

REDESCRIPTION AND SYSTEMATIC POSITION OF *PTEROCARIS* HELLER, 1862 (CRUSTACEA: DECAPODA: CARIDEA)

Arthur Anker

Laboratoire de Biologie des Invertébrés Marins et Malacologie, Muséum National d'Histoire Naturelle, 55, rue de Buffon, F-75005 Paris, France.
Email: anker@mnhn.fr

Peter C. Dworschak

Dritte Zoologische Abteilung, Naturhistorisches Museum Wien, Burggring 7, A-1014 Wien, Austria. Email: Peter.Dworschak@nhm-wien.ac.at
(Author to whom correspondence should be addressed.)

ABSTRACT. – The enigmatic caridean shrimp *Pterocaris typica* Heller, 1862, is redescribed and illustrated in detail after the rediscovery of the unique female holotype in the Crustacea Collection of the Museum of Natural History in Vienna. Heller did not specify the systematic position of the genus *Pterocaris* within the Caridea. Several subsequent workers (H. Coutière, D. M. Banner & A.H. Banner, M.L. Christoffersen) discussed the systematic position of this curious shrimp in relation to the family Alpheidae without having the possibility to examine the type. It is concluded here that the genus is indeed best placed within the Alpheidae. However, several highly unusual features (autapomorphies), which clearly indicate a specialized life style - especially the flattened and expanded abdominal pleura and the long simple setae covering almost the entire dorsal surface - make it difficult to find any close relatives among other alpheid genera. It is assumed that the extreme rarity of *P. typica* is due to a cryptic life style of the shrimp, which could live either inside galls among corals, on the surface of its invertebrate host or in a completely different habitat such as sedimentary bottoms.

KEY WORDS. – *Pterocaris typica*, Alpheidae, redescription, phylogeny, C. Heller, C.L. Doleschall, Indonesia, *Paratypton*.

HISTORICAL INTRODUCTION

The genus *Pterocaris* was erected by Camill Heller in 1862 (Heller, 1862) for a highly unusual shrimp sent to the Museum of Natural History in Vienna (NHMW) from "Amboina" (Ambon, Moluccas, Indonesia) by Carl Ludwig Doleschall (1827-1859), who was a remarkable physician, researcher and collector of numerous interesting specimens for the Vienna Museum. He practised in Java and later on Ambon until his early death, and published numerous scientific papers, mainly on Arachnida and Insecta (Stagl, 1999). During his life in Ambon he also met Alfred R. Wallace, who admired his collection of Lepidoptera. Heller had no information on the habitat of this unique specimen, and we were unable to find any further data on Doleschall's collections of Crustacea in his correspondence with Vincenz Kollar, who was "Vorstand des kayslerlich-königlichen zoologischen Hofkabinettes" in Vienna. We assume that the specimen Heller described as *Pterocaris typica* was sent by Doleschall under the name "*Apus* (?) sp., (sehr schlecht

erhalten)" meaning "*Apus* (?) sp. [= *Triops*, Notostraca] (in very poor condition)" as this is the only entry among numerous other crustaceans in the book of acquisitions (1859, III.) which could refer to this shrimp.

Long after the description the type of *P. typica* was considered as lost, since several workers who requested or searched for it in the Vienna Museum (Alexander J. Bruce, Albert H. Banner & Dora M. Banner) were not successful. D.M. & A.H. Banner (1985) supposed that it might be displaced, for example placed together with phyllosoma larvae.

In 1993, all the Natantia (sensu Holthuis, 1993) of the Crustacea Collection in alcohol had to be transferred for safety reasons to the newly constructed basement storage room and all the information which could be deciphered from the labels was hastily entered into a database. The current placement of *Pterocaris* on the shelves in the basement storage room is not among the Alpheidae (cabinets 6-8), but

after the Stenopodidea and before numerous unidentified *Natantia* (cabinet 15). This means that during this activity, V. Stagl - then part-time assistant curator at the then Crustacea-Arachnoidea-Myriapoda Collection - came across the specimen long after all alpheids have been entered. This indicates the misplacement on the original shelves among the "*Natantia* indet."

During the ongoing work on a type catalogue of the Crustacea Collection of the NHMW (Dworschak & Stagl, in prep.), one of us (PCD) became aware of the type in the database and on the shelf while cross-checking all the species described by Camill Heller and the material present in the collections.

The original description of *Pterocaris typica* by Heller (1862) is detailed but far from complete and the species has never been found again. The rediscovery of its unique type specimen in the NHMW gave us the opportunity of a redescription and a reevaluation of its systematic position, which is presented in this paper.

MATERIAL AND METHODS

The holotype of *P. typica* (NHMW 7982) was examined and illustrated with the aid of a stereo microscope (Nikon SMZ-10A) equipped with a camera lucida. After its rediscovery the type was in reasonably good condition, although partly incomplete. The body was lacking most of the appendages on the left side, including the mouthparts, the third maxilliped, first to fourth pereopods (fifth pereopod was still feebly attached), and the second pleopod. From these only the first and the second chelipeds (P1 and P2), and also two walking legs, probably third and fourth pereopods detached from the left side, were found loose in the same jar. As the exact origin of these two legs is difficult to establish (Heller's figure of P3 does not help much as it does not respect the proportions), in this study they will be termed "P 3/4". All other detached appendages, including all dissected mouthparts, are missing. Moreover, some appendages are absent on the right side, and were not found in the jar; these are the third and fourth pereopods (first, second and fifth are still attached, second is broken at third carpal segment). Table 1 summarises the condition of the specimen prior to and after the dissection:

The mouthparts were dissected and illustrated by Heller (1862: Pl. 1, figs. 10 - second maxilliped, 11 - first maxilliped, 12 - maxilla, 13 - mandible; here reproduced in Fig. 1), with the exception of maxillula (Mx1), which was not illustrated. In order to verify the exactness of Heller's figures we decided to dissect the remaining mouthparts. After the drawing of the underside of the body was made, the mouthparts and the third maxilliped were carefully dissected from the right side, without damaging first and second pereopods. The only other appendages detached were the left fifth pereopod, the coxa of the left first pereopod, the left first pleopod and the right second pleopod. The former three appendages or the parts of appendages were not

Table 1. Condition of the holotype of *Pterocaris typica* prior to and after present dissection.

appendage	right	left	dissection
eystalks	+	+	not detached
antennule	+	+	not detached
antenna	+	+	not detached
mandible	-	+	detached
maxillula	-	+	detached
maxilla	-	+	detached
maxilliped 1	-	+	detached
maxilliped 2	-	+	detached
maxilliped 3	-	+	detached
pereopod 1	+	+	(loose) right not detached
pereopod 2	+	+	(broken) (loose) right not detached
pereopod 3	-	?	(loose)
pereopod 4	-	?	(loose)
pereopod 5	+	+	left detached
pleopod 1	+	+	left detached
pleopod 2	+	-	right detached
pleopods 3-5	+	+	neither detached
uropod	+	+	not detached
telson		+	not detached

illustrated by Heller, while the last one was illustrated very superficially.

Prior to the dissection the specimen was coloured with the Chlorazole Black E (Sigma Aldrich, CAS-Nr. 1937-37-7), and photographs of the specimen in different views were taken with a Pentax SFXN with a 50 mm macro lens or attached to a Leica Wild M3Z stereo microscope. For details of the long setae the camera was mounted on a Leitz Diaplan microscope with interference contrast.

Other material examined: ovigerous female (syntype) of *Paratypton siebenrockii* Balss, 1914 (NHMW 6714).

REDEFINITION OF *PTEROCARIS* HELLER, 1862

Carapace and abdominal segments strongly compressed dorso-ventrally; carapace with latero-anterior projections; dorsal integuments (carapace, abdominal pleurites, telson, uropods) covered by long, hair-like setae. Cardiac notch not distinct. Pleurites of abdominal segments greatly expanded; first covering all posterior half of carapace; second covering posterior part of first and pleurites of all following segments, latter less expanded. Rostrum small, triangular; orbital teeth lacking; eyes partially visible, their basal and median portions covered by rostrum. Antennular peduncle stout; first article with strong ventral carina; stylocerite well developed; second article shortest; third article bearing two flagella, outer flagellum biramous. Basicerite of antenna with large, blunt ventro-lateral tooth; carpocerite short, not exceeding scaphocerite; flagellum thick; scaphocerite soft and without distinct lateral spine. Mouthparts and third maxilliped not especially modified, except maxilla bearing broadened

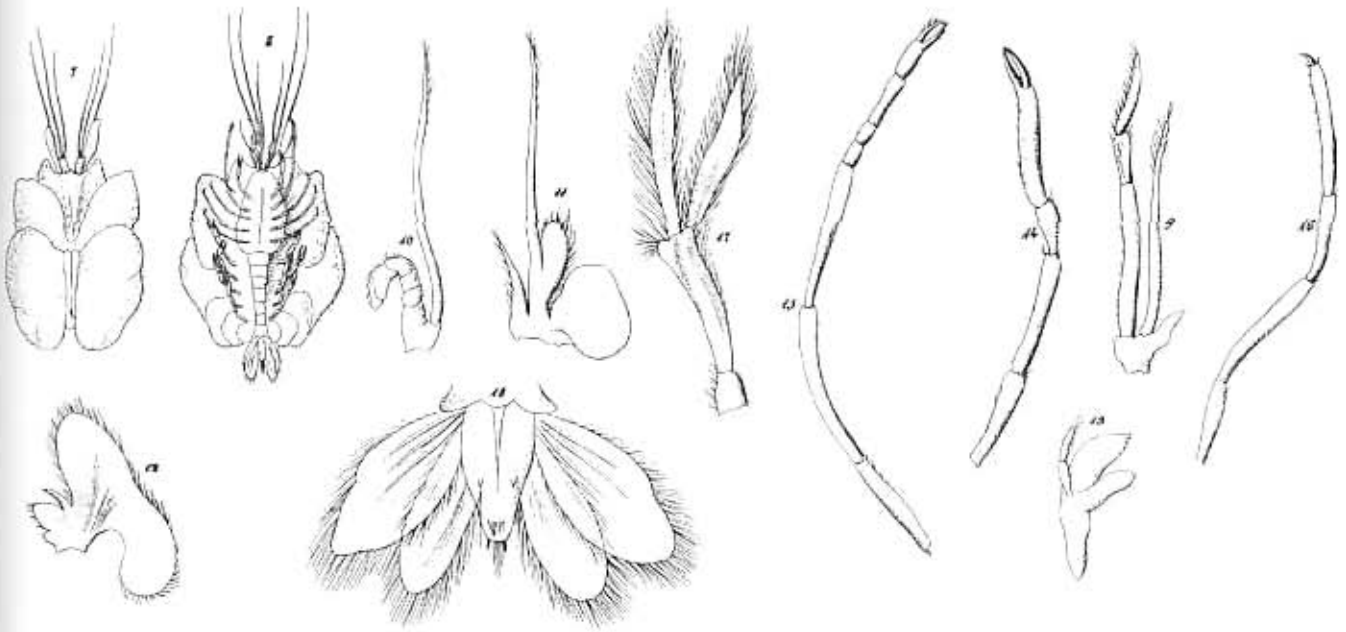


Fig. 1. *Pterocaris typica* Heller, 1862 (NHMW 7982) as illustrated by Heller (1862: Pl. 1 figs. 7-18); original size of figure - no scale was given - rearranged.

scaphognathite. Third maxilliped pediform, not expanded; lateral plate produced and acute; arthrobranch and epipod lacking; ultimate segment unarmed. First pereopods of female symmetrical, carried extended; merus elongated, unarmed, ventrally flattened; carpus long, cylindrical; chela only slightly enlarged and simple, cutting edges of fixed finger and dactylus unarmed (first pereopods of male unknown, but possibly similar). Second pereopod with carpus four-jointed, first longest; chela small and simple. Third to fifth pereopods robust; ischium, merus and carpus unarmed; propodus weakly armed, fifth pereopod lacking grooming brush; dactylus robust and simple. First four abdominal segments visible in dorsal view; sixth abdominal segment without articulated flap, with latero-posterior angles produced. Pleopods situated proximally to abdominal sternites; first pleopod with endopod only slightly smaller than exopod; second to fifth female pleopod with endopod bearing slender appendix interna; male pleopods unknown. Uropods largely exceeding telson; exopod with small lateral spine and straight diaeresis; endopod without special features. Telson with two pairs of dorsal spines; posterior margin slightly rounded, with two pairs of lateral spines; anal tubercles absent. Branchial formula; five pleurobranchs (P1-P5); no arthrobranchs; no podobranchs; two epipods (Mxp1 and Mxp2); three exopods (Mxp1-3).

REDESCRIPTION OF *PTEROCARIS TYPICA* HELLER, 1862

Body strongly compressed dorso-ventrally. Dorsal integuments, especially anterior portion of carapace, abdominal pleurites, telson, and uropods, covered by long (500 - 1500 μm , 15-20 μm diameter at their base) simple setae (Fig. 2D). Carapace appearing soft, flattened, with latero-anterior projections covering dorsally basal articles of antennae. Pleurites of first abdominal segment soft,

somewhat rugose, laterally and anteriorly expanded, covering almost entire carapace (Figs 2A, 3A); pleurites of second abdominal segment also expanded, covering posterior portion of first abdominal pleurites and all following pleurites; third, fourth and especially fifth pleurites much less expanded, dorsally completely covered by second pleurites and visible only in ventral view.

Rostral process (Figs 3B, 8A) small, dorsally flattened, acute and almost triangular in shape, reaching to about middle of first antennular article, scarcely covered by hair-like setae and somewhat delimited from the rest of carapace. Orbital teeth lacking. Eyes partially visible in dorsal view (their basal and median part covered by rostrum); with weak antero-medial processes; corneas not distinct (Fig. 9A). Pterygostomial angles (as represented by above mentioned anterior projections of carapace) produced and rounded; cardiac notch absent (Fig. 10A).

Antennules short; antennular peduncles stout; first article with strong ventral carina (Fig. 9B); stylocerite well developed, reaching third article, its apex rather blunt (Fig. 9A); second article very short, about half of first and also shorter than following article; third article robust, bearing two multiarticulated flagella, inner flagellum being somewhat thicker than outer flagellum; each article of these flagella bearing a row of setae (these rows of setae are better developed on inner flagellum); outer flagellum bifurcating at third-fourth article (Fig. 9C), secondary flagellum weak and with few aesthetascs.

Antennal peduncles exceeding antennular peduncles; small external process present near insertion of antenna (Fig. 9B); basicerite robust, with large, blunt ventro-lateral tooth; carpocerite short, not exceeding scaphocerite; flagellum thick; scaphocerite fringed with small setae on outer and inner margins, without distinct lateral spine, unusually

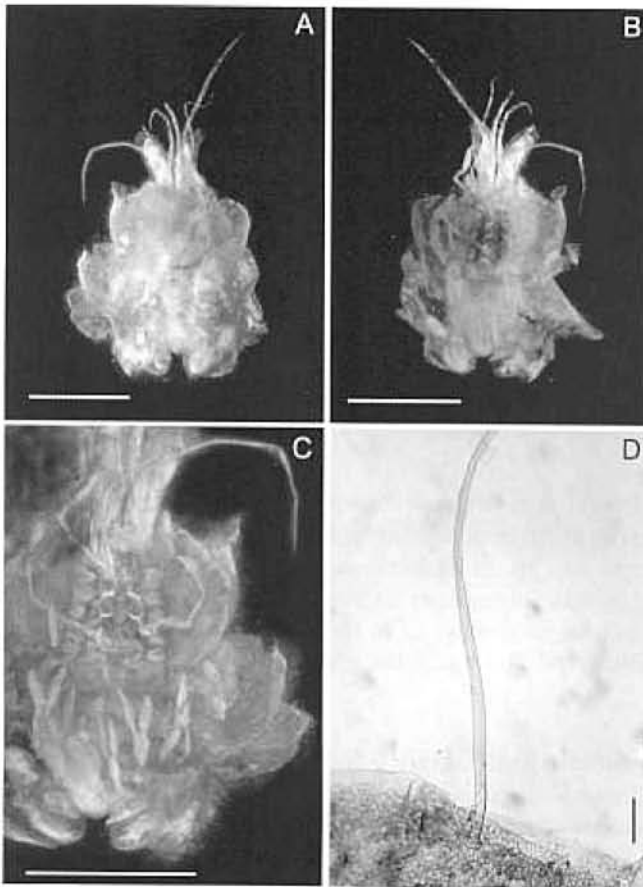


Fig. 2. *Pterocaris typica* Heller, 1862 (NHMW 7982). A, habitus, dorsal view; B, same, ventral view; C, detail of B; D, seta under microscope. Scale = 1 cm (A-C); = 100 μ m (D).

inflated and soft (feature certainly not due to long conservation in alcohol).

Mouthparts (Figs 5A-H) not especially modified: mandible with incisor process bearing five teeth, molar process and two-jointed palp; maxillula with endopodite bilobed and setose; maxilla with scaphognathite expanded and with inferior lacinia (lower endite) reduced, lacking setae; all maxillipeds with long exopods; first maxilliped with well developed caridean lobe and epipod, palp slender; second maxilliped with well developed epipod, without podobranch. Third maxilliped (Fig. 5G) pediform, not expanded, reaching to distal margin of carpocerite; coxa with lateral plate produced and acute; antepenultimate segment as long as penultimate and ultimate segments together, bearing numerous setae on inner margin; penultimate segment only 0.35 of length of antepenultimate segment; ultimate segment slightly less than twice as long as penultimate segment, with numerous rows of thick setae on mesio-inferior margin, superior margin and tip without distinct spines, but with long setae on distal portion; arthrobranch and epipod lacking.

First pereiopods (Figs 6A-E) symmetrical and carried extended, at least in preserved specimen (see remark below), with dactylus in ventral, slightly lateral position (Figs 9B-C); when fully extended tips of chela reaching beyond carpocerite of antenna, but not exceeding scaphocerite; coxa with tubercle on outer superior margin, without epipod;

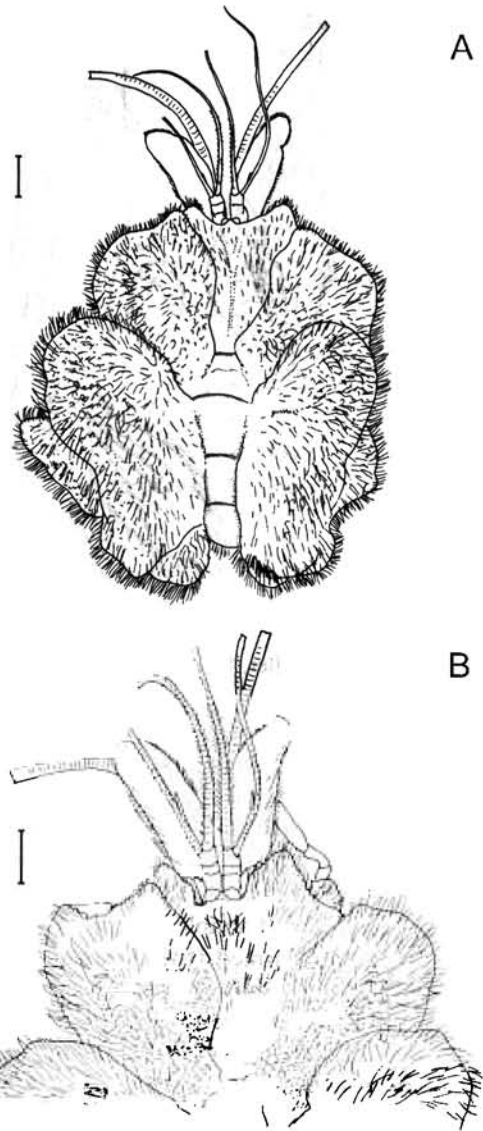


Fig. 3. *Pterocaris typica* Heller, 1862, female (NHMW 7982). A, habitus; B, anterior part, in dorsal view. Scale = 2 mm.

ischium elongated, unarmed; merus elongated, unarmed, ventrally strongly flattened, but not excavated; carpus long, cylindrical; chela (Fig. 6C) simple, not especially enlarged; palm twice as long as dactylus, with weak crest proximal to dactylar articulation, without notable sculpture (except some projections obviously due to damaged cuticula); dactylus of left chela bearing weak crest on outer proximal margin (Fig. 6C), not visible on right chela (possibly artefact); fixed finger and dactylus slightly gaping, tips with few setae, incompletely crossing; cutting edges of fixed finger and dactylus without teeth or other type of armature.

Second pereiopods (Fig. 6F) longer than first pereiopods, almost reaching anterior margin of scaphocerite; carpus 4-segmented, first segment much longer than sum of following three, proportions of carpal segments approximately equal to 7 : 1.25 : 1 : 2.5; chela small and simple, bearing numerous setae on dactylus and fixed finger. Third to fifth pereiopods (description based on appendages P3/4 and P5) robust; coxa without epipods; ischium relatively long, unarmed; merus and carpus unarmed, with exception of minute disto-inferior spinules of carpus; propodus of P3 and P4 weakly armed: 3

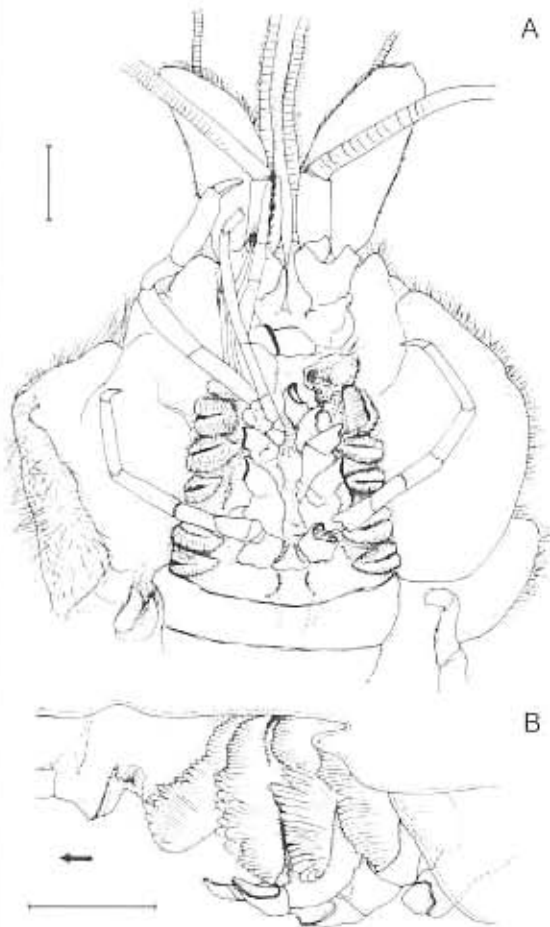


Fig. 4. *Pterocaris typica* Heller, 1862 (NHMW 7982). A: anterior part in ventral view; B: lateral view of pleurobranchs, left side (arrow indicating position of head). Scale = 1 mm.

spinules along inferior margin and a distal pair of short spinules proximal to dactylus, propodus of P5 without grooming brush; dactylus robust, simple, curved (Fig. 7).

Abdomen and telson flexed ventrally (in preserved specimen); median portion of first four abdominal segments visible in dorsal view (Fig. 2A, 3A); sixth abdominal segment without articulated flap, but with latero-posterior angles and preanal plate somewhat produced towards telson (Fig. 9D). Pleopods situated more (fifth, fourth) or less (first, second) close to abdominal sternites; first pleopod with endopod only slightly smaller than exopod; second to fifth pleopod with endopod bearing slender appendix interna. Uropods largely exceeding telson; exopod and endopod equal in length; exopod with small lateral spine and straight diaeresis (Fig. 8D); endopod without special features. Telson broad, tapering distally, with two pairs of dorsal spines situated in relatively deep depressions (Fig. 8E); posterior margin slightly rounded, with two pairs of lateral spines, inner spines distinctly curved and about twice longer than outer spines; between these spines at least seven long and thick plumose setae; anal tubercles absent. Branchial formula as given for the genus. Size: carapace length: ca. 8 mm; total length: ca. 23 mm (10 Linien); total width: ca. 20 mm (9 Linien), telson length: 2.2 mm.

Distribution. – Collected in Ambon, Moluccan Islands,

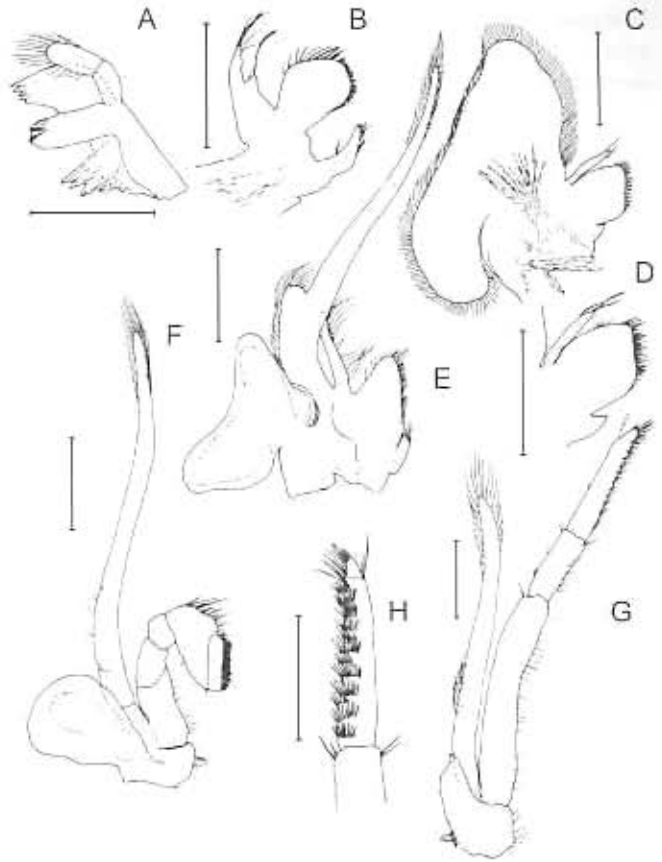


Fig. 5. *Pterocaris typica* Heller, 1862 (NHMW 7982), right mouthparts. A, mandible, inner view; B, maxillula; C, maxilla; D, same, endites; E, first maxilliped; F, second maxilliped; G, third maxilliped; H, same, mesial view of ultimate segment. Scale = 1 mm.

Indonesia. Known only from type locality.

Remark: The specimen has the attached first cheliped clearly in extended position; however, it is important to note that the merus of the first cheliped is flattened on its ventral side - possibly to accommodate the chela in flexed position.

DISCUSSION

Comparison with Heller's description. – For the mid-19th century Heller's description can be considered as very long and detailed (almost four full-text pages), and his illustrations are rather numerous (altogether 12 figures - reproduced here in Fig. 1), although not always accurate. The main insufficiencies of the original description were the absence of detailed information on the branchial formula (although pleurobranchs are clearly visible in ventral aspect and were noted as "blättrigen Kiemen" in the text, they were not illustrated on Pl. 1 fig. 8), and the absence of the detailed drawings of several important regions, e.g. the frontal region and the caudal fan. Moreover, Heller's description and illustrations apparently contain several important errors. During the re-examination of the type we observed that the outer flagellum clearly bifurcates in two flagella, one very short, while Heller illustrated the outer flagellum as entire (cf. Pl. 1 figs. 7 and 8). The first maxilliped was obviously

badly dissected since the endites and the lower part of the epipod are absent (Pl. I fig. 11). The same holds true for the second maxilliped, illustrated without epipod by Heller (Pl. I fig. 10), while we found a well developed and elongated epipod on this appendage. Also, the articulation between the two distal articles of the endopod of the second maxilliped is not as illustrated in Heller's Pl. I fig. 10. The abdominal appendages and the telson were very briefly described and the illustrations contain numerous errors. The second pleopod and all the following pleopods have a well developed, slender appendix interna; however, there is no appendix interna on Heller's figure of the second pleopod (Pl. I fig. 17). The uropods were illustrated inexactly, without lateral spine and without transverse suture (Pl. I fig. 18), while both structures (lateral spine small but distinct) are clearly present. Finally, the telson has four dorsal spines instead of two originally illustrated (Pl. I fig. 18), and there are also two pairs of posterior spines, and not one, as shown by Heller in the same figure. It should be noted, however, that the dorsal spines of the telson are difficult to see, being partially hidden by long, hair-like setae, and also because they are appressed and

situated in rather deep depressions.

Systematic position. – The discussion of the phylogenetic position of *Pterocaris* is very difficult, mainly because of the profound modification of its morphology. Heller (1862) did not place his genus in any particular family, mentioning only that it belongs to the Caridea.

Comparatively few publications mention *Pterocaris*, despite its uniqueness and interest for the taxonomy of the Caridea. To our knowledge the first to mention this genus in a revision of caridean families was Kingsley (1880: 421), who placed it in the subfamily Alpheinae Dana, 1852. Coutière (1899: 331-332) discussed this genus in detail in his famous and important monograph of the family Alpheidae. As for some reason it was impossible for him to study the type specimen, he reproduced and discussed the figures published by Heller, and gave the generic diagnosis based mainly on Heller's description and illustrations. He preferred to keep *Pterocaris* in the Alpheidae, but made several remarks on the singular position of this genus within the family. In his evolutionary

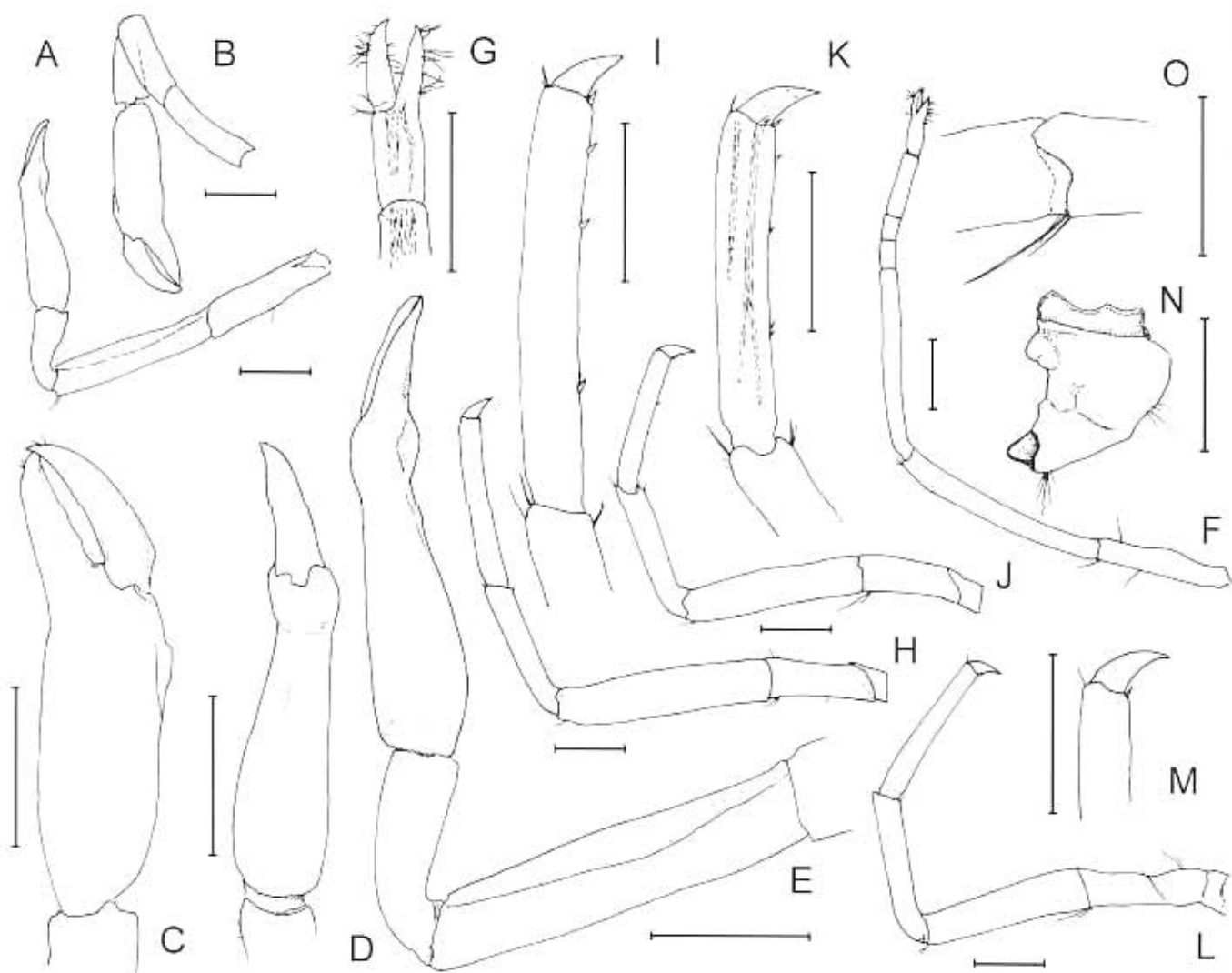


Fig. 6. *Pterocaris typica* Heller, 1862 (NHMW 7982). A, left first pereiopod, dorsal view; B, same, mesial view; C, same, chela enlarged; D, same, ventral view of chela; E, same as in A, enlarged; F, left second pereiopod; G, same, chela; H, pereiopod 3/4; I, same, propodus + dactylus; J, another pereiopod 3/4; K, same, propodus + dactylus; L, left fifth pereiopod, M, same, distal part of propodus + dactylus; N, same as in A, outer view of coxa; O, same as in J, ischial setae. Scale = 1 mm.

tree (Coutière, 1899: 353), *Pterocaris* is placed close to *Automate* de Man, 1888. Borradaile (1921), however, addressed *Pterocaris* briefly as a hippolytid shrimp. The position within the Alpheidae was accepted by Holthuis (1955), Balss (1957) and apparently also by Chace (1992), as he did not mention *Pterocaris* at all, obviously considering it as a member of Alpheidae. When *Pterocaris* was taken into cladistic analysis of the superfamily Alpheoidea it came out as the sister group to the clade Ogyrides + Alpheidae (Christoffersen, 1987: 354, Fig. 5). Three years later the same author proposed a new family Pterocarididae to accommodate the genus *Pterocaris* (Christoffersen, 1990: 97). The diagnosis of the family was as follows: "Body strongly compressed dorsolaterally [sic!] in adult; pleura of first and second abdominal somite strongly produced anteriorly and posteriorly, respectively, covering most of carapace and remaining abdomen in adult." In his updated survey of the caridean genera, Holthuis (1993) lists the family Pterocarididae among the synonyms of the Alpheidae, thus placing the genus again into the latter family. To our

knowledge the only other recent papers partly dealing with *Pterocaris* were D.M. & A.H. Banner (1985), who gave a brief diagnosis based on Heller's description, and Bruce (1987), who mentioned its unusual habitus and rarity.

The pleurites of the second abdominal segment cover dorsally the posterior part of the pleurites of the first and also the pleurites of the following, third abdominal segment. This is an important autapomorphy of all Caridea. Therefore, *Pterocaris* is clearly a caridean shrimp. The unique specimen is clearly an adult and not a larval stage: all the mouthparts and other morphological structures appear completely developed; the protopods of pleopods bear elongated setae, as found in ovigerous females, and damaged remnants, possibly of eggs, may still be found on the ventral surface of the abdomen.

The present study shows that despite its numerous autapomorphic characters, there are no convincing arguments to take *Pterocaris* out of the family Alpheidae, although it is clear that the genus occupies a very singular position within this family. The four features that are unusual for Alpheidae, and therefore would possibly exclude *Pterocaris* from this family, are: (1) unusually long simple setae covering almost all of the dorsal surface; (2) dorso-ventrally flattened body with greatly expanded abdominal pleurites; (3) scaphocerite lacking lateral spine, being unusually soft and fringed on both margins with small setae; (4) absence of a cardiac notch. Features (1) and (2) are clearly of adaptive nature and can be compared with expected reservation to the extreme lateral compression in the alpeid genus *Racilius* Paulson, 1875, or to the setose dorsal surface in other alpheids, e.g.

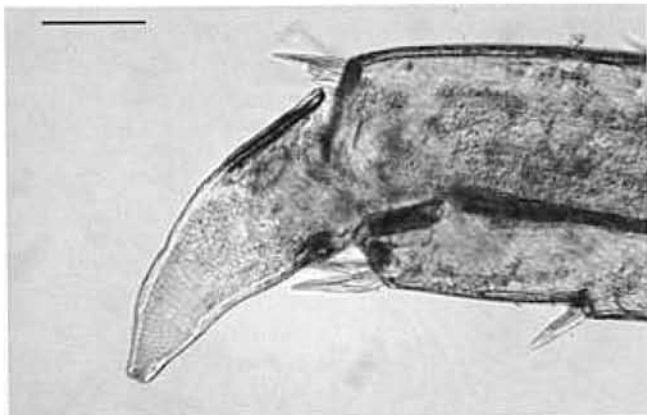


Fig. 7. *Pterocaris typica* Heller, 1862 (NHMW 7982). left pereopod 3/3. Scale = 100 μ m.

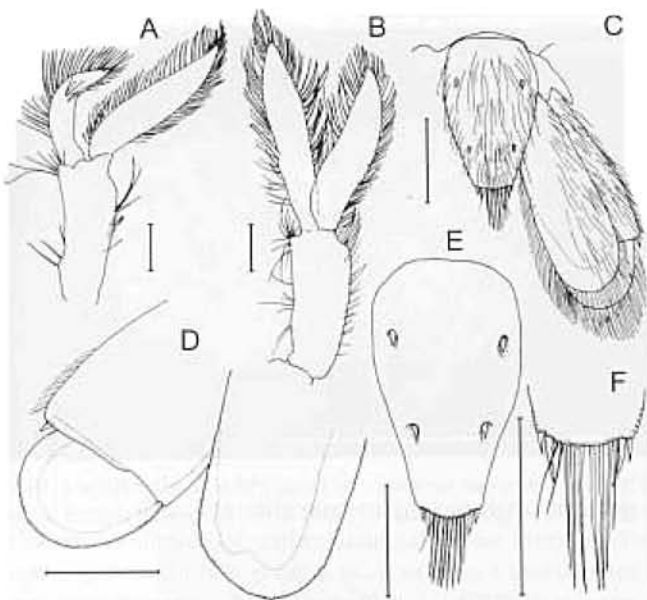


Fig. 8. *Pterocaris typica* Heller, 1862 (NHMW 7982). A, left first pleopod; B, right second pleopod; C, caudal fin; D, distal part of left uropod; E, telson; F, same, posterior margin (drawn without camera lucida). Scale = 1 mm.

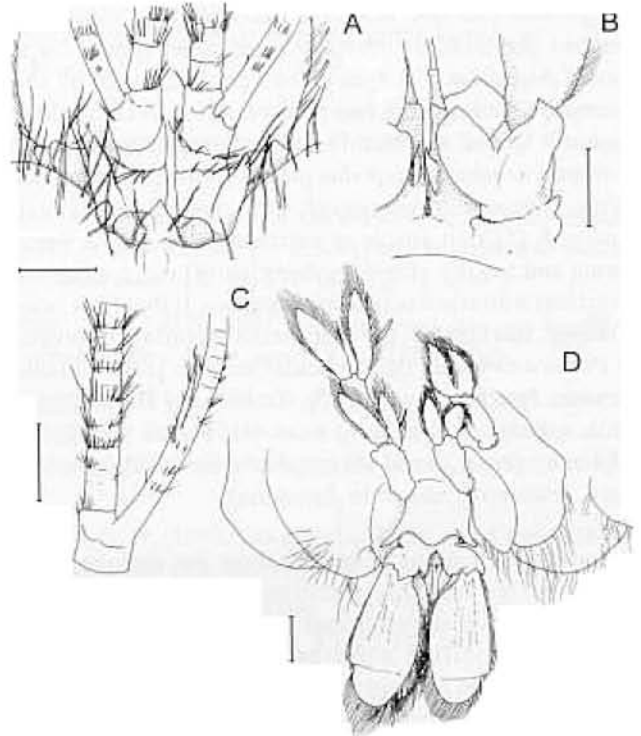


Fig. 9. *Pterocaris typica* Heller, 1862 (NHMW 7982). A, frontal region enlarged, dorsal view; B, antennules and antennae, ventral view; C, inner and outer flagella of right antennule, dorsal view; D, posterior abdomen and caudal fin, ventral view. Scale = 1 mm.

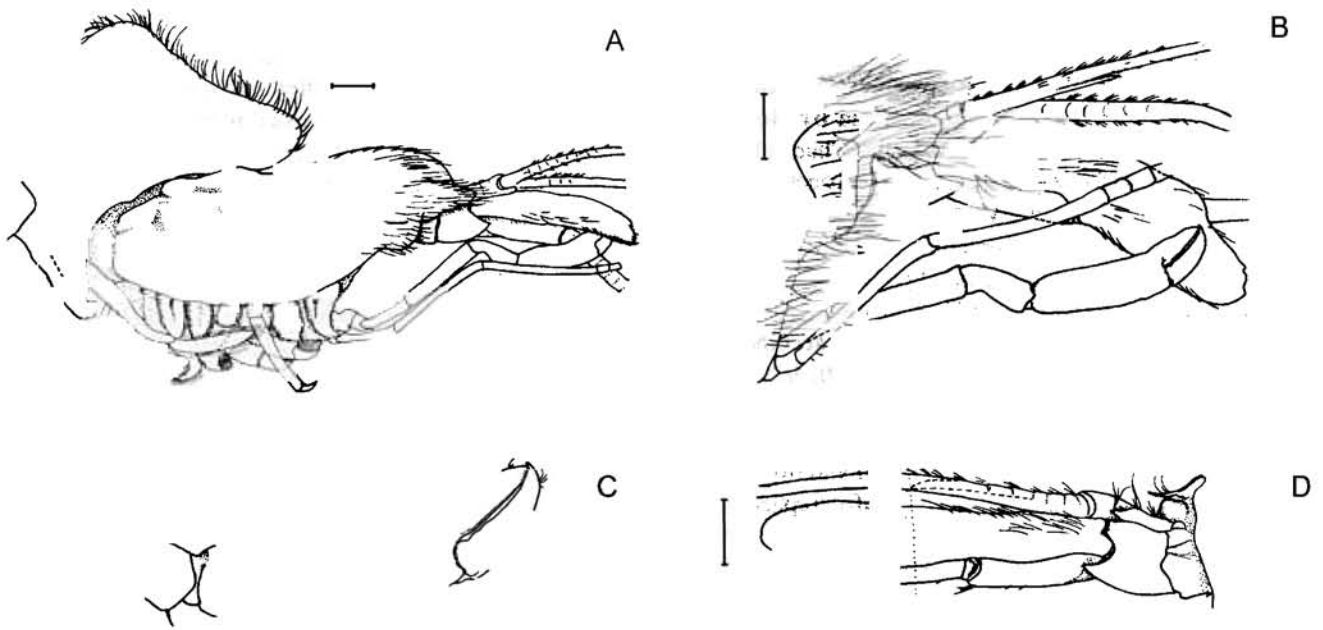


Fig. 10. *Pterocaris typica* Heller, 1862 (NHMW 7982). A, cephalothorax in right lateral aspect, abdominal segments lifted to show carapace; B, frontal region and chelipeds, seen in right lateral view (carapace in natural position); C, right chela enlarged; D, frontal region, seen in left lateral view (lateral lobes of carapace lifted to show antennules and eyes). Scale = 1 mm.

Salmoneus setosus Manning & Chace, 1990. The regression of the cardiac notch, considered to be an important diagnostic feature of the Alpheidae (Coutière, 1899, Chace & Kensley, 1992), is probably directly related to the dorso-ventral compression of the whole body (the posterior region of the carapace is completely covered by first abdominal pleurites). Moreover, the cardiac notch is reduced in some incontestably alpheid species, e.g. in *Alpheus (Thunor) saxidomus* Holthuis, 1980, or again, in most specimens of *Racilius compressus* Paulson, 1875. On the other side, some of the features displayed by *Pterocaris* are rather typical for the family Alpheidae: (1) eyes at least partly covered by short rostrum; (2) telson with two pairs of dorsal and two pairs of posterior spines; (3) third maxilliped distally unarmed and with well developed epipodial plate; (4) first pereiopod more robust than second pereiopod, with chela at least slightly enlarged; (5) first article of antennule with strong ventral carina and usually shaped stylocerite; (6) outer antennular flagellum with small accessory flagellum. It should be noted, however, that some of the characters supporting the position of *Pterocaris* within the Alpheidae are also present in other caridean families (e.g. (4), (5), (6) in many Hippolytidae), while others are shared by most, but not all members of Alpheidae (e.g. (3), and (5) not shared by *Synalpheus* Bate, 1888, feature (6) absent in *Automate*).

Unfortunately nothing is known about the ecology of this shrimp, so we can only speculate about the ancestors of *Pterocaris*. We suppose that these ancestors were not especially modified alpheids, possibly close to some primitive recent alpheid genera such as *Potamalpheops* Powell, 1979.

Habitat. – As mentioned above, we have no information on the habitat of *Pterocaris*. The specimen certainly came from Ambon as most crustaceans received from Doleschall were

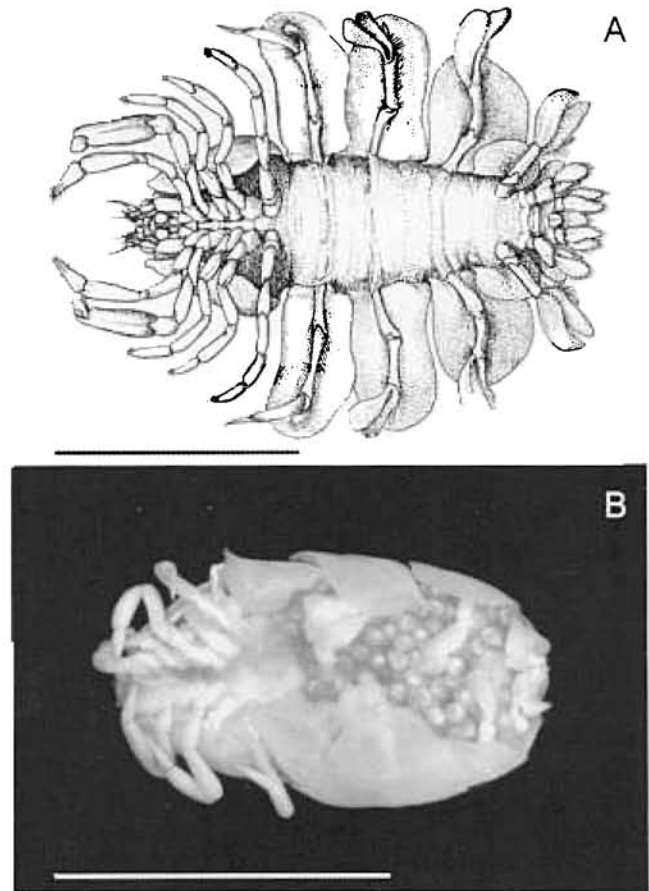


Fig. 11. *Paratypton siebenrocki* Balss, 1914. A, after Balss (1915: Fig. 19); B, ovigerous female (NHMW 6714), ventral aspect. Scale = 1 cm.

collected during his stay there (Stagl, 1999). Only a few originated from his journey from Batavia (via Java, Celebes and Ternate) to Ambon and those are clearly labelled with "Ternate".

Most crustacean species listed in the book of acquisitions are marine: many live among corals (e.g. the alpheids *Alpheus lottini* Guérin, 1829 and *Synalpheus coutieri* Banner, 1953; the brachyurans *Trapezia*, *Chlorodiella*, *Chlorodius*, *Atergatis*, *Eriphia*, the stomatopod *Gonodactylus*, stenopodids and palinurids), others are found on shallow back-reef sands (like *Portunus*, *Calappa* and *Thalamita*), sandy beaches (like *Ocypode*) or mangroves (like *Macrophthalmus*, *Uca* and *Thalassinia*). The presence of a few specimens of *Macrobrachium* indicates that freshwater habitats were also sampled. Nonetheless, crustaceans constitute - among all the insects, spiders and fishes - only a very small part of all the animals sent by Doleschall to Vienna (see Stagl, 1999). During his last years, Doleschall could not collect himself and trained native people who brought him the specimens. Therefore, *Pterocaris* could originate virtually from every habitat available on the island of Ambon.

One explanation for its rarity could be its possible association with another marine organism, combined with a highly cryptic life style. For some unknown reason, Coulière (1899: 20) speculated that this species is associated with echinoderms. D.M. Banner & A.H. Banner (1985) suspected that it lives as a symbiont where the flattened shape would be an advantage as within the mantle cavity of bivalves.

An association with another organism would also explain the profound modification of its morphology. To our knowledge there are no other examples of such an extreme development of abdominal segments within the Caridea. Several pontonine shrimps, for instance *Ctenopontonia* Bruce, 1979, and *Paratypton* Balss, 1914, have expanded abdominal pleurites, especially in females. The unique species of *Paratypton*, which appears similar to *Pterocaris* in some aspects, is known to live in gall-like chambers or cysts made in living corals (Borradaile, 1921, Bruce, 1969), whereas *Ctenopontonia cyphastreophila* Bruce, 1979, is known to live in the grooves of a coral (Bruce, 1994). We examined the ovigerous female from the type series of *Paratypton siebenrocki* Balss, 1914, deposited in the NHMW. This female shows some similarities to *Pterocaris* in having similar antero-lateral projections of the carapace, and the extremely developed first and second abdominal segments (Fig. 11A). Also, the frontal region with the short, triangular rostrum is very similar. The abdominal pleura of the female *Paratypton* are not really flattened, but rather cover laterally the pleopods with attached eggs (Fig. 11B), and this might also be the case in living *Pterocaris*. In contrast to *Pterocaris*, however, *Paratypton* has no trace of long setae, the scaphocerite is rather normally developed, the third maxilliped is short and stout, not pediform.

Also, being dorsoventrally flattened, *Pterocaris* probably lives on the surface of - rather than inside - an invertebrate host, which could be a coral, a gorgonian or a short-spined irregular sea-urchin. The simple dactyls of P3/4, however, suggest a free-living lifestyle. Another possible habitat could be a sedimentary environment, either marine, brackish or freshwater.

Many workers (e.g. A.H. and D.M. Banner, A.J. Bruce, C.H.J.M. Fransen and probably others) searched for this unique shrimp in the field, but were unsuccessful. We can only hope that the present contribution will attract more attention to this mysterious and extraordinary shrimp, especially of people working with other marine invertebrates in Indonesia, and that it will soon be rediscovered and studied in the field.

ACKNOWLEDGEMENTS

Our thanks are due to D. Doumenc (BIMM-MNHN, Paris) for the financial support which enabled AA the travel to Vienna, to V. Stagl for important historical background information and to P. Noël for helpful suggestions. We also thank A.J. Bruce and an anonymous reviewer for constructive comments.

LITERATURE CITED

- Balss, H., 1915. Expeditionen S.M. Schiff "Pola" in das Rote Meer. Nördliche und südliche Hälfte. 1895/96-1897/98. Zoologische Ergebnisse. XXX. Die Decapoden des Roten Meeres. I. Macruren. *Denkschr. Kais. Akad. Wiss. Wien, math.-naturwiss. Kl.*, **91**: 1-38.
- Balss, H., 1957. Decapoda. VIII. Systematik. In: H.G. Bronn's *Klassen und Ordnungen des Tierreichs*. Akademische Verlagsgesellschaft, Leipzig, Band 5, Abteilung 1, Buch 7, Lieferung **12**: 1505-1672.
- Banner, D.M. & A.H., 1985. The alpheid shrimp of Indonesia, based upon J.G. de Man's "The Decapoda of the Siboga Expedition, Part II: Family Alpheidae" (1911). *Mar. Res. Indones.*, **25**: 1-79.
- Borradaile, L.A., 1921. On the coral-gall prawn *Paratypton*. *Mem. Proc. Manchester Lit. Phil. Soc.*, **65**(11): 1-10, figs. 1-11a.
- Bruce, A.J., 1969. Notes on some Indo-Pacific Pontoniidae XIV. Observations on *Paratypton siebenrocki* Balss. *Crustaceana*, **17** (2): 171-186, figs 1-5, pl 1
- Bruce, A.J., 1987(1988). Shrimps that live on tropical echinoderms. *Underwater*, **17**: 92-94, 9 figs.
- Bruce, A.J., 1994. *A synopsis of the Indo-West Pacific genera of the Pontoniinae (Crustacea: Decapoda: Palaemonidae)*. Koeltz Scientific Books, Königstein, 172 pp., 70 figs.
- Chace, F.A. Jr., 1992. On the classification of the Caridea (Decapoda). *Crustaceana*, **63**(1): 70-80.
- Chace, F.A. Jr. & B. Kensley, 1992. The cardiac notch in decapods. *J. Crust. Biol.*, **12**(3): 442-447.
- Christoffersen, M.L., 1987. Phylogenetic relationships of hippolytid genera, with an assignment of new families for the Crangonoidea and Alpheoidea (Crustacea, Decapoda, Caridea). *Cladistics*, **3**(4): 348-362.
- Christoffersen, M.L., 1990. A new superfamily classification of the Caridea (Crustacea: Pleocyemata) based on

- phylogenetic pattern. *Z. Zool. Syst. Evolutionsforsch.*, **28**: 94-106, 8 figs.
- Coutière, H., 1899. Les "Alpheidae", morphologie externe et interne, formes larvaires, bionomie. *Ann. Sci. Nat., Zool., sér.*, **8**, **9**: 1-560, fig. 1-409, pls. 1-6 (or Masson et Cie Ed., Paris).
- Heller, C., 1862. Beiträge zur näheren Kenntnis der Macrouren. *Sb. math.-naturwiss. Cl. kais. Akad. Wiss.*, **45**(1): 389-426, pls. 1-2.
- Holthuis, L.B., 1955. The recent genera of the Caridean and Stenopodidean shrimps (Class Crustacea: Order Decapoda: Supersection Natantia) with keys to their determination. *Zool. Verh., Leiden*, **26**: 1-157.
- Holthuis, L.B., 1993. *The recent genera of the Caridean and Stenopodidean Shrimps (Crustacea Decapoda): with an appendix on the order Amphionidacea*. Nationaal Natuurhistorisch Museum, Leiden, 328 pp., 312 figs.
- Kingsley, J.S., 1880. On a collection of Crustacea from Virginia, North Carolina, and Florida, with a revision of the genera of Crangonidae and Palaemonidae. *Proc. Acad. Nat. Sci. Phila.*, **1879**: 383-427.
- Stagl, V., 1999. Carl Ludwig Doleschall - Arzt, Forscher und Sammler. *Quadrifina*, **2**: 195-203.