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Rediscovery of the holotype of *Paeduma cylindraceum* (Bell, 1859) and description of a new genus of Hexapodidae (Decapoda, Brachyura)

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ABSTRACT

The hexapodid genus *Paeduma* Rathbun, 1897 (replacement name for *Amorphopus* Bell, 1859) was established without figure for a species from an unknown locality, *P. cylindraceum* (Bell, 1859) (described as *Amorphopus cylindraceus* Bell, 1859). *Paeduma cylindraceum* was never reported ever since, and the holotype was considered lost. The examination of the holotype of *Paeduma cylindraceum* permits to know its provenance (the Galápagos Islands or alternatively somewhere on American Pacific coast) and the exact nature of the supposedly rudimentary fifth ambulatory leg (P5) described by Bell (1859). The “rudiment” is in fact the external and exposed portion of the apodeme of P4 and not an “aborted” pereopod. The two other species subsequently attributed to *Paeduma* are referred to *Hexalaughlia* n. gen. A new diagnosis for *Paeduma* is provided, and the status of the extant and fossil *Stevea* Manning & Holthuis, 1981 is re-considered. Evaluation of *Paeduma* has prompted some new views on the family Hexapodidae, and the presence for the first time of two genera of the family in the Americas, *Paeduma* and *Stevea*.

KEY WORDS

Crustacea,
Decapoda,
Brachyura,
Hexapodidae,
Amorphopus,
Paeduma,
Stevea,
Hexalaughlia n. gen.,
vestigial coxa,
male gonopore,
new genus.

RÉSUMÉ

Découverte de l'holotype de Paeduma cylindraceum (Bell, 1859) et description d'un nouveau genre d'Hexapodidae (Decapoda, Brachyura).

Le genre *Paeduma* Rathbun, 1897 (nom de remplacement pour *Amorphopus* Bell, 1859) a été établi sans illustration pour une espèce de provenance inconnue, *P. cylindraceum* (Bell, 1859) (décrite sous le nom *Amorphopus cylindraceus* Bell, 1859). Elle n'a jamais été retrouvée depuis et l'holotype était considéré comme perdu. L'examen de l'holotype de *Paeduma cylindraceum* permet de connaître son origine (Galapagos ou quelque part sur la côte pacifique américaine) et la nature exacte du rudiment de dernière patte ambulatoire (P5) décrit par Bell (1859). Le « rudiment » est en fait la partie la plus externe, exposée, de l'apodème de P4, ce qui ne constitue nullement un périopode « avorté ». Les deux autres espèces attribuées ultérieurement à *Paeduma* sont placées dans *Hexalaughlia* n. gen. Une nouvelle diagnose de *Paeduma* est fournie et le statut du genre actuel et fossile *Stevea* Manning & Holthuis, 1981 reconsidéré. L'étude de *Paeduma* permet une nouvelle appréciation de la famille des Hexapodidae, et tout d'abord la présence de deux genres de cette famille sur la côte pacifique américaine, *Paeduma* et *Stevea*.

MOTS CLÉS

Crustacea,
Decapoda,
Brachyura,
Hexapodidae,
Amorphopus,
Paeduma,
Stevea,
Hexalaughlia n. gen.,
coxa vestigiale,
gonopore mâle,
genre nouveau.

INTRODUCTION

For a long time, the diagnosis of the Hexapodidae Miers, 1886 has taken into account the characters of an enigmatic genus, *Amorphopus* Bell, 1859 (type species by monotypy: *A. cylindraceus* Bell, 1859; gender masculine), which was replaced by *Paeduma* Rathbun, 1897 (Rathbun 1897; see under Type species of the latter). The type species of *Paeduma* became *P. cylindraceum* (Bell, 1859) by monotypy, the gender of the genus being considered neuter according to Manning & Holthuis (1981).

Bell's genus was described from an unknown locality and without figures, for a single species which has never been reported since.

Amorphopus was assigned by Bell (1859) to the Pinnotheridae De Haan, 1833, to which at that time *Hexapus* De Haan, 1835 was also referred. Subsequently Miers (1886: 275) included both genera in his subfamily Hexapodinae Miers, 1886 within the Pinnotheridae (see also Ortmann 1894). Hexapodid crabs were then referred to the Goneplacidae MacLeay, 1838 (Alcock 1900; Borradaile 1907; Stebbing 1910; Tesch 1918; Barnard 1950; Monod 1956; Serène 1964, 1968; Glaessner 1969; Gordon 1971; Sankarankutty 1975; Sakai

1976; Crane 1981; Crane & Quayle 1986; Dai & Yang 1991). Ontogenetic data have suggested a close relationship to the Goneplacidae (Pereyra Lago 1988). In cases when the Goneplacidae is considered a distinct superfamily (d'Udekem d'Acoz 1999; Collins *et al.* 2003), it includes Hexapodidae.

The Hexapodinae was elevated to family level by Guinot (1978: 214), and this arrangement was followed by subsequent authors (Manning & Holthuis 1981; Bowman & Abele 1982; Abele & Felgenhauer 1982; Schram 1986; Pereyra Lago 1988; Huang *et al.* 2002; Karasawa & Kato 2003; Guinot & Quenette 2005). A suprafamilial level, Hexapodoidea, was even suggested (Guinot 1978: 214, 285), followed by Glaessner (1980: fig. 22), Morris & Collins (1991: 28), and Schweitzer *et al.* (2000: 55). In a more recent discussion on the differentiation of the fossil Hexapodidae from similar forms (Schweitzer & Feldmann 2001: 331), hexapodid crabs were included within the Xanthoidea, as in the updated classification of Martin & Davis (2001: 75). This view was again discussed by Schweitzer (2005: 291). Elucidation of the relationships of the Hexapodidae is currently under study (Guinot, Tavares & Castro unpublished data).

The Hexapodidae was until recently characterized by the complete loss of the last pereopod, except in *Paeduma* where this pereopod is considered rudimentary. Bell (1859: 28) described the P5 as “reduced to a mere rudiment, in the form of a minute tubercle inserted in a little notch at the base of the first joint of the fourth pair, and scarcely discernible by the naked eye”. *Paeduma* is therefore considered as having the last pereopod “aborted” instead of completely lost. Thus, the diagnosis of the Hexapodidae by Miers (1886: 275) and subsequent authors mentions that the P5 is altogether aborted (as in most hexapodids) or rudimentary (as in *Paeduma*). The precise condition of P5, however, was not discussed in the two other species originally referred to *Paeduma*, *P. chuenensis* (Rathbun, 1909) and *P. orientalis* (Rathbun, 1909).

The condition of P5 in *P. cylindraceum* remained unknown for nearly 150 years. Both Bell's genus and species were mentioned by a few authors (Miers 1886; Alcock 1900; Stebbing 1910; Tesch 1918; Gordon 1971; Sankarankutty 1975; Guinot 1979), without reporting new specimens. Manning & Holthuis (1981) gave a new diagnosis of *Paeduma* combining unfortunately the characters given by Bell (1859) for the type species (*P. cylindraceum*), and those shown by the two other *Paeduma* species; they also included a key of all hexapodid genera.

The holotype of *Amorphopus cylindraceus* Bell, 1859 could not be traced for a long time (Gordon 1971: 108). This species was not included by DiMauro (1982) in his list of many of Bell's presumably lost types for the species described between 1835 and 1855, and deposited in the dry crustacean collection of the Zoological Collections, University Museum, Oxford, UK. With the help of curator S. De Grave, the holotype of *Paeduma cylindraceum* has now been found in the Oxford Museum, and its approximate origin (Galápagos or somewhere else on the Pacific coast of America), and characteristics have been determined.

The comparison of *Paeduma cylindraceum* with the two other *Paeduma* species from the western Pacific has shown that they are sufficiently distinct to justify the proposal of a new genus. Thus, *Hexalaughlia* n. gen. is herein established, and the diagnosis of *Paeduma* is emended. The status of

the genus *Stevea* Manning & Holthuis, 1981, the only other hexapodid representative known from the Americas, is also reconsidered based on the study of photographs of the holotype of *S. williamsi* (Glassell, 1938).

Also discussed in this study is Guinot, Tavares & Castro (unpublished data) statement regarding the presence in the Hexapodidae of a vestigial P5 coxa, articulated on reduced sternite 8. The “rudiment” observed in *Amorphopus* by Bell (1859) is located differently, does not correspond to a vestigial P5 coxa, and merely represents the external, exposed portion of the apodeme of P4.

ABBREVIATIONS

G1	first male pleopod (or first gonopod);
G2	second male pleopod (or second gonopod);
mxp2, mxp3	second and third maxillipeds;
P1-P5	first to fifth pereopods.

Measurements of carapace length and carapace width are given in millimeters (mm).

The specimens remain deposited at:

MNHN	Muséum national d'Histoire naturelle, Paris;
OUMNH	Zoological Collections, University Museum, Oxford, UK;
SDSNH	San Diego Museum of Natural History;
USNM	National Museum of Natural History, Smithsonian Institution, Washington D.C.

SYSTEMATICS

HETEROTREMATA Guinot, 1977

Family HEXAPODIDAE Miers, 1886

Hexapodinae Miers, 1886: 275. — Ortmann 1894: 690. — Alcock 1900: 293, 329. — Borradaile 1907: 468, 485. — Tesch 1918: 150, 237. — Monod 1956: 340, 361. — Balss 1957: 1658. — Imaizumi 1959: 276. — Serène 1964: 270; 1968: 93. — Glaessner 1969: R527. — Gordon 1971: 106. — Sakai 1976: 522, 553. — Collins & Morris 1978: 977. — Crane 1981: 3. — Dai & Yang 1991: 393, 417.

Hexapodidae – Guinot 1978: 212; 1979: 16, 43, 114, 145, 155, 167, 215, 220, 261, 267. — Manning & Holthuis 1981: 166. — Glaessner & Secretan 1987: 9. — Saint Laurent 1989: 154, footnote, 157. — Beschin *et al.*

1994: 191. — Guinot & Richer de Forges 1997: 496, table 1. — Ng 1998: 1061, 1081. — Guinot & Bouchard 1998: 660. — Huang *et al.* 2002: 651. — Schweitzer *et al.* 2000: 55. — Von Sternberg & Cumberlidge 2001: 332. — Martin & Davis 2001: 75. — Schweitzer & Feldmann 2001: 330, 331. — Schweitzer 2003: 1107; 2005: 289. — Karasawa & Kato 2003: 129. — Guinot & Quenette 2005: 334.

EXTANT GENERA (SOME INCLUDE FOSSIL SPECIES). — *Hexapinus* Manning & Holthuis, 1981 (type species by original designation: *Hexapus latipes* De Haan, 1835); *Hexaplex* Doflein, 1904 (type species by monotypy: *Hexaplex megalops* Doflein, 1904); *Hexapus* De Haan, 1835 (type species by subsequent designation, International Commission of Zoological Nomenclature: *Cancer sexpes* Fabricius, 1798); *Lambdophallus* Alcock, 1900 (type species by monotypy: *L. sexpes* Alcock, 1900); *Latohexapus* Huang, Hsueh & Ng, 2002 (type species by original designation: *L. granosus* Huang, Hsueh & Ng, 2002); *Paeduma* Rathbun, 1897 (type species by monotypy: *Amorphopus cylindraceus* Bell, 1859); *Hexa-laughlia* n. gen. (type species by present designation: *Thaumastoplax orientalis* Rahbun, 1909); *Parahexapus* Balss, 1922 (type species by monotypy: *P. africanus* Balss, 1922); *Pseudohexapus* Monod, 1956 (type species by monotypy: *Hexapus (Pseudohexanus) platydactylus* Monod, 1956); *Spiroplax* Manning & Holthuis, 1981 (type species by original designation: *Thaumastoplax spiralis* Barnard, 1950); *Stevea* Manning & Holthuis, 1981 (type species by original designation: *Hexapus williamsi* Glassell, 1938); *Thaumastoplax* Miers, 1881 (type species by monotypy: *T. anomalipes* Miers, 1881); *Tritoplax* Manning & Holthuis, 1981 (type species by original designation: *Hexapus stebbingi* Barnard, 1947).

FOSSIL GENERA. — *Goniocyopoda* Woodward, 1867 (type species by monotypy: *G. edwardsi* Woodward, 1867); *Palaeopinnixa* Via, 1966 (type species by original designation: *P. rathbunae* Schweitzer, Feldmann Tucker & Berglund, 2000; originally *Pinnixa eocenica* Rathbun, 1926, see Schweitzer *et al.* 2000). *Globihexapus* Schweitzer & Feldmann, 2001 (type species by monotypy: *G. paxillus* Schweitzer & Feldmann, 2001) was recently removed to the Pinnotheridae (Nyborg 2002; Schweitzer 2005).

REMARKS

Hexapodid crabs were often regarded as having sternal male genital openings (Barnard 1950: 283, key; Balss 1957: 1658). The family was assigned either to the Thoracotremata (or Catometopa) (Guinot 1978 provisionally; Schram 1986; Schweitzer *et al.* 2000; von Sternberg & Cumberlidge 2001) or to

the Heterotremata (Guinot 1979; Saint Laurent 1989; Guinot & Richer de Forges 1997; Guinot & Bouchard 1998; Martin & Davis 2001), the latter implying a true coxal condition of the male openings.

Hexapodids are considered as highly modified and specialized. Many species are known to live in annelid tubes or on hydroids. Tesch (1918: 238) commented that their commensalistic mode of life “has brought about not only the cylindrical shape of the body, but also the disappearance of the posterior legs, which, by the fact that they are inserted at a higher level than the preceding pairs, perhaps would rather impair the animal’s moving up and down in the tubes of Annelids and Hydrozoa”.

The P5 were presumed to be absent in all Hexapodidae, except in *Paeduma*. Thus, the corresponding sternite 8 was supposedly also lacking. Sternite 8 was seen as a triangular piece remaining visible dorsally (Barnard 1950: 300, fig. 56g, k, under “sternite 5”). A line dividing it into two parts has been observed in *Hexapus stebbingi* Barnard, 1947 (Gordon 1971, figs 1, 2). The hypothesis that a portion of the reduced sternite 8 may have an appendicular origin was formulated by Guinot (1979: 115, fig. 32). In fact, sternite 8 is present, although markedly reduced and concealed under the abdomen, with only a very small exposed portion. P5 vestigial coxae were clearly indicated, but not figured, by Saint Laurent (1989: 154, footnote). Such a vestigial coxa was confirmed by several dissections of *Hexaplex megalops* Doflein, 1904 by Guinot, Tavares & Castro (unpublished data), and it is supposedly characteristic to all Hexapodidae. The presence of a vestigial P5 coxa, from which the penis emerges, has necessitated a new interpretation of the hexapodids, which are no longer hexapods in term of anatomy (at least the males) but are clearly true decapods. Male Hexapodidae actually have five pairs of legs, with an extremely reduced P5 which lacks all its articles except for the vestigial coxa, which is concealed under the abdomen.

Genera within the Hexapodidae are essentially distinguished by the shape of the eyes and mxp3, the shape and degree of fusion of the male abdomen, the development of sternal grooves on the thoracic sternum, the frequent presence of a stridulating ap-

paratus (in the family at least two different shapes of one of its two components), and the structure of the G1. Some characters, such as the G1, show such a wide range of variation that subfamilies could be considered.

In addition to the dorsal location and reduction of sternite 8 and the partial loss of P5 in males, the Hexapodidae show other characteristics that are not found in most other Eubrachyura Saint Laurent, 1980: loss of the exopodite of pleopods of somite 2 in females, persistence of structures for the abdominal maintaining in adult females, and female abdomen not markedly sexually dimorphic. Guinot & Quenette (2005: 334, fig. 29b) discussed the possible relationships of the Hexapodidae with other eubrachyuran families characterized by reduced P5, in particular the Retropiumidae Gill, 1894, females of which show the same features (loss of the exopodite of pleopods of somite 2 in females, persistence of structures for the abdominal maintaining in adult females) as the Hexapodidae.

Genus *Paeduma* Rathbun, 1897 (Figs 1; 2)

Amorphopus Bell, 1859: 27-29. — Miers 1886: 275. — Alcock 1900: 293. — Stebbing 1910: 315. — Tesch 1918: 238 (key). — Serène 1968: 93. — Gordon 1971: 108. — Sankarankutty 1975: 4. — Guinot 1979: 114, 215.

Paeduma Rathbun, 1897: 163. — Gordon 1971: 108. — Guinot 1979: 114. — Schweitzer *et al.* 2000: 55. — Schweitzer & Feldmann 2001 *pro parte*: 332, 335, 345.

Non *Paeduma* – Manning & Holthuis 1981: 168, 173. — Karasawa 1990: 25. — Huang *et al.* 2002: 652, table 1. — Schweitzer 2005: 289.

TYPE SPECIES. — *Amorphopus cylindraceus* (Bell, 1859), by monotypy. *Amorphopus* Bell, 1859 is an invalid junior homonym of *Amorphopus* Audinet-Serville, 1838 (Insecta), therefore was replaced by *Paeduma* Rathbun, 1897 (p. 163), substitute name, from the Greek “rudiment” in allusion to the fifth pair of legs (Rathbun 1897: 163, footnote). Genus *Paeduma*: gender neuter according to Manning & Holthuis (1981), thus the type species is *Paeduma cylindraceum* (but gender masculine

according to Huang *et al.* 2002, who are not followed in the present paper).

EMENDED DIAGNOSIS (male holotype of *P. cylindraceum*). — Body thick, nearly cylindrical, narrowing anteriorly, markedly convex, transversely flattened. Dorsal surface with regions indistinct, grooves not marked except for extremely weak traces of cervical and branchiocardiac grooves. Lateral margin arcuate anteriorly, then divergent, posteriorly convergent. Front depressed, relatively narrow (6.4 times in carapace width), with distinct thickened ridge, more advanced laterally than in midline, with very weak, obtuse projection medially. Antennae with articles 2+3 covered by antennules. Epistome relatively developed. Orbits transverse, situated in straight line, not dorsally expanded, rimmed. Eyes movable, small, lying transversally, with cornea small, narrower than stalk. Buccal cavity with sides convergent anteriorly. Mxp3 of “normal” type (i.e. operculiform), broad, nearly filling entire field. Endopod with broad ischion and merus; anteroexternal margin of merus oblique; propodus, carpus and dactylus slender; palp cylindrical; dactylus longer than propodus but extending only two-thirds of ischion, close to its border. Exopod wide, with long but concealed flagellum (not shown in Fig. 2C). Thoracic sternum very wide. Sternites 1-2 forming a narrow, triangular piece extending between bases of mxp3, clearly separated from sternite 3; sternite 3 distinct but not delimited by suture; sternite 4 much developed; sternites 5-7 similarly developed, high; sternite 8 not aligned with preceding sternites, strongly reduced, only visible dorsally as small, ornamented plate inserted between sternite 7 and abdominal somite 1. Episternites 4-5 similarly elongated, pointed; episternites 6-7 similarly rounded; episternite 7 forming projection overhanging posterolateral angle of carapace. Sutures 4/5 to 6/7 nearly parallel, equidistant. Sternal grooves or trenches absent. Sterno-abdominal cavity elongated, reaching sternite 3. Male abdomen very long, extending beyond bases of mxp3, extremely narrow, specially at level of somite 6 and telson; strong constriction at level of abdominal somite 6 opposite to middle part of thoracic sternite 5. Somites 1, 2 free, approximately similar in size; somites 3-5 fused, forming distally-truncated triangle; somite 6 as extremely long, linear, undivided piece; its proximal part markedly constricted; telson elongated, rounded at tip. Gonopods concealed under abdomen, shape unknown (dry condition of specimen). G1 supposedly relatively slender (because of narrowness of abdomen), not recurved posteriorly or doubled recurved into a 8-shaped figure; G2 probably small. Chelipeds markedly unequal in male, robust, thick; large cheliped with palm nearly as long as wide, gap between fingers; fingers armed with blunt teeth; small cheliped with closer fingers. Dactyli on each side with striae on inner surface. P2-P4 short, rather similar in size, shape. P5 not visible on the outside, reduced to

a vestigial coxa in males, absent in females. Stridulating apparatus of two striated parts. Pterygostomian region with an oblique row of rather thick, short, spaced sticks (about 14), progressively diminishing in size to show externally as rounded granules; dactylus provided with numerous thin, long, closed striae on whole length of inner surface (except for apex).

GEOGRAPHICAL DISTRIBUTION. — Galápagos Islands (Garth 1946, 1991; Hickman & Zimmerman 2000) or possibly Pacific coast of South America.

REMARKS

Bell's *Amorphopus* (= *Paeduma*) was established without indicating locality and without figures, which may explain why *Paeduma cylindraceum* was never reported since its description.

The P5 was considered a “mere rudiment, in the form of a minute tubercle inserted in a little notch at the base of the first joint of the fourth pair, and scarcely discernible by the naked eye” (Bell 1859: 28). Bell did not believe that a leg could vanish completely in a decapod. De Haan (1835: 35, under *Hexapus sexpes* Fabricius, 1798) correctly remarked: “Nullum indicium quinti paris, neque sub abdomine ulli reconditi” (= “no sign of a fifth pair, or is any hidden under the pleon”). Stebbing (1910: 315) corrected Bell's statement “six pairs of legs beside the claws” to “three pairs of legs”.

Two of Bell's statements need comment.

1) The location of the P5 rudiment showing as a tubercle at the base of the P4 does not correspond to the normal place of the coxa of an appendage (always articulated on the sternite). This location, which might be interpreted as the result of the displacement of the P5 in the reduction process of sternite 8, does not match with the interpretation of an hexapodid P5 vestigial coxa that is concealed under the abdomen (Saint Laurent 1989; Guinot, Tavares & Castro unpublished data).

2) A similar “tubercle” was seen by Bell (1859: 29) at the base of the P4 in dorsal view of *Hexapus sexpes* (Fabricius, 1798) figured by De Haan (1835: pl. D, pl. 11, fig. 6). The small figure of De Haan (1835: pl. 11, fig. 6) does not allow to be sure of the presence of such a tubercle, but the presence in *H. sexpes* of a structure similar to that of *P. cylindraceum* is confirmed here.

Bell's “mere rudiment” on the P4 coxa of *P. cylindraceum* (Figs 1A; 2D) actually corresponds to the external portion of the apodeme of the P4 coxa, i.e. the apodemal platelet. It is exposed in a notch of the proximal border of the P4 coxa, and shows externally as a calcified strip extending through the arthrodial cavity as usual. The apodemal platelet is clearly visible in the dry holotype of *P. cylindraceum*, as well as in a number of hexapodids (for instance in *Hexapus sexpes*). The supposed P5 rudiment seen by Bell (1859) definitely is not a vestige of P5, but corresponds to a portion of the P4.

Actually, apodemal platelets are present on P2-P4 coxae in all the hexapodid genera that were examined, although this could not be confirmed in the holotype of *P. cylindraceum* because of its dry condition. The apodemal platelets are also visible ventrally on the basis-ischion of P2-P4 in the *P. cylindraceum*'s holotype as well as in other hexapodids. Such apodemal (coxal and ischio-basal) platelets are present to a variable extent on P2 to P5 in other eubrachiuran families. It seems, however, that the coxal platelets are particularly well visible on the pereopods of the Hexapodidae, and on the P4 in particular. Authors such as Huang *et al.* (2002) who have discussed other species of *Paeduma*, viz. *P. orientalis*, unfortunately have not provided enough information.

As previously mentioned, Manning & Holthuis (1981) gave erroneous characters for *Paeduma* because they combined the characters briefly provided by Bell (1859) for *P. cylindraceum*, the type species, and those shown by the two other species of *Paeduma*, *P. orientalis* and *P. chuenensis*. The latter two are herein placed in *Hexaloughlia* n. gen. Manning & Holthuis (1981) indicated for *Paeduma* “third and fourth and fourth [*sic*] and fifth male abdominal somites fused” (p. 168, in the key) and “third and fourth and fifth and sixth somites fused” (p. 173, 175). We put another interpretation, hypothetically: abdominal somites 3-5 fused in *Paeduma* and in *Hexaloughlia* n. gen.

Manning & Holthuis' (1981) assertion that the gonopods of *Paeduma* are slender and recurved posteriorly is applicable to the gonopods of *Hexaloughlia* n. gen. The gonopods of *Paeduma* (*P. cylindraceum*) are unknown because of the dry condition of the

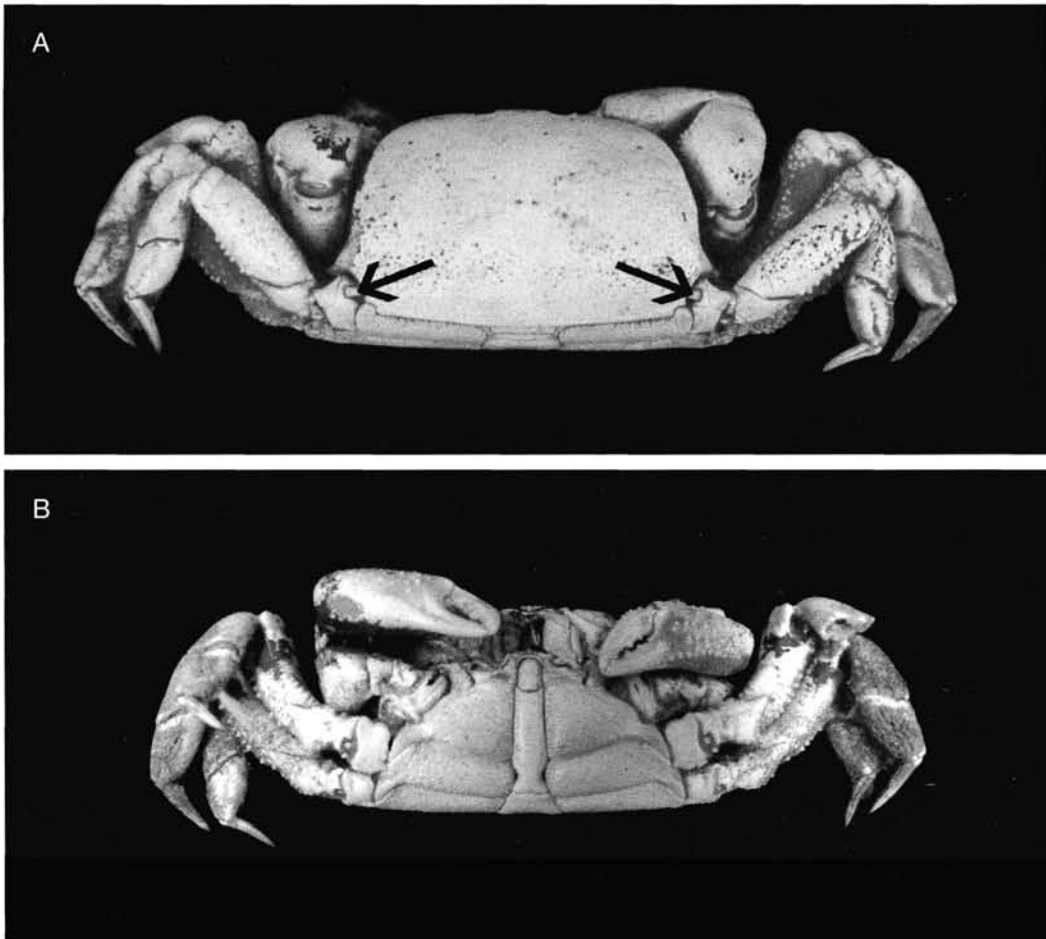


FIG. 1. — *Paeduma cylindraceum* (Bell, 1859), holotype ♂ 15.3 × 23.5 mm, dry, with two Bell's handwritten labels: "*Amorphopus*" and "*Am: cylindraceus* male sign. Gallapagos [sic] Mr Cuming" (OUMNH 15693): **A**, dorsal view, showing apodemal platelets of P4 coxae (indicated by arrows); **B**, ventral view.

holotype, but they are probably neither recurved posteriorly nor doubly recurved into an 8-shaped figure as in *Hexalaughlia* n. gen. Bell's (1859) description of *P. cylindraceum* does not mention pterygostomian stridulating striae, which explains why this character is missing in the generic diagnosis of *Paeduma* provided by Manning & Holthuis (1981: 173: "pterygostomian region lacking oblique striae"). Manning & Holthuis attributed to *Paeduma* two other species, *P. orientalis* and *P. chuenensis*, that lack a stridulating apparatus. In contrast, Manning & Holthuis (1981: 177) did characterize *Stevea wil-*

iamsi by the presence of stridulating pterygostomian striae, a condition confirmed herein.

Paeduma cylindraceum (Bell, 1859)
(Figs 1; 2)

Amorphopus cylindraceus Bell, 1859: 27. — Serène 1968: 93.

Paeduma cylindraceum — Rathbun 1897: 163. — Gordon 1971: 108. — Crane 1981: 3. — Manning & Holthuis 1981: 173.

MATERIAL EXAMINED. — Holotype, ♂ 15.3 × 23.5 mm, dry and in good condition, with Bell's handwritten labels: "Amorphopus" (placed above specimen) and "Am: cylindraceus male sign. Gallapagos [sic] Mr Cuming" (placed below specimen). Registration number: OUMNH 15693 (S. De Grave pers. comm.).

DESCRIPTION OF DRY MALE HOLOTYPE

Granules absent on dorsal surface of carapace, present only on lateral borders, more developed at level of P4; with numerous pits except medially. Large cheliped with palm much inflated; outer surface covered by coarse, rounded granules, more numerous on inferior half near superior border; proximal superior border of dactylus coarsely granulated, prehensile margin armed with two distinct blunt teeth; fixed finger curved, granulated, prehensile margin armed with strong proximal tooth and less distinct teeth; marked gap between fingers. Small cheliped much reduced; no marked gap between pointed fingers; outer surface of palm covered by coarse, blunt granules, closer on inferior half near superior border; dactylus with superior border coarsely granulated except distally, prehensile margin armed with several triangular teeth; fixed finger with two rows of strong granules, prehensile margin armed with several triangular teeth. Thoracic sternum ornamented with marked granules along border of sterno-abdominal cavity and sutures; surface punctate. Sutures 4/5 to 6/7 equidistant; sternites 1-2 advanced between mxp3; sternite 3 distinct but not demarcated by suture; sternite 4 well developed, with latero-anterior projections; sternites 5 to 7 inflated, of about same size. Sternite 7 tilted, its posterolateral corner (episternite 7) forming a marked projection which fits with a notch on border of carapace (interlocking mechanism carapace/sternum). Sternite 8 present but extremely reduced and concealed under carapace, except for small plate exposed dorsally, calcified, ornamented. Pereopods 2-4 with margins of meri ornamented with salient, blunt granules. Setae on surfaces of P2 and P3 meri, on surfaces of P2-P4 carpi and propodi; longer setae on margins of distal articles. P4 coxa with a markedly discernible apodemal platelet; ischio-basis with a ventral apodemal platelet. P5 vestigial coxa concealed under abdomen.

REMARKS

The particular spelling of Galápagos, with a double "l", i.e. "Gallapagos", is consistent on labels of Bell's dry collection (see DiMauro 1982: 158: a fact which "does help substantiate that it is Bell's collection"), and was similarly used by H. Milne Edwards (1838: 12). It should be stressed that the Galápagos origin of this unique specimen must be taken with caution because of a possible exchange of labels between material collected by Cuming in the Galápagos and along the South American mainland coast. Several species collected by Cuming and reported by Bell "have been turned up along the mainland coast of south America from Santa Elena Bay, Ecuador, to the Bay of Panama, localities also visited by Cuming" (Garth 1946: 343; see also Garth 1958: 71; DiMauro 1982: 156).

Genus *Stevea* Manning & Holthuis, 1981 (Fig. 3)

Stevea Manning & Holthuis, 1981: 168, 177. — Beschin *et al.* 1994: 191. — Schweitzer *et al.* 2000: 55. — Schweitzer & Feldmann 2001: 337, 345 (key). — Huang *et al.* 2002: 653, table 1. — Schweitzer 2005: 289.

TYPE SPECIES. — *Hexapus williamsi* Glassell, 1938, by original designation.

SPECIES INCLUDED. — One extant species, *S. williamsi*. For the status of the fossil species *Stevea cesarii* Beschin, Busulini, De Angeli & Tessier, 1994, from the Eocene of Italy, see Fossil Hexapodidae.

DESCRIPTION

See Manning & Holthuis (1981: 168, 177), in amending the features concerning the male abdomen which, instead of "second through sixth somites fused", shows weak but distinct sutures.

REMARKS

The genus *Stevea* was established by Manning & Holthuis (1981) to separate from *Hexapus* De Haan, 1835 emend. (type species: *Cancer sexeps* Fabricius, 1798; genus established in 1833 but without nominal species) the American species *H. williamsi* Glassell, 1938 (p. 445, pl. 35, figs 1-4). *Stevea williamsi* appears to be known with

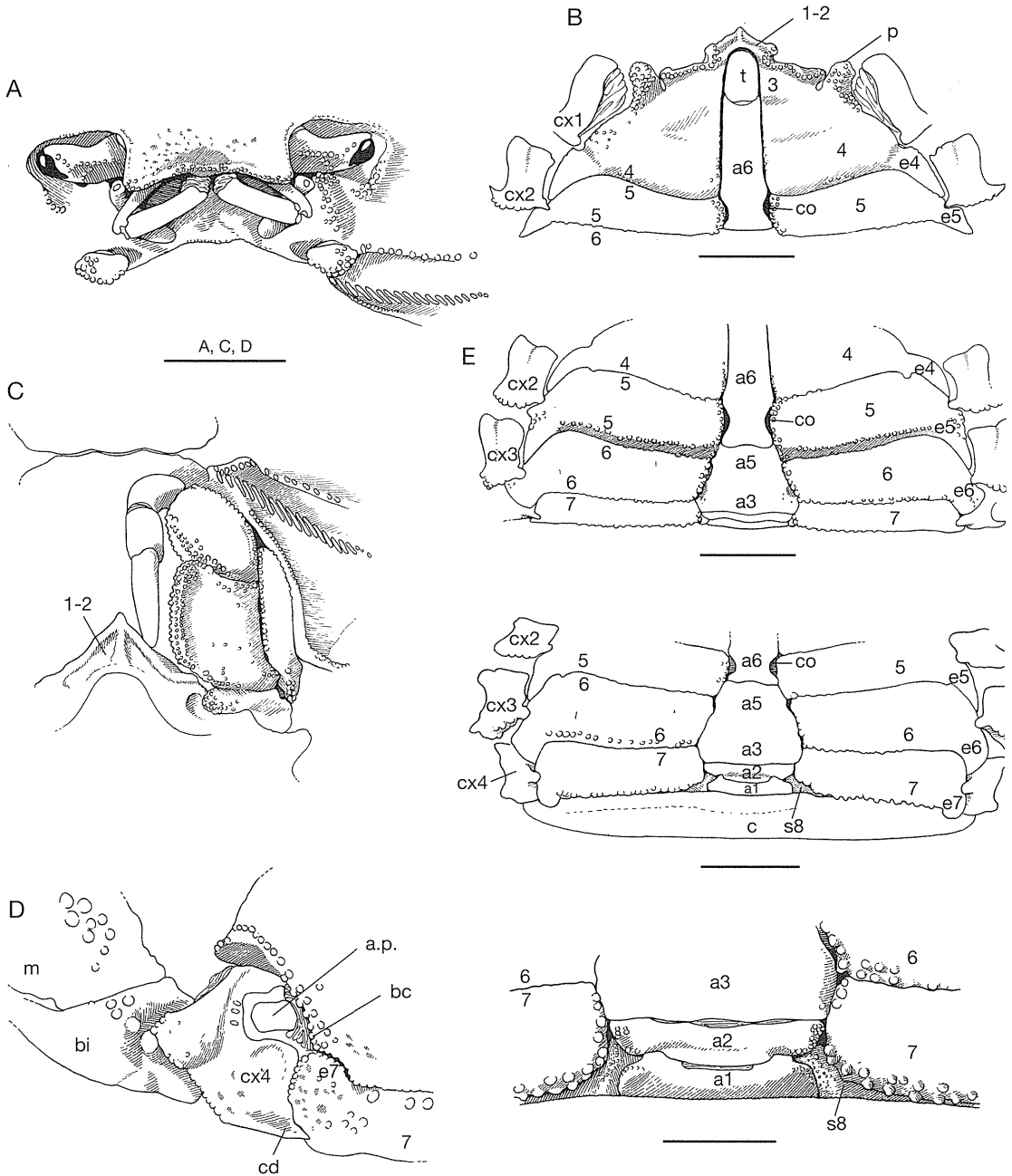


FIG. 2. — *Paeduma cylindraceum* (Bell, 1859), holotype ♂ 15.3 × 23.5 mm, dry, "Gallapagos [sic] Mr Cuming" (OUMNH 15693): **A**, frontal view; **B**, different views of thoracic sternum and abdomen; **C**, mpx3 and stridulating striae; **D**, proximal articles of left P4, with apodemal platelet; **E**, posterior view of thoracic sternum to show reduced sternite 8. Abbreviations: **a.p.**, apodemal platelet; **a1-a6**, abdominal segments 1-6; **bc**, carapace border; **bi**, basis-ischion; **c**, carapace; **cd**, articular condyle of cx4 on thoracic sternite 7; **co**, constriction at level of abdominal somite 6; **cx1-cx4**, coxae of P1-P4; **e4-e7**, épisternites 4-7; **m**, merus; **p**, projection of sternite 4; **s8**, exposed portion of sternite 8; **t**, telson; **1-7**, sternites 1-7; **4/5-6/7**, thoracic sternal sutures 4/5-6/7. Scale bars: 2.5 mm.

certainty from the male holotype only, 5.8×8.6 mm, from San José, Guatemala (SDSNH No. 3940; ex Cat. No1158). The female 9.4×14.4 mm, from the Gulf of Tehuantepec, west coast of Mexico (USNM 170897), identified to *H. williamsi*, may well prove to belong to *Paeduma*, a direct comparison with the holotype of *H. williamsi* being necessary.

Glassell (1938: 445, pl. 35, fig. 4) illustrated the male abdomen of *S. williamsi* as having several weak sutures; however, this does not correspond exactly to his text: "Only the 1st and 7th segment [telson] are articulated; the five interior segments are coalesced". This is probably why Manning & Holthuis (1981) indicated for *Stevea* "male abdomen with three somites, second through sixth fused". Examination of the male holotype and photographs by L. L. Lovell (Fig. 3B, C) indicate that Glassell's sketch, showing several abdominal sutures, is correct. The abdominal somites of the holotype (which are wider than in *Paeduma*) are separated by several weak but visible sutures so that in *Stevea* abdominal somites seem to be distinct, although all not articulated. There is no constriction. In these respects *S. williamsi* appears to be distinct from *P. cylindraceum* where, hypothetically, the abdominal somites 3-5 are completely fused and where there is a marked constriction at the level of somite 6, leaving an empty space on each side (Fig. 2B, E).

The first gonopods of the male holotype of *S. williamsi* are essentially straight, with only a slight distal curvature (L. L. Lovell pers. comm.). Because of the dry condition of the holotype of *P. cylindraceum*, it is not possible to compare the gonopods to those of *Stevea*. In *S. williamsi* the meri of P2-P4 show rows of tubercles, those on P2 being more numerous (L. L. Lovell pers. comm.).

A stridulating apparatus similar to that of *Paeduma* (Fig. 2A, B) is mentioned in Manning & Holthuis' (1981: 177) diagnosis of *Stevea*. According to Glassell (1938: 445, pl. 35, fig. 2), in *S. williamsi* there is "a tubercle on the inner distal face [of the palm of the cheliped] which engages with the stridulations of the epimera". Actually, in both sexes of *Stevea*, the symmetrical rows of thick and spaced pterygostomial stridulating striae are more likely rubbed by very thin and closed striae located on

the inner part of the dactylus of both chelipeds, as in *P. cylindraceum*. In the female of *S. williamsi* (USNM 170897) the exposed portion of sternite 8 is small, as in the male of *P. cylindraceum* (Fig. 2B, E).

Despite some similar features, *P. cylindraceum* and *S. williamsi* are distinct. The question of the specific versus generic level of these differences, which concern mainly the male abdomen and the gonopods, is beyond the scope of this study, and should be addressed in a revision of the family Hexapodidae. Two genera, *Paeduma* and *Stevea*, are thus so far known from the Pacific coast of South America.

See below for the fossil record of *Stevea*.

Stevea williamsi (Glassell, 1938) (Fig. 3)

Hexapus williamsi Glassell, 1938: 445, pl. 35, figs 1-4. — Hendrickx 1995: 139, list.

Stevea williamsi — Stephensen 1946: 182 (incorrect spelling).

Stevea williamsi — Manning & Holthuis 1981: 177. — Beschin *et al.* 1994: 191. — Schweitzer & Feldmann 2001: 337. — Huang *et al.* 2002: 653, table 1.

MATERIAL EXAMINED. — Holotype, ♂ 5.8×8.6 mm, San José, Guatemala (SDSNH No. 3940; ex Cat. No. 1158; examined and photographed by L. L. Lovell and W. A. Newman; with reservation, ♀ 9.4×14.4 mm, Gulf of Tehuantepec, west coast of Mexico (USNM 170897).

DESCRIPTION

See Glassell (1938) and above.

Genus *Hexalaughlia* n. gen. (Fig. 4)

Paeduma — Manning & Holthuis 1981 *pro parte*: 173, 174. Non *Paeduma* Rathbun, 1897: 163 (substitute name for *Amorphopus* Bell, 1859).

Thaumastoplax — Rathbun 1909: 113; 1910: 346, 347. — Tesch 1918 *pro parte*: 238, 239. — Sakai 1935 *pro parte*: 195; 1939 *pro parte*: 577, 578; 1976: 553, 555. —

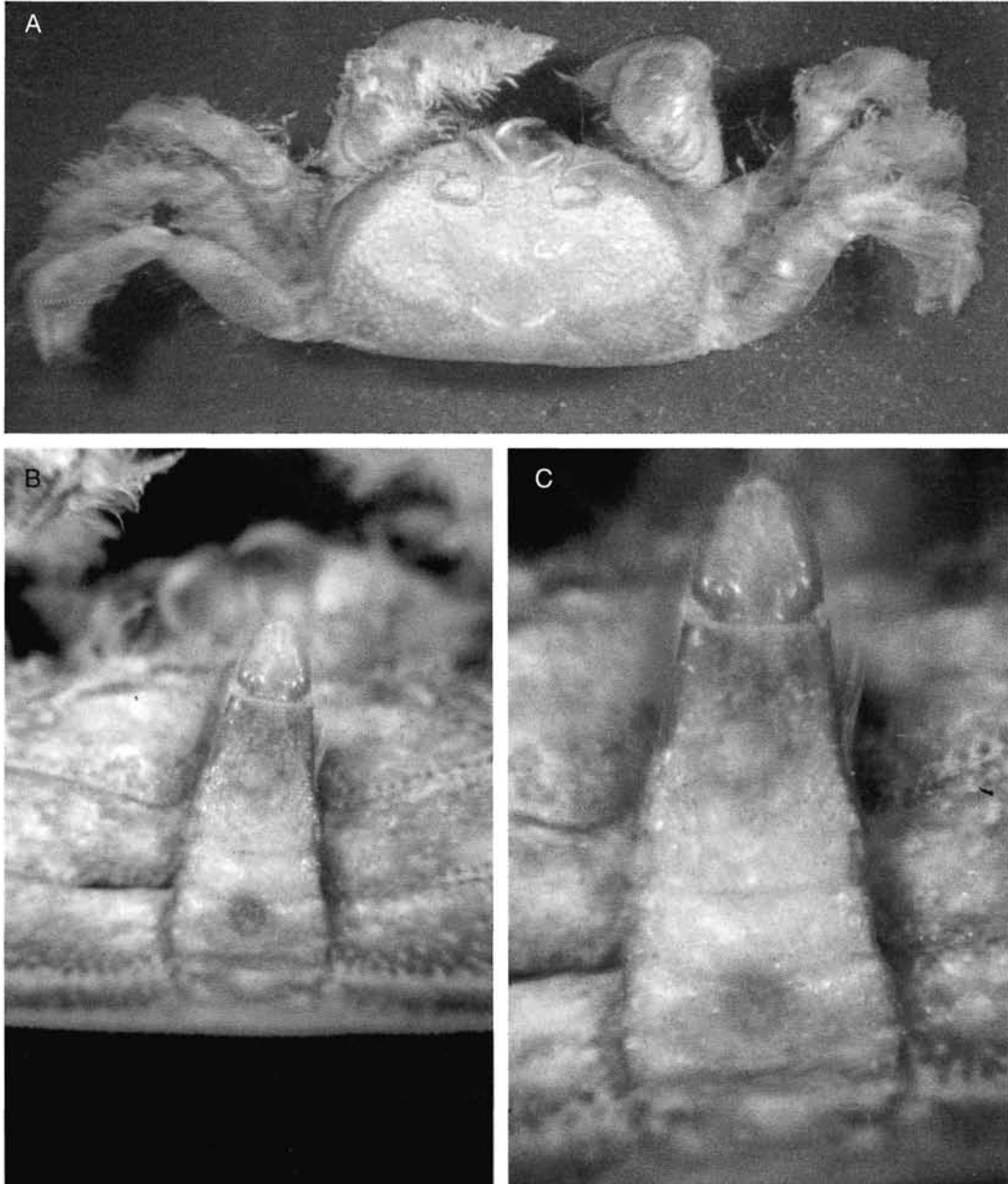


FIG. 3. — *Stevea williamsi* (Glassell, 1938), holotype ♂ 5.8 × 8.6 mm, San José, Guatemala (SDSNH No. 3940; ex Cat. No. 1158): **A**, dorsal view; **B**, ventral view; **C**, abdomen. Photographs by L. L. Lovell and W. A. Newman.

Imaizumi 1959 *pro parte*: 276. — Dai & Yang 1991 *pro parte*: 393, 419. Non *Thaumastoplax* Miers, 1881 (type species by monotypy: *T. anomalipes* Miers, 1881).

Paeduma — Karasawa 1990 *pro parte*: 25. — Huang *et al.* 2002 *pro parte*: 652, table 1. — Schweitzer & Feldmann 2001 *pro parte*: 332, 345.

TYPE SPECIES. — *Thaumastoplax orientalis* Rathbun, 1909, by present designation.

OTHER SPECIES INCLUDED. — *Thaumastoplax chuenensis* Rathbun, 1909.

ETYMOLOGY. — It is a pleasure to dedicate this new genus to Dr Patsy A. McLaughlin, in recognition of her considerable contribution to scientific knowledge. Gender: feminine.

GEOGRAPHIC DISTRIBUTION. — Western Pacific.

DESCRIPTION

Carapace wider than long, longitudinally convex, transversely flat. Dorsal surface with regions indistinct, except for a faint H-shaped median depression; gastric region may be sharply outlined. Lateral margin anteriorly arcuated, then straight (not diverging), sometimes marked by raised line. Antennae not covered by antennules. Front slightly deflected, thin. Epistome reduced. Orbits oval, in common straight line, not dorsally expanded, rimmed. Eyes movable, small, transversal, with small cornea. Buccal cavity much broader than long, anteriorly arcuated, sides anteriorly divergent. Mxp3 somewhat pediform, slender, inclined, gaping, leaving mxp2 only partly visible. Endopod with short, mesially expanded ischion; merus narrow, inclined; carpus short; propodus as long as broad, considerably dilated and with mesial expansion distally; dactylus lanceolated, with very long setae entering sterno-abdominal cavity. A wide hiatus between palp and ischium, partly filled by fringes of setae. Exopod without flagellum. Pterygostomian region without row of stridulatory striae. Thoracic sternum wide. Sternites 1-2 forming wide, triangular piece extending between bases of mxp3, prolonging into sternite 3 without marked delimitation; sternite 4 much developed; sternites 5-7 similarly developed, high; sternite 8 reduced, visible dorsally only as minute plate inserted between sternite 7 and abdominal somite 1, most part hidden under carapace. Episternites 4-5 similarly elongated, pointed; episternites 6-7 similarly rounded, episternite 7 forming projection overhanging the posterolateral angle of carapace (interlocking apparatus). Sutures 4/5, 5/6 and 6/7 nearly equidistantly parallel. Sternal grooves or trenches absent in both sexes. Sterno-

abdominal cavity elongated, reaching sternite 3. Male abdomen very long, extending beyond bases of mxp3, moderately narrow, specially at level of somite 6 and telson; no marked constriction at level of somite 6. Somites 1, 2 free, of about the same size, not much elongated transversally; somites 3-5 fused in undivided piece, anteriorly narrowing; somite 6 as relatively long plate; telson relatively short, bluntly triangular. Abdomen not maintained by prominences of press-button type [to be verified], appearing maintained between oblique slopes of deep sterno-abdominal cavity. Gonopods concealed under abdomen, slender, recurved posteriorly, apex apparently naked. Chelipeds equal in male, short; palm of large cheliped higher than long, may be ornamented with granules. P2-P4 markedly unequal, with P3 granulous, very developed, longer, thicker (in particular the merus) than subequal, smooth P2, P4; all articles fringed with long, thick setae. No stridulating apparatus.

REMARKS

The recent discovery of the holotype of *P. cylindraceum* (Bell, 1859), type species of the American genus *Paeduma*, has allowed its comparison with two other species described from Thailand and referred to *Paeduma* by Manning & Holthuis (1981: 173). As a result, a new genus, *Hexalaughlia* n. gen., is established for those two species: *H. chuenensis* (Rathbun, 1909) n. comb., and *H. orientalis* (Rathbun, 1909) n. comb.

Hexalaughlia n. gen. may be distinguished from *Paeduma* by the following characters: mxp3 pediform, slender, endopod recurved, with dilated ischium and propodus, and exopod without flagellum (Fig. 4A) (mxp3 operculiform, endopod with narrow propod, exopod with flagellum in *Paeduma*, Fig. 2C); stridulating striae lacking (row of oblique striae in *Paeduma*, Fig. 2A, C); thoracic sternum with sternites 1-3 forming a triangular piece, without marked delimitation (Fig. 4B) (a narrow triangle in *Paeduma*, Fig. 2B); male abdomen markedly wider in *Hexalaughlia* n. gen. than in *Paeduma* (where it appears somewhat linear); somite 6 moderately long, without constriction in *Hexalaughlia* n. gen. (Fig. 4B-D) (somite 6 as very long, narrow, basally constricted plate in *Paeduma*,

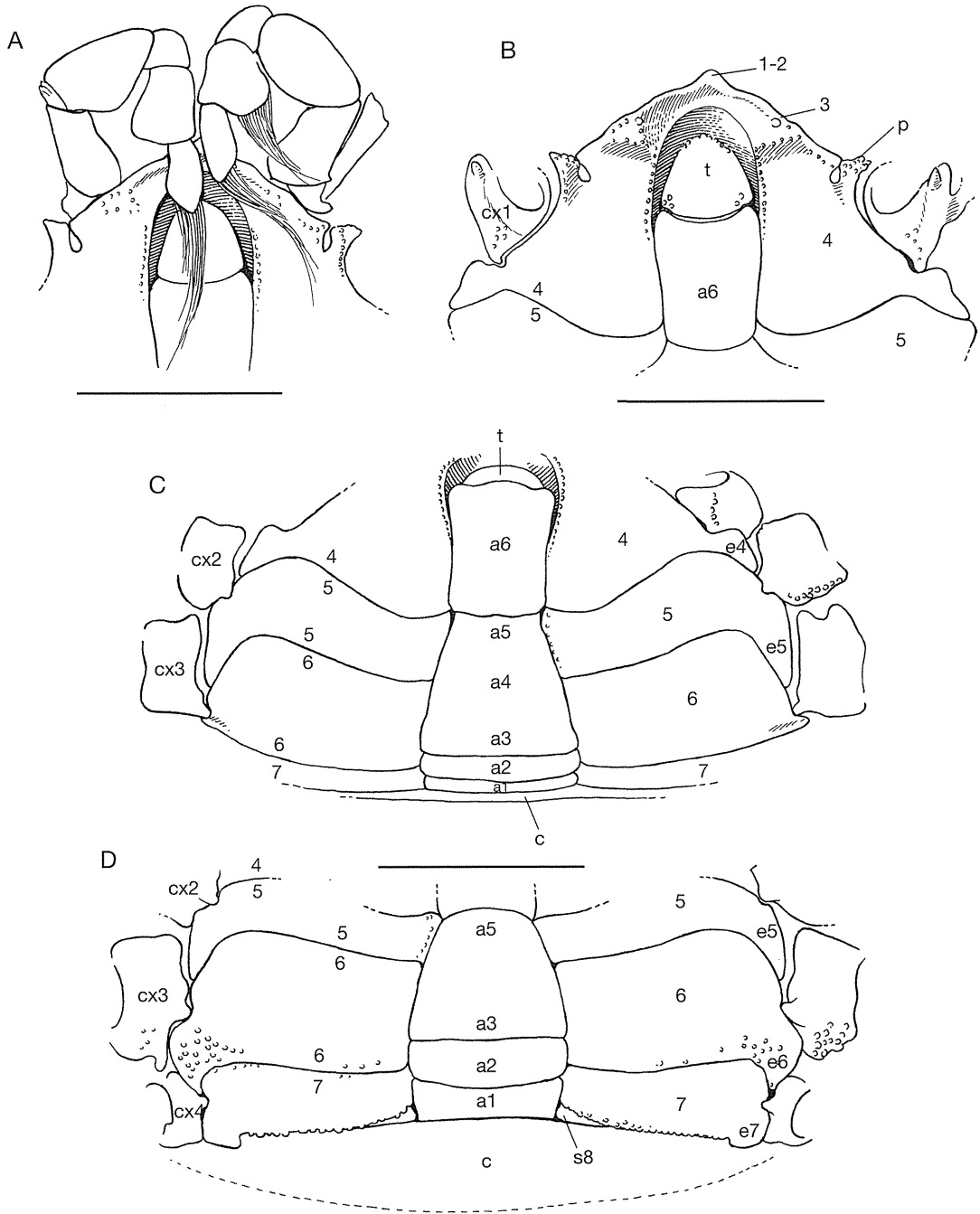


FIG. 4. — *Hexalaughlia? orientalis* (Rathbun, 1909) n. comb., ♂ 5.5 × 8 mm, Japan, *Albatross*, stn 4964, 27.VIII.1906, 37 fms, det. *Thaumastoplax orientalis* (USNM 46392): **A**, mpx3 (flagellum of exopod not shown); **B-D**, different views of thoracic sternum and abdomen. Abbreviations: **a1-a6**, abdominal segments 1-6; **c**, carapace; **cx1-cx4**, coxae of P1-P4; **e4-e7**, épisternites 4-7; **p**, projection of sternite 4; **s8**, exposed portion of sternite 8; **t**, telson; **1-7**, sternites 1-7; **4/5-6/7**, thoracic sternal sutures 4/5-6/7. Scale bars: 2.5 mm.

Figs 1B; 2B); telson rather short, bluntly triangular in *Hexaloughlia* n. gen. (elongated and rounded at tip in *Paeduma*); chelipeds equal in *Hexaloughlia* n. gen. (strong heterochely in *Paeduma*); P2-P4 markedly unequal, with P3 stout, much larger than P2 and P4, ornamented with strong granules in *Hexaloughlia* n. gen. (P2-P4 subequal, nearly similar in size and shape, and weak ornamentation in *Paeduma*, Fig. 1).

Contrary to Manning & Holthuis' (1981) assertion, *Paeduma* does not resemble *Thaumastoplax*. In contrast, *Hexaloughlia* n. gen. is close to *Thaumastoplax* by its pediform and recurved mxp3 (Fig. 4A), the absence of a flagellum on mxp3 exopod, absence of stridulating pterygostomial striae, and unequal P2-P4. *Hexaloughlia* n. gen., however, differs from *Thaumastoplax* by the narrower carapace; the relative size of the ambulatory legs, the P2 and P4 being subequal and P3 much stouter (P2 slender, P3 very stout and P4 thicker than P1 in *Thaumastoplax*); G1 recurved posteriorly and 8-shaped (slender, only sinuous, with apex directed anteriorly in *Thaumastoplax*).

Hexaloughlia orientalis
(Rathbun, 1909) n. comb.
(Fig. 4)

Thaumastoplax orientalis Rathbun, 1909: 113; 1910: 347, fig. 33, pl. 2, fig. 1. — Tesch 1918: 239 (key). — Sakai 1934: 316, fig. 24; 1935: 193, fig. 100; 1939: 579, pl. 102, fig. 3; 1976: 555, fig. 300a, b. — Imaizumi 1959: 276, fig. 5. — Takeda 1982: 200, fig. 593. — Dai & Yang 1991: 419, fig. 205(3-4), pl. 56(6).

Paeduma orientale – Manning & Holthuis 1981: 174, fig. 35. — Karasawa 1990: 25.

Paeduma orientalis – Huang et al. 2002: 652, table 1.

MATERIAL EXAMINED (specific identification with reservation). — **Japan**. From Kobe, Tomaga Shima Lt., *Albatross*, stn 4964, 65 m, 34°05'30"N, 134°56'40"E, 27.VIII.1906, *Thaumastoplax orientalis*, ♂ 5.5 × 8 mm (USNM 46392).

REMARKS

It was not possible to examine the type material of *Thaumastoplax orientalis* from Thailand. The

Albatross Japanese specimen bears a label from R. B. Manning indicating that it represents a new species. Manning & Holthuis (1981: 174) add that this genus also includes "... a species from Japan, identified by earlier workers with *T. [Thaumastoplax] orientalis*, which we believe represents a new species, the description of which is in preparation". The first occurrence outside Thailand was by Sakai (1934). There are several other Japanese records (see Sakai 1976; Takeda 1982), although that material should be examined to see if it actually represents *H. orientalis* n. comb.

Hexaloughlia chuenensis
(Rathbun, 1909) n. comb.

Thaumastoplax chuenensis Rathbun, 1909: 113; 1910: 346, figs 34, 35. — Tesch 1918: 239 (key).

Paeduma chuenense – Manning & Holthuis 1981: 174, fig. 35.

REMARKS

Hexaloughlia chuenensis n. comb., known from a young male, and not reported since its description from Thailand by Rathbun (1909, 1910), differs from *P. orientalis* by a narrower carapace, slightly more marked dorsal areolation, less angled anterolateral margins, wider fronto-orbital margin, and narrower walking legs.

FOSSIL HEXAPODIDAE

The family Hexapodidae includes a relatively small number of extant genera, distributed throughout Indo-West Pacific, eastern Pacific, and eastern Atlantic regions, some being monospecific, and several species endemic to South Africa. This represents a more restricted distribution than in the fossil record and suggests that hexapodids are a highly specialized group that has remained conservative, and has adapted to a small number of specialized ecological niches (Schweitzer & Feldmann 2001: 332). With several robust fossil records, the Hexapodidae is one among several eubranchyuran families known from pre-Eocene

occurrences, and one of the families known with certainty from the Cretaceous. According to Schweitzer (2005: 291) such a conservative specialization suggests that the Hexapodidae is not a likely candidate to contain the ancestral xanthoids. The hexapodid lineage presumably survived as refugium species.

A key of extant and fossil Hexapodidae and similar genera, including both *Paeduma* and *Stevea*, was provided by Schweitzer & Feldmann (2001: 337, 344, 345; see also Schweitzer 2005: 289). The distinctive characters of *Stevea* given by Schweitzer & Feldmann (2001: 337) were according to the erroneous diagnosis of Manning & Holthuis (1981), as previously explained. Most references to *Paeduma* in the literature (except for the mention of the type species, *P. cylindraceum*) correspond to *Hexaloughlia* n. gen.

Stevea cesarii Beschin, Busulini, De Angeli & Tessier, 1994 (p. 191, fig. 8, pl. 10), from the Eocene of Italy, shows a well preserved thoracic sternum, which is typically hexapodid, and a male abdomen without constriction. The abdominal somites 2-6 are fused (De Angeli pers. comm.) but traces of sutures are visible, which corresponds to extant *Stevea* (rather than to *Paeduma*). There was no mention of striae on the pterygostomial region in the description by Beschin *et al.* (1994: pl. 10, fig. 4b), and no striae can be discerned from their figures. A sketch and examination of a specimen, kindly provided by A. De Angeli, have nevertheless confirmed the presence of a row of stridulating striae, which are typical of *Paeduma* and *Stevea*. The hexapodid figured as *S. cesarii* on the same plate (Beschin *et al.*: pl. 10, fig. 2) from limit Ypresian-Lutetian (instead of Middle Lutetian), and with a different carapace shape, is not *S. cesarii*, and instead belongs to another new species (De Angeli pers. comm.).

A fossil without oblique pterygostomial striae, from the Miocene of central Japan was assigned to the genus *Paeduma* by Karasawa (1990: 25, pl. 8, fig. 14, as *Paeduma* sp.), who followed Manning & Holthuis' (1981) diagnosis. A stridulating apparatus is nevertheless diagnostic of *Paeduma* and *Stevea*, so the generic status of this Japanese hexapodid needs to be reviewed.

The nearly complete loss of P5 is a problem in recognizing fossil hexapodids because the legs, in particular P5, are often lost during fossilisation. Among the criteria that could be used are the shape of sternites 5-7 (well developed, equal and subrectangular) and the strong reduction of sternite 8, and perhaps even without visible trace.

Several fossil crabs truly lacking P5 (instead of lost during fossilisation) have been attributed to the Hexapodidae. The first verified occurrence for this condition was for the Paleocene *Gonicypoda rajasthanica* Glaessner & Rao, 1960. More recently, *G. tessieri* Rémy & Tessier, 1954, from the Maastrichtian, has been confirmed as another fossil member of the Hexapodidae (see Crane 1981; Crane & Quayle 1986; Schweitzer & Feldmann 2001; Feldmann & Schweitzer 2004; Schweitzer 2005).

Morris & Collins (1991), who described *Prepaeduma decapoda* Morris & Collins, 1991 from the Pliocene, considered *Prepaeduma* to be an ancestor to *Paeduma* in which P5 was not yet fully suppressed (Schweitzer *et al.* 2000: 55). Beschin *et al.* (1994) justifiably doubted the placement of *Prepaeduma* in the Hexapodidae. Finally Schweitzer & Feldmann (2001: 335, 339) clearly demonstrated that the type material of the Pliocene *P. decapoda* was a composite. The holotype (Morris & Collins 1991: fig. 56), without preserved pereopods, exhibits the seven sternites that are diagnostic of the Hexapodidae (in particular the well developed and similar sternites 5-7). Conversely, the paratype, which has a small but visible P5 (Morris & Collins 1991: fig. 57), has been referred to *Orthakrolophus bittneri* (Morris & Collins, 1991), of the Chasmocarcininae Serène, 1964 (Collins *et al.* 2003: 218, pl. 7, fig. 2). Collins *et al.* (2003: 220, pl. 7, fig. 8) provided a revised description of the true *Prepaeduma decapoda*, and referred it to *Hexapus*. *Hexapus decapodus* is a true hexapodid, with well visible seven thoracic sternites only, and shows five or six long stridulating ridges on the pterygostomial regions, typical of *Hexapus* (e.g., *H. sexpes*).

For a discussion of the fossil representatives of *Thaumastoplax*, see Imaizumi (1959) and Collins & Morris (1976, 1978).

REMARKS ON THE HEXAPODID STRIDULATING APPARATUS

The stridulating apparatus consists in *Paeduma* of a prominent, narrow, and oblique row of rather thick striae on the pterygostomial region (Fig. 2A, B), and thin striae on the inner surface of the dactyl of both chelipeds. The same kind of stridulating mechanism is present in *Hexaplax* Doflein, 1904 (Doflein 1904; Tesch 1918; see also Guinot-Dumortier & Dumortier 1960: 122, plectrum erroneously indicated on the propodus). The pars stridens and plectrum are well differentiated and consist of specialized striae, although in *Hexaplax* the distinction between these two structures lacks precision. In *Stevea williamsi*, thick and spaced pterygostomial striae are rubbed by thin and closed striae on the inner part of the dactylus of both chelipeds, as in *P. cylindraceum*. The fossil *Stevea cesarii* shows a similar stridulating pterygostomial row of striae.

A slightly distinct stridulating mechanism exists in a few other Hexapodidae. In *Hexapus sexpes* for instance, there is an area with several oblique and elongated striae disposed near the anterolateral angles of the buccal cavity; they are rubbed by thin, closed striae on the inner surface of the dactyl of both chelipeds (A. Milne-Edwards 1873: 254, pl. 12, fig. 1a; Tesch 1918: 240; Guinot-Dumortier & Dumortier 1960: 130, fig. 9; Manning & Holthuis 1981: fig. 32b; Manning 1982: 159, fig. 1d). Fossil *Hexapus* species probably show an area of oblique pterygostomial striae, as in *Hexapus pinfoldi* Collins & Morris, 1978, from Eocene of Pakistan, with 14 oblique and postero-laterally directed pterygostomial striae, sometimes irregularly arranged (Glaessner & Secretan 1987: 8, pl. 1, figs 5b, 6; Beschin *et al.* 1994: 194). A similar area exists in the extant *Lambdophallus sexpes* Alcock, 1900, but the striae seem to be fewer and thicker (Alcock 1900: 330; Alcock & McArdle 1903: pl. 62, fig. 1a). *Hexalaughlia orientalis* n. comb. and *H. chuenensis* n. comb. lack a stridulatory apparatus.

A stridulating apparatus was described as a prominent ridge in *Goniocypoda edwardsi* Woodward, 1867 and probably also in *G. quaylei* Crane, 1981, both from the Upper Eocene of Hampshire (Crane 1981: 6, 7, fig. 8D). This is an additional character

supporting assignment of *Goniocypoda* Woodward, 1867 to the Hexapodidae.

Acknowledgements

My most sincere appreciation to S. De Grave (Curator of the collections of OUMNH) who found the holotype of *Amorphopus cylindraceus* among Bell's material, considered to be lost; to Lawrence L. Lovell who kindly arranged with the San Diego Museum of Natural History the loan of the holotype specimen of *Stevea williamsi* and provided information and photographs (with the help of W. A. Newman). Special thanks to A. Crosnier (MNHN) for his kind help; M. Hendrickx (EMU Estación Mazatlán, Universidad Nacional Autónoma, México) for information and comments; R. Lemaître (USNM) who loaned material for study and carefully reviewed the manuscript; A. De Angeli (Associazione Amici del Museo Civico "G. Zanano", Montecchio Maggiore, Italy) for providing paleontological data and who permitted the examination of the Eocene *Stevea cesarii*; M. Tavares (Museu de Zoologia, Universidade de São Paulo) who generously shared useful discussions, and to P. Castro (California State Polytechnic University, Pomona) who critically read through an earlier draft of the manuscript and improved it with constructive comments.

Original drawings are due to Michèle Bertoncini (MNHN): we express our profound thanks for her invaluable contribution, which made this paper sound and comprehensive. The photographs were prepared by Laurent Albenga (MNHN).

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