



Discovery of the first hermit crab (Crustacea: Decapoda: Parapaguridae) associated with hydrothermal vents

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Abstract: A new species of hermit crab of the family Parapaguridae, *Paragiopagurus ventilatus*, is described from hydrothermal vent habitats in the Tashi fishing grounds, northeastern Taiwan, at depths of 128 to 281 m. The discovery of this new species is significant in that it is the first confirmed, fully identified hermit crab known from hydrothermal vents, although the association of *Paragiopagurus ventilatus* with this environment does not appear to be «obligate». This new species is the 17th in the genus *Paragiopagurus* Lemaître, 1996, and is distinguished primarily by the dense, long plumose setae with bacterial strands on the anterior sternal region, including outer surfaces of bases and ischia of third maxillipeds, and mesial and ventral surfaces of ischia and meri of the first three pereopods; striae on the ocular acicles; shape and armature of the right cheliped; ventromesial armature of dactyls of second and third pereopods; and armature of anterior lobe of sternite XII.

Résumé : Découverte du premier bernard l'hermite (Crustacea : Decapoda : Parapaguridae) associé aux sources hydrothermales. Une nouvelle espèce de bernard l'hermite de la famille des Parapaguridae, provenant des sources hydrothermales de la zone de pêche de Tashi, nord-est de Taïwan, entre 128 et 281 m, est décrite. La découverte de cette nouvelle espèce est la première confirmée et complètement identifiée d'un bernard l'hermite provenant de sources hydrothermales, bien que l'association de *Paragiopagurus ventilatus* avec cet environnement n'apparaissent pas nécessairement obligatoire. Cette nouvelle espèce est la 17^{ème} dans le genre *Paragiopagurus* Lemaître, 1996, et se distingue tout d'abord par : les longues et denses soies plumeuses porteuses de rangées de bactéries dans la région antérieure, y compris les faces externes du basis et de l'ischion du troisième maxillipède, les faces ventrales et latérales de l'ischion et du mérus des trois premiers péréiopodes ; les stries sur les ossicules oculaires, la forme et l'armature du chélipède droit ; l'armature ventro-latérale du dactyle des seconds et troisièmes péréiopodes ; l'armature du lobe antérieur du sternite XII.

Keywords: Hydrothermal vents, hermit crab, Parapaguridae, *Paragiopagurus*, new species, Taiwan.

Introduction

The occurrence of anomurans in the vicinity of hydrothermal vents or cold-seeps is well known. In particular, a good

number of species of Lithodidae, Galatheidae, and Chirostylidae have been either described or reported from these deep-sea environments around the world oceans (see summary by Chevaldonné & Olu, 1996). However, despite many studies over two decades since the discovery of vent biological communities (Suess et al., 1985), hermit crabs (Paguroidea *sensu* McLaughlin, 2003) have rarely been seen or collected in these remarkable environments, and at

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most have been reported to genus or family level, such as «*Parapagurus*» (de Saint Laurent, in Chevaldonné & Olu, 1996), or «Paguridae-unknown sp.» (Barry et al., 1996). Thus, the discovery of a new species of hermit crab in samples recently obtained by a joint Taiwanese-French expedition in hydrothermal vent environments from the Tashi fishing grounds, on the northeastern coast of Taiwan, is of considerable significance. This new species of the family Parapaguridae Smith, 1882 is the 17th so far known in the genus *Paragiopagurus* Lemaitre, 1996, and is the first hermit crab confirmed and fully identified from a vent community, although it remains to be studied whether it is an «obligate» associate of these vents systems or not.

All specimens were obtained in depths from 128 to 281 m, using a beam-trawl directly over hydrothermal vent sites, and operated from the fishing trawler «*Chung-Tung Long*». The beam trawl was pulled over known vent areas for 30 minutes, at a speed of 1.5 knots. A description of the Taiwanese-French expedition, and the complete station data, can be found in Richer de Forges et al. (in press). The specimens used remain deposited in the collections of the National Taiwan Ocean University, Keelung (NTOU), and MNHN, except for three specimens deposited in the National Museum of Natural History, Washington, D.C. (USNM). The general morphological terminology follows Lemaitre (1999). The term «bacteriophage setae», introduced by Segonzac et al. (1993: 550) for the hydrothermal vent shrimp *Rimicaris exoculata* Williams & Rona, 1986, is used to refer to specialized plumose setae that facilitate growth of bacterial strands. The measurements in millimeters included in the material examined are of shield length (sl), measured from the midpoint of the rostrum to the midpoint of the posterior margin of the shield. Other abbreviations used in the manuscript are: CP, from the French «Chalut à perches», meaning beam-trawl; ov, ovigerous; stn, station. The overall length of the right cheliped is measured dorsally, from the tip of the fingers to the proximal margin of the merus; the length and width of the chela and carpus are measured dorsally.

Systematics

Family Parapaguridae Smith, 1882
Genus *Paragiopagurus* Lemaitre, 1996
Paragiopagurus ventilatus sp. nov.
(Figs. 1-5)

Type material: Taiwan. Holotype: M 5.6 mm, stn CP 113, 24°50.8'N, 121°59.9'E, 281 m, 21 May 2001 (NTOU A00438). Paratypes: stn CP 81, 24°50.5'N, 121°59.9'E,

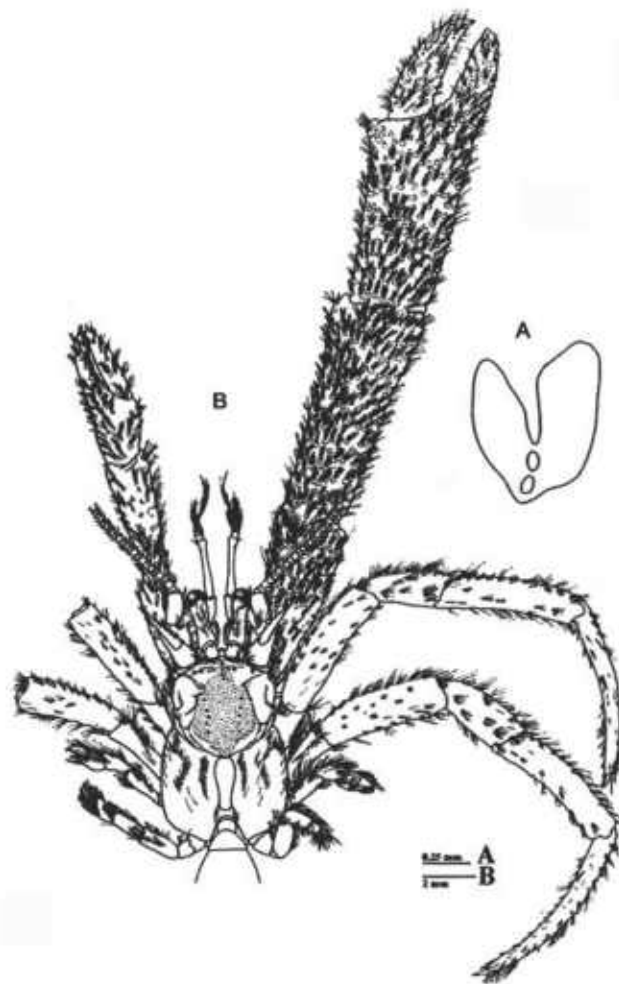


Figure 1. *Paragiopagurus ventilatus*, sp. nov. A. paratype, male 5.6 mm, Taiwan, stn CP 113 (MNHN-Pg 6736). B. holotype, male 5.6 mm, Taiwan, stn CP 113 (NTOU A00438). A. gill lamella. B. whole specimen except for abdomen, and carpi, propodi and dactyl of left second and third pereopods.

Figure 1. *Paragiopagurus ventilatus*, sp. nov. A. paratype mâle 5,6 mm, Taiwan, stn CP 113 (MNHN-Pg 6736). B. holotype mâle 5,6 mm, Taiwan, stn CP 113 (NTOU A00438). A. lamelle branchiale. B. spécimen entier sauf l'abdomen ; carpe, propodie et dactyle des second et troisième péréiopodes gauches.

205 m, 8 May 2001: 1 M 5.6 mm (MNHN-Pg 6735); same station data as holotype: 2 M 5.4, 5.8 mm, 1 ov. F 3.8 mm (MNHN-Pg 6736), 1 M 5.4 mm, 2 ov. F 4.2, 4.4 mm (USNM 1068936), 6 M 4.5-5.7 mm, 1 ov F 4.9 mm (NTOU A00439); stn CP 114, 24°51.0'N, 121°51.3'E, 128-250 m, 21 May 2001: 1 M 5.1 mm (MNHN-Pg 6737).

Description

Eleven pairs of biserial gills (Fig. 1A). Shield (Fig. 1B)

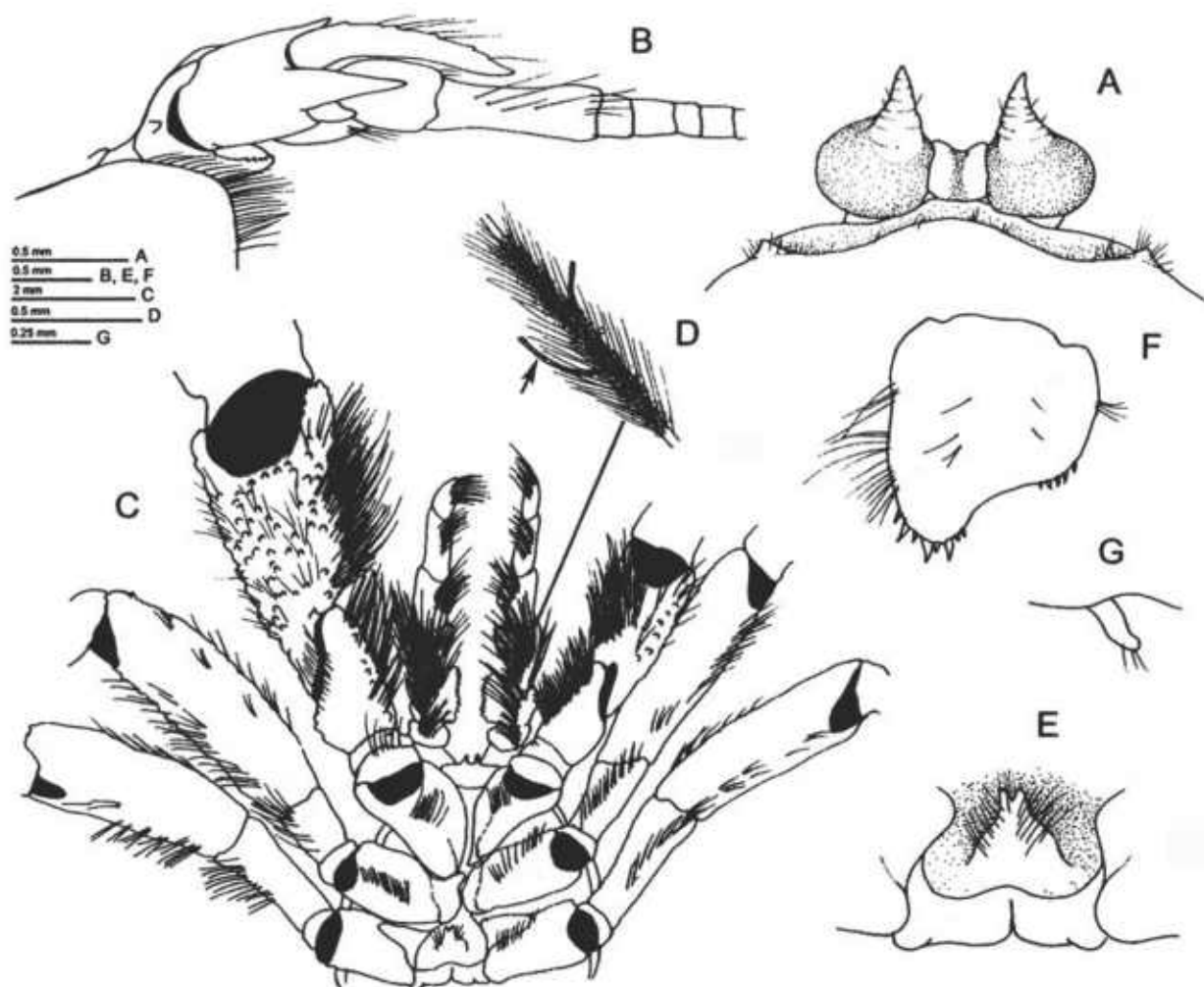


Figure 2. *Paragiopagurus ventilatus*, sp. nov. Holotype, male 5,6 mm Taiwan, stn CP 113 (NTOU A00438). A. ocular acicles, rostrum, and lateral projections, dorsal view. B. right antennal peduncle, and anterodistal margin of branchiostegite, lateral view. C. thoracic region showing third maxillipeds, and part of chelipeds and second and third pereopods, ventral view. D. magnified section of plumose seta from outer surface of third maxilliped (arrow indicates bacterial strand; stippling represents mucus-like substance). E. anterior and posterior lobes of thoracic sternite XII (third pereopods), ventral view. F. telson, dorsal view; G. left second pleopod, lateral view.

Figure 2. *Paragiopagurus ventilatus*, sp. nov. Holotype mâle 5,6 mm Taiwan, stn CP 113 (NTOU A00438). A. ossicules oculaires, rostre et projections latérales, vue dorsale. B. pédoncule antennaire droit et bord antérodistal du branchiostégite, vue latérale. C. région thoracique montrant les troisièmes maxillipèdes, une partie des chélipèdes et des seconds et troisièmes péréiopodes, vue ventrale. D. partie agrandie d'une soie plumeuse de la face externe du troisième maxillipède (la flèche indique la rangée de bactéries; les pointillés représentent une substance muqueuse). E. lobes antérieurs et postérieurs du sternite thoracique XII (troisième péréiopodes), vue ventrale. F. telson, vue ventrale. G. second pléopode gauche, vue latérale.

approximately as broad as long; dorsal surface weakly calcified along midline and sometimes anterior portions; with scattered short setae. Rostrum broadly rounded, with short mid-dorsal ridge. Anterior margins of shield weakly con-

cave; lateral projections subtriangular, with small terminal spine; anterolateral margins sloping; ventrolateral margins each with small spine anteriorly; posterior margin broadly rounded. Anterodistal margin of branchiostegite (Fig. 2B)

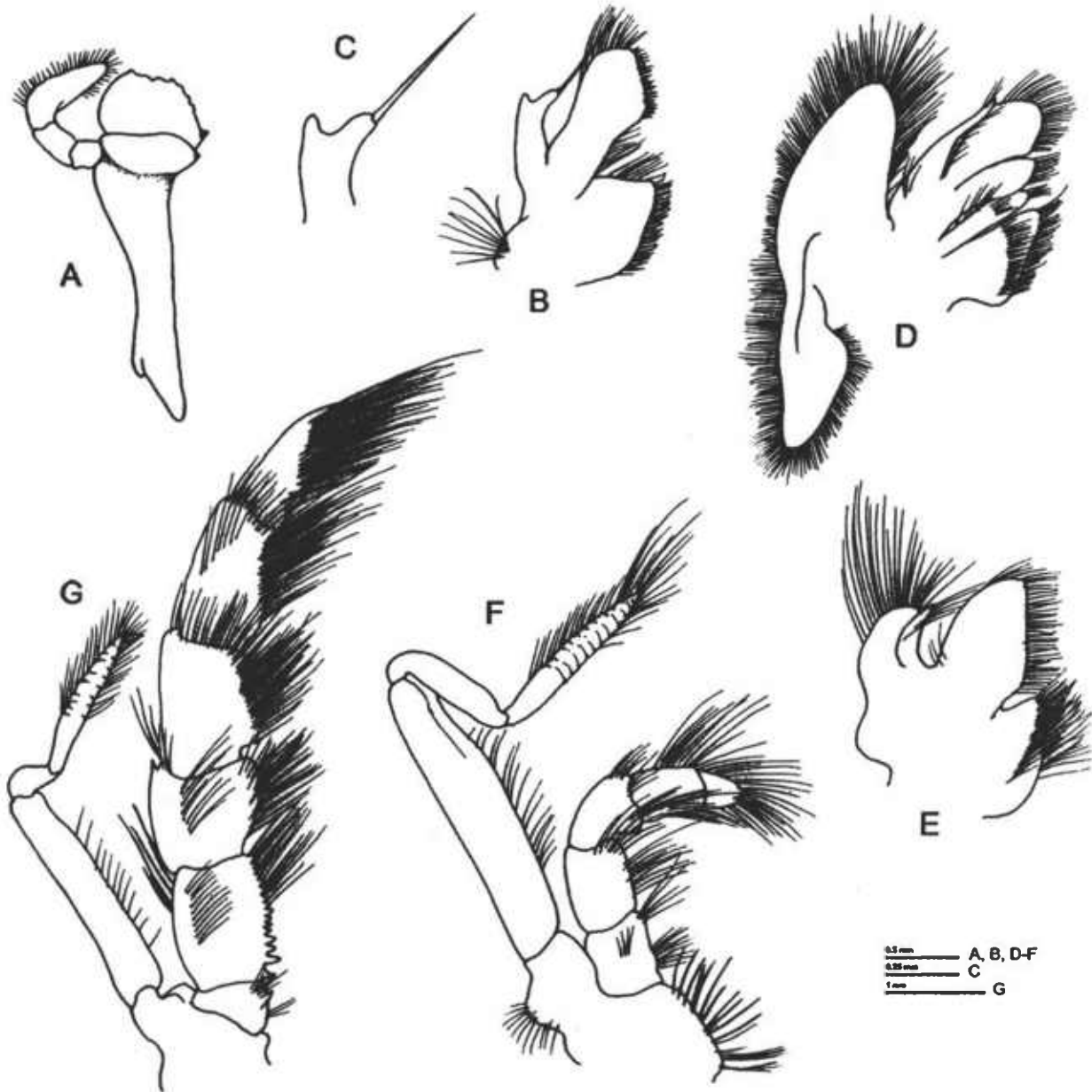


Figure 3. *Paragiopagurus ventilatus*, sp. nov. Paratype, male 5.6 mm, Taiwan, stn CP 113 (MNHN-Pg 6735). Left mouthparts, internal view. A. mandible. B. maxillule. C. distal end of endopod of same. D. maxilla. E. first maxilliped. F. second maxilliped. G. third maxilliped.

Figure 3. *Paragiopagurus ventilatus*, sp. nov. Paratype mâle 5,6 mm, Taiwan, stn CP 113 (MNHN-Pg 6735). Pièces buccales gauches, vue interne. A. mandibule. B. maxillule. C. extrémité distale de l'endopodite du maxillule. D. maxille. E. premier maxillipède. F. deuxième maxillipède. G. troisième maxillipède.

rounded, unarmed, setose.

Ocular peduncles more than half length of shield, with short setae on dorsal surface. Cornea slightly dilated. Ocular acicles subtriangular, terminating in strong, simple

spine (rarely bifid) with transverse striae (Fig. 2A); separated basally by less than basal width of 1 acicle.

Antennular peduncles exceeding distal margins of corneas by nearly entire length of ultimate segment, with

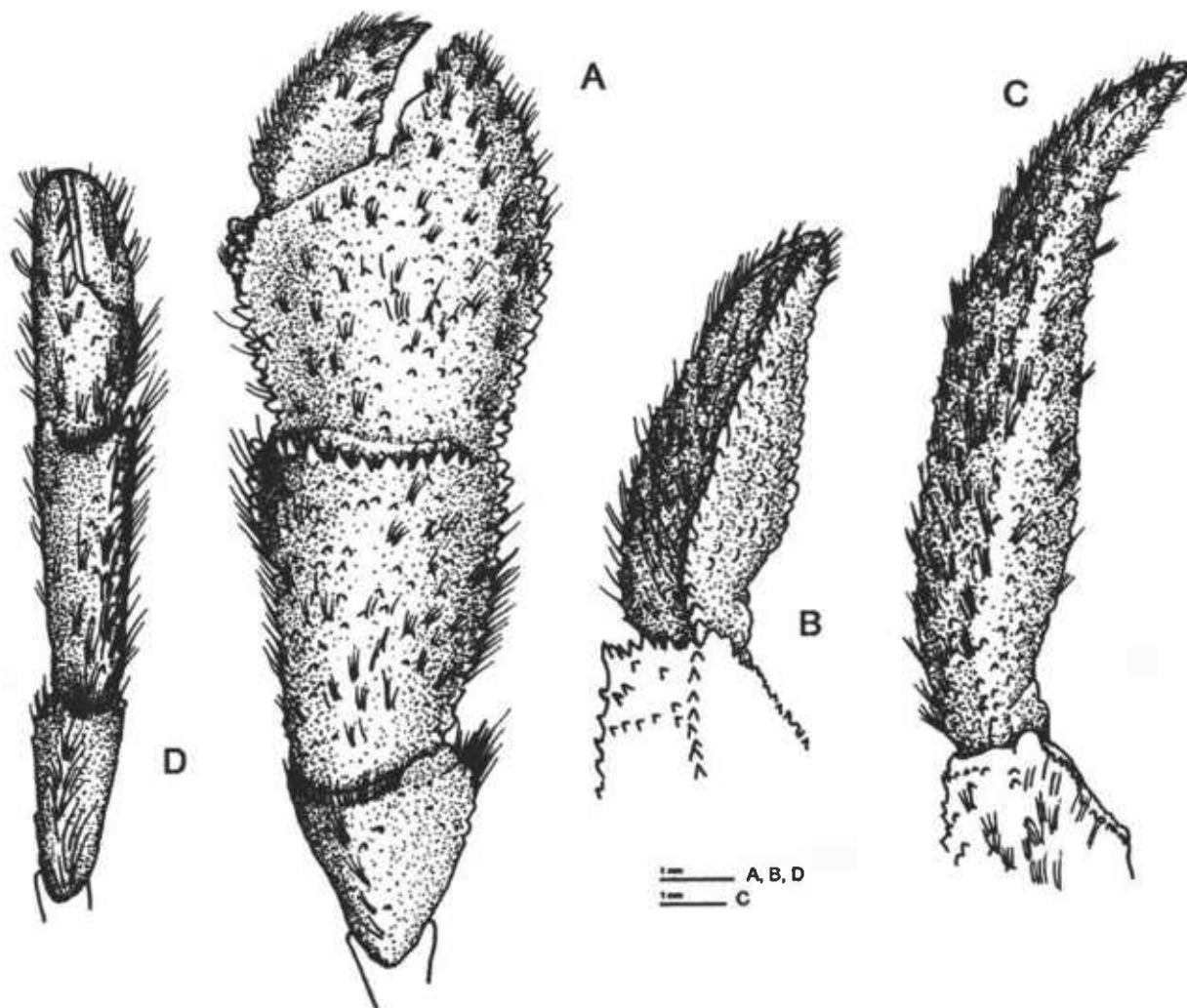


Figure 4. *Paragiopagurus ventilatus*, sp. nov. A, B, D. paratype, ovigerous female 4.9 mm, Taiwan, stn CP 113 (NTOU A00439). C, holotype, male 5.6 mm Taiwan, stn CP (NTOU A00438). A, female right cheliped, dorsal view. B, chela of same, lateral view. C, male right chela, lateral view. D, female left cheliped, dorsal view.

Figure 4. *Paragiopagurus ventilatus*, sp. nov. A, B, D. paratype femelle ovigère 4,9 mm. Taiwan, stn CP 113 (NTOU A00439). C. holotype mâle 5,6 mm Taiwan, stn CP 113 (NTOU A00438). A. chélipède droit femelle, vue dorsale. B. pince du même chélipède, vue latérale. C. pince droite mâle, vue latérale. D. chélipède gauche femelle, vue dorsale.

scattered setae dorsally; ventral flagellum with 4 or 5 articles. Ultimate segment about twice as long as penultimate. Basal segment with strong ventromesial spine; lateral face with distal subrectangular lobe usually armed with 1 or 2 small spines, and strong spine proximally.

Antennal peduncles (Fig. 2B) reaching to about distal margin of corneas. Fifth segment unarmed but with setae on lateral and mesial margins. Fourth segment unarmed, lacking spine on dorsolateral distal angle. Third segment with strong ventromesial distal spine. Second segment with dor-

solateral distal angle produced, terminating in strong, simple spine reaching slightly beyond midpoint of acicle; mesial margin with small spine on dorsolateral distal angle. First segment with spine on lateral surface; ventromesial angle produced, with row of 5 or 6 small spines laterally. Antennal acicle nearly straight or weakly curved outward (dorsal view), reaching to distal margin of cornea, terminating in strong spine; mesial margin setose, armed with row of 4-6 spines (rarely 8 or 9) diminishing in size distally. Flagellum reaching to about distal margin of palm of right

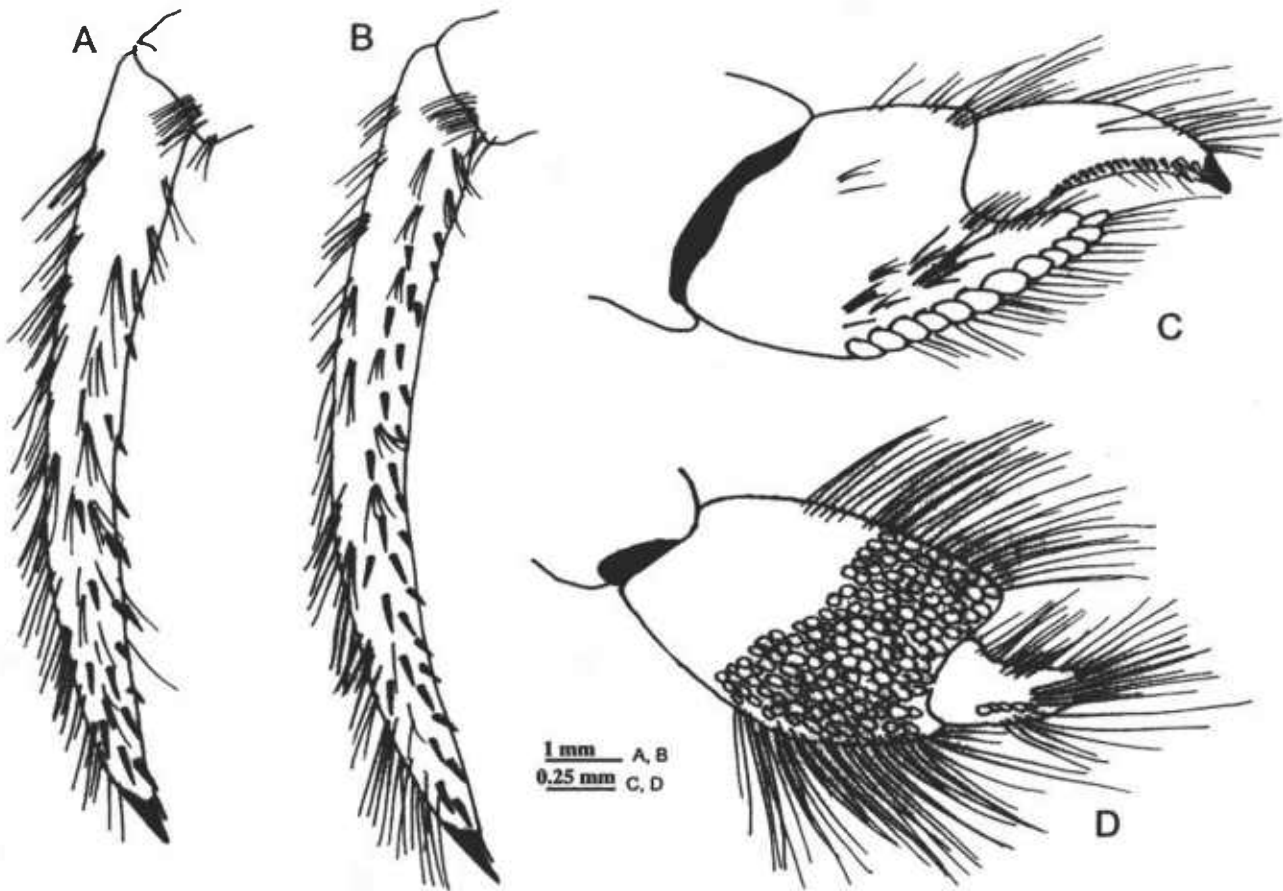


Figure 5. *Paragiopagurus ventilatus*, sp. nov. Holotype, male 5.6 mm Taiwan, stn CP 113 (NTOU A00438). A. B. dactyl of right second (A) and right third (B) pereopod, mesial view. C. propodus and dactyl of right fourth pereopod, lateral view. D. propodus and dactyl of right fifth pereopod, lateral view.

Figure 5. *Paragiopagurus ventilatus*, sp. nov. Holotype mâle 5,6 mm Taiwan, stn CP 113 (NTOU A00438). A. B. dactyle des second (A) et troisième (B) périopodes droits, vue latérale. C. propode et dactyle du quatrième périopode droit, vue latérale. D. propode et dactyle du cinquième périopode droit, vue latérale.

cheliped; with short setae < 1 to 2 flagellar articles in length.

Mandible (Fig. 3A) with 3-segmented palp; cutting edge calcified, somewhat cristiform, with small corneous tooth medially; molar process with small corneous tooth medially. Maxillule (Fig. 3B, C) with external lobe of endopod moderately developed, not recurved, internal lobe with long terminal seta. Maxilla (Fig. 3D) with endopod slightly exceeding distal margin of scaphognathite. First maxilliped (Fig. 3E) with endopod slightly exceeding exopod in distal extension. Second maxilliped (Fig. 3F) without distinguishing characters, except for mesiolaterally flattened flagellum. Third maxilliped (Fig. 3G) stout; with basis, ischium merus, carpus, propodus, and dactyl about same length (measured along lateral margin); outer face of basis, and

ischium, with long, dense, plumose bacteriophage setae (Fig. 2D) denser on larger male specimens (sl > 5.0 mm); crista dentata with about 16 corneous-tipped teeth; basis with small mesial spine. Sternite of third maxillipeds with small spine on each side of midline; with mesiolaterally flattened flagellum. Epistome usually with small, straight simple to trifid epistomial spine, or rarely unarmed.

Chelipeds markedly dissimilar; proportions and armature of right strongly affected by size and sex (see *Variations*). Right cheliped about 3 times as long as sl in females (Fig. 4A), or up to 6.9 times as long as sl in males (Figs. 1B, 4A). Chela somewhat dorsoventrally flattened in females, less so in males; dorsal and ventral surfaces with numerous blunt to sharp spines or tubercles, most with tuft of setae near base anteriorly. Fingers slightly curved ven-

tromesially, terminating in small, blunt corneous claws; cutting edges each with row of small blunt, or broadly rounded, unequal calcareous teeth, and distal row of small corneous teeth. Dactyl shorter (males) or longer (females) than mesial margin of palm, set at weakly oblique angle to longitudinal axis of palm; mesial margin well defined by row of spines or tubercles; ventromesial face concave. Fixed finger much broader basally in females than in males. Palm longer than broad in males or broader than long in females; lateral margin more distinctly delimited by spines or tubercles in females (Fig. 4B) than in males (Fig. 4C); mesial face rounded, females with dorsomesial margin distinctly delimited by row of spines or tubercles. Carpus armature and setation similar to that of chela; length/width ratio ranging from 1.2 in females to as much as 2.7 in males; dorsodistal margin with row of strong (females) or weak (males) spines; ventrolateral margin well delimited by spines (females) or not delimited (males); mesial surface rounded, with small tubercles, ventromesial distal margin with row of small blunt spines. Merus armature and setation similar to that of carpus; with ventromesial and ventrolateral row of small spines; mesial and ventral surfaces with dense, long plumose bacteriophage setae, more dense in large males. Ischium with dense, long plumose bacteriophage setae on distomesial and dorsal surfaces. Coxa with ventrodorsal row of setae.

Left cheliped (Figs. 1B, 4D) well calcified; reaching at most to level of distal 0.75 of carpus of right cheliped in large males (sl > 5.0 mm), or slightly beyond level of base of dactyl of right cheliped in females. Fingers terminating in sharp corneous claws; dorsal and ventral surfaces unarmed except for tufts of setae; cutting edges each with row of closely-set small corneous teeth. Dactyl shorter (males) or longer (females) than palm. Palm dorsal surface with tufts of setae and small tubercles on dorsal surfaces; ventral surface with tufts of setae. Carpus with irregular rows of small spines or tubercles obscured by tufts of setae on dorsal surface, and 1 or 2 strong dorsodistal spines; dorsodistal margin with 1-3 small spines laterally; lateral and ventral surfaces with tufts of setae and some small tubercles or spines; mesial surface with tufts of setae. Merus with rows of small tubercles or spines on dorsal and ventral surfaces, and dense, long bacteriophage setae on proximomesial and ventral surfaces; ventrolateral and ventromesial distal margins each with row of small spines. Ischium unarmed but with scattered tufts of setae on lateral surface, and usually dense, long bacteriophage setae on distomesial and dorsal surfaces. Coxa with ventromesial row of setae.

Ambulatory legs or second and third pereopods (Figs. 1B, 5A, B) similar from right to left except for slightly longer meri on right; reaching when fully extended to about level of proximal third of palm of right cheliped in males, or slightly exceeding right cheliped in females. Dactyl 1.4-

1.7 times as long as propodus, broadly curved, terminating in sharp corneous claw usually with long bristle at base ventrally; dorsal margin with tufts of setae; ventromesial surface with irregular rows of 18-40 corneous spines (more numerous on third pereopod). Propodus, carpus, and merus with tufts or short transverse rows of setae on all surfaces. Carpus with small dorsodistal spine. Merus with ventrodorsal row of small spines or tubercles (second pereopod), or lacking tubercles (third pereopod); ventral margin with long bacteriophage setae proximally, more dense on second pereopod than on third. Ischium and coxa with ventromesial row of setae; ischium with small, blunt spine distally (second pereopod) or without spine (third pereopod), and long bacteriophage setae on ventral margin. Anterior lobe of sternite XII (third pereopods, Fig. 2E) subsemicircular, setose, with strong subterminal simple or more often, bifid spine.

Fourth pereopod (Fig. 5C) subchelate; merus, carpus, and propodus with setae on dorsal and ventral margins. Dactyl subtriangular, terminating in sharp corneous claw; with ventrolateral row of small corneous spinules. Propodus longer than wide, rasp formed of 1 row (at least distally) of rounded scales.

Fifth pereopod (Fig. 5D) chelate. Propodal rasp extending slightly beyond mid-length of segment. Dactyl with row of small rounded scales on ventral surface (in lateral view), lacking subterminal corneous tooth on prehensile margin.

Uropods and telson markedly asymmetrical. Telson (Fig. 2F) with weak or obsolete transverse suture; dorsal surface with scattered short setae; lateral margins with long (left) or short (right) setae; posterior margin separated by broad, shallow cleft, into rounded projections armed with relatively few short, corneous spines, some often ventrally curved.

Male lacking first pleopods; with unpaired left second pleopod rudimentary, uniramous (Fig. 2G). Female with rudimentary second right pleopod.

Colour (in life)

Shield and cephalic appendages cream with some faded pink areas. Chelipeds and ambulatory legs red or pink; propodi and dactyls of ambulatory legs each with faded pink or white stripe on lateral face.

Housing

Found living in gastropod shells of the buccinid genus *Siphonalia*. The shells were covered with a fine layer of sediment, but no evidence of epibionts or bacterial growth.

Etymology

The specific name is derived from the Latin *ventilo*, air,

with the suffix *-atus*, meaning ventose, and used as an adjective. The name is in reference to the gas believed to escape through the Tashi hydrothermal vents, where this new species was discovered.

Variations

The 12 males and 4 ovigerous females known of this new species show a remarkable degree of morphological variation in the right cheliped related to sex and size. The ratio of right cheliped length/shield length ranges in males from 3.9 in the smallest specimen (sl = 4.5 mm) to 6.9 in the largest (sl = 5.6 mm); in females the ratio ranges from 3.2 in the smallest (sl = 3.8 mm) to 3.3 in the largest (sl = 4.9 mm). In the specimens examined, the elongation of the right cheliped is particularly pronounced in specimens sl \geq 5.0 mm. The right chela in females (Fig. 4B) is more dorsoventrally flattened than in males (Fig. 4C), the former having the dorsolateral and dorsomesial margins of the chela well defined by rows of spines, whereas in the latter the dorsolateral and dorsomesial margins are weakly defined by low tubercles.

The bacteriophore setae on the outer surfaces of bases and ischia of the third maxillipeds, the mesial surfaces and ventral margins of the ischia and meri of the chelipeds, and the ventral margins of ischia and meri of the second and third pereopods, are more dense in large males (sl \geq 5.0 mm).

Distribution

Known so far only from the Tashi fishing ground, north-eastern coast of Taiwan near Kueishan Island (Turtle Mountain Island). Depth: 128 to 281 m.

Remarks

Paragiopagurus ventilatus is clearly distinguished from other congeners by several morphological features, including the presence of bacteriophore setae on the third maxillipeds, chelipeds, and second and third pereopods. Although many paragiopagurid species have dense setation patterns, particularly on the chelipeds, and sometimes also second and third pereopods, none have the bacteriophore setae (Fig. 2C, D) present in *P. ventilatus*. These bacteriophore setae are covered around the rachis with a mucus-like substance, and have bacterial strands. Other distinguishing features include the striae on the dorsal surface of the spines of the ocular acicles (Fig. 2A); the irregular rows of spines on the ventromesial margins of the dactyls of second and third pereopods (Fig. 5A, B); and the bifid spine on the anterior lobe of sternite XII (third pereopods). This new species is one of six *Paragiopagurus* species in which males lack first pleopods, and have unpaired rudimentary left pleopod; the others are: *P. acutus* (de Saint Laurent,

1972), second *P. bicarinatus* (de Saint Laurent, 1972), *P. hirsutus* (de Saint Laurent, 1972), *P. hobbiti* (Macpherson, 1983), and *P. ruticheles* (A. Milne-Edwards, 1891).

Habitat and specialized morphology

The habitat characteristics of the Tashi fishing grounds where hydrothermal vents are found have been described by Bouchet & von Cosel (in press), and generally consists of gently sloping bottoms of fine sediments with some coral outcrops. Many hydrothermal vents occur from shallow water down to 700 m, and frequently gas bubbles are seen by fishermen on the water surface. Photographs of the smoking vents and associated communities are available, although none show hermit crabs (T.-Y. Chan, pers. comm.). In the more shallow vents, in depths of about 15 m, the endemic grapsid crab, *Xenograpsus testudinatus* Ng, Huang & Ho, 2000, known to be associated with thermal habitats (Ng et al., 2000), is quite abundant and has frequently been photographed. The relatively shallow depth of the Tashi vents appears to be a reason for the intrusion of atypical faunal components such as *X. testudinatus* and *Paragiopagurus ventilatus*.

Paragiopagurus ventilatus appears to be a member of the biological communities that lives close but do not depend exclusively, on the chemosynthetically-based vent ecosystems, perhaps attracted by the high food supply available. As such, this new species is probably not part of the «obligate» fauna living in these vent habitats. The trawl samples where this new species was found included blocks of a sulphur compound with many mussel specimens of *Idas* (Bivalvia: Mytilidae), numerous *X. testudinatus* crabs, and unidentified carideans and thalassinid specimens (T.-Y. Chan, pers. comm.). In situ observations of *P. ventilatus* were not obtained, and thus it was not possible to determine how close to the vents this new species might live, or estimate the degree, if any, of ecological dependency («obligate» vs. «non-obligate») of this new species on the chemosynthetically-based vent ecosystem. However, based on the contents of trawl catches, and especially the bacteriophore setae (Fig. 2D) present on the buccal and proximal segments of chelipeds and second and third pereopods, it is clear that *P. ventilatus* lives in close vicinity of the vents where bacterial growth is facilitated by nutrient rich vent water (Van Dover, 1995). A somewhat similar, dense setation pattern has been documented in other decapods associated with hydrothermal vents or seeps, such as the galatheids *Shinkaia crosnieri* Baba & Williams, 1998 (see Baba & Williams, 1998: fig. 4B, D), and *Munida magniantennulata* Baba & Türkay, 1992 (see Baba & de Saint Laurent, 1992: 326), although no bacterial growth was mentioned for either of these galatheids. In contrast, Felder & Kensley (2004) did observe in the axiid *Calaxius carneyi* Felder & Kensley, 2004, dense setae fouled with flocculent

debris possibly derived from the seep environments where this species was found.

The very long right cheliped (at least in males) of *P. ventilatus* might appear to be another adaptation related to feeding in vent habitats. However, long chelipeds may not necessarily be related to the vent habitat, and more likely is an adaptation related to life in soft, deep-sea substrates. Other parapagurids that are not associated with vent environments can also have remarkably long right chelipeds, such as *Parapagurus nudus* (A. Milne-Edwards, 1891), *P. alaminos* Lemaître, 1986, *P. saintlaurentae* Lemaître, 1999, and *Sympagurus andersoni* (Henderson, 1896) (see Lemaître, 1986, 1999, 2004).

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