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Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa

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Abstract

The patterns of complexity of the male and female sexual openings in Brachyura, which have been the source of uncertainties and conflicting opinions, are documented, together with a study of the morphologies of the coxal and sternal gonopores in both sexes, penises, spermathecae, and gonopods. The vulvae, male gonopores and penises are described among selected taxa of Eubrachyura, and their function and evolution examined in the context of a wide variety of mating behaviours. The location of female and male gonopores, the condition of the penis (coxal and sternal openings and modalities of protection), and related configurations of thoracic sternites 7 and 8, which are modified by the intercalation of a wide sternal part (thoracic sternites 7 and 8) during carcinisation, show evidence of deep homology. They represent taxonomic criteria at all ranks of the family-series and may be used to test lineages. Of particular significance are the consequences of the posterior expansion of the thoracic sternum, which influences the condition, shape, and sclerotisation of the penis, and its emergence from coxal (heterotreme) to coxo-sternal, which is actually still coxal (heterotreme), in contrast to a sternal emergence (thoracotreme).

The heterotreme-thoracotreme distinction results from two different trajectories of the vas deferens and its ejaculatory duct via the P5 coxa (Heterotremata) or through the thoracic sternum (Thoracotremata). Dissections of males of several families have demonstrated that this major difference not only affects the external surface (perforation of the coxa or the sternum by the ejaculatory duct) but also the internal anatomy. There is no evidence for an ejaculatory duct passing through the articular membrane between the P5 coxa and the thoracic sternum in any Brachyura, even when the sternal male gonopore is very close to the P5 coxa. Trends towards the coxo-sternal condition are exemplified by multistate characters, varying from a shallow depression to a long groove along expanded sternites 7 and 8, and ultimately their complete, extended junction typifying the most derived coxo-sternal condition. The coxo-sternal condition is indicative of a long evolutionary history, as evidenced by the presence of multistate characters (e.g., Dorippidae, Goneplacoidea) or by a single, well-established condition (e.g., Chasmocarcinidae, Ethusidae, Panopeidae Eucratopsinae, Rhizopidae, Scalopidiidae). The penial area proves to be an essential diagnostic feature in Brachyura, with a value comparable to that of the gonopods. Penis protection is ubiquitous in Brachyura irrespective of length, and several modalities of protection prevail, which necessitate different modifications of associated structures. A long penis in a gutter developed from a partial invagination of sternite 8 induces the formation of a new “suture” at the same level as the preceding suture 6/7. Such a “supplementary suture 7/8” exists among unrelated heterotreme families (e.g., Ethusidae, Panopeidae Eucratopsinae, Pseudorhombilidae, Rhizopidae). A fully protected penis, concealed in a groove within a complete invagination of sternite 8 in the form of two contiguous plates, evolved independently (homoplasy) in Palicoidea and Chasmocarcinidae (Goneplacoidea), with sternite 8 present as a single plate in females. In condylar protection, described for the first time and occurring in several heterotreme families, the penis emerges from the extremity of the P5 coxo-sternal condyle or from its anterior border instead of from the coxa itself. A penis precisely lodged in a small excavation on sternite 8, which is lined by a row of stiff setae, is unique to Brachyura, and represents a new synapomorphy of the Homoloidea.

Five modalities of penis protection are recognised in Podotremata, eight in Eubrachyura (six in Heterotremata and two in Thoracotremata). Special attention has been paid to Dorippoidea (Dorippidae and Ethusidae), which shows transformation series from coxal to coxo-sternal conditions. The coxo-sternal condition is not an intermediate towards the thoracotreme organisation, and a step in heterotreme evolution is the adoption of the coxo-sternal condition. An extreme carcinisition may also result in the sternal arrangement of male gonopores in the form of a “sternitreme” disposition, as in the case of Hymenosomatoidea, which displays a broad thoracic sternum and true sternal male gonopores (as in thoracotremes) together with several plesiomorphic traits that are assumed to represent an old, deeply-rooted heterotreme clade. A sternitreme condition evolved independently in the most ancestral heterotreme clades (such as Hymenosomatoidea) and in Thoracotremata. The older the lineage of a heterotreme is, the higher the possibility of having evolved carcinisation. Evidence that “derived” traits may be the consequence of a strong carcinisation, rather than being recently acquired, necessitates reconsidering certain character states in Brachyura. Eubrachyurans can only evolve either the heterotreme or the thoracotreme arrangement, the consistency of the inferred ancestral characters states providing a useful criterion for evaluating ancestral trait reconstructions. A widened thoracic sternum together with sternal gonopores may be present in carcinised heterotremes such as hymenosomatoids. The thoracic sternum provides a reliable complex of characters that must be carefully interpreted. The hypothesis of a coxo-sternal disposition in Cryptochiroidea and Pinnotheroidea, generally considered thoracotremes, is rejected, and an alternative interpretation of their status is discussed. A new interpretation of the phylogeny of Cryptochiroidea is outlined, but the origin of Pinnotheroidea remains puzzling.

The sella turcica, frequently regarded a synapomorphy of Eubrachyura, is redefined as the structure formed by the endosternal intertagmal phragma that connects the tagma/thorax and the tagma/abdomen to thoracic interosternite 7/8. It is here termed the “brachyuran sella turcica” and is shown to be synapomorphic to all Brachyura. The Eubrachyura synapomorphically shares the fusion of the thoracic interopleurite 7/8 with the brachyuran sella turcica, forming the “eubrachyuran sella turcica”. In contrast, some Podotremata (Cyclodorippoidea and Raninoidea) share a connection between the sella turcica and the thoracic interosternite 6/7.

Six main patterns of the thoracic sternum in relation to variations in sutures 4/5–7/8 are recognised in Eubrachyura, whereas several subpatterns that include variations in the median line are distinguished. The evolution of the thoracic sternum and axial skeleton is reassessed in Podotremata and Eubrachyura. A posteriormost location of the male gonopore (coxal or sternal) in relation to sternite 8 characterises many brachyurans (Cryptochiroidea, Hymenosomatoidea, Majoidea, Matutidae, Menippidae, Orithyioidea, Parthenopoidea, Ucididae, Grapsoidea - including Percnidae, Plagusiidae, Varunidae), in contrast to a location close to suture 7/8 in other groups. The thoracic sternum/pterygostome junction, which has multistate characters, is shown to be a valuable taxonomic criterion. The shapes of the sterno-abdominal depression and sterno-abdominal cavity provide diagnostic features that are helpful in suprageneric assignments.

The monophyly of Brachyura, Eubrachyura, and Thoracotremata is reaffirmed. The monophyly of Brachyura is supported by the interdependence of the two pairs of gonopods and penis. An abdomen permanently flexed and held by the pereopods and/or the homoloid press button (on sternite 4) or typical eubrachyuran press-button (on sternite 5) may be considered a synapomorphy of Brachyura, the absence of this condition considered a loss. The double abdominal-locking system (“double peg”) on sternite 5, a device discovered in three families of the extinct Palaeocorystoidea from the Upper Aptian, is similar to the double hook present in living lyreidids, although it is lost in all other raninoid extant members. New evidence shows that the abdominal holding was an early occurrence for a brachyuran crab. The Raninoidea, sister to Palaeocorystoidea, is characterised by gymnopleurity, a condition that results from the lifting of the carapace and thus the exposure of several pleurites. The narrowing of the body and thoracic sternum, almost certainly associated with their burrowing behaviour, is a diagnostic feature of raninoid evolution, in contrast to the widening observed in the remaining Brachyura. The monophyly of Heterotremata is discussed. Although the correct assignment of the coxal male gonopore and sternal female gonopore (vulva) at the base of Decapoda and Eubrachyura, respectively, left no synapomorphies to support the Heterotremata, the group nevertheless should be regarded as the sister group to Thoracotremata. The controversial monophyly of Podotremata is discussed and arguments are presented against the suppression of this taxon. The distinction of Homoloidia from Dromioidia is argued, and a classification of Podotremata, which considers the fossil record whenever possible, is presented. The earliest brachyurans are re-examined, and a new interpretation of the phylogeny of several basal eubrachyuran groups (Dorippoidea, Inachoididae, Palicoidea, Retroplumoidea) is proposed. *Stenorhynchus* shares a number of characters with the Inachoididae that differentiate them from Inachidae, and also has some distinctive features that warrants its assignment to a separate inachoidid subfamily, Stenorhynchinae, which is resurrected.

The concealment strategies among Brachyura are documented and discussed. Podotremes use carrying behaviour, often combined with burying and concealment under substrates, whereas living within a host, burying, and decoration are used by heterotremes, burrowing being essentially a thoracotreme strategy. Locomotion in relation to the orientation of the pereopods provides evidence of phylogenetic position, most of podotremes primarily having a forward instead of a sideways locomotion. Dorippids, which combine carrying behaviour and burying, can also walk forwards, a corroboration of their basal position in Eubrachyura. The Palicidae constitutes the second non-podotreme group in which carrying behaviour is, for the first time, documented. Carcinisation and subsequent adjustments are re-examined, particularly the reduction and folding of the abdomen. An analysis of cephalic condensation provides evidence roughly similar to that supported by other characters.

The present study of the morphology and evolution of the sexual openings and complementary characters did not result in taxonomic changes within the section Eubrachyura, the hierarchical relationships of taxa above the superfamily not being formalised in a new classification but only suggested, such as in the discussions on the affinities between Palicoidea, Retroplumoidea, and Hexapodoidea, between Dorippoidea and Hymenosomatoidea, and between Hymenosomatoidea and Inachoididae.

In contrast, as a result of the confused nomenclatural situation in the taxonomy of the section Podotremata and in the absence of Rules for the nomenclature of higher taxa in the *International Code of Zoological Nomenclature* (1999), it is necessary to use new ranks above the superfamily, which therefore belong in the class-series. In order to accommodate the high diversity of living podotremes and the robust podotreme fossil record, four subsections, which correspond to the four main clades of podotreme crabs, are diagnosed and named, with the suffix ***–IFORMIA*** (at least for three of the subsections) to distinguish them from family-series nomina. They are: Dynomeniformia **nom. nov.** (to replace Dromiacea that was initially established in 1833 by De Haan as a family and shown to be unavailable for a high-ranked taxon of the class-series), Homoliformia Karasawa, Schweitzer & Feldmann, 2011 **new status**, Cyclodorippiformia **nom. nov.**, and Gymnopleura Bourne, 1922, a nomen already used by many authors. The nomenclatural rationale behind our decisions is discussed in "Classification and nomenclatural ranks" and implemented in Appendix II.

The nomen Homolidae cannot be credited to De Haan (1839), who simply quoted and Latinised (only one simple transcription in Latin) H. Milne Edwards’ (1837) nomen *Homoliens* without an intention to adopt it as valid and place it in the nomenclatural hierarchy, and is therefore nomenclaturally unavailable under the *International Code of Zoological Nomenclature*. As the nomen *Homoliens* H. Milne Edwards, 1837, fulfils all the requirements making it nomenclaturally available under the *Code*, the authorship of the the family and superfamily is credited to H. Milne Edwards, 1837, as Homolidae H. Milne Edwards, 1837, and Homoloidea H. Milne Edwards, 1837, respectively.

The fossil Telamonocarcininae is elevated to a familial rank within the Dorippoidea, i.e., as Telamonocarcinidae **new status**. The fossil Basinotopidae is downgraded to a subfamilial rank within the Dromiidae, as Basinotopinae **new status**, at the same rank as the extant Sphaerodromiinae.

Key words: Crustacea, Decapoda, Brachyura, Podotremata, Eubrachyura, Heterotremata, Thoracotremata, morphology, evolution, monophyly, plesiomorphy, homoplasy, synapomorphy, phylogeny, fossil record, nomenclature, class-series, sections, subsections, carcinisation, sexual openings, gonopores, spermatheca, vulva, penis, gonopods, thoracic sternum, thoracic sternal sutures, thoracic sternal patterns, thoracic sternum/pterygostome junction, gymnopleurity, abdomen, uropods, axial skeleton, sella turcica, P5 coxa, coxo-sternal condition, sternitreme condition, sperm plugs, penis protection, condylar protection, cephalic condensation, mating, reproduction, concealment behaviour, carrying behaviour, decoration behaviour, burying, burrowing, locomotion, megalopa, Dromiacea, Dromiidae, Homolodromiidae, Dynomenidae, Dromioidea, Homolidae, Homoloidea, Cyclodorippoidea, Homoliformia **new status**, Dynomeniformia **nom. nov**., Cyclodorippiformia **nom. nov**., Gymnopleura, Telamonocarcinidae **new status,** Basinotopinae **new status**.

Introduction

The mid-body location of the sexual openings, or gonopores, in the class or subphylum Crustacea (see *Classification and nomenclatural ranks*), has always figured prominently in recognising the group, but substantial variations in the exact location of the gonopores has generally been considered of taxonomic importance only at the class or ordinal ranks (see Schram & Koenemann 2004: 86). The location of the male and female gonopores is important at all hierarchical levels in the extant fauna of the infraorfer Brachyura Latreille, 1802 (see *Classification and nomenclatural ranks*), which comprises 39 superfamilies and 98 families for 1,359 genera and 7,073 valid species (Ng, Guinot & Davie 2008, updated; Ng, Guinot & Davie 2010, updated; P.K.L. Ng, pers. comm. 2012), thus with a higher diversity than previously realised. The significance of this remarkable fact is the main objective of this work.

The female and male brachyuran gonopores are exclusively associated with the thoracic somites 6 and 8 respectively, but are located either on the coxae of the appendages or on the trunk somites. The sexual openings in both sexes are not uniformly placed among brachyurans. The female oviduct opens on the coxa of the third thoracic pereopod (P3 gonopore in podotreme crabs), or on the sternum of the corresponding somite, that is, the sixth somite of the cephalothorax (vulva in eubrachyuran crabs, heterotremes as well as thoracotremes).

The male ejaculatory duct opens either on the coxa of the last thoracic pereopod (P5) (Figs. 1A–C, 8A–F, H, 9, 10–13, 15, 27, 28, 30A, D, 31A–E, 34, 44, 46B, 49B, 52A, B, 55), including the cases with a coxo-sternal condition (Figs. 8G, I–K, 14, 16–22, 24, 30B, C, E, F, 32, 34), or on the sternum of the corresponding somite, that is, the last somite of the cephalothorax (thoracic somite 8) (Figs. 1D, E, 23, 26, 33, 35, 36). A sternal location of the female and male gonopores as in Brachyura is unique within Decapoda Latreille, 1802. The Podotremata Guinot, 1977, refers to Brachyura with both the female and male openings on the appendages, specifically on the P3 and P5 coxae respectively (Guinot 1977a, b). In contrast, the Eubrachyura Saint Laurent, 1980 (Saint Laurent 1980a, b) refers to the other (non-podotreme) Brachyura with female openings on the thoracic sternum (vulvae), and comprises Heterotremata Guinot, 1977, with the male openings on the P5 coxae, and Thoracotremata Guinot, 1977, with the male openings on the thoracic sternum.

Our knowledge of the external genital region of the Brachyura is limited, particularly in males, in which the location of the penises and the shape of abdomen and posterior thoracic sternites are variously influenced by several factors. The diagnoses of several brachyuran families are contradictory in this respect because taxonomic descriptions often do not consider the characters provided by the sexual openings. As a result, the systematic position of a number of families is unstable and may well be erroneous.

The Palicidae Bouvier, 1898, is a striking example of a family where the different points of view have led to divergent taxonomic assignments. The male gonopores of palicids, which sometimes were not explicitly mentioned (Bouvier 1897a, b; 1898; Rathbun 1918; Williams 1984), have been considered either coxal (Borradaile 1907; Sakai 1976) or sternal (Calman 1900), thus sometimes resulting in the inclusion of Palicidae among the thoracotremes (Alcock 1900b; Balss 1957; Martin & Davis 2001; Brösing 2002, 2008; Brösing *et al*. 2007; Wetzer *et al*. 2009; Felder *et al*. 2009; Schweitzer *et al*. 2010). The confusion arose due the fact that in Palicidae the male gonopores are coxo-sternal, a condition where the orifices are clearly located in the P5 coxae, and therefore the gonopores are definitely not sternal (Fig. 32; Guinot 1978a; Guinot & Bouchard 1998; Castro 2000). A similar