Larvae of two species of *Trizocheles* (Decapoda: Anomura: Paguroidea: Pylochelidae: Trizochelinae), description of the adult of one, and preliminary implications of development on pylochelid phylogeny

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Abstract

The larvae of two species of the pylochelid genus *Trizocheles* are described from prematurely hatched specimens and compared with earlier described larvae of *Pylocheles* (*Pylocheles*) and *Pomatocheles*. Although all are lecithotrophic and exhibit marked advanced development, differences in the larval morphology among the three genera are profound. Consideration is given to these differences as they relate to development in the entire Paguroidea, and the possible impact they may have on pylochelid phylogeny. As one of the *Trizocheles* species is undescribed, adults as well as larvae are described and illustrated.

Key words: Decapoda, Anomura, Paguroidea, Pylochelidae, Trizochelinae, *Trizocheles*, *Pylocheles*, *Pomatocheles*, new species, advanced and lecithotrophic development, phylogeny

Introduction

As noted by McLaughlin *et al.* (2007), the Paguroidea provide a wide range of evolutionary enigmas. This is especially true for the Pylochelidae. Forest (1987) considered these "symmetrical" hermit crabs a heterogeneous assemblage whose phylogenetically significant characters were difficult to identify. So distinctive were the majority of genera, that only *Pylocheles* A. Milne-Edwards, 1880 and *Cheiroplatea* Miers, 1876 appeared sufficiently closely related to be grouped together in a single subfamily. The other five subfamilies, three monotypic, exhibited a vast array of distinct morphological attributes that Forest (1987) disclosed in his very detailed and thorough study.

Only two reports have been published regarding development in pylochelids: Konishi & Imafuku (2000) for *Pomatocheles jeffreysii* Miers, 1879, and Saito & Konishi (2002) for *Pylocheles* (*Pylocheles*) *mortensenii* (Boas, 1926). The former account was based on a single specimen hatched from an ovigerous female held in an aquarium. Konishi & Imafuku (2000) referred to this larva as a hatchling because although enclosed in the embryonic cuticle of a decapod prezoea, its appendages were indicative of abbreviated development. Saito & Konishi (2002) reported on ten larvae that hatched in the laboratory and were preserved promptly. These larvae were referred to as first stage zoeae, although their development also was described as advanced. The larvae of these two species demonstrated morphological diversity similar to that seen in their respective adults.

Recently, an ovigerous female of *Trizocheles spinosus spinosus* (Henderson, 1888), preserved upon collection, was made available to us, together with two dozen or so of her eggs that hatched at the time of preservation. From these we observed heterochronic development in a series of simultaneously and prematurely

hatched larvae, and found their zoeal morphology markedly different from both *Pomatocheles* and *Pyloche-les*.

Gore (1985) and others, following Williamson (1982), have identified, with Roman numerals, the series of stages (instars of Anger 2001) in the zoeal phase of development and specified the developmental levels of specific larval characters that define these stages. However, in his classic review of larvae of decapod Crustacea, Gurney (1942) used names for the stages that various decapods went through as had been proposed by earlier carcinologists. The term metazoea was used by some authors for brachyuran larvae to identify zoeae that had rudimentary appendages behind the maxillipeds and non-brachyuran larvae with more than two pairs of thoracic exopods in the first stage after hatching (Gurney 1942; Anger 2001), but Williamson (1982) considered it and other similar prefixes of little practical use. Generally speaking, Williamson's terminology can readily be applied to most paguroid (sensu McLaughlin *et al.* 2007) larvae, but because of the combination of lecithotrophically influenced reduction in feeding appendages and heterochronically advanced development of nearly all other zoeal structures in the pylochelids now known, none of these defined stages of the zoeal phase accurately categorize these specimens. Therefore, we have chosen to substitute the older term metazoea for Konishi & Imafuku's (2000) hatchling, Saito & Konishi's (2002) first stage zoea, and our *T. s. spinosus* "preemies."

Additionally, a second, and undescribed, species of *Trizocheles* was found in the collections of the Muséum national d'Histoire naturelle, Paris, which included an ovigerous female with three larvae, similarly prematurely hatched. Adults of the new species and the metazoeae of both species are described and illustrated herein and these larvae are compared with the larvae of the previously described pylochelid species. The differences among the larvae of these taxa, representing three genera in three subfamilies, are profound.

The ovigerous female and metazoeae of *Trizocheles s. spinosus* were borrowed from the National Institute of Water and Atmospheric Research, Wellington (NIWA), [formerly the New Zealand Oceanographic Institute (NZOI)], and are being returned to that institution. The holotype and most paratypes of *Trizocheles vaubanae* **n. sp.**, including metazoeae, are deposited in the Muséum national d'Histoire naturelle, Paris (MNHN); a pair of paratypes is deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). With the exception of metazoea, terminology for the larval descriptions follows that of McLaughlin & Gore (1988), and for adults that of McLaughlin (2003). EBISCO is the acronym for Exploration de la Biodiversité et ISolement en Mer du COrail; the abbreviations sl and cl are used for shield length of adults and carapace length of metazoeae, which are measured from the tip of the rostrum or midpoint of the rostral lobe to the midpoint of the posterior margin of the shield or carapace, respectively. The abbreviations SMIB, DW, CP, R/V, stn and ovig. are used for Substances Marines d'Intérêt Biologique, Warén dredge, Charcot dredge, research vessel, station, and ovigerous, respectively.

Larval development

Family Pylochelidae Bate, 1888

Subfamily Trizochelinae Forest, 1987

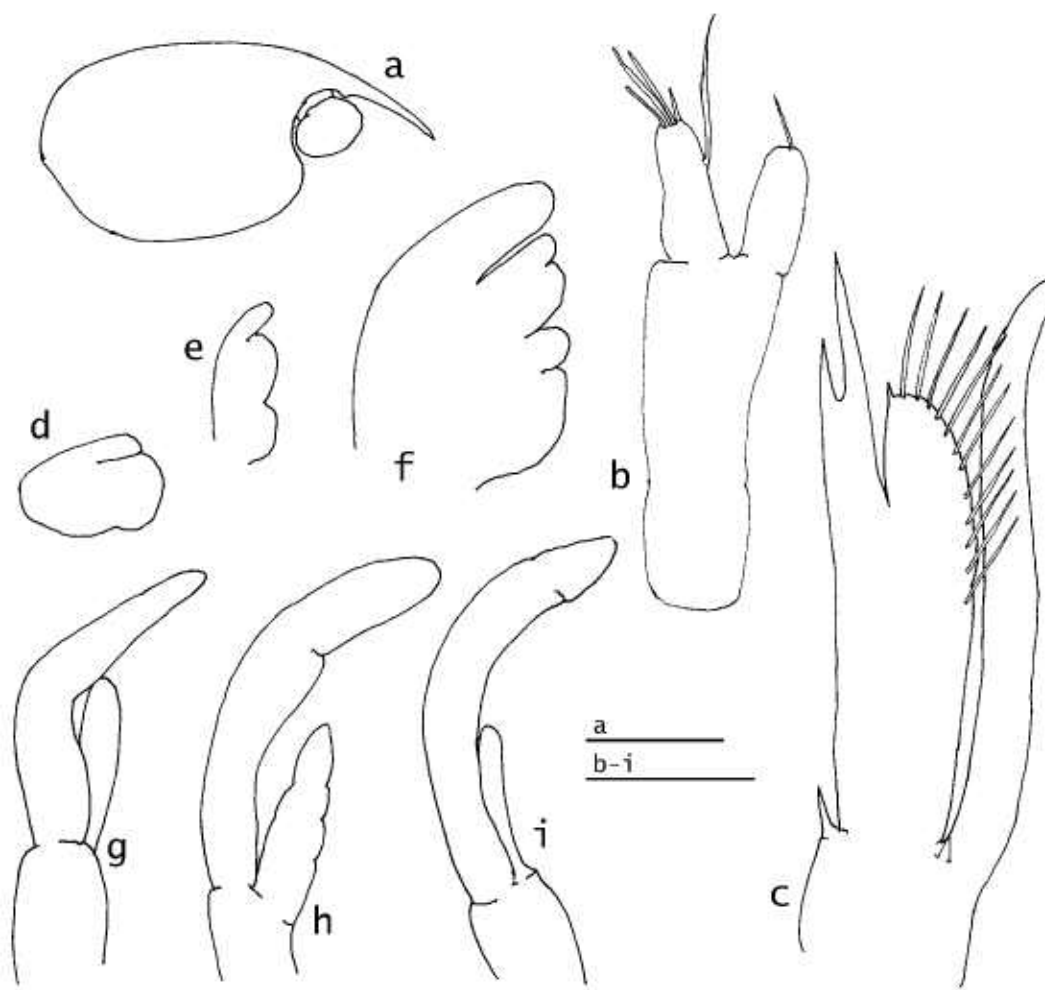**Genus *Trizocheles* Forest, 1987**

Trizocheles spinosus spinosus (Henderson, 1888)
Pylocheles spinosus Henderson, 1888: 101, pl. 11, fig. 1.
Trizocheles spinosus spinosus. — Forest, 1987: 202, figs. 47d, 66g, 69c, 70.

Material examined. Twenty-six specimens, cl (including rostrum) = 1.8–2.1 mm; 10 dissected. All specimens hatched from single ovigerous female at time of preservation; additional eggs less developed. Female (sl = 6.6 mm), R/V *Kaharoa* stn Z9852, 37°28.15'S, 177°06.71'E, 250–310 m, 5 Jun 1999 (NIWA 43797).

Description. Yolk granules usually present.

FIGURE 1. Metazoea of *Trizocheles spinosus spinosus* (Henderson, 1888). a, carapace (lateral view); b, antennule; c, antenna; d, mandible; e, maxillule; f, maxilla; g, first maxilliped; h, second maxilliped; i, third maxilliped. Scales: 1 mm (a), and 0.25 mm (b–i).

Carapace (Fig. 1a). Globoid, lacking spines and setae, posterior margins rounded; rostrum approximately 0.2 of carapace length, moderately slender, frequently directed somewhat downward.

Eyes. Stalked, corneas large.

Antennule (Fig. 1b). Biramous, with protopod elongate, unsegmented; endopod varying from nearly equal in length to approximately twice length of exopod, naked or with 1 terminal seta; exopod varying from naked to bearing 1 short terminal seta and 3 or 4 aesthetascs, 1 aesthetasc on inner margin.

Antenna (Fig. 1c). Biramous; protopod unsegmented, with small spine at endopodal junction and larger spine at scaphocerite junction; base of protopod sometimes enlarged, with internally directed lobe of future antennal gland orifice apparent; endopod varying from approximately half length of scaphocerite to nearly equal to tip of distolateral spine. Scaphocerite with 11 or 12 setae, often only partially evaginated, on inner margin, upper margin with or without small spine; distolateral spine subdistal in origin and very prominently bifid.

Mandible (Fig. 1d). Varying from indistinguishably fused to epistome to subquadrate in structure with unsegmented, naked palp.
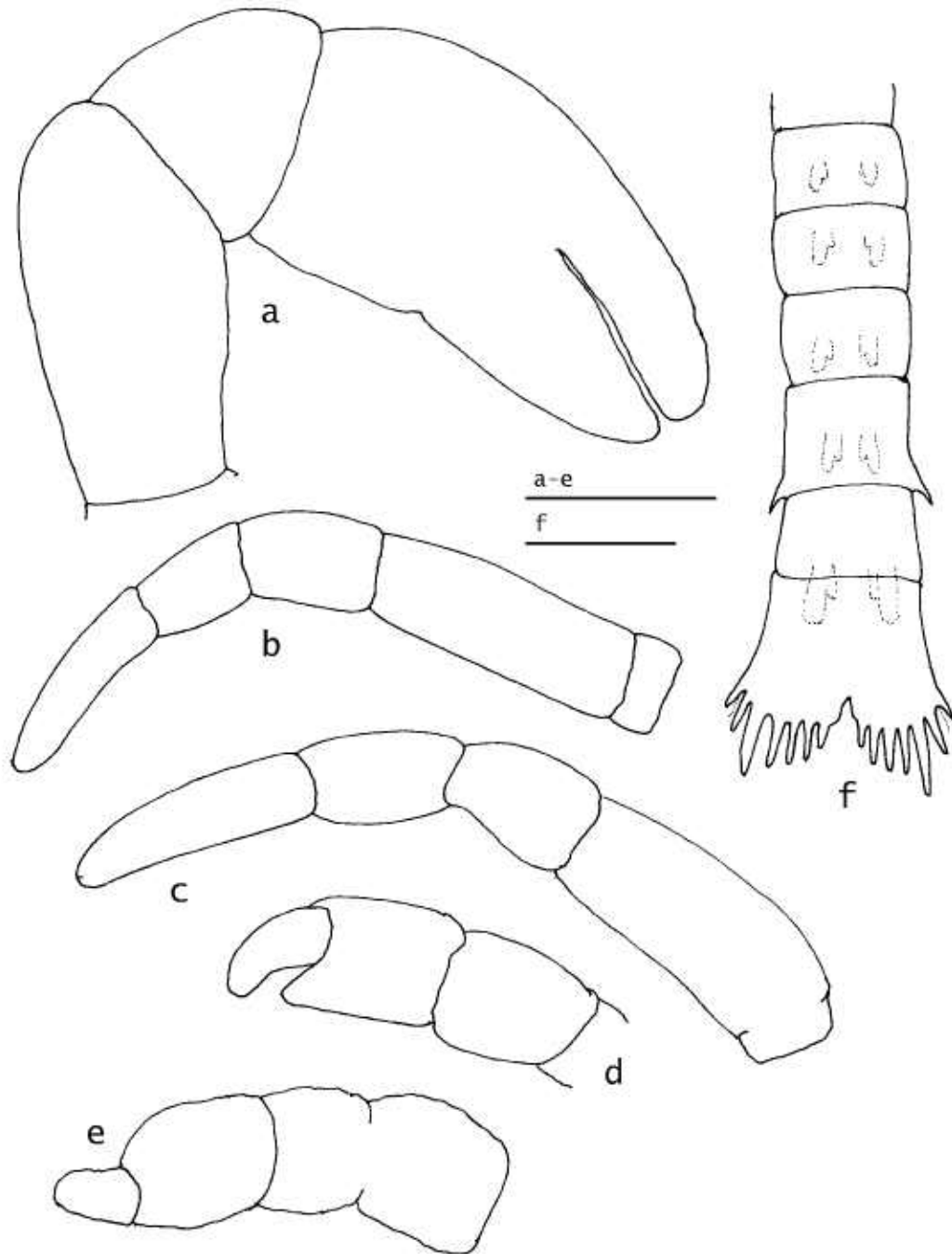
Maxillule (Fig. 1e). Often indiscernible, occasionally with buds of endites and endopod developed, all lacking setae.

Maxilla (Fig. 1f). Varying from bilobed bud to moderately well developed appendage with bilobed coxal and basial endites, and scaphognathite, endopod apparent or not; all lacking setae.

First maxilliped (Fig. 1g). Protopod unsegmented; exopod elongate; endopod varying from rudimentary to subequal in length to exopod, both lacking setae and segmentation.

Second maxilliped (Fig. 1h). Protopod unsegmented; exopod elongate, varying from unsegmented to incompletely 2-segmented; endopod varying from unsegmented and subequal in length to exopod to appreciably shorter than exopod and faintly 4-segmented, setae lacking.

Third maxilliped (Fig. 1i). Protopod unsegmented; exopod elongate, varying from faintly to incompletely 2-segmented; endopod unsegmented, varying from rudimentary to moderately well developed bud.

FIGURE 2. Metazoea of *Trizocheles spinosus spinosus* (Henderson, 1888). a, cheliped; b, second pereopod; c, third pereopod; d, fourth pereopod; e, fifth pereopod; f, pleon and telson. Scales: 0.25 mm (a–e), and 1 mm (f).

Chelipeds (Fig. 2a). Chela with dactyl distinguishable, articulation with palm usually not apparent; carpus and merus delineated, unarmed; setae entirely lacking.

Pereopods 2 and 3 (Fig. 2b, c). Dactyls, propodi, carpi and meri varying from partially to clearly delineated, no terminal claws apparent; setae entirely lacking.

Pereopod 4 (Fig. 2d). Dactyl semichelate; remaining segments partially to clearly delineated; setae entirely lacking.

Pereopod 5 (Fig. 2e). Dactyl partially to clearly delineated, simple, terminal; remaining segments partially to clearly delineated; setae entirely lacking.

Pleon (Fig. 2f). Six-segmented, with telson clearly separated; pleomeres 1–4 and 6 unarmed, pleomere 5 with pair of moderately prominent posterolateral spines; uniramous or weakly biramous pleopod buds present on pleomeres 2–5; pleomere 6 with uni- or biramous uropod buds.

Telson (Fig. 2f, 4h). Short and moderately stout; terminal margin with broad V-shaped median cleft and 8 + 8 processes, all articulated, 3–8 each with long, fine marginal setae, fourth process longest.

Trizocheles vaubanae n. sp.

Material examined. 3 specimens, cl (including rostrum) approximately 1.8–2.0 mm (carapaces damaged); two dissected. All specimens hatched from single ovigerous female at time of preservation. Female (sl = 4.2 mm), EBISCO stn DW 2606, 19°36.0'S, 158°42.0'E, 442–443 m, 18 Oct 2005 (MNHN-Pg 7776).

Description. Yolk granules present.

Carapace. Globoid, lacking spines and setae, posterior margins rounded; rostrum approximately 0.2 of carapace length, quite slender, directed downward.

Eyes. Stalked, corneas large.

Antennule (Fig. 3a). Biramous; protopod elongate, unsegmented; endopod shorter than exopod, naked; exopod with 2 short terminal setae and 2 or 3 aesthetascs, 1 long aesthetasc on inner margin.

Antenna (Fig. 3b). Biramous; protopod with spine at endopodal junction and larger spine at scaphocerite junction; endopod overreaching tip of distolateral spine of scaphocerite. Scaphocerite with 7 moderately long setae and 1 very short seta proximally on inner margin, upper margin with 2 or 3 setae; distolateral spine subdistal in origin, prominent, simple, lateral margin with or without small spine-like protuberance at midlength.

Mandible (Fig. 3c). Subquadrate with large, unsegmented, naked palp.

Maxillule (Fig. 3d). Bilobed bud.

Maxilla (Fig. 3e). Well developed, with bilobed coxal and basial endites, endopod and scaphognathite, all lacking setae.

First maxilliped (Fig. 3f). Protopod unsegmented; exopod unsegmented, elongate, 4 slightly evaginated setae visible distally beneath cuticle; endopod short, unsegmented.

Second maxilliped (Fig. 3g). Protopod unsegmented; exopod unsegmented, elongate, 4 slightly evaginated setae visible distally beneath cuticle; endopod approximately 0.3 length of exopod, unsegmented.

Third maxilliped (Fig. 3h). Protopod unsegmented; exopod unsegmented, elongate, naked; endopod slight shorter than exopod, unsegmented, naked.

Chelipeds (Fig. 4a). Dactyl clearly defined, but still fused to palm, longer than fixed finger; segments all unarmed and lacking setae.
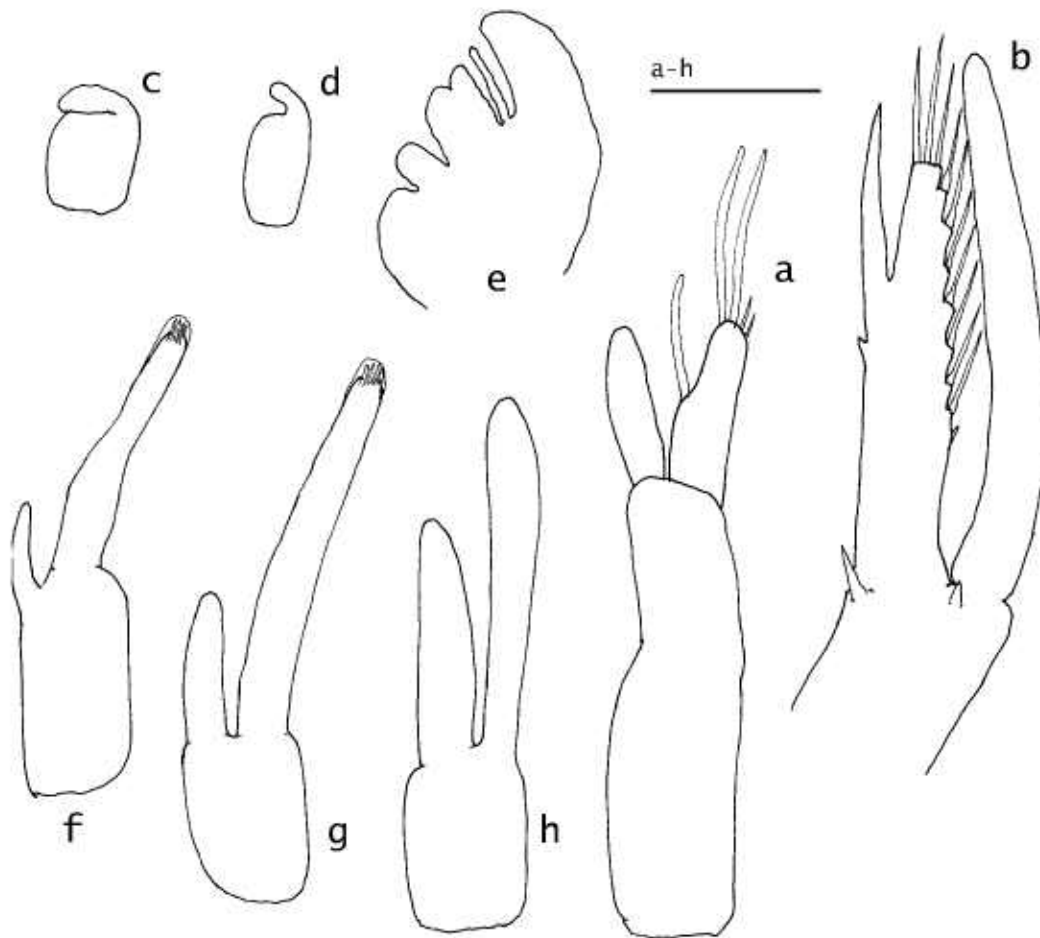
Pereopods 2 and 3 (Fig. 4b, c). Dactyls short, stout, terminal claws apparent; all segments unarmed and lacking setae.

Pereopods 4 and 5 (Fig. 4d, e). Dactyls developed but still fused to propodi.

Pleon (Fig. 4f). Six-segmented, with telson clearly separated; pleomeres 1–4 and 6 unarmed, pleomere 5 with pair of moderately long posterolateral spines; biramous pleopod buds present on pleomeres 2–5; ple-
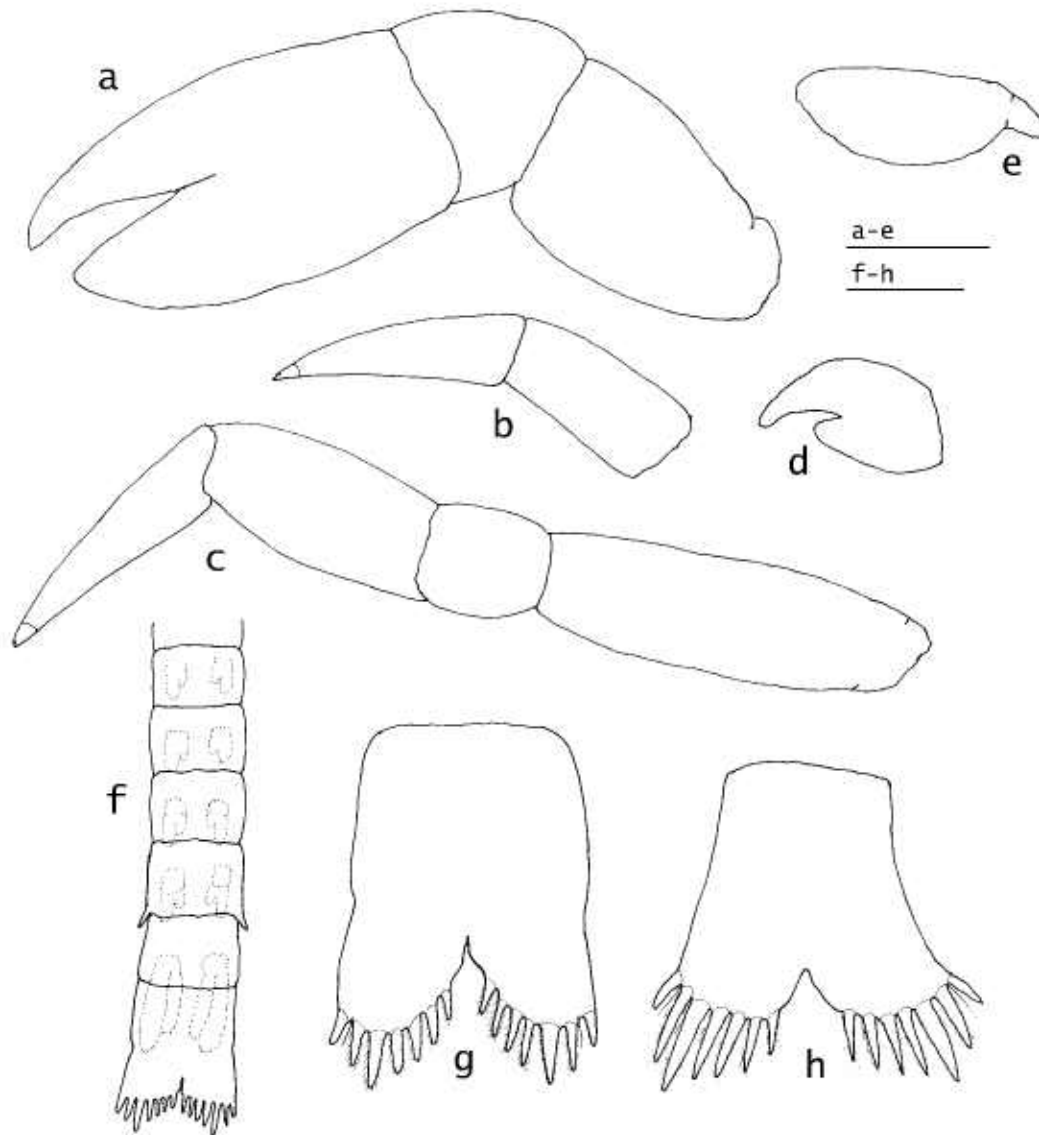
omere 6 with biramous uropods, lacking setae.

Telson (Fig. 4f, g). Moderately long; terminal margin with narrow V-shaped median cleft and 8 + 8 processes, all articulated, 3–8 each with fringe of marginal setae, fourth process longest.

FIGURE 3. Metazoea of *Trizocheles vaubanae* **n. sp.** a, antennule; b, antenna; c, mandible; d, maxillule; e, maxilla; f, first maxilliped, g, second maxilliped; h, third maxilliped. Scale: 0.25 mm.

Remarks. In advanced development, morphological characters appearing in later zoeal stages are shifted backward or compressed into first and second stages. However when compression of morphological features unites with elimination and/or shortening of durations of stages, a highly advanced larva results (Gore 1985). Development in *Trizocheles* is clearly quite advanced and also lecithotrophic as it is in *Pomatocheles* and *Pylocheles*. As previously noted, all of the larvae of *Trizocheles* are believed to have hatched prematurely as the females were preserved. The variation in development of the appendages seen in the several dissected specimens of *T. s. spinosus* indicated that the embryos were not all at the same level of development when they hatched. Whether this disparity resulted from differences in initial egg deposition or from irregularities in the embryonic molt cycles among individuals can not be determined from the material available.

As the present larval descriptions are based on prematurely hatched specimens, some of the larval differences seen between the two species simply may be variations in developmental levels. However, metazoeae of these two species of *Trizocheles* are readily distinguished from one another by the structure of the antennae, which is consistent for each species. In *T. s. spinosus*, the subdistal lateral spine of the scaphocerite is prominently bifid, but it is simple in *T. vaubanae* **n. sp.** Although the development of the uropodal endopods was greater in the latter species, both species appeared to be near the end of their embryonic molt cycles and would hatch either as megalopae or in the last zoeal stage before metamorphosis.

FIGURE 4. Metazoea of *Trizocheles vaubanae* **n. sp.**, a–g: a, cheliped; b, second pereopod; c, third pereopod; d, fourth pereopod; e, fifth pereopod; f, pleon and telson; g, telson. *Trizocheles spinosus spinosus* (Henderson, 1888), h: telson. Scales: 0.25 mm (a–e), 1 mm (f), and 0.5 mm (g–h).

Subfamily Pomatochelinae Stebbing, 1914

Pomatocheles Miers, 1879

Pomatocheles jeffreysii Miers, 1879
Pomatocheles jeffreysii Miers, 1879: 49, pl. 3, fig. 2, 2a–d.

Material examined. One specimen, cl = 1.3 mm (examination and description by Konishi & Imafuku 2000).

    Remarks. Konishi & Imafuku (2000) considered the cuticular covering of the "hatchling" of *P. jeffreysii* prezoeal-like, but recognized the advanced development of the stalked eyes, pereopods, and uropods of the larva. The authors did not, however, mention the juvenile-like development of the maxillule and the first max-illiped. Nonetheless, the telson, as illustrated (Konishi & Imafuku 2000, fig. 2M) was clearly zoeal, although quite distinct from any described taxon. The apparent absence of an anomuran hair may have been an anomaly

of their single specimen; however, the number of telsonal marginal processes (13) approaches that of *Pyloche-les* (*P.*) *mortensenii* and the few parapagurid larvae known, as well as the unusual larva of the pagurid *Lithopagurus yucatanicus* Provenzano, 1968. Although no aesthetascs or setae were evaginated, the biramous condition of the antennule of *P. jeffreysii* also indicated a late stage of zoeal development. No protopodal spine or spines were described or illustrated for the antenna, an absence seen in larvae of porcellanids but not in paguroids. The larva is also notable for the lack of a rostrum and pleonal armature.

Konishi & Imafuku (2000) were of the opinion that as all of the setae were invaginated, their larva of *Pomatocheles jeffreysii* had hatched prematurely. These authors believed that the advanced developmental stage of the larva indicated that either it would have been released as, or have been followed at the next molt by, a megalopa or more advance juvenile stage. The well developed uropods lend support to their supposition.

Subfamily Pylochelinae Bate, 1888

Genus *Pylocheles* A. Milne Edwards, 1880

Subgenus Pylocheles A. Milne Edwards, 1880

Pylocheles (*Pylocheles*) *mortensenii* (Boas, 1926)

Pylocheles Mortensenii Boas, 1926: 40, figs. 1, 5, 6, 10A, 11B, 13, 14, 18, 25A.
Pylocheles (Pylocheles) mortensenii. — Forest, 1987: 51, figs. 2a, 3a, 5a, b, 7a, 8a–i, 9a–d, 10a, b, 12a–d, 41a, pl. 2C.

Material examined. Ten specimens, cl = 2.0–2.3 mm; three dissected (examination and description by Saito & Konishi 2002).

Remarks. Although Saito & Konishi (2002) referred to their larvae as a first zoea, they noted the stalked condition of the eyes, existence of a mandibular palp, well developed pereopods, six pleonal somites and the occurrence of uropodal buds. However, the presence of only four natatory setae on the exopods of each first and second maxilliped was viewed as a typical first zoeal character.

The antennule of *P.* (*P.*) *mortensenii* was described as being incompletely segmented and lacking processes, although Saito & Konishi's (2002, fig. 3A) figure might be interpreted as having the bud of one ramus (presumably the exopod) developed but lacking aesthetascs. Clearly, the antennule was in an early stage of development. The antenna as described and illustrated also appeared to be of an early zoeal stage, whereas the mandible, with its two-segmented palp was comparable to mandibular development seen in a late stage zoea. The maxillule was described as reduced, but whether this condition was a reflection of lecithotrophy or transition to the juvenile state is uncertain. The first and second maxillipeds had the endopods reduced, but appeared typically zoeal in structure, in contrast to the third maxilliped where the endopod had five incipient segments.

Saito & Konishi (2002) concluded that the larvae of *Pylocheles* (*P.*) *mortensenii* were free-swimming upon hatching, and while not cultured, the authors suggested that at least one subsequent larval stage would follow. Although staked eyes and developing pereopods, uropods, and pleopod buds are indicative of advanced development, the generally typical early zoeal stage antennule and antennal of the larvae would sustain their conclusion.

Discussion

As noted by both Konishi & Imafuku (2000) and Saito & Konishi (2002), the presence of large amounts of yolk in the larvae of *Pomatocheles* and *Pylocheles* (*Pylocheles*), together with the reduction in development

of feeding appendages suggested that both were lecithotrophic (non feeding) in their larval stages. Both species of *Trizocheles* are similarly provided with substantial amounts of yolk and their mouthparts are poorly developed; therefore it is reasonable to assume that full lecithotrophy (cf. Anger 2001: 111) is common among pylochelid larvae.

Provenzano (1971) summarized what appeared to be distinguishing characters of the larvae of pagurids, parapagurids, diogenids and coenobitids based on the data, published and unpublished, available to him at the time. Although our knowledge of paguroid development has increased appreciably in the last 35 years, his basic data for these families are still accurate; development in the Pylojacquesidae is unknown. However, relatively few of Provenzano's (1971) characters are applicable to taxa exhibiting lecithotrophic reduction in feeding appendages and advanced development. In the case of the pylochelids, we have found only characters associated with the carapace, antenna, pleon and telson meaningful in evaluating potential relationships.

Carapace. The metazoeae of all three pylochelid genera are characterized by globular carapaces with rounded posterolateral margins. Rounded posterolateral carapacial margins are typical of diogenid (except *Calcinus* Dana, 1851), parapagurid, and coenobitid zoeae, whereas these margins are most frequently sharply pointed or drawn out and spiniform in pagurids. Saito & Konishi (2002) differentiated *Pylocheles* (*P.*) *mortensenii* from diogenid larvae by the presence of a pair of anterolateral marginal spines (suborbital spines of Saito & Konishi; pterystomial spines of Gurney 1942 and de Saint Laurent-Dechancé 1964) and an oblique row of small spines on lateral surface of the carapace. However, within the Diogenidae, a pair of anterolateral carapace spines was described for larvae of *Paguristes* species by Rice & Provenzano (1965), Provenzano (1978) and Tirmizi & Siddiqui (1988). Similarly, anterolateral spines were described for some species of *Parapagurus* Smith, 1879 sensu lato by de Saint Laurent-Dechancé (1964) and Williamson & von Levetzow (1967). Numerous carapace spinules were described for the early zoeal stages of *Trizopagurus magnificus* (Bouvier, 1898) by Provenzano (1967) and lateral carapace spines for *Pylopaguropsis atlantica* Wass, 1963 by Provenzano (1971). Consequently, it does not appear that carapace armature, or lack thereof, is of phylogenetic significance, although it may be useful in distinguishing metazoeae of *Pylocheles* (*Pylocheles*) from *Pomatocheles* and *Trizocheles*.

Unless it is an anomaly of the single specimen, one carapace character that is noteworthy about *Pomatocheles jeffreysii* is the absence of a rostrum. In all other paguroid zoeae, even those with abbreviated development, and including the metazoeae of *Pylocheles* (*P.*) *mortensenii* and *Trizocheles*, a rostrum is present.

Antenna. The considerable length of the endopod of the antenna in *Pomatocheles jeffreysii* suggests an advanced stage of development. Thus, the apparent absence of a protopodal spine or spines is also unique. At least one protopodal spine develops, if not in the first zoeal stage, at least later, in all known paguroid larvae, as well as in albuneids, and galatheids except *Cervimunida* Fagetti, 1960 (Gore 1979), porcellanids, and perhaps chirostylids where only early first zoeae of three species have been described (Pike & Wear 1969; Ogawa & Matsuzaki 1992). A distolateral spine on the scaphocerite is typical of pagurid larvae and several diogenid genera, but is absent, or lost after stage I in parapagurids and some diogenid genera. In *Pylocheles* the spine is also present and distolateral in origin, but in *Pomatocheles* and *Trizocheles* it is distinctly subdistal.

Pleon. Only in *Pylocheles* (*P.*) *mortensenii* are pleomeres 2–5 armed and in this species they are described as long and paired dorsolateral spines. Saito & Konishi (2002) suggested that the pleonal armature was similar to that of the deep water lobster, *Metanephrops challengeri* (Balss, 1914), as described by Wear (1976) and the brachyuran, *Cymonomus bathamae* Dell, 1971, as reported by Wear & Batham (1975). However, a pair of dorsal spines on pleomere 5 has been reported for zoeae of *Birgus latro* Linnaeus, 1767 by Reese & Kinzie (1968) and dorsolateral plus unpaired median dorsal spines have been described for species of *Coenobita* Latreille, 1829 by Provenzano (1962), Nakasone (1988), and Harvey (1992); whereas dorsolateral pleonal spines are common in pagurid zoeae, as are posterodorsal marginal spines. Long dorsal and dorsolateral spines are also described for the few galatheoid chirostylid larvae known (Ogawa & Matsuzaki 1992), so it is probable that pleonal armature has evolved independently numerous times. In *Trizocheles* only pleomere 5

has a pair of dorsolateral spines, whereas all pleomeres are unarmed in *Pomatocheles jeffreysii* as they are in parapagurids.

Telson. The terminal margins of the telsonal lobes are slightly to distinctly convex in *Trizocheles* and *Pylocheles*, but slightly concave in *Pomatocheles*. In the first zoeal stage of diogenids and pagurids this margin varies from convex to straight, becoming less convex in subsequent stages. It is faintly convex in zoea I in parapagurids but becomes increasingly concave in later stages.

The number of telsonal processes in Zoea I in all paguroids is 7+7, with the first process typically a small spine, the second process represented by an "anomuran hair", and processes 3–7 plumodenticulate setae of which the fourth most frequently is the longest. The number usually, although not always, increases in subsequent zoeal stages to 8+8 (most pagurids), 8+1+8 (most diogenids and coenobitids) or 11–13 (parapagurids) with processes added medially. Interestingly, in the Galatheidae, the typical 7+7 with an increase to 8+8 is seen in *Galathea* Sars, 1889, but in other galatheid genera considerably more processes are added in later zoeal stages (Gore, 1979). However, larvae of the Porcellanidae increase the telsonal processes by the addition of only one median process (7+1+7) in the second and usually final stage. McLaughlin *et al*. (2004) considered the higher number plesiomorphic.

In the prematurely hatched metazoeae of *Trizocheles* the number of processes is 8+8, and considering the advanced development of the uropods, it is unlikely that additional processes would be added at hatching. These larvae appear to have reached their maximum compliment of telsonal processes. In contrast, the telsons of both *Pomatocheles jeffreysii* and *P. (P.) mortensenii* have considerably more processes. However, in addition to the larvae of the two *Trizocheles* species, one very prematurely hatched larva of *Pylocheles* (*Bathycheles*) *profundus* Forest, 1987 was discovered and found to have only 7+7 telsonal processes. This observation prompts the question of whether larval development in these subgenera of *Pylocheles* is really so different, or if the very premature larva of *P. (B.) profundus* was at an early stage of telsonal development and several more processes would be added prior to hatching? Helluy & Beltz (1991) found embryonic telsonal development in the lobster *Homarus americanus* H. Milne Edwards, 1837 to be 6+6 setae in the egg nauplius, but increased to 15+15 by the time the metanauplius was ready to hatch. Of course, the available data are too meager to permit anything more than speculation at this point. However, Makarov's (1968a, b) hypothesis of obligatory and non-obligatory staging, if correct, might provide an explanation. Makarov found in species of crangonid and hippolytid shrimp that larvae were "obliged" to pass through three larval stages, but in some species, additional, non-obligatory stages could be added. If the decapod egg nauplius has six telsonal processes, and the paguroid metanauplius (prezoea) has 7+7 telsonal processes (cf. Gurney 1942, fig. 13D), the number in the third obligatory stage of most paguroids, as in the metazoea of *Trizocheles*, would then be 8+8. In contrast, the larger numbers seen in the zoeae of *Pylocheles*, *Pomatocheles*, the parapagurids and *Lithopagurus* perhaps were reached during one or more non-obligatory stages, with these compressed into early metazoeae in *Pylocheles* and *Pomatocheles*.

One attribute of the telson of *Pylocheles* (*P.*) *mortensenii* that is not seen in the metazoeae of either *Pomatocheles* or *Trizocheles*, is also atypical of most paguroids. While the outermost spiniform process in many is fused with the telson, that process is typically small; it is the fourth process that is slightly larger in most first stage zoeae and increases in size in successive stages. However, the outermost spine-like process in *P. (P.) mortensenii* is not only fused, but appreciably longer than any of the other processes, a condition known previously in paguroids only in species of the genus *Spiropagurus* Stimpson, 1858, as described by Dechancé (1962). That this large spine actually is homologous with the outermost process in other taxa is demonstrated by the position of the adjacent anomuran hair; however, the telsonal margin is straight, without a cleft, in *Spiropagurus*. In *Pylocheles* (*P.*) *mortensenii* this margin is convex, with a distinct median cleft, and is reminiscent of the telson of the first zoeal stage of the albuneid, *Lophomastix japonica* Duruflé, 1889, as described by Konishi (1987). In subsequent zoeal stages of *L. japonica*, the outermost process becomes reduced and articulated, whereas the fourth becomes fused and elongated. In view of the Saito & Konishi's (2002) sugges-

tion of at least one additional zoeal stage in the development of *P.* (*P.*) *mortensenii*, it is quite possible that telsonal development in this taxon is not as unusual as it would appear from the known larvae.

The morphological diversity noted among the larvae of the three pylochelid genera lends support to Forest's (1987) observation that differences seen among the adults in the six subfamilies might warrant the elevation of each to familial rank. Even so, Forest was of the opinion that all pylochelid genera were more closely allied to the Diogenidae than to the Paguridae and Parapaguridae. Our limited larval data do not support that supposition. The metazoeae of all three genera do share carapace form with the Diogenidae, but also with the Parapaguridae. In development of the distolateral spine of the scaphocerite, only *Pylocheles* is similar to pagurid and some diogenid zoeae; the subdistal origin seen in *Pomatocheles* and *Trizocheles* is, as far as known at present, unique among paguroids. The telsonal margins and processes in the *Trizocheles* metazoeae more closely approach those seen in pagurids than in either diogenids or parapagurids, whereas the telsons of *Pomatocheles* and *Pylocheles* cannot easily be allied to any other paguroids. Richter & Scholtz (1994) suggested that the Pylochelidae was paraphyletic. However, the differences seen in the larval data now available, support the recently completed cladistic analysis (Lemaitre *et al.*, in press), which indicated at least three evolutionary branches.

Taxonomy

Family Pylochelidae Bate, 1888

Subfamily Trizochelinae Forest, 1987

Genus *Trizocheles* Forest, 1987
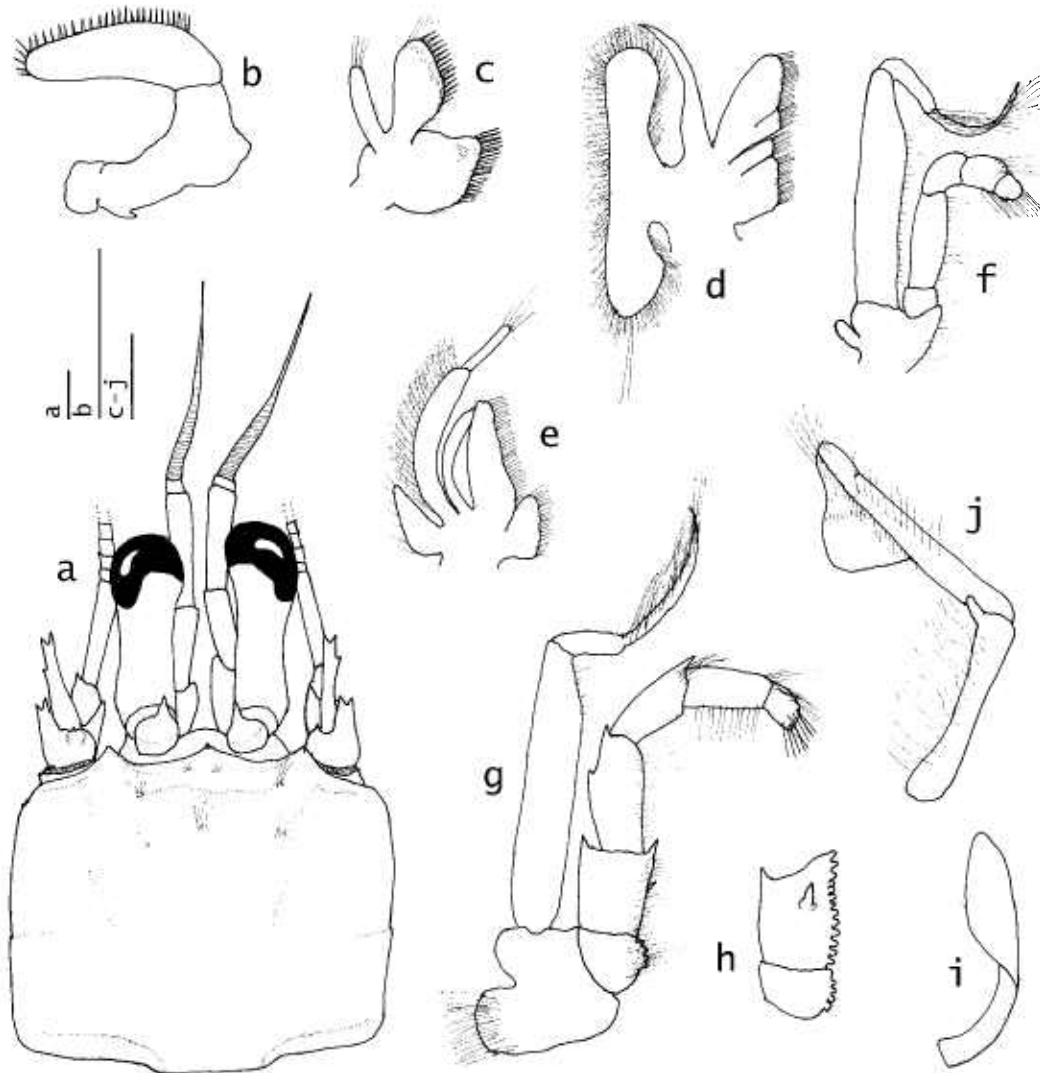
***Trizocheles vaubanae* n. sp.**
(Figs 5, 6)

Type material. New Caledonia. *Holotype*: ovigerous female (sl = 7.8 mm) NORFOLK 2 stn CP 2050, 23°42'S, 168°16'E, 377 m, 24 Oct 2003 (MNHN-Pg 7766).

Paratypes: 1 ovig. female (2.4 mm), BIOCAL, stn DW 66, 24°55.43'S, 168°21.67'E, 505–515 m, 3 Sep 1985 (MNHN-Pg 7767); 1 male (sl = 2.2 mm), SMIB 3, stn CP 1, 22°53.0'S, 167°12.0'E, 437 m, 5 Feb 1986 (MNHN-Pg 7768); 2 males (sl = 2.7, 2.9 mm), CHALCAL 2, stn DW 72, 24°54.5'S, 168°22.3'E, 527 m, 28 Oct 1986 (MNHN-Pg 7769); 1 male (sl = 4.3 mm), BERYX 2, stn DW 38, 23°38'S, 167°39'E, 550–690 m, 19 Oct 1992 (MNHN-Pg 7770); 1 female (sl = 2.4 mm), NORFOLK 2, stn DW 2147, 22°50'S, 167°16'E, 496 m, 4 Nov 2003 (MNHN-Pg 7771); 1 male (sl = 2.7 mm), stn 2050, same data as holotype, (MNHN- Pg 7772); 2 males (sl = 2.6, 2.8 mm), 1 ovig. female (3.6 mm), stn DW 2057, 24°40'S, 168°39'E, 555–565 m, 25 Oct 2003 (MNHN-Pg 7773); 1 ovig. female (sl = 3.4 mm), stn CP 2061, 24°37'S, 168°40'E, 620–1040), 25 Oct 2003 (MNHN-Pg 7774); 1 male (sl = 2.3 mm), 1 female (sl = 2.4 mm), 3 ovig. females (sl = 2.4–3.3 mm), stn DW 2081, 25°54'S, 168°22'E, 500–505 m, 28 Oct 2003 (MNHN-Pg 7775); 1 male (sl = 5.1 mm) stn DW 2087, 24°56'S, 168°22'E, 518–586 m, 28 Oct 2003 (USNM 1114242); 1 ovig. female (sl = 7.2 mm), EBISCO, stn DW 2584, 19°38.0'S, 158°44.0'E, depth not recorded, 15 Oct 2005, (USNM 1114243); 1 ovig. female (sl = 4.2 mm, with prematurely hatched metazoeae), stn DW 2606, 19°36.0'S, 158°42.'E, 442–443 m, 18 Oct 2005, (MNHN-Pg 7776).

Solomon Islands. 1 female (sl = 4.8 mm), SALOMON 2, stn CP 2261, 8°01.9'S-156°54.1'E, 433-470 m, Nov 2004 (MNHN-Pg 7778).

Other material examined. **New Caledonia.** 1 ovig. female (2.0 mm), SMIB 4, stn DW 55, 23°24.1'S, 168°04.5'E, 260 m, 9 Mar 1989 (MNHN Pg 7777).

Description. Shield (Fig. 5a) distinctly broader than long, and longer than calcified posterior carapace; dorsal surface with moderately long, deep, transverse groove subrostrally. Cervical groove clearly delineated laterally. Shield lateral margins each with slight indentation to small spine in proximal half. Posterior median plate well delineated, broad anteriorly and narrowing posteriorly, moderately well calcified; sulci cardiobranchialis not apparent. Branchiostegites weakly calcified anterodorsally; dorsal margin unarmed, usually few spinules on distal margin. Rostrum typically broadly triangular, with or without small marginal spinule, approximately reaching level of lateral projections, occasionally obsolete. Lateral projections well developed, each with marginal spine.

FIGURE 5. *Trizocheles vaubanae* **n. sp.**, a, ovig. female holotype (sl = 7.7 mm) (MNHN-Pg 7766), b–j, male paratype (sl = 4.3 mm) (MNHN-Pg 7770). a, shield and cephalic appendages (aesthetascs and some setae omitted); b, mandibular palp (left, inner surface); c, maxillule (left, outer face); d, maxilla (left, outer surface); e, first maxilliped (left, outer surface); f, second maxilliped (left, outer surface); g, third maxilliped (left, outer surface); h, basis and ischium of third maxilliped (left, inner surface); i, male first pleopod (left, anterior face); j, male second pleopod (left, anterior face). Scales: 1 mm.

Ocular peduncles 0.5–0.8 length of shield; corneas 0.3–0.5 of peduncular length. Ocular acicles moderately small, acutely triangular, calcified only in anterior halves; widely separated.

Antennular peduncles overreaching distal corneal margins by 0.5–0.7 lengths of ultimate segments. Ulti-

mate segment approximately equal in length to penultimate segment or slightly shorter. Basal segment with spine on statocyst lobe laterally and spinule at ventrodistal margin.

Antennal peduncles reaching midlength of corneas; with supernumerary segmentation. Fifth segment unarmed; fourth segment with spine at dorsodistal margin; third segment with spine at ventrodistal margin; second segment with dorsolateral distal angle produced, with terminal bifid spine, dorsomesial distal angle with small spine; first segment with 2 or 3 small spines ventrolateral margin.
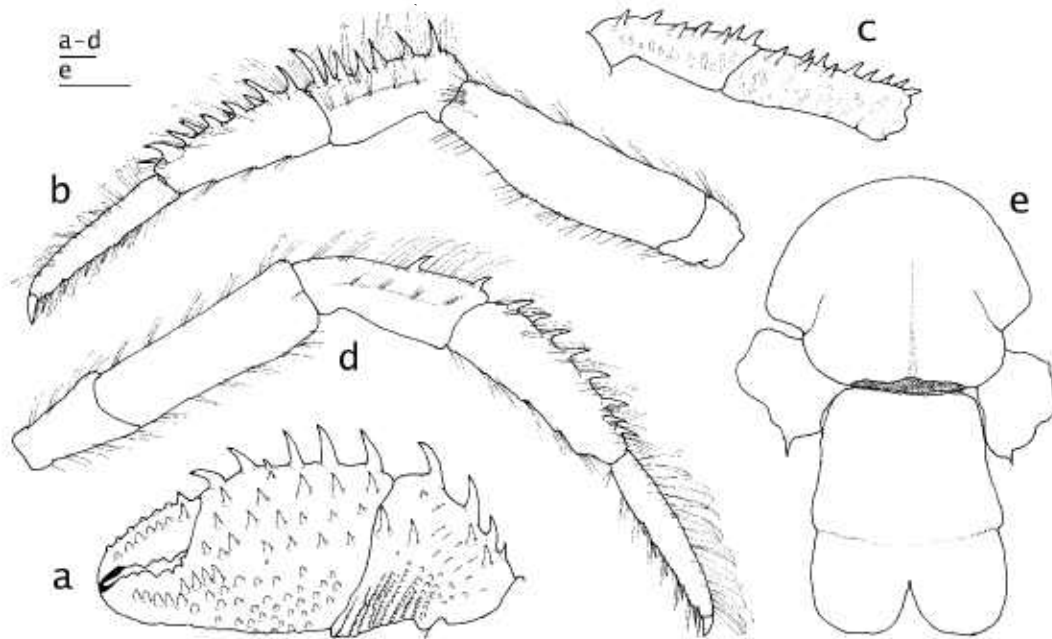
Antennal acicle short, not reaching beyond midlength of ocular peduncle (exclusive of cornea), usually terminating in bifid spine, rarely simple, mesial margin with 1 or 2 spines, lateral margin unarmed or with 1 spine in distal half. Antennal flagella as short as carapace; most articles each with 2–4 short to moderately long setae.

Second segment of mandibular palp (Fig. 5b) with roundly subrectangular dorsomesially projected lobe and dorsoproximal small spiniform protuberance. Maxillule (Fig. 5c) with external lobe of endopod obsolete. Maxilla (Fig. 5d) 2 very long setae on ventral margin of proximal lobe of scaphognathite. First maxilliped (Fig. 5e) with well developed, marginally setose epipod. Second maxilliped (Fig. 5f) with small tubular epipod. Third maxilliped (Fig. 5g, h) with unarmed exopod; endopod with 3 or 4 small teeth on basis; ischium with well developed crista dentata, 1 accessory tooth, 1 dorsodistal and 1 ventrodistal spine; merus with 1 dorsodistal and 1 smaller subdistal spine; carpus with dorsodistal spine; termination simple.

Chelipeds subequal and symmetrical; with propodal-carpal rotation of approximately 45°; chelae and carpi (Fig. 6a) each with moderate covering of long setae on upper and outer surfaces not concealing armature. Dactyl 0.6–0.7 length of palm, with moderately narrow hiatus between dactyl and fixed finger; upper margin with 1 or 2 large, corneous-tipped spines proximally and row of much smaller, often subacute, spines; outer face also with large corneous-tipped proximal spine and row of smaller spines extending to or nearly to tip; cutting edge with row of moderately large, calcareous teeth, terminating in prominent corneous claw; inner face with few scattered setae. Palms 1.5–1.7 length of carpus; upper margin with row of prominent large spines, outer surface of palms with 4 rows of smaller spines, lower outer surface with scattered small tubercles; fixed finger with distinct row of subacute marginal spines and adjacent row of small tubercles, cutting edge with row of moderately large calcareous teeth and terminal corneous claw. Carpus subtrapezoidal; upper margin with 2 large and 1 or 2 somewhat smaller spines, outer surface with 3 or 4 spines; outer lower face with several rows of stridulatory rods and tubercles; inner face with 1 or 2 small tubercles and tufts of short setae; ventral surface smooth. Merus subtriangular; dorsal margin with spine, often corneous-tipped, at distal margin and row of setae proximally, mesial and lateral faces unarmed, ventromesial and ventrolateral margins each with row of small tubercles or spines; ventral surface with 1 or 2 small tubercles proximally. Ischium with row of large spines on ventromesial margin.

Second and third pereopods (Fig. 6b–d) equaling or slightly overreaching chelipeds. Dactyls 0.1–0.2 longer than propodi; dorsal and mesial faces each with tufts of stiff setae; ventral margins each usually with 5–7 corneous spines and tufts of setae. Propodi 0.2–0.3 longer than carpi; dorsal margins of second pereopods each with tufts of long setae, irregular often incomplete double row of acute large spines, single or incomplete double, also irregular row on third, often fewer in number; mesial faces of second pereopods each with numerous stridulatory tubercles or short ridges, scattered or forming irregular rows, third unarmed or with row of quite small, widely-spaced tubercles; ventral surfaces of second pereopods each with few scattered setae, occasionally corneous spine at ventrodistal margin, third with or without corneous spinule at ventrodistal margin and row of widely spaced protuberances and tufts of setae, occasionally concealing additional corneous spinule(s); lateral faces unarmed. Carpi of both second and third pereopods each with dorsal row of prominent spines and tufts of moderately long setae in large individuals, third often with only 1–3 spines in small specimens, lateral faces each with shallow median longitudinal sulcus; mesial faces of second pereopods each with row of prominent stridulatory ridges. Meri of second pereopods each often with row of small spinules or tubercles on ventral margin, sometimes not discernable, third only with few tufts of setae. Fourth

pereopods semichelate; each with propodal rasp consisting of several rows of corneous scales; propodi and carpi each with dorsodistal spine. Fifth pereopods chelate; propodal rasp well developed.

FIGURE 6. *Trizocheles vaubanae* **n. sp.**, ovig. female holotype (sl = 7.7 mm) (MNHN-Pg 7766). a, chela and carpus of left cheliped (outer face); b, left second pereopod (lateral view); c, propodus and carpus of left second pereopod (mesial view); d, right third pereopod (lateral view); e, tergite of sixth pleomere, protopods of uropods, and telson (dorsal view). Scales: 1 mm.

Pleon with tergite 1 moderately well calcified; tergites 2–5 weakly calcified, pleura weakly delineated; tergite of pleomere 6 (Fig. 6e) roundly subquadrate, with deep lateral incisions and shallow median longitudinal sulcus; terminal margin straight, slightly sinuous, or with shallow to moderately deep, broad, median concavity, unarmed. All tergites and telson usually with covering of short setae.
Uropods symmetrical; protopods each with posteriorly directed spine. Telson with faint lateral indentations dividing telson into unequal anterior and posterior portions; posterior lobes considerably shorter, separated by deep median cleft, terminal margins rounded, unarmed but with fringe of fine setae.

Males with paired first pleopods (Fig. 5i) 2-segmented, distal segments each terminally spatulate; paired second pleopods (Fig. 5j) also 2-segmented, spatulate terminal segments quite broad; pleopods 3–5 each with exopod well developed, endopod reduced.

Females with slender, 2-segmented first pleopods each with numerous setae marginally and terminally.

Etymology. This species is named for the research vessel R.V. *Vauban*, from which the first specimens were collected.

Habitat. Carcinoecia usually missing; one specimen found occupying a gastropod shell and another lodged in the lumen of a piece of a dead stony coral.

Distribution. New Caledonia, Solomon Islands; 377–620 m, possibly as shallow as 260 m or as deep as 1040 m.

Variation. Variations in the number of ventral spines on the dactyls of the ambulatory legs and on the dorsal surfaces of the carpi of the third pereopods appear to be functions of size. Small specimens typically had five spines on the dactyls and one or two on the carpi; these often increased in number with increased animal size; however, in the large female holotype, the dorsal surface of the third left carpus had four spines, but only two on the right. The terminal margin of the sixth pleomere also appeared influenced by animal size. The margin typically was straight in small specimens but appeared more sinuous with increased size, because mar-

ginal calcification diminished, ultimately giving the impression of a broad median concavity in the largest individuals.

Remarks. *Trizocheles vaubanae* **n. sp.** is most closely allied to *T. s. spinosus* and *T. s. bathamae* Forest & de Saint Laurent, 1987 in having spines on the dorsal margins of the propodi and carpi of both the second and pereopods as well as prominently developed stridulatory rods and/or tubercles on the mesial faces of the second pair. However, like *T. pulcher* Forest, 1987 and *T. pilgrimi* Forest & McLaughlin, 2000, the propodal spines of *T. vaubanae* **n. sp.** form one or two, usually incomplete, irregular rows rather than the single regular row seen in the two subspecies of *T. spinosus. Trizocheles pulcher* and *T. pilgrimi* are immediately distinguished from the new species by having the dorsal spines on the propodi of only the second pereopods; the propodi of the third pereopods are unarmed or each has only a small dorsodistal spine. The ovigerous female from SMIB 4, stn DW 55, differs from the other females in having only a distal pair of spines on the propodus of each second pereopod rather than the typical row(s). Whether this is because of its smaller size is uncertain, but it only can questionably be assigned to *T. vaubanae* **n. sp.** It is not considered a paratype.

Acknowledgements

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