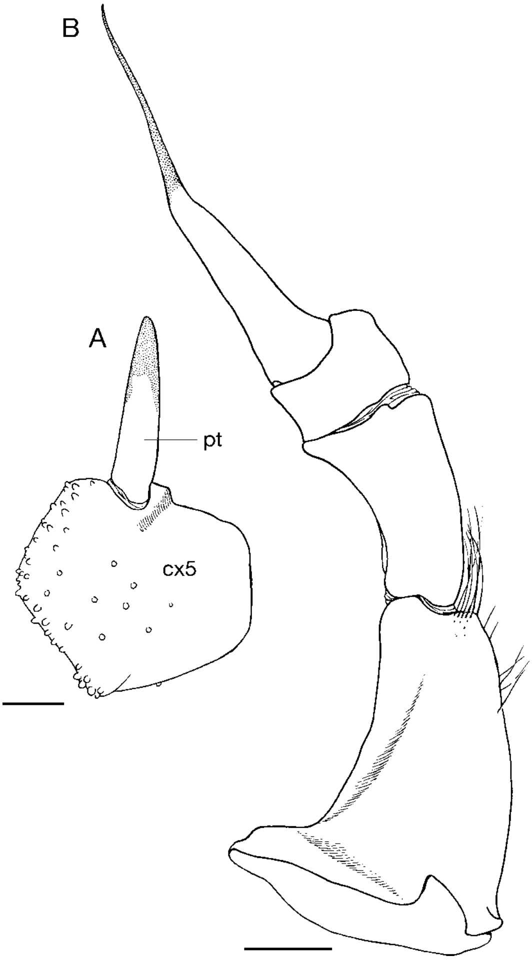

FIG. 20. — *Hypoconcha panamensis* Smith, 1869; **A**, Panama, ♂ 20 × 21 mm (MNHN-B 21597), coxa of P5, with mobile penial tube; **B**, México, ♂ 27 × 28 mm (EMU 2941), G2, without exopod. Abbreviations: **cx5**, coxa of P5; **pt**, penial tube. Scale bars: 1 mm.

The taxonomic position of *Desmodromia* (not examined) is puzzling. As in *Hypoconcha* the carapace, although not membranous on posterior half, is poorly calcified and flattened; the eaves overhang the eyes; and P4-P5 end in upturned dactylus which supposedly holds a shell. *Hypoconcha* and *Desmodromia* differ from one another as follows: 1) epipod present on P1 (absent in *Desmodromia*); 2) narrow ventral uropods (dorsal and well-developed in immature female of *D. tranterae* McLay, 2001); 3) female sternal sutures 7/8 ending rather posteriorly in *Hypoconcha* (Fig. 19A) (between P2 in *Desmodromia*); and 4) abdominal holding never involving uropods and provided by structure on P1 coxa, or, more usually, without coxal differentiation (provided by a differentiation of P2 coxa involving uropods in *Desmodromia*). It is not known if in *Desmodromia* (such as in *Hypoconcha*) the female thoracic sternites 7 and 8 are tilted, and if the male pleopodal formula is complete and the P5 coxa differentiated into penial mobile tube since males are unknown. The lack of information on the morphology of male abdomen and of details on the P4 and P5 grasping apparatus make it difficult to compare it with the very specialized *Hypoconcha*.

Presently, the subfamily Hypoconchinae n. subfam. includes six species, all belonging to *Hypoconcha* Guérin-Méneville, 1854: *H. arcuata* Stimpson, 1858; *H. californiensis* Bouvier, 1898; *H. lowei* Rathbun, 1933; *H. panamensis* Smith, 1869; *Cancer parasiticus* Linnaeus, 1763; and *H. spinosissima* Rathbun, 1933.

The larval development is only known for two species, *H. parasitica* (see Lang & Young 1980, as *H. sabulosa*) and *H. arcuata* (see Kircher 1970). It is abbreviated to only three zoeal stages and a megalopa. We examined an ovigerous female (6 mm length) of *H. parasitica* (MNHN-B 28279) with less than 40 rather large eggs.

Subfamily SPHAERODROMIINAE n. subfam.
(Figs 21-24; 28E-G)

TYPE GENUS. — *Sphaerodromia* Alcock, 1899 by present designation (type species: *Dromidia kendalli* Alcock & Anderson, 1894 by monotypy. Gender: feminine).

GENERA INCLUDED. — *Eodromia* McLay, 1993 (type species: *Eodromia denticulata* McLay, 1993 by monotypy); *Sphaerodromia* Alcock, 1899.

DESCRIPTION

Carapace longer than wide or as long as wide, subglobose. Lateral margins subparallel; anterolateral margin long, joining buccal cavern instead of exorbital angle, and separated from short posterolateral margin by deep notch. Dorsal surface with regions not defined or almost indistinct; subhepatic area more or less inflated. Branchial groove not marked. Front projecting well beyond orbits. Rostrum noticeably deflexed. Presence of two pseudorostral lobes extending uninterruptedly around supraorbital margin. Orbits oblique, deeply hollowed on lateral sides of carapace; supra- and infraorbital margins entire, forming a sort of eave, orbital border almost continuous. Proepistome widely triangular, in front of well-defined epistome. Ocular stalk short and thick. Antennules with basal article strongly developed. Antenna: first article beak-like; basal article with exopodal scale markedly developed, as long or longer than following article; internal angle weakly or not produced. Mxp3 operculiform; coxae approximated.

Thoracic sternum narrow. Gynglymes of thoracic sternites 1-3 largely spaced from each other, stepped at lower plane. Sternites 1-3 not visible; sternite 4 forming plate overhanging or just touching bases of mxp3 (Fig. 21A, B). Episternites 4 and 5 more or less elongated and wide, their gynglymes in almost terminal location. When male abdomen flexed against ventral surface, anterior portion of sternite 4 and lateral part (i.e. episternite 4) exposed, while episternite 5 is completely covered by uropod and hardly or not visible at all (Fig. 21A). Sutures 4/5 and 5/6 very short, only lateral and not clearly visible; sutures 6/7 and 7/8 oblique. Female sternal sutures 7/8 short; apertures of spermathecae very minute, behind level of P3 gonopore, located laterally, and either completely exposed (*Sphaerodromia* pro parte, for example *S. lamellata* Crosnier, 1994), or concealed under the lateral heightening and fold of sternite 8 (*Sphaerodromia*

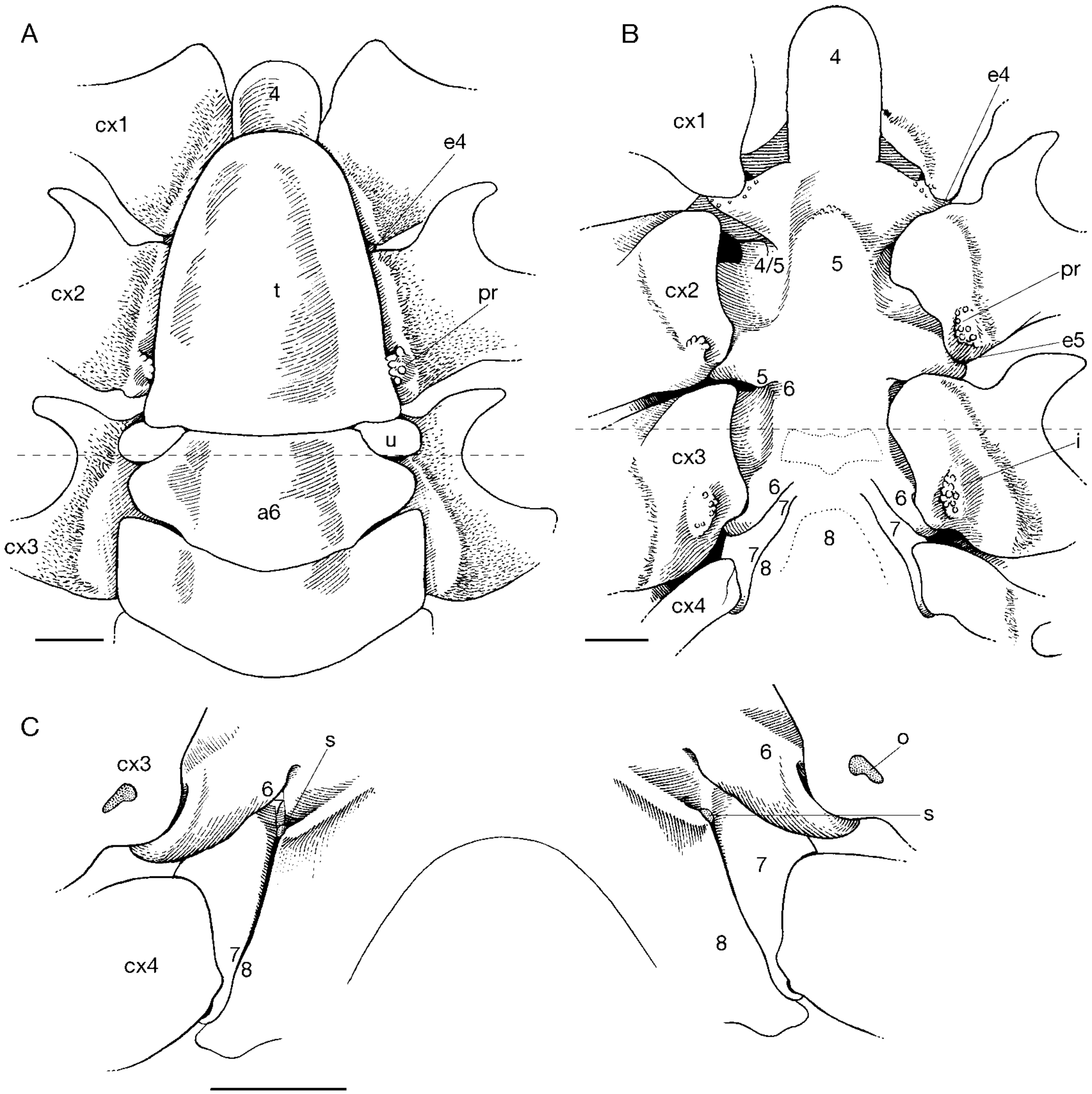

FIG. 21. — *Sphaerodromia ducoussoi* McLay, 1991; **A**, **B**, Tuamotu, ♂ 43.2 × 43 mm, holotype (MNHN-B 22172), thoracic sternum without and with abdomen; **C**, Tuamotu, Mururoa, ♀ 41.4 × 40.9 mm, paratype (MNHN-B 22173), spermathecae, behind level of P3. Abbreviations: **a6**, abdominal segment 6; **cx1**-**cx4**, coxae of P1-P4; **e4**, **e5**, episternites 4, 5; **i**, prominence on P3 coxa, covered by abdomen and inefficient for abdominal holding; **o**, female gonopore; **pr**, holding prominence; **s**, aperture of spermatheca; **t**, telson; **u**, uropod; **4-8**, sternites 4-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 2.5 mm.

pro parte, for example *S. ducoussoi* McLay, 1991, Fig. 21C; *Eodromia*, Fig. 24C).

Abdomen long but not reaching mxp3, once folded; pleural parts well recognizable, all segments free; segment 6 noticeably expanded laterally (*Sphaerodromia*, Figs 21A; 22; *Eodromia*, Fig. 24A, B); telson long. Vestigial male pleopods 3-5 present, either biramous (*Sphaerodromia*, Fig. 22) or uniramous (*Eodromia*, Fig. 24A). Male uropods as elongated dorsal plates, exposed but deeply inserted between abdominal segment 6 and telson (the base of which covering uropod), included in the outline of abdomen, *viz.* not really salient nor movable, occupying a relatively

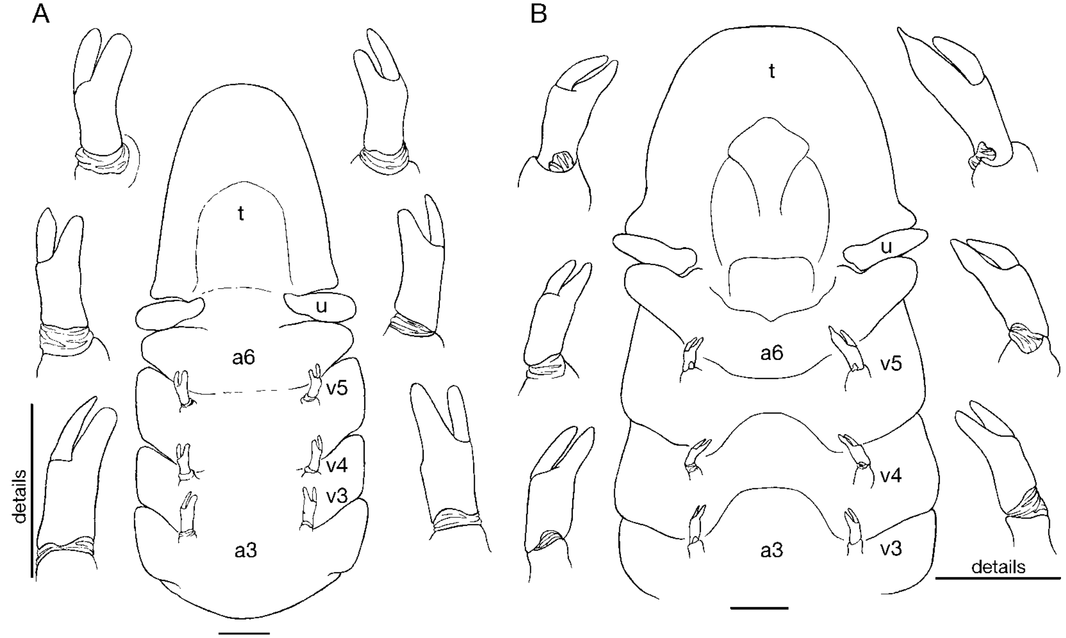

FIG. 22. — *Sphaerodromia* Alcock, 1899, biramous vestigial male pleopods on segments 3-5 with details on each side; **A**, *S. ducoussoi* McLay, 1991, Tuamotu, Tuanake, ♂ 43.2 × 43 mm, holotype (MNHN-B 22172); **B**, *S. nux* Alcock, 1899, Madagascar, ♂ 60 × 67 mm (MNHN-B 6872). Abbreviations: **a3**, **a6**, abdominal segments 3, 6; **t**, telson; **u**, uropod; **v3**-**v5**, biramous vestigial pleopods 3-5. Scale bars: A, 2.5 mm; B, 2 mm.

large portion of lateral margin of abdomen, playing no role in holding of abdomen (*Sphaerodromia*, Figs 21A; 22; *Eodromia*, Fig. 24A, B). Dimorphism of uropods marked. Female uropods deeply inserted, rather developed, occupying large part (*Sphaerodromia*) or whole part (*Eodromia*) of abdominal external margin posteriorly to telson, and well visible dorsally (*Sphaerodromia* and *Eodromia*).

Holding of male abdomen not really efficient when provided by granulous prominence on P2 coxae involving telson in its anterior part (*Sphaerodromia*, where the abdomen is loosely retained). Always, a prominence on P3 coxae, covered by abdomen and inefficient (Fig. 21B).

Epipod present on chelipeds; podobranch either present (*Sphaerodromia*) or absent (*Eodromia*). P2 and P3 with epipods, with or without podobranchs (*Sphaerodromia*), or without epipods (*Eodromia*).

Chelipeds stout, with fingers close along most of length; dactylus with a large proximal tooth and rest of prehensile margin very thin and smooth; fixed finger with marked proximal teeth and several smaller ones. P2 and P3, very long, neither lobed nor nodose; propodus very long, bearing distal propodal spine. P4 and P5 reduced, shorter than preceding ones, similar in size, oriented in a different way than P2 and P3, only P5 dorsal; subcheliform apparatus formed by multiple distal propodal spines opposing dactyli, three to five; no spines on outer propodal margin; presence of spines on inner margin of P4 and P5 dactylus. P5 without spines on outer dactylus margin.

Male coxa of P5 strongly modified, extended, without movable penial tube, in the two genera (*Sphaerodromia*, Figs 23A; 28E, F; *Eodromia*, Fig. 28G).

G1 with well-developed apical plate. G2 long, with styliform flagellum, exopod present but of variable length (*Sphaerodromia*, Fig. 23B; presence to be verified in *Eodromia*).

Carrying behaviour

Large pieces of sponges for *Sphaerodromia* (McLay & Crosnier 1991; McLay 1991, 1993;

Crosnier 1994); camouflage data not known in *Eodromia*.

REMARKS

Differences between *Sphaerodromia* and other dromiids were already discussed (McLay & Crosnier 1991; McLay 1991, 1993). They concern the shape of carapace, the presence of podobranchs on pereopods, the presence of distal propodal spine on P2 and P3, and the arrangement of spines to form the subchelate mechanism of P4 and P5. The condition is similar in *Eodromia*, except that podobranchs and epipods on P2 and P3 are lost, an absence that must be regarded as a more advanced character state (McLay 1993: 131). A unique character of the Sphaerodromiinae n. subfam. is the long P2 and P3 propodus (with distal spine) and the not strongly curved dactylus. The propodus is shorter and without distal spine, and dactylus curved in the Dromiinae n. status. In the Sphaerodromiinae n. subfam. and Dromiinae n. status, the inner margin of dactylus on P2 and P3 bears several spines (whereas it is smooth, or nearly smooth, in the Hypoconchinae n. subfam.).

The study in this review of morphological structures often neglected before revealed that the sphaerodromiine genera share a combination of characters found nowhere else within the Dromiidae. In *Sphaerodromia* and *Eodromia*, the coxa of P5 is extended to form conical expansion in which the penis is completely enclosed. The coxa and penis thus form a single structure (Figs 23A; 25B, D; 28E-G). In contrast, in the Dromiinae n. status (Fig. 28H-J) and Hypoconchinae n. subfam. (Figs 20A; 28K) the male coxa of P5 is not modified to enclose penis and there are two independent structures: the unmodified P5 coxa and the long, sclerotized penis emanating from male gonopore. The dromiine and hypoconchine movable structures, here named "penial tube", end in soft tip (see Patterns of P5 coxa and penis; Fig. 28).

The Sphaerodromiinae n. subfam. (Figs 21C; 24C) have short female sternal sutures 7/8, so the apertures of spermathecae lie, always laterally, in the vicinity of female gonopores on P3, that is, behind level of P3. In *Sphaerodromia lamellata*, the suture 7/8 is shorter than in *S. ducoussoi* (Fig. 21C) or *S. kendalli* (Alcock & Anderson, 1894), and the spermathecal aperture lies posteriorly and is not concealed under raised part of

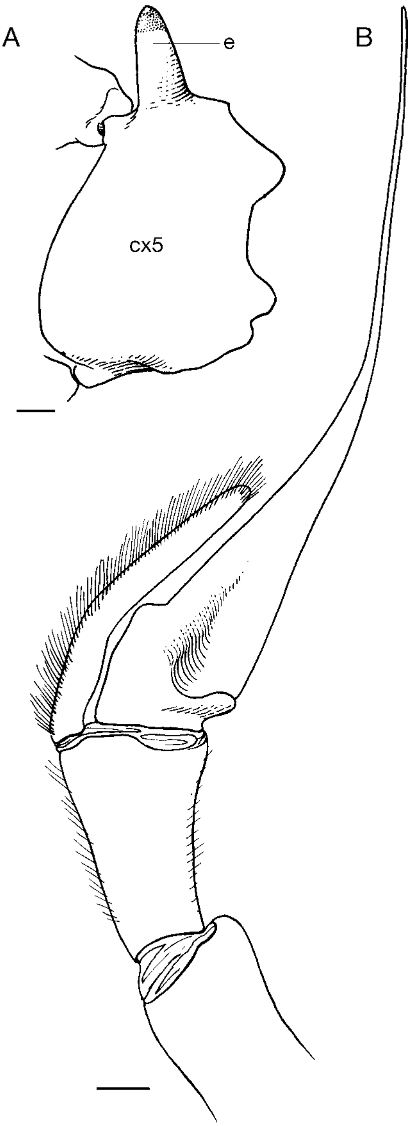

FIG. 23. — *Sphaerodromia nux* Alcock, 1899, Madagascar, ♂ 60 × 67 mm (MNHN-B 6872); **A**, coxa of P5, modified and elongated into process enclosing penis and not forming penial tube; **B**, G2, with long exopod. Abbreviations: **cx5**, coxae of P5; **e**, elongation of P5 coxa enclosing penis. Scale bars: 1 mm.

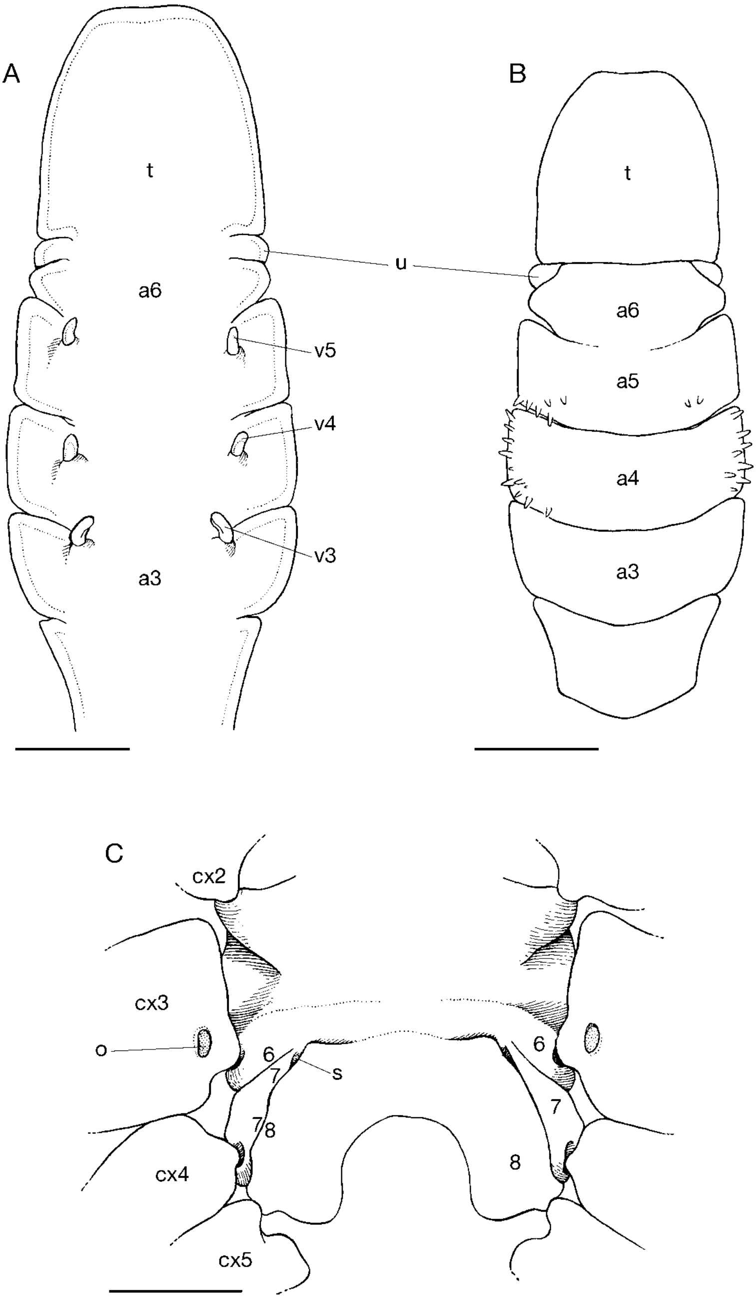

Fig. 24. — *Eodromia denticulata* McLay, 1993, Indonesia, Kai Islands, Tanimbar Island, KARUBAR (MNHN-B 26327); **A**, **B**, ♂ 4.9 × 4.5 mm, abdomen, ventral and dorsal views; note elongated uniramous vestigial pleopods on segments 3-5; **C**, ovigerous ♀ 5 × 4.5 mm, thoracic sternum and spermathecae, with aperture at level of P3. Abbreviations: **a3**-**a6**, abdominal segments 3-6; **cx2**-**cx5**, coxae of P2-P5; **o**, female gonopore; **s**, aperture of spermatheca; **t**, telson; **u**, uropod; **v3**-**v5**, vestigial pleopods 3-5; **6**-**8**, sternites 6-8; **6/7**, **7/8**, thoracic sternal sutures 6/7, 7/8. Scale bars: 0.5 mm.

sternite 8. Conversely, all the Dromiinae n. status show extremely long female sutures 7/8, so that the spermathecae open far beyond level of P3, sometimes at level of P1 or beyond. Therefore, in the dromiine females the sternites 7 and 8 occupy much of the ventral surface of cephalothorax, and the thoracic sternum appears dramatically distorted. The only exception is *Stebbingdromia plumosa* n. comb., where the spermathecae open between P3 (Fig. 17C). In the dromiine genera the spermathecae open apart or together, each spermathecal aperture being often positioned on more or less prominent tubercle; in a few genera the spermathecae open on a single tubercle. It is worth noting that the position of the apertures of spermathecae in relation to female gonopores on P3 coxae and the kind of penial structure seem to be related. Thus, in considering the sphaerodromiine condition, the location of the apertures about level of coxae of P3 seems to be connected with a short and non-articulated penis. Conversely, a spermathecal aperture positioned far beyond coxa of P3 appears to be connected with a long, sclerotized and movable penis (penial tube). This condition is found in the Dromiinae n. status (again, the only exception is the atypical *Stebbingdromia plumosa* n. comb., which has short female sutures 7/8 and penial tube; Figs 17A, C; 18A).

The Hypoconchinae n. subfam. show a different combination: sternal sutures 7/8 relatively short (Fig. 19A) and the presence of a penial tube (Figs 20A; 28K). In the Hypoconchinae n. subfam. the female sternal sutures 7/8 are slightly extended forward, more than in the Sphaerodromiinae n. subfam. (where they are behind level of P3) but not so far forward as in the Dromiinae n. status. In this respect Dromiinae n. status and Hypoconchinae n. subfam. differ less from one another than from Sphaerodromiinae n. subfam.

The Sphaerodromiinae n. subfam. also shares the absence of spines on outer margin of propodus of P4 and on outer margin of dactylus of P5.

Within the Sphaerodromiinae n. subfam., *Sphaerodromia* and *Eodromia* seem to be very closely related to one another as they share a number of characters unique among the Dromiidae. The *Sphaerodromia* species are relatively large (width more than 65 mm in *S. nux* Alcock, 1899), while *Eodromia denticulata* McLay, 1993 is very small, with ovigerous females measuring only 4.5 mm width. In *Sphaerodromia* and *Eodromia* the basal antennal article bears a long exopodal scale, extending "beyond joint of segments three or four" (Mc Lay 1993: 127), and its internal corner is not or only weakly produced.

In *Sphaerodromia* (Fig. 21A, B) and *Eodromia*, the long male abdomen covers most part of thoracic sternum, except anterior part of sternite 4 which is in contact with mxp3. In *Sphaerodromia* (Figs 21A; 22) and *Eodromia* (Fig. 24A, B), the male abdominal segment 6 is expanded laterally. In *Sphaerodromia* and *Eodromia*, no specialized structures are found for an efficient abdominal holding, so the male abdomen is rather loosely retained beneath cephalothorax (the granulous prominences found on P2 and P3 coxae are inefficient).

Sphaerodromia and *Eodromia* share the subcheliform system formed by multiple distal propodal spines on the dactyli. The minute apertures of spermathecae, at level of P3, are more or less concealed under fold of sternite 8.

Vestigial pleopods are always present in male Sphaerodromiinae n. subfam.: they are biramous in *Sphaerodromia* (Fig. 22) and uniramous in *Eodromia* (Fig. 24A). In male Sphaerodromiinae n. subfam. Pl3 to Pl5 occur with immovable uropods showing as intercalary dorsal plates. This combination of characters (Pl3-Pl5 combined with dorsal uropods) is known from only a few genera and species of Dromiinae n. status: *Dromia* pro parte (Fig. 27), *Moreiradromia* n. gen. (Fig. 14B) and *Stebbingdromia* n. gen. (Fig. 18C; Table 1).

The G1 of *Sphaerodromia* is provided by apical plate, and the G2 (Fig. 23B) with exopod. McLay (1993: 132) indicated that the first pairs of pleopods of the male paratype of *Eodromia denticulata* (8.2 × 7.8 mm; MNHN-B 22545) were "not properly developed". This specimen has several pairs of pleopods and a P5 coxa not extended: it seems to be an abnormal individual. In a male specimen (4.5 mm width; MNHN-B 26327), the P5 coxa is elongated and both G1 and G2 are developed; an apical plate is clearly present on G1 as in *Sphaerodromia*, whereas an exopod is not discernible on the G2, which is typically prolonged by styliform flagellum.

Presently, the subfamily Sphaerodromiinae n. subfam. consist of six species including among two genera: 1) *Sphaerodromia* (*Sphaerodromia brizops* McLay & Crosnier, 1991; *Sphaerodromia ducoussoi*; *Dromidia kendalli*; *Sphaerodromia lamellata*; *Sphaerodromia nux*); 2) *Eodromia* (*Eodromia denticulata*).

The close relationship between *Sphaerodromia* and *Eodromia*, both with many ancestral characteristics, was already noted by McLay (1993: 130, 228). McLay *et al.* (2001: 741, table 3) recently predicted that the larvae of these two genera should also have primitive features. McLay (1993: 131) noted that the absence of epipods on P2-P3 and of podobranch on chelipeds must be regarded as the more advanced character states of *Eodromia*.

Our investigation suggests that the Sphaerodromiinae n. subfam. is a basal group within the Dromiidae. Several sphaerodromiine plesiomorphic characters, that is, a male P5 coxa modified and extended in a process (in contrast to a mobile penial tube in the Dromiinae n. status and Hypoconchinae n. subfam.), the male vestigial pleopods on abdominal segments 3-5, the short female sutures 7/8, and the apertures of spermathecae positioned near female gonopores on P3 coxae, are also found in the two other families of Dromiacea, Homolodromiidae Alcock, 1900 and Dynomenidae Ortmann, 1892. An exopod present on G2, sometimes well-developed (*Sphaerodromia nux*, Fig. 23B) or shorter (*S. brizops*, *S. lamellata*), is shared with the Dynomenidae, but not with the Homolodromiidae.

It is worth noting that the spermatozoal ultrastructure of *Sphaerodromia* (*S. lamellata*) allies the genus more closely to the dynomenid *Metadynomene tanensis* (Yokoya, 1933) than to the advanced dromiid (dromiine) *Stimdromia lateralis* (Gray, 1831) (Guinot *et al.* 1998: 91, 93, 94, fig. 8), which is in accordance to the plesiomorphic condition of the Sphaerodromiinae n. subfam.

About the status of *Sphaerodromia lethrinusae* Takeda & Kurata, 1976, see under *Dromidiopsis* sensu nobis.

Whether *Parasphaerodromia* Spiridonov, 1992 belongs to the Sphaerodromiinae n. subfam. is not certain but seems unlikely. Based on the original description of *Parasphaerodromia subglobosa* Spiridonov, 1992, type species and the only representative of the genus, McLay (1993: 122, 183, 184) synonymized the species with *Dromidia spongiosa*, now *Platydromia spongiosa* n. comb. (see above, Fig. 15), but furnished no arguments for doing so. As a result, *Parasphaerodromia* is merged into *Platydromia* Brocchi, 1877. The synonymy between *Parasphaerodromia subglobosa* Spiridonov, 1992 and *Platydromia spongiosa* n. comb. shall very likely to be confirmed in the future (see above, under *Platydromia*). Our view is that the establishment of dromiid taxa necessitates the adequate description and illustration of essential characters such as the thoracic sternum and uropods; details of the carapace and legs alone are usually insufficient.

DISCUSSION

THE STATUS OF THE GENUS *FRODROMIA* MCLAY, 1993 (FIGS 25; 26)

The genus *Frodromia*, which consists of two species (*Petalomera atypica* T. Sakai, 1936, type species by original designation; and *Petalomera reticulata* T. Sakai, 1974), is not more related to the Sphaerodromiinae n. subfam. than to Dromiinae n. status. The sphaerodromiine characters of *Frodromia* are as follows: elongated shape of carapace, with subparallel lateral borders (see McLay 1993: figs 6a, 17d); long male telson (Fig. 25A, C); vestigial male pleopods 3-5 present (Fig. 25C); male uropods showing as deeply inserted and obliquely oriented dorsal plates; short female sternal sutures 7/8; apertures of spermathecae lying not very far from P3 coxae, i.e. close to female gonopores on P3 (Fig. 26); male

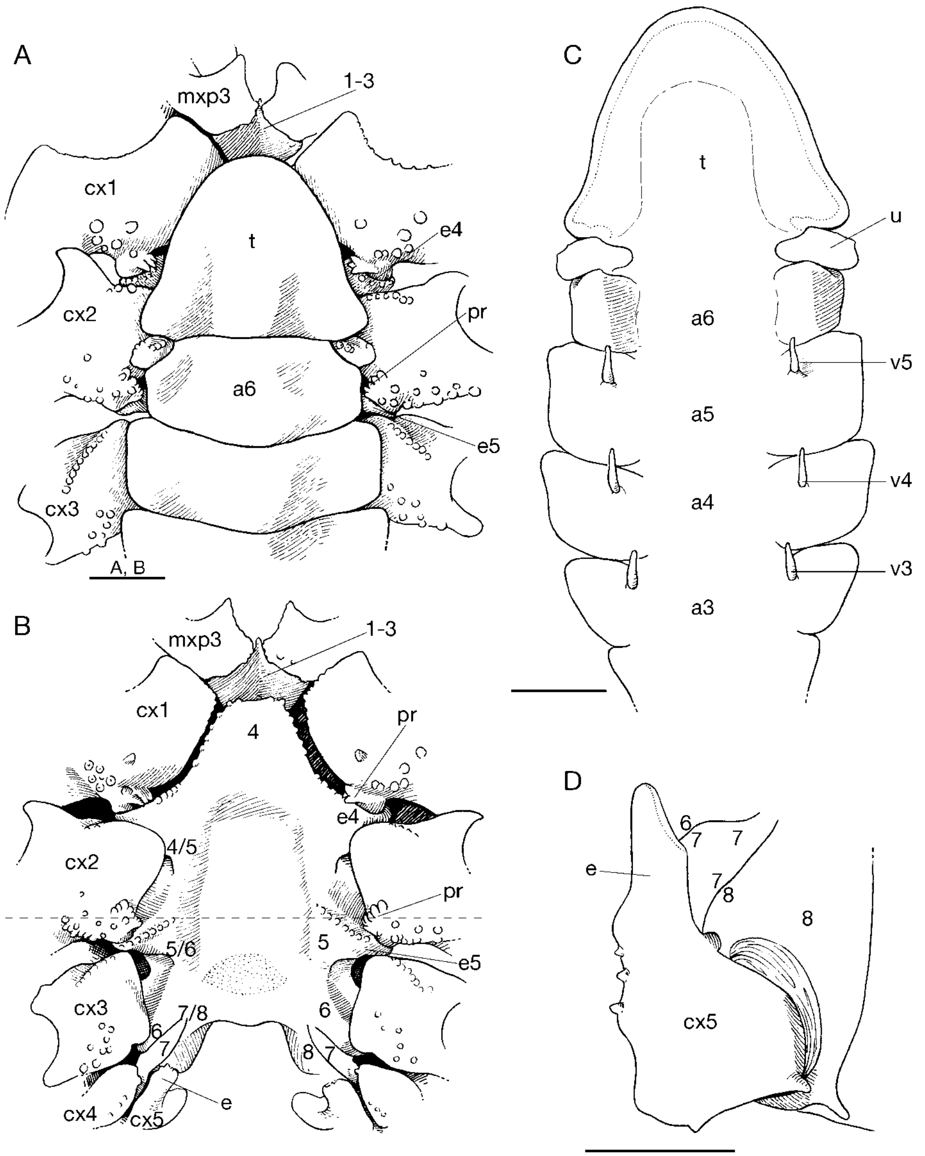

FIG. 25. — *Frodromia atypica* (Sakai, 1936), New Caledonia, MUSORSTOM 4, CP 171, ♂ 10.6 × 9.5 mm (MNHN-B 22559); **A**, **B**, thoracic sternum, with and without abdomen; **C**, abdomen, ventral view; note uropods showing as intercalary dorsal plates and elongated uniramous vestigial pleopods on segments 3-5; **D**, P5 coxa, modified and elongated into process enclosing penis and not forming penial tube. Abbreviations: **a3-a6**, abdominal segments 3-6; **cx1-cx5**, coxae of P1-P5; **e**, elongation of P5 coxa enclosing penis; **e4**, **e5**, episternites 4, 5; **mxp3**, external maxilliped; **pr**, holding prominence on P1 and P2; **t**, telson; **u**, uropod; **v3-v5**, vestigial pleopods 3-5; **1-3**, sternites 1-3; **4-8**, sternites 4-8; **4/5-7/8**, thoracic sternal sutures 4/5-7/8. Dotted line indicates difference in level. Scale bars: 1 mm.

P5 coxa strongly modified, without "articulated", movable penial tube (Fig. 25D); P2 and P3 with long propodus and not strongly curved dactylus (see McLay 1993: fig. 6d); presence of a prominence on P3 coxae, covered by abdomen, but inefficient for abdominal holding.

Nevertheless, *Frodromia* is distinguished from the Sphaerodromiinae n. subfam. by several characters: two pseudorostral teeth, one at each side of rostrum (two pseudorostral lobes extending uninterruptedly around supraorbital margin in *Sphaerodromia* and *Eodromia*); sutures 7/8 almost longitudinal (oblique in *Sphaerodromia* and *Eodromia*); exopod of antenna with internal angle produced (weakly or not produced in *Sphaerodromia* and *Eodromia*); mxp3 with coxae not approximated (approximated in *Sphaerodromia* and *Eodromia*); sternites 1-3 visible (Fig. 25A) (not exposed in *Sphaerodromia* and *Eodromia*); sternite 4 covered by abdomen when flexed (exposed in *Sphaerodromia* and *Eodromia*); apertures of spermathecae raised, each on a tubercule, and visible (Fig. 26) (often concealed in *Sphaerodromia*); abdominal segment 6 not expanded laterally (Fig. 25A, C) (noticeably expanded in *Sphaerodromia* and *Eodromia*); abdominal holding efficient, by means of marked granulous prominence on P1 coxae acting at base of telson and of another prominence on P2 coxae acting with (probably mobile) uropods (Fig. 25A, C) (abdominal holding not really efficient, not involving uropods in *Sphaerodromia* and *Eodromia*); podobranchs absent on pereopods (present in *Sphaerodromia* but absent in *Eodromia*); fingers of chelipeds with prehensile margins toothed (fingers of chelipeds, each with one marked proximal tooth and close along most of length of prehensile margins, and no other marked teeth on dactyl margin in *Sphaerodromia* and *Eodromia*); P2 and P3 without distal propodal spine (with a distal propodal spine in *Sphaerodromia* and *Eodromia*); subchelate mechanism of P4 and P5 with dactyli opposed by one (on P4) or two (on P5) propodal spines (multiple distal propodal spines opposing dactyli, three to five, in *Sphaerodromia* and *Eodromia*); G1 sharply tipped (a well-developed apical plate in *Sphaerodromia*); G2 without exopod (with exopod, at least in *Sphaerodromia*). The camouflage of *Frodromia* is provided by ascidians (Sakai 1936; McLay 1993).

The combination of characters of *Frodromia* does not secure its position in any dromiid subfamily, and whether or not this genus belongs to the Sphaerodromiinae n. subfam. deserves further investigation. *Frodromia* seems apart within the Sphaerodromiinae n. subfam., but several of its features (such as loss of apical plate on G1 and exopod on G2, reduction of spines of P4 and P5 subcheliform apparatus, efficiency of abdominal holding) may be regarded as more advanced character state, such as features of *Eodromia* compared with those of *Sphaerodromia*. It should be noted that *Frodromia* is the only case in the Dromiidae where the female gonopore on P3 coxa opens very close to anterior border of coxa and at summit of tubular process, which is proximally armed with strong spur (*Frodromia atypica*, Fig. 26; *F. reticulata*, not examined, condition to be verified). In *Frodromia atypica* the P3 coxa is dimorphic since the male does not possess such a process.

PATTERNS OF UROPODS AND VESTIGIAL MALE PLEOPODS 3-5

Unlike other Decapoda, the uropod is never biramous in the Brachyura (Podotremata, Heterotremata and Thoracotremata). The brachyuran uropod shows a wealth of morphological variation, even if its primary function is related to the abdominal holding against thoracic sternum.

In the majority of the families of the Heterotremata and Thoracotremata (Eubrachyura) the uropod shows as a socket situated on ventral surface of abdominal segment 6 and is homologous to the ancient uropod. The socket is the hollow part of the press-button mechanism (Guinot & Bouchard 1998: 682, table 3). Conversely, the uropod is diversely modified in the Podotremata. Always uniramous, it shows either as a ventral lobe or plate (Homolodromiidae, Dromiidae *pro parte*), or as a calcified dorsal plate (Dynomenidae, Dromiidae *pro parte*), or as a socket (Homoloidea, Lyreidinae), all homologous. The term “vestigial uropod” is mistaking as this structure actually represents a wealth of character states (Guinot & Tavares 2001: fig. 15). The uropod is completely lost in the podotreme families Cymonomidae Bouvier, 1897, Phyllotymolinidae Tavares, 1998, Cyclodorippidae Ortmann, 1892, and in the Raninoidea de Haan,

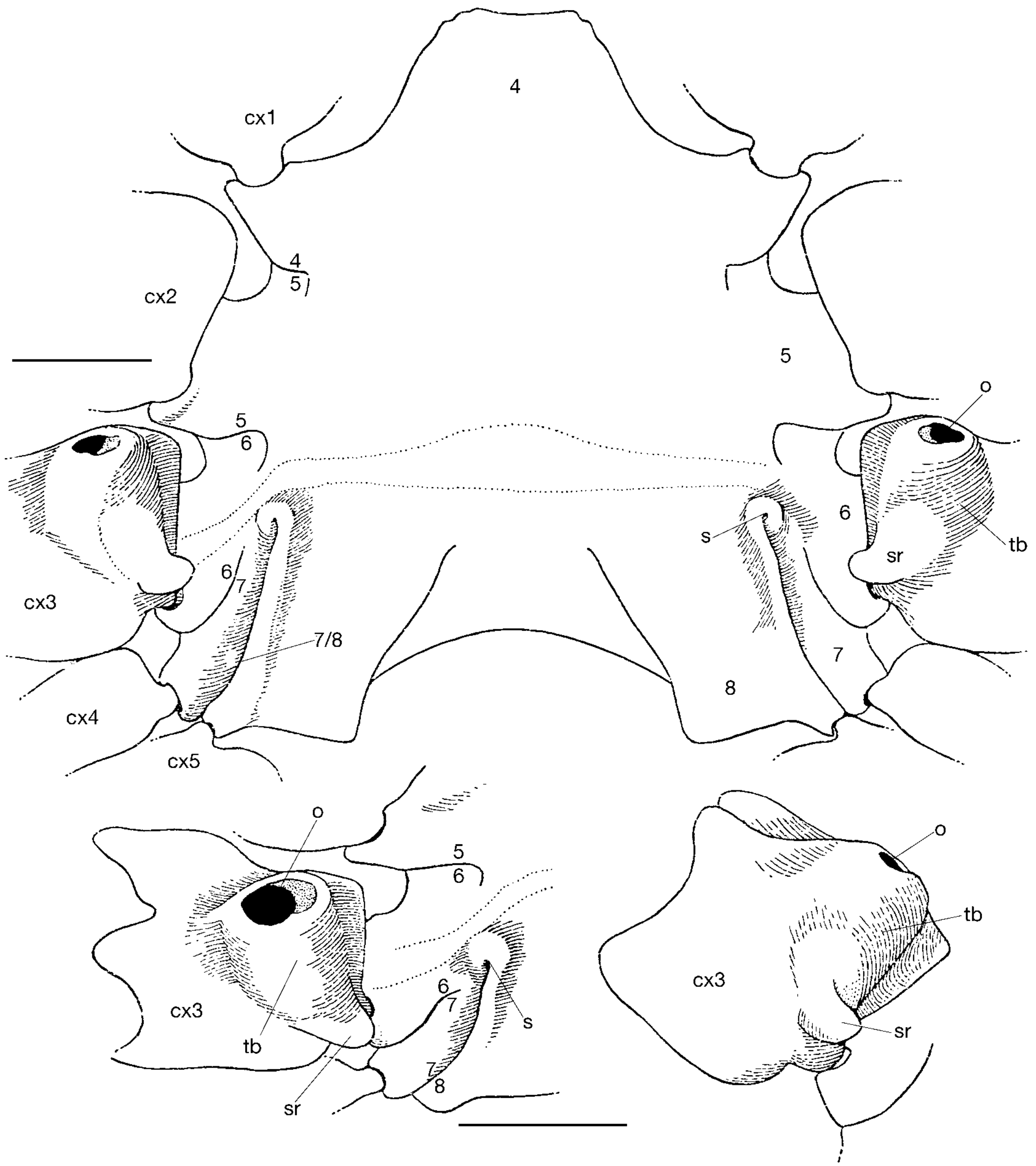

FIG. 26. — *Frodromia atypica* (Sakai, 1936), New Caledonia, MUSORSTOM 4, CP 171, ♀ 8.5 × 7.3 mm (MNHN-B 22560), thoracic sternum and spermathecae with two detailed views (lower) of coxa of P3; note apertures of spermatheca behind level of female gonopores located near anterior border of coxa, at summit of tubular process. Abbreviations: **cx1**-**cx5**, coxae of P1-P5; **o**, female gonopore; **s**, aperture of spermatheca; **sr**, spur of P3 coxa; **tb**, tubular process of P3 coxa, with gonopore at its extremity; **4**-**8**, sternites 4-8; **4/5**-**7/8**, thoracic sternal sutures 4/5-7/8. Scale bars: 1 mm.

1839 (Lyreidinae Guinot, 1993 excepted). The total loss of the uropod may be interpreted as a synapomorphy of the Archaeobrachyura Guinot, 1977 *sensu* Guinot & Tavares 2001 (Cymonomidae, Phyllotymolinidae, Cyclodorippidae, Raninoidea *pro parte*).

The dromiacean uropod is generally simply referred as "vestigial". Such an oversimplification does not reflect the diversity of uropod patterns found within the group. The dynomenid uropod always shows as a well-developed dorsal plate, sexually dimorphic, not markedly prominent, even in males, and not efficient in maintaining the broad abdomen.

The dromiid uropod is more diverse. It often shows as a calcified and exposed dorsal plate, with a marked sexual dimorphism in terms of size and shape. This plate is placed between segment 6 and telson. It does not have the same place or orientation than a vestigial male pleopod than may remain on preceding segments. Among dromiids, the dorsal uropods are more or less salient and movable in males (and immature females) and very often play major role in the abdominal holding. The dromiid uropod can also show as a ventral plate, more or less developed and calcified, never visible dorsally in either sex, sometimes very reduced and resembling a soft lobe (*Austrodromidia australis*, Fig. 1C), or sometimes indistinct (*A. octodentata*, Fig. 2B).

The dromiid uropod can also show as a calcified platelet, obliquely oriented, and so deeply inserted ventrally that it is no longer markedly salient, but still exposed dorsally (*Stebbingdromia* n. gen., Fig. 17B; *Sphaerodromia*, Figs 21A; 22; *Eodromia*, Fig. 24A, B; *Frodromia*, Fig. 25A, C). This condition is herein named "intercalary platelet" and has been indicated as a dorsal uropod in Table 1. Even though visible dorsally, intercalary platelets are not involved (or only weakly so) in abdominal holding.

In some cases the differentiation between intercalary platelets and ventral plates is not easy. In *Dromidia hirsutissima* (Fig. 5B, C) for instance, the uropod is oblique and deeply inserted ventrally, actually quite similar to the intercalary platelet condition, but hardly visible dorsally. In this particular, the uropod of *D. hirsutissima* could be regarded as intermediate between dorsal and ventral plate. The ventral uropods of *Lamarckdromia globosa* n. comb. (Fig. 10B, C) and *Hypoconcha* spp. (Fig. 19B, C) are also very different, rounded and narrow/oblique respectively. In Table 1 we consider the uropods of *Dromidia*, *Lamarckdromia* n. gen. and *Hypoconcha* as ventral.

In dromiids the uropods are only rarely completely lost (as in *Ascidiophilus*). There are no known cases of an uropod modified into socket.

The uropodal plate, whether dorsal, intercalary or ventral, is the transformation of the biramous uropod of the megalopa. The role of uropod in abdominal holding deserves further investigation, the lobe or ventral plate being too ventral to be truly efficient. Conversely, uropods as dorsal plates have generally proved to be very efficient, acting together with coxal structures on thoracopods. The evolution of the biramous uropod into dorsal plate is likely to represent a specialized structure functionally adapted to act in the holding of abdomen, even though not used by all species.

Information on the kind of uropods is still lacking for a number of dromiid genera, and the presence of uropods still needs confirmation in a few genera. In *Tunedromia* McLay, 1993 the uropods are indicated as absent in both sexes (Takeda 2001: 220). The uropods are absent in females of *Epipedodromia* André, 1932, but the male condition is unknown. In *Austrodromidia* McLay, 1993, the uropods have been reported as "reduced and concealed or absent" (McLay 1993: 185). Actually, the uropods of *A. australis*, type species of *Austrodromidia*, and of *A. octodentata* have not been properly described. In *A. australis* the uropods are very small ventral plates (Fig. 1B, C), whereas in *A. octodentata* they show as indistinct, nearly obsolete ventral plates (Fig. 2B), perhaps an indication that *Austrodromidia* is heterogeneous.

It is actually important that the uropod condition and the male pleopodal formula be determined jointly in the Dromiacea. It is still not known if the male Pl3-Pl5 remain as vestiges in many basal Podotremata (plesiomorphy). The vestiges are: 1) always biramous in Dynomenidae (uniramous in *Dynomene praedator* A. Milne Edwards, 1879) and in Dromiidae *pro parte* (*Sphaerodromia*); and 2) uniramous in Homolodromiidae and Dromiidae *pro parte* (at various stages of vestigial

TABLE 1. — Pleopodal formula in the dromiid genera, including the condition of the uropod, dorsal, ventral or absent. Genera in bold have a complete pleopodal formula. The condition in *Conchoecetes* needs to be verified. *Pl3-Pl5 are present in *Exodromidia spinosa*, while only Pl5 seems to be present in *E. spinosissima* and *E. bicornis*. The enigmatic genus *Frodromia* is not listed.

Uropod as dorsal plate	Uropod as ventral plate	Uropod absent	Male vestigial pleopods
DROMIINAE n. status			
Alainodromia			absent
		Ascidiophilus	absent
	Austrodromidia		absent
	?*Barnadromia*		?
Conchoecetes			absent
Cryptodromia			absent
Cryptodromiopsis			absent
Desmodromia			?
Dromia			absent or present
	Dromidia		present
Dromidiopsis			absent
Epigodromia			absent
		?*Epipedodromia*	?
	Eudromidia		?
	Exodromidia		present*
Fultodromia			absent
	Haledromia		?
Hemisphaerodromia			?
Homalodromia			absent
	Lamarckdromia n. gen.		absent
Lauridromia			absent
Lewindromia n. gen.			absent
Mclaydromia n. gen.			absent
Moreiradromia n. gen.			present
Paradromia			?
Petalomera			absent
	Platydromia		present
	Pseudodromia		absent
	Speodromia		?
Sternodromia			absent
Takedromia			absent
		?*Tunedromia*	?
Stebbingdromia n. gen.			present
HYPOCONCHINAE n. subfam.			
	Hypoconcha		present
SPHAERODROMIINAE n. subfam.			
Eodromia			present
Sphaerodromia			present

condition). The male pleopods 3-5 have been lost in a number of Dromiidae and in all remaining Podotremata (Homolidea and Archaeobrachyura *sensu* Guinot & Tavares 2001).

The present study revealed the presence of vestigial male Pl3-Pl5 in several dromiid species. Because Pl3-Pl5 are frequently much reduced, sometimes to short papillae, they are easily overlooked and remain undescribed. Rudimentary Pl3-Pl5 are often dissimilar in length, as for example in *Stebbingdromia plumosa* n. comb. (Fig. 18C).

Because not enough attention has been paid to the male pleopodal formulae, the character remains unknown in a number of dromiid genera: 1) *Barnardromia* (uropods reduced, not visible); 2) *Eudromidia* (uropods very reduced, not visible dorsally); 3) *Haledromia* (uropods very reduced, concealed); 4) *Speodromia* (uropods as ventral plates); 5) *Epipedodromia* (uropods

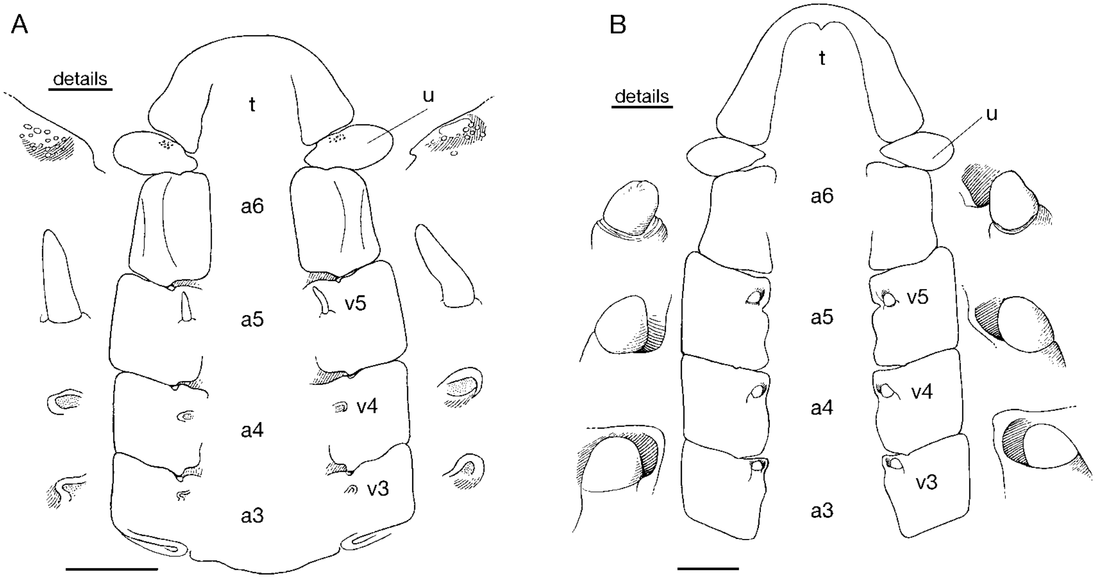

Fig. 27. — *Dromia* Weber, 1795, uropods and vestigial male pleopods on segments 3-5 with details on each side; **A**, *Dromia personata* (Linnaeus, 1758), Cape Fréhel, ♂ 47 × 59 mm (MNHN-B 22049); **B**, *D. bollorei* Forest, 1974, Ivory Coast, ♂ 71.5 × 85 mm, paratype (MNHN-B 21932). Abbreviations: **a3-a6**, abdominal segments 3-6; **t**, telson; **u**, uropod; **v3-v5**, vestigial pleopods 3-5. Scale bars: A, B, 5 mm; details, 1 mm.

indicated as absent); and 6) *Tunedromia* (uropods absent). In these genera (not examined) the presence of vestigial pleopods has not been investigated.

When information on the type of uropod and male pleopodal formula are combined, four patterns emerge in the Dromiidae (Table 1): 1) vestigial pleopods Pl3-Pl5 combined with dorsal plates; 2) Pl3-Pl5 combined with ventral plates; 3) presence of uropods and no Pl3-Pl5; and 4) all abdominal appendages completely lost. We found no case so far of vestigial pleopods occurring in the absence of uropods.

The condition Pl3-Pl5 combined with dorsal plates has been found in all Sphaerodromiinae n. subfam. but only in a few Dromiinae n. status. In the male Sphaerodromiinae n. subfam., Pl3-Pl5 occur along with intercalary plates, which are exposed dorsally. Pl3-Pl5 are biramous in *Sphaerodromia* (Fig. 22), uniramous in *Eodromia* (Fig. 24A); they are also uniramous in *Frodromia* (Fig. 25C). The genera and species of Dromiinae n. status with (uniramous) vestigial pleopods combined with dorsal plates are as follows: *Dromia* pro parte, i.e., in *D. personata* (Linnaeus, 1758) (Fig. 27A), *D. bollorei* Forest, 1974 (Fig. 27B), *D. marmorea* Forest, 1974, and also in "*Dromia*" *wilsoni* (Fulton & Grant, 1902), *Moreiradromia* n. gen. (*M. antillensis* and *M. Sarraburei*, Fig. 14B, C), and *Stebbingdromia* n. gen. (*S. plumosa* n. comb., Fig. 18C).

Vestigial pleopods combined with ventral uropods (i.e., a complete male pleopodal formula) occur in the Hypoconchinae n. subfam. (*Hypoconcha*, Fig. 19B) and (with certainty) in only a very limited number of genera and species of the large subfamily Dromiinae n. status, as follows: 1) in the monospecific *Dromidia* (*D. hirsutissima*, Fig. 5B, C); and 2) in *Exodromidia spinosa* (Studer, 1883), type species of *Exodromidia* Stebbing, 1905 (p. 64). The other two species of *Exodromidia*, *E. spinosissima* (Kensley, 1977) and *E. bicornis* (Studer, 1883) only have a long Pl5, whereas Pl3-Pl4 seem to be absent (the inclusion of these two last species in *Exodromidia* has been already questioned; see

Guinot 1995: 187; Guinot & Bouchard 1998: 624; Bouchard 2000).

The present study of *Pseudodromia* and *Ascidiophilus* has confirmed the absence of vestigial male pleopods as well as the presence of ventral uropods in *Pseudodromia*, and the complete loss of both Pl3-Pl5 and uropods in *Ascidiophilus*. The uropod condition remains vague in the dromiid genera whose uropods are described in the literature as "concealed" (see above and Table 1). Within family Dromiidae a complete male pleopodal formula occurs in the Sphaerodromiinae n. subfam. (intercalary platelets, exposed dorsally), in the Hypoconchinae n. subfam. (ventral narrow uropods), and in a very limited number of Dromiinae n. status (Dromiinae *pro parte*, see Table 1).

PATTERNS OF P5 COXA AND PENIS

Several morphological structures remain overlooked or very poorly investigated in the Brachyura. Among these is the coxa of P5 in the male with its associated penis (Guinot 1978, 1979a, b). In the Brachyura the male gonopore opens on coxa of last thoracic pereopod (Podotremata and Hetrotremata) or on thoracic sternum (Thoracotremata). The vas deferens always prolongs itself into penis, whose role is to penetrate inside the base of male first pleopod, or gonopod. Conversely to the podotreme condition, with a single basal opening, or foramen, for the introduction of both penis and second gonopod, in the Eubrachyura (Hetrotremata and Thoracotremata) the completely closed first gonopod is provided with two distinct basal foramina: one for the insertion of penis ("foramen proximal externe") and the other for the insertion of male second pleopod ("foramen proximal interne") (Guinot 1979a: 239, figs 60-68). That supports the monophyly of the non-podotreme brachyurans.

The Eubrachyura show a rather conservative condition for the male P5 coxa, while diverse modalities for the protection of penis exist (see Guinot 1969a-c, 1979a, b; Hartnoll 1975; Tavares 1992, 1997). The coxa itself is only slightly modified or not modified at all (for the special condition in the Leucosiidae Samouelle, 1819, see Guinot 1979a: fig. 45). In contrast, the Podotremata exhibit several markedly different patterns of coxal morphology, related to sperm transfer.

The Homolodromiidae and Dynomenidae share a totally modified P5 coxa, which is modified in a continuous hard extension, simply enclosing penis which ends in small extrusion formed by the soft extremity of vas deferens (Guinot 1978: 231; 1979a: 191, 194, figs 43C, G, 63A, B; 1995: 174, fig. 4; McLay 1999: 460, fig. 14f). This first type of modification involves an elongation at different degrees of the P5 coxa. As shown in Fig. 28, the modification involves either the whole coxa, which is more or less regularly tapered (Dynomenidae, Fig. 28C, D), or only anterior part, which is abruptly constricted just anteriorly to P5 articular condyle on thoracic sternite 8 (Homolodromiidae, Fig. 28A, B). The extension of the coxa takes different shapes which, in the case of the Homolodromiidae and Dynomenidae, is family specific. In the Homolodromiidae there is a reduced P5, completely rejected dorsally (P4 is only subdorsal), whereas in the Dynomenidae there is an obliquely directed and very small last pereopod. In *Homolodromia* A. Milne Edwards, 1880 (Homolodromiidae) the tubular process is specially long and hard. The details of the P5 coxa (length, direction) seem useful to separate the dynomenid genera.

Two substantially different patterns were found during this study in the family Dromiidae, opposing the Sphaerodromiinae n. subfam. to the Dromiinae n. status and Hypoconchinae n. subfam. Our view is that both patterns evolved independently and thereby are not homologous.

The two sphaerodromiine genera *Sphaerodromia* (Figs 23A; 28E, F) and *Eodromia* (Fig. 28G), and also *Frodromia* (Fig. 25B, D) share with the Homolodromiidae and the Dynomenidae a modified and elongated P5 coxa that encloses the penis. The *Sphaerodromia* pattern is very close to that found in the Homolodromiidae (Fig. 28A, B): a marked constriction of the coxal

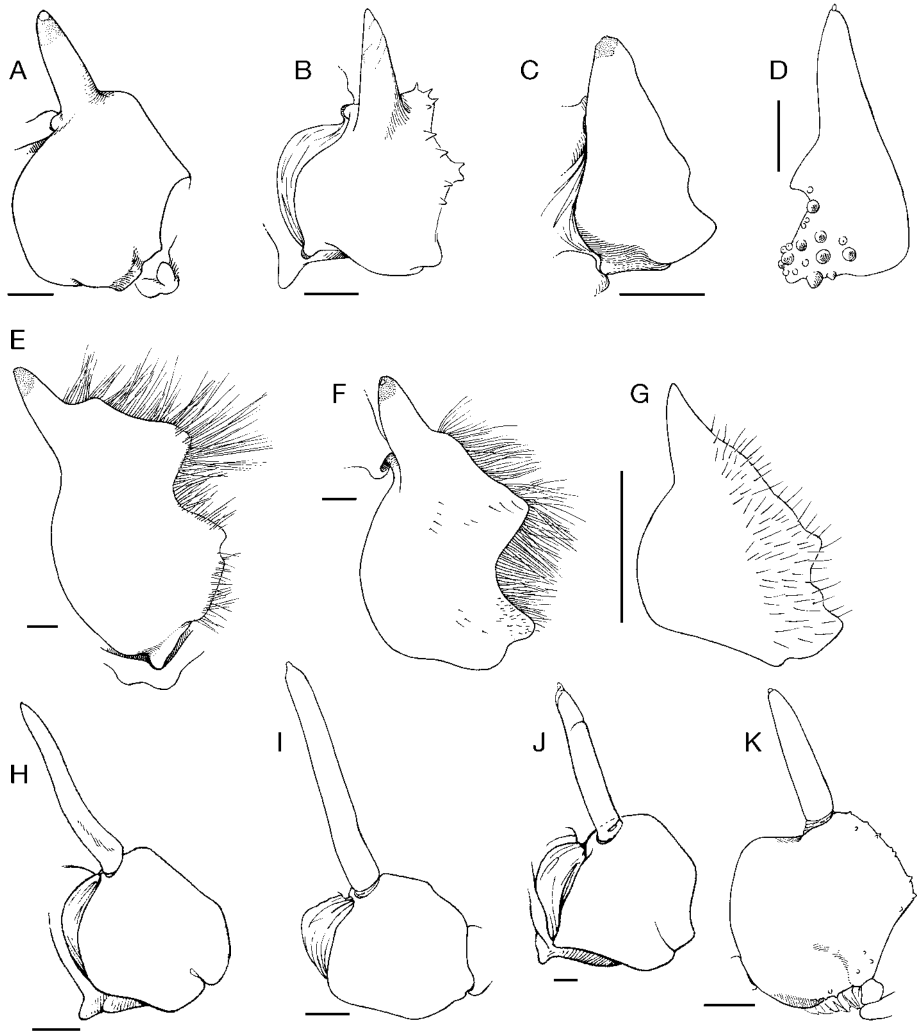

Fig. 28. — Patterns of male coxa of P5 in the Dromiacea de Haan, 1833; **A**-**G**, pattern with coxa modified and elongated into process enclosing penis and not forming penial tube; **A**, **B**, Homolodromiidae Alcock, 1900; **A**, *Homolodromia paradoxa* A. Milne Edwards, 1880, Bahamas, *Gerda*, stn 190, ♂ 24 × 15 mm (RMNH); **B**, *Dicranodromia mahieuxii* A. Milne Edwards, 1883, Bay of Biscay, *Le Travailleur*, stn 9, ♂ 9 × 6.5 mm, holotype (MNHN-B 21681); **C**, **D**, Dynomenidae Ortmann, 1892; **C**, *Dynomene hispida* Guérin-Méneville, 1832, New Caledonia, ♂ 8.8 × 11.5 mm (MNHN-B 22091); **D**, *Paradynomene tuberculata* Sakai, 1963, New Caledonia, 11 mm width (MNHN-B 24780); **E**-**G**, Sphaerodromiinae n. subfam. (Dromiidae); **E**, *Sphaerodromia ducoussoi* McLay, 1991, Tuamotu, ♂ 43.2 × 43 mm, holotype (MNHN-B 22172); **F**, *Sphaerodromia lamellata* Crosnier, 1994, New Caledonia, ♂ 47.8 × 42.6 mm, holotype (MNHN-B 24724); **G**, *Eodromia denticulata* McLay, 1993, Kai Islands, KARUBAR, ♂ 4.9 × 4.5 (MNHN-B 26327); **H**-**K**, pattern with coxa not modified but prolonging into mobile penial tube; **H**-**J**, Dromiinae de Haan, 1833 n. status (Dromiidae); **H**, *Moreiradromia antillensis* (Stimpson, 1858) n. comb., French Guiana, stn 33, ♂ 18 × 18 mm (MNHN-B 22030); **I**, "*Dromia*" *wilsoni* (Fulton & Grant, 1902), Guézé coll., ♂ 22 × 37 mm (MNHN-B 26254); **J**, *Lauridromia dehaani* (Rathbun, 1923), Gulf of Suez, Monod det. *Dromia dormia*, ♂ 42 × 45 mm (MNHN-B 21998); **K**, Hypoconchinae n. subfam. (Dromiidae), *Hypoconcha californiensis* Bouvier, 1898, Gulf of California, ♂ 20.3 × 19.4 mm, syntype (MNHN- B 22066). Corneous regions stippled. Scale bars: A, D-F, H-K, 1 mm; B, C, G, 0.5 mm.

article just anterior to articular condyle of P5 coxa, forming a narrow process, well demarcated from the rest of the coxa.

Since the extended coxa is a sexual modification of the male, the female does not have a modified coxa. An elongated P5 coxa is therefore a unique characteristic of the male in the Dynomenidae, Homolodromiidae and Sphaerodromiinae n. subfam.

The remaining Dromiidae, that is, the Dromiinae n. status (Fig. 28H-J) and Hypoconchinae n. subfam. (Figs 20A; 28K), fall into the second pattern sharing an ordinary unmodified P5 coxa. The vas deferens protrudes from gonopore to form long, sclerotized tube, which is completely independent from coxa and movable; from tube emerges the soft tip of penis. In *Dromia personata*, for example, the soft male vas deferens passes through the foramen in the coxa, becoming protected by a thick cuticle (Hartnoll 1975: 665, figs 1A, 4A). It is not a simple extrusion or evagination of the vas deferens, since it becomes a differentiated and movable independent structure, supported by long calcified sclerite. We propose to name it "penial tube". The external sclerotized penial tube is unique to members of the subfamilies Dromiinae n. status and Hypoconchinae n. subfam., and constitutes one of longest penial structure ever found in the Podotremata in particular and in the Brachyura in general. The only other brachyuran crabs with a long penial tube is the family Dorippidae MacLeay, 1838, where the vas deferens arises from coxal gonopore to form a tube which may remain exposed and sclerotized, as in the subfamily Dorippinae (see Guinot 1979a: 195, fig. 46F; 1979b: figs 2, 3). Amongst the Podotremata, the Raninoidea combine an elongated P5 coxa and a more or less long and soft penis (see Guinot 1979a: 194, fig. 43F).

No intermediate stages between the two patterns (P5 coxa extended/P5 coxa not modified and prolonging into sclerotized mobile penial tube) were found amongst the Dromiacea. Although of different shapes from group to group, the elongated male P5 coxae are typically found in the most basal Podotremata (Homolodromiidae, Dynomenidae and Sphaerodromiinae n. subfam.). The Homolodromiidae, Dynomenidae and Sphaerodromiinae n. subfam. have all short female sternal sutures 7/8. The long and mobile penial tube is present only in two dromiid subfamilies, the Dromiinae n. status and Hypoconchinae n. subfam. In the Dromiinae n. status there are long female sternal sutures 7/8 and the apertures of spermathecae are located far anteriorly than the female genital openings on P3 coxae. As in these dromiines the spermathecal apertures end on a more or less prominent tubercule, it is possible that mating requires a particular arrangement of the male copulatory system, involving both gonopods and the penis. The only exception is the atypical dromiine *Stebbingdromia plumosa* n. comb., with its long penial tube (Fig. 18A) and short female sutures 7/8 ending near gonopores on P3 (Fig. 17C). The male G2 of *Stebbingdromia plumosa* n. comb., stout and without needle-like flagellum (Fig. 18B), represents a unique pattern that differs from that of all other Dromiidae and all Dromiacea as well. Unlike the Dromiinae n. status, the Hypoconchinae n. subfam. combines a penial tube (Figs 20A; 28K) and short female sutures 7/8 that end near gonopores on P3 (Fig. 19A).

In the Dromiinae n. status and Hypoconchinae n. subfam. the penial tubes are always symmetrical, and in the numerous species that were examined no significant differences were observed in the calcification of the penial tube.

It is evident that either the modification of the P5 coxa or the formation of an independent penial tube in the Podotremata is tied with the marked change in the alignment of the arthrodial cavities of posterior pereopods. The last thoracomere(s) are tilted, often almost perpendiculary to preceding ones. All the families of Podotremata have P4 + P5 or P5 alone modified (Guinot 1991, 1995; Guinot & Richer de Forges 1995; McLay 1993, 1999; Tavares 1993, 1996, 1998; Guinot & Tavares 2000). Either the whole P5 is mobile and completely raised on the back of the crab and therefore a carrying behaviour is well-developed (as in Homolodromiidae, Dromiidae, Homolidae, Latreilliidae, Cyclodorippidae) (Guinot *et al.* 1995), or it is only the P5 coxa (not the whole leg) which is dorsal, that is, a dorsal location of the P5 arthrodial cavity. Even in the Dynomenidae, where P5 are carried alongside the body and not capable of carrying a camouflaging object, the P5 coxa (with its arthrodial cavitiy) is moved dorsally.

In the two groups of basal Podotremata (Dromiacea, except Dynomenidae, and Homolidea) the thoracic pereopods may perform several functions: 1) P2 for walking and holding of abdomen; 2) P3 for walking, abdominal holding, and reproduction; 3) P4 for walking and, in some cases, for camouflage; and 4) P5 for reproduction and camouflage. This is perhaps why the walking is so slow in dromiacean crabs.

It is not surprising to find a kind of penial tube in the Dorippinae (Eubrachyura) where the two posterior legs (P4 and P5) are dorsal and prehensile to hold a sessile animal or shell for camouflaging, as in Dromiinae n. status and Hypoconchinae n. subfam.

The shape of the P5 coxa provides an invaluable tool for recognition of families among the fossil Podotremata. Because the fragile mobile penial tube of the Dromiinae n. status and Hypoconchinae n. subfam. is connected to the coxa through a delicate membrane, it cannot be fossilized and does not remain attached. In this case, male fossil specimens will show only unmodified coxa. Conversely, the hard elongated coxa of the Homolodromiidae, Dynomenidae and Sphaerodromiinae n. subfam. is far more easily preserved in the fossil record. As a result, a homolodromiid, dynomenid, or sphaerodromiine fossil crab could be easily recognized by a greatly expanded P5 coxa, whereas a dromiine or hypoconchine would present an unmodified coxa and no penial tube. The gonopores are very difficult to see in fossils, thus the shape of the male P5 coxa may be a good character not only to separate the podotreme families but also to recognize the sex of individuals.

There is little or no information on the mechanism for the discharge of the sperm into the penial tube and, therefore, into gonopods, as well as on the mobility and ultrastructure of the P5 coxa and penis (see Hartnoll 1975).

The P5 coxa in the Anomura

H. Milne Edwards (1837: 239) described in the Anomura the tubular prolongations on the coxae of *Coenobita* Latreille, 1829. Actually, two types of coxal modifications related to sperm transfer are shown by the hermit crabs. The first consists of an elongation of the male P5 coxa, on one or both sides. This occurrs in only a few genera: *Coenobita*, tubes not present in all species (Coenobitidae Dana, 1851); some *Porcellanopagurus* Filhol, 1885, and *Solitariopagurus* Türkay, 1986 (Paguridae Latreille, 1802; McLaughlin pers. comm.; Lemaitre pers. comm.).

The second type of coxal modification refers to the development of a "sexual tube", known for more than 150 years (Henderson 1888, 1893). The term "tube sexuel" seems to have been introduced by A. Milne Edwards & Bouvier (1892: 188). Currently, more than half of the genera in the family Paguridae and one of the two genera of the Coenobitidae show the development of some type of tube emanating from one or both gonopores on the P5 coxae. The tubes are often asymmetrical, sometimes filamentous or coiled, membranous or slightly calcified (Saint Laurent-Dechancé 1966; McLaughlin & Hogarth 1998; McLaughlin 2000; McLaughlin & Lemaitre 2000, 2001; Lemaitre & Tudge 2001; McLaughlin pers. comm.). But the hermit crabs tubes are quite different from the brachyuran tubes, because their function is not associated with male pleopods (Lemaitre & Tudge pers. comm.). It is not known how insemination takes place in hermit crabs. It probably occurs externally because spermatophores have been seen attached to various parts of specimens in species having sexual tubes. In hermit crabs without sexual tubes (e.g. the diogenid *Clibanarius* Dana, 1852 and the coenobitid *Birgus* Leach, 1815) the sperm mass definitely is attached to the sternum. Both, the details on the copulatory behaviour known to date and the absence of male structures to be used to introduce the sperm into the females, suggest that fertilization occurs externally (Lemaitre & Tudge pers. comm.).

SHELL-CARRYING BEHAVIOUR

Shell-carrying is relatively rare in the dromiid genera. The posterior legs, P4 and P5, are generally reduced and modified (oriented subdorsally and/or dorsally, ending in special prehensile apparatus) for carrying an object. In the commonest condition, P4 and P5 are roughly similar, P5 being either slightly longer and more slender, or markedly longer than P4 (in *Pseudodromia*). The grasping mechanism is represented by a subchelate ending, usually formed by one or several distal propodal spines opposing the dactylus, the number and location being often different on P4 and P5.

The camouflage among dromiids typically includes soft material such as sponges, ascidians, and weeds. Occasionally, hard material such as a large shell is encountered. Shell-carrying has been reported, for example, in the dromiine *Austrodromidia octodentata* (Hale 1925: 406, pl. 40A; 1927: 108, 109). Curiously, shell-carrying (using a *Pecten* shell) has never been observed again in this species. In *Austrodromidia*, P4 and P5 are not really different from the P4 and P5 of other dromiids. They are therefore similarly shaped, both reduced, and end in subchelate apparatus formed by one (on P5) or two (on P4) distal propodal spines opposing the dactylus; a long spine on the outer margin of P5 dactylus may also be involved.

In other dromiids the two last pereopods show a different pattern. *Desmodromia* (2001b: 1-8, figs 1d, 2d, 3), recently described for two Australian species collected without camouflage material, supposedly may carry bivalve shells (McLay 2001b: 7, 8). On both P4 and P5, which do not look very dissimilar in shape, the dactyli are very small but stout, curved simply and without opposing propodal spines. Thereby, they do not form a subchelate mechanism such as in most Dromiidae which carry soft material, even in *Austrodromidia*, which occasionally may carry a shell.

All the species of *Hypoconcha* (Hypoconchinae n. subfam.) and *Conchoecetes* (Dromiinae n. status) are by far the best known examples of permanent shell-carrying behaviour in the family. These species are adapted to hold and fit inside the valve of a lamellibranch mollusk (Nicolson 1776; Lamarck 1818; Crane 1937; Rathbun 1937; Schmitt 1965; Brusca 1980; Williams 1984; Hendrickx 1997; Ng *et al.* 2000: 157-159). Their two last legs (P4 and P5) are dissimilar in size and shape, markedly modified but in different ways (Guinot & Tavares 2000).

On a photograph of *Austrodromidia octodentata* published by Hale (1925: pl. 40A), the crab is shown sheltered beneath the valve with its cephalic parts situated near the umbo of shell. *Hypoconcha* has an opposite posture inside the shell (see Rathbun 1937: pl. 8, fig. 6, pl. 9, figs 4, 5 "in its natural habitat"). Its body is very small and thin in relation to the large shell which is kept very close to carapace. The crab, which is well concealed, probably walks slowly while carrying the shell, perhaps trailing it, without standing much off the ground. The carapace can be pressed against the inner concave surface shell, with the setae aiding "in a tight seal", and only P2 and P3 are used in locomotion, altough the crab may rest on the tips of chelipeds as well (Wicksten 1986b: 19). The posture of *Conchoecetes* under the shell is known by photographs of live *C. artificiosus* (Fabricius, 1798). The individual is hiding under the shell but remains partially exposed (Ng *et al.* 2000: fig. 1b); in another photograph (Nishimura 1987: pl. M) the crab was completely concealed by the shell.

Conchoecetes exhibits a particular combination of P4-P5, dissimilar in position, size, and shape. The P4, not dorsal, are markedly heavy, each with a thick propodus bearing a mobile process which more or less sinks in a socket, and with a long, curved dactylus. The P5 are very thin and end in simple, upturned dactylus. This arrangement in *Conchoecetes* allows the bivalve shell to be inserted between the mobile process and the curved dactylus. Detailed information, however, is lacking. This highly-specialized mechanism is the only of its kind in the Brachyura.

The disposition in *Hypoconcha*, also with P4-P5 different in position and size, is distinct. The P4 are not dorsal, and are robust but shorter than the P5. In both P4 and P5, the dactylus is crescent-shaped, upturned and mobile in a notch at the end of the stout propodus. The shell of the lamellibranch is held by the posterior legs and also by the angular abdomen inserted under the hinge (Rathbun 1937: 44, pl. 9, figs 4, 5; Wicksten 1986b: 19; Hendrickx 1997). *H. arcuata* clings so tightly to its shell that the removal of the valve without crushing the crab is almost impossible (Williams 1984: 257). It is not uncommon to find crabs carrying a shell markedly larger than carapace (Hendrickx pers. comm.; see Schmitt 1965: fig. 62; Brusca 1980).

KEY TO FAMILIES OF DROMIACEA AND SUBFAMILIES OF DROMIIDAE

The suprafamilial level, Homolodromioidea (with the single family Homolodromiidae) and Dromioidea (with families Dromiidae and Dynomenidae), is not specified in this key.

1. Both P4 and P5 modified, reduced, subdorsal or dorsal, with terminal prehensile apparatus. Pleopodal formula variable in males, either complete (vestigial pleopods Pl3-Pl5 combined with dorsal or ventral plates) or incomplete (no vestigial pleopods Pl3-Pl5). Uropods showing as dorsal plates or ventral lobes, absent exceptionally. Female sternal sutures 7/8 short or long, spermathecal apertures diversely located. Exopod present or absent on G2. Male P5 coxa modified and elongated, or unmodified and with independent penial tube 2

— Only P5 modified, very reduced, obliquely directed, somewhat rigid, without real prehensile apparatus. Male pleopodal formula complete in males. Pl3-Pl5 as biramous vestiges in males (uniramous in *Dynomene praedator*). Uropods always present, showing as large dorsal plates in both sexes, not efficiently involved in abdominal holding. Female sternal sutures 7/8 short, spermathecal apertures lying close to gonopores on P3. Exopod always present on G2. Male P5 coxa modified, elongated, prolonging into hard process enclosing penis .... Dynomenidae

2. Mxp3 pediform. Male pleopodal formula always complete. Pl3-Pl5 as uniramous vestiges in males. Uropods showing as ventral lobes, never involved in abdominal holding. Male abdomen with distinct pleurae; telson very long, reaching mxp3. Endophragmal skeleton regularly layered; phragmae interfingered to each other. Female sternal sutures 7/8 short, spermathecal apertures lying close to gonopores on P3. Exopod absent on G2. Male P5 coxa modified, elongated, prolonging into hard process enclosing penis .... Homolodromiidae

— Mxp3 operculiform. Male pleopodal formula variable. Pl3-Pl5 sometimes as vestiges in males. Uropods showing as salient dorsal plates (often efficiently involved in holding of abdomen), or as ventral plates, absent exceptionally. Male abdomen with pleurae sometimes distinct; telson variously shaped. Endophragmal skeleton not regularly layered; phragmae fused to each other. Female sternal sutures 7/8 short or long, spermathecal apertures close to or far from female gonopores on P3. Exopod present or absent on G2. Male P5 coxa modified or unmodified ...... Dromiidae (3)

3. Male P5 coxa modified, elongated, prolonging into hard process enclosing penis. P2 and P3 propodus long and provided with distal spine; inner margin of dactylus of P2 and P3 with numerous spines. Male pleopodal formula complete. Pl3-Pl5 as biramous (or uniramous) vestiges. Uropods showing as dorsal plates, exposed but deeply inserted medially, intercalary. Female sternal sutures 7/8 short, spermathecal apertures not reaching level of gonopores on P3. Exopod may be present on G2, length variable .... Sphaerodromiinae n. subfam.

— Male P5 coxa unmodified, bearing long movable, "articulated", sclerotized tube, from which emerges penis ("penial tube"). P2 and P3 propodus of variable length, usually without distal spine; inner margin of dactylus of P2 and P3 spinous or smooth. Male pleopodal formula complete or incomplete. Female sternal sutures 7/8 short or long, spermathecal apertures beyond gonopores on P3, sometimes far beyond (except *Stebbingdromia plumosa* n. comb.). Exopod absent on G2 4

4. Front and lateral margins greatly expanded, covering all parts of head, except antennal flagella; eyes displaced in ventral location. Carapace hourglass-shaped; dorsal surface flattened, very thin, membranous, specially in posterior half. Male abdomen widely triangular, generally flexed at right angles in the middle. Male pleopodal formula complete: Pl3-Pl5 as uniramous vestiges in males; uropods always as ventral plates. Female sternal sutures 7/8 relatively short, entirely located on bent posterior part of sternum, spermathecal apertures showing as minute pores, always apart, slightly beyond female gonopores on P3. P2 and P3 propodus short, never armed with distal spine; inner margin of dactylus smooth or nearly smooth. P4 and P5 dissimilar, with peculiar, contorted dactylus, movable in a hollow at the end of propodus, and ending in corneous hook. Always carrying a valve of lamellibranch mollusk .... Hypoconchinae n. subfam.

— Front not expanded; eyes visible dorsally. Carapace dorsal surface convex, more or less calcified. Male abdomen relatively narrow and rather long, variously shaped, but never triangular. Male pleopodal formula variable, complete or incomplete. Uropods either as salient dorsal plates or as ventral plates, exceptionally absent. Female sternal sutures 7/8 long (except *Stebbingdromia plumosa* n. comb.), spermathecal apertures generally showing as minute pores, far beyond gonopores on P3 (except *S. plumosa* n. comb.), and ending either apart or together. P2 and P3 propodus short, not armed with distal spine (except *S. plumosa* n. comb.); inner margin of dactylus with spines. P4 and P5 roughly similar in size (P5 often slightly longer than P4) and shape (except *Conchoecetes*, with P5 much smaller than P4 and both ending in different terminal apparatus) .... Dromiinae n. status (5)

5. G2 long, with a needle-like flagellum. Female sutures 7/8 long, spermathecal apertures generally far beyond gonopores on P3, showing as very minute pores (perhaps except *Stebbingdromia plumosa* n. comb.), exceptionally as slits (*Sternodromia*). Male pleopodal formula variable .... Dromiinae n. status (list of genera included, p. 49)

— G2 short (slightly shorter than G1) and stout, without needle-like flagellum. Female sutures 7/8 short, spermathecal apertures beside gonopores on P3, shape of spermathecal apertures unknown. Male pleopodal formula complete .... *Stebbingdromia* n. gen.

Illustration

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