A review of *Pseudionella* Shiino, 1949 (Crustacea: Isopoda: Bopyridae), with the description of a new species parasitic on *Calcinus* hermit crabs from Easter Island

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Abstract.—Two pairs of bopyrids collected on Easter Island, from the hermit crab Calcinus imperialis Whitelegge, belong to the genus Pseudionella Shiino (=Pseudasymmetrione Adkinson & Heard, new synonymy) and are described as P. akuaku n. sp. This is the first record of any bopyrid isopod from Easter Island and the first Pseudionella known to parasitize hermit crabs of the genus Calcinus. A review of the species of Pseudionella, with keys to males and females, is provided and includes a significant range extension for P. deflexa Bourdon.

Bopyrid isopods found in the branchial chambers of hermit crabs are restricted to the subfamily Pseudioninae. Seven genera have been erected exclusively for species of hermit crab branchial parasites, including Pseudionella Shiino, 1949, with one Pacific and one Atlantic taxon, and Pseudasymmetrione Adkinson & Heard, 1978, with one Atlantic species. Additionally, nine species of the heterogeneous (and probably paraphyletic) genus Pseudione Kossman, 1881, are known from hermit crabs; other Pseudione spp. occur on a broad range of decapod taxa, including carideans, nephropids, thalassinoids, galatheoids, and lithodids.

One of us (CBB) collected a series of hermit crabs from Easter Island (Rapa Nui) during August 1999. Two of these crabs contained mature female bopyrids, each with a male attached to the ventral side of the pleonites. Provisional identification of these specimens indicated that they appeared to belong to the genus *Pseudasymmetrione* Adkinson & Heard. However, an examination of *Pseudasymmetrione* type material showed that genus to be a synonym of *Pseudionella* Shiino, and our specimens cannot be placed into any of the three described species now placed in that genus. These specimens are described as a new species of *Pseudionella* which is most closely related to an Atlantic congener, *P. markhami* (Adkinson & Heard).

Methods

Hermit crabs inhabiting gastropod shells were collected intertidally on Easter Island during August 1999. The data label in the vial containing the parasitized specimens was badly damaged during shipping of specimens from Easter Island to New York and, consequently, no specific locality can be determined. Specimens were preserved in 70% ethanol. The shells were cracked using a vise and the crabs removed and examined for parasites. Collection of a single female *Pseudionella deflexa* was made on Andros Island, Bahamas in September 2000 using methods identical to those above.

Drawing tube sketches made of the spec-

imens were scanned into a Macintosh[®] computer. Images were then prepared using the programs Adobe Photoshop[®] and Adobe Illustrator[®].

Shield length (SL) is provided as an indicator of size for the host crabs. Isopod size is given as total body length (anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.01 mm using an ocular micrometer.

Specimens of the new species and *P. de-flexa* are deposited in the Division of Invertebrate Zoology, American Museum of Natural History, New York, U.S.A. (AMNH). Specimens of *Pseudasymmetrione markhami* were borrowed from the National Museum of Natural History (Naturalis), Leiden, the Netherlands (RMNH) and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

Family Bopyridae Rafinesque, 1815

- Subfamily Pseudioninae Codreanu, 1967 Genus Pseudionella Shiino, 1949
- Pseudionella Shiino, 1949:60-61 (type species by monotypy: Pseudionella attenuata Shiino, 1949).
- "Undescribed genus" Markham, 1978:110. *Pseudasymmetrione* Adkinson & Heard, 1978:409, 412 (type species by monotypy: *Pseudasymmetrione markhami* Adkinson & Heard, 1978) (new synonymy).
- not *Pseudionella*, Shiino, 1958:41 (*=Bo-pyrissa* Nierstrasz & Brender à Brandis, 1931).

Diagnosis.—Female with seven pereonites and five pleonites plus pleotelson, all laterally distinct. Frontal lamina entire. Lateral plates very short. Marsupium enclosed by well-developed oostegites. Five pairs of lamellar pleopods, anterior two pairs biramous with exopodite distally bilobed; posterior three pairs uniramous. Uropoda uniramous. Male with seven distinct pereonites and five distinct pleonites plus pleotelson, pleonites markedly reduced in width from pereonites. Five pairs of uniramous tuberculiform or flap-like pleopods.

Remarks.—The addition of the new taxon described below to Pseudionella, and the synonymy of Pseudasymmetrione, requires some modifications to the original diagnosis of Shiino (1949). The frontal lamina is entire, although Shiino (1949) called it rudimentary in the type species. The first two pairs of pleopods in the female are biramous with the endopodite bilobed at the tip, while the last three pairs are uniramous. Both Shiino (1949) and Adkinson & Heard (1978) considered the coalescence of the head with the first pereonite in the male to be of great importance, but this character can vary between individuals within a species (e.g., Stegophryxus hyphalus Markham, 1972:38) and we are unconvinced in its reliability as a diagnostic feature. The pleotelson of the male is either a simple cone (as in P. attenuata and P. deflexa) or has lateral projections (as in P. markhami and the new species) which may represent reduced lateral plates on the sixth pleonite (=pleotelson).

The synonymy of Pseudasymmetrione with Pseudionella was suggested, but not formally proposed, by Bourdon (1979). Bourdon (1979) noted that the one, perhaps significant, difference between the two taxa was the form of the male pleotelson (simple in Pseudionella and with fused lateral plates in Pseudasymmetrione) but wondered if this was sufficient for the establishment of a separate genus. We agree that the four characters given as diagnostic for Pseudasymmetrione by Adkinson & Heard (1978) do not appear to warrant separation of the genera: the female dorsal segmentation is medially indistinct in both P. markhami and the new species, but is variable between the specimens of the new species, and therefore not a good character; the frontal lamina of Pseudionella is not reduced or absent, as stated by Shiino (1949), and there is little difference in this character between the four species; the coxal plates of P. markhami are well developed, but are reduced in the other taxa including the new species; and contrary to the statement of

Adkinson & Heard (1978), males of P. markhami do possess pleopods, but of a form more reduced than those seen in P. attenuata and P. deflexa. The only character left to discriminate between the two genera is the shape of the male pleotelson which, as noted by Bourdon (1979), was not included in the original diagnosis of Pseudasymmetrione. In our opinion, this single difference does not warrant separate generic status for these species. We propose that Pseudionella contains two species-groups, each with one Atlantic and one Pacific taxon: P. attenuata and P. deflexa; P. markhami and the new species from Easter Island. Note that Pseudionella pyriforma Shiino, 1958, does not belong in this genus, but to Bopyrissa Nierstrasz & Brender à Brandis, 1931 (see Bourdon 1979, Markham 1982). Pseudionella appears closely allied to the diverse genus Pseudione which contains species with very similar female morphology, but with five pairs of biramous pleopods in the females (e.g., Nierstrasz & Brender à Brandis 1931, Shiino 1933). The males of Pseudionella also resemble those of Pseudione, but have more laterally constricted pleonites. Although Pseudionella contains several clearly apomorphic characters (e.g., uniramous pleopods 3-5 in females, narrowed pleonites in males) as compared to Pseudione, a detailed phylogenetic analysis is needed to fully understand the relationships between these genera and the others in the subfamily.

Pseudionella attenuata Shiino, 1949

Pseudionella attenuata Shiino, 1949:62–63, fig. 2.

Material examined.-unavailable.

Type locality.—Seto, Wakayama Prefecture, Japan (Shiino 1949, type specimens (if extant) in National Science Museum, Tokyo).

Distribution and host.—Japan, on Pagurus sp. (Shiino 1949, as Eupagurus sp.).

Remarks.—No specimens have been reported subsequent to the two type speci-

mens. Unfortunately it has not been possible to directly examine the types, nor to even confirm if they are still extant, as Shiino's material is in a very poor state of organization (M. Takeda, pers. commun. 15 Jun 1999). The female type was dextral, which suggests that it came from the right branchial chamber of the host.

Pseudionella markhami (Adkinson & Heard, 1978), new combination

"Undescribed ... species" Markham, 1978: 110.

- Pseudasymmetrione markhami Adkinson & Heard, 1978:412–414, figs. 1–3.—Markham, 1988:8–9, fig. 2.
- "Pseudasymmetrione ... undescribed species" Adkinson & Heard, 1978:417.

Material examined.-Holotype: sinistral female (3.14 mm) infesting left branchial chamber of Pagurus annulipes (Stimpson) (sex and size unknown). Morehead Channel, Carteret County, North Carolina, U.S.A., R. W. Heard coll., 26 Aug 1963 (USNM 170590). "Allotype": male (0.99 mm) same data as holotype (USNM 170590). Paratypes: female (2.14 mm) and male (0.89 mm) infesting male host (1.7 mm SL), female (2.00 mm) and male (0.78 mm) infesting male host (1.7 mm SL), female (2.86 mm) and male (0.87 mm) infesting female host (2.1 mm SL), all females sinistral and infesting left branchial chambers of P. annulipes, Morehead Channel, Carteret County, North Carolina, U.S.A., R. W. Heard coll., 25 Jun 1970 (USNM 170593); non-types: dextral female (3.14 mm), and male (0.99 mm), infesting [presumed right] branchial chamber of Iridopagurus iris (A. Milne Edwards) (sex and size unknown), Sta. P-757, 11°41'N, 69°21'W, off Peninsula de Paraguaná, Venezuela, 161-187 m, R/V Pillsbury coll., 27 Jul 1968 (USNM 172224); sinistral female (3.14 mm), male (1.57), sinistral female (1.26 mm), male (0.72 mm) infesting Pagurus brevidactylus (Stimpson) (host sexes, sizes and infested branchial chambers unknown), Punta de Betin, Santa Marta, Dept. Magdalena, Colombia, under stones, 1–2 m, coll. H. G. Müller, 4 Feb 1986 (RMNH 7042); sinistral female (1.26 mm), infesting *Pagurus stimpsoni* (A. Milne Edwards & Bouvier) (host sex, size, and infested branchial chamber unknown), Punta de la Aquia, ca. 4 km east of Santa Marta, Dept. Magdalena, Colombia, on coral rubble, 17– 19 m, coll. H. G. Müller, 9 Jan 1986 (RMNH 7058).

Type locality.—Morehead Channel, Carteret County, North Carolina, United States (Adkinson & Heard 1978, type specimens in USNM, Zoologiske Museum Copenhagen, and the collection of D. Adkinson).

Distribution and hosts.—North Carolina, U.S.A., on Pagurus annulipes (Stimpson) (Adkinson & Heard 1978, herein); Venezuela, on Iridopagurus iris (A. Milne Edwards) (Markham 1978, Adkinson & Heard 1978, herein); Colombia (Atlantic), on Pagurus brevidactylus (Stimpson) and P. stimpsoni (A. Milne Edwards & Bouvier) (Markham 1988, herein).

Remarks.—The pereonites and pleonites of male P. markhami are much more compacted than in the other three taxa in the genus, but the shape of the male pleotelson and the form of the male pleopods are very close to the new species from Easter Island. Although Adkinson & Heard (1978) did not designate an allotype, the male accompanying the female holotype is of equivalent status. Markham (1988) correctly identified the above cited specimens of Pseudionella markhami from Colombia, but inaccurately drew the male pleotelson of RMNH 7042 as having two slender projections; the shape is identical to that of the male allotype and of the other specimens in RMNH. Adkinson & Heard (1978) indicated that Markham's (1978:110) "undescribed new genus and species" from Venezuela appeared to be an undescribed Pseudasymmetrione (=Pseudionella). However, examination of those two specimens indicated no notable differences from P. markhami, other than the unique dextral orientation of the female.

Pseudionella deflexa Bourdon, 1979

Pseudionella deflexa Bourdon, 1979:139– 141, fig. 1.

Material examined.—sinistral female (2.5 mm, with one female and three male *Cabirops* cryptoniscid isopods in the brood chamber), infesting male *Pagurus brevidac-tylus* (Stimpson) (2.1 mm SL), Station 409R, 24°53'13.3"N, 77°54'47.2"W, sand/ algal plain, 1.2–1.8 m, Andros Island, Bahamas, coll. C. B. Boyko, 1 Sep 2000 (AMNH 18204).

Type locality.—24°35′5″S, 46°31′W, 45 m, Brazil (Bourdon 1979).

Distribution and hosts.—Brazil, on Pagurus criniticornis (Dana) (Bourdon 1979); Bahamas, on Pagurus brevidactylus (Stimpson) (herein).

Remarks.—The Bahamas specimen represents a new host record and a significant range extension for the species, which was previously known only from Brazil. The females of this species are extremely close to those of *P. markhami*, but can be distinguished by more delineated segmentation of the pereonites, less pronounced coxal plates (especially on the posterior pereonites), and less pronounced lateral projections on the pleotelson. The males of the two species are easily distinguished by the presence (*P. markhami*) or absence (*P. deflexa*) of lateral projections on the pleotelson and by the different forms of the pleopods.

Pseudionella akuaku, new species Figs. 1–4

Material examined.—Holotype: sinistral female (1.44 mm), infesting left branchial chamber of male *Calcinus imperialis* Whitelegge (2.0 mm SL; AMNH 18187), inhabiting shell of *Planaxis akuana* Rehder, Easter Island, intertidal, coll. C. B. Boyko, Aug 1999 (AMNH 18201). Allotype: male (0.91 mm), same data as holotype (AMNH 18202). Paratypes: sinistral female (1.75 mm), male (1.26 mm) infesting left branchial chamber of male *Calcinus imperialis*

(2.0 mm SL; AMNH 18187), inhabiting shell of *Planaxis akuana* Rehder, Easter Island, intertidal, coll. C. B. Boyko, Aug 1999 (AMNH 18203).

Type locality.—Easter Island, territory of Chile, Pacific Ocean.

Description.—Female (Figs. 1, 2), based on holotype: Body length 1.44 mm, maximal width 1.19 mm, head length 0.48 mm, head width 0.52 mm, pleon length 0.45 mm. Pereon weakly S-shaped; head deflected to the right and pleon weakly to the left. Body outline broad at pereon, narrow at pleon and elongated (Figs. 1A, B). Dark spot or band of pigmentation at junction of all coxal plates and pereonites (in dorsal view).

Head weakly produced with anterior lamina raised and recurved along distal margin. Eyes present, large relative to cephalon, occurring near posterolateral corners of raised lamina edge (but absent in paratype female). Antenna (Fig. 2A) of three articles; antennule (Fig. 2A) of three articles, all segments with fine scales bearing setae on distal margins, distal margins of segments with setae. Maxilliped (Fig. 2B) with elongate rounded spur; palp subcircular with distal narrow, rounded projection; posterior margin setose. First oostegite proximal lobe ovate, distal lobe subtriangular, internal ridge smooth (Figs. 2C, D).

Pereon broadest across pereonite 4, tapering anteriorly and posteriorly. Coxal plates on sides of pereonites all similar but larger on left side of body. Oostegites sparsely covered in minute tubercles; posteriormost oostegite with fringe of setae on posterior margin. Pereopods 3-6 of about same size; pereopods 1, 2, and 7 (Fig. 2E, F) slightly smaller and shorter. Dorsal margins of dactylus and basis, and ventral margins of propodus, carpus, and merus with numerous plate-like scales bearing setae on distal margins; short setae at distal tip of propodus. First two pereopods surrounding head region; no large gaps between any pereopods.

Pleonites 1 and 2 with extended lanceo-

late, distally rounded, biramous pleopods and uniramous short lateral plates; exopodite of pleopod 1 bilobed, endopodite smaller and entire; exopodite and endopodite of pleopod 2 entire; pleonites 3-5 with lanceolate, uniramous pleopods and uniramous short lateral plates (Fig. 2G); lateral plates slightly reduced and pleopods markedly reduced in size from anterior to posterior; pleotelson (Fig. 2H) appears trifid distally as a result of incomplete fusion of segment with sixth pair of lateral plates, all projections subequal in length and width, with pair of large broad lanceolate, distally rounded, uropods. Lateral plates and uropods with dense covering of scales bearing setae on distal margins (Fig. 2I).

Male (Figs. 3, 4), based on allotype: Length 0.91 mm, head length 0.13 mm, head width 0.28 mm, pleon length 0.21 mm. Occurring on ventral side of pleon of female; directed anteroposteriorly.

Head suboval, widest posteriorly, distinct from with first pereonite (Figs 3A, B). Large eyes (relative to cephalon) near posterolateral margin. Antenna of five articles, distally setose; extending posterolaterally from head; antennule of three articles; antennae and antennule with scattered small scales bearing setae on distal margins (Fig. 4A).

Pereonites 3 and 4 broadest, tapering anteriorly and posteriorly. All pereonites directed laterally. Irregular dark pigmentation pattern at junction of body and pereonite lateral projections and on first three pleonites. All pereopods (Figs. 4B, C) subequal, all articles distinctly separated, no scales apparent on dorsal or ventral surfaces.

Pleonites tapering posteriorly and directed laterally. All pleonites distinctly segmented, weakly produced laterally and markedly narrower than pereonites. No midventral tubercles (Figs. 3B, 4D). Pleotelson (Fig. 4D) notched medially with minute anal cone, produced distolaterally into rounded lobes, distolateral corners of lobes with scales and setae; uropods absent.

Distribution and host.-On hermit crabs,

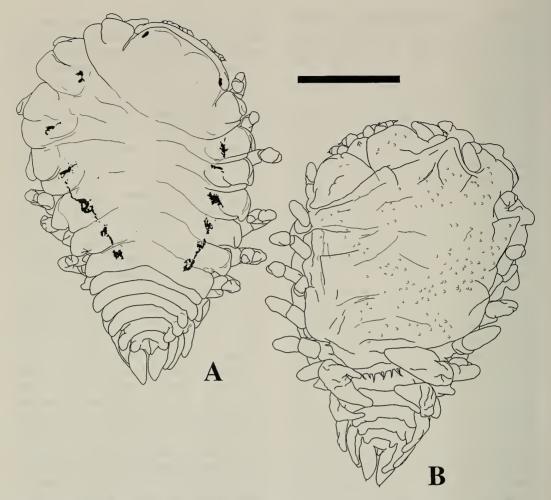


Fig. 1. *Pseudionella akuaku*, new species. Female, 1.44 mm, AMNH 18201, holotype. A, dorsal view; B, ventral view. Scale = 500μ m.

Calcinus imperialis from Easter Island; intertidal.

Etymology.—The specific name *akuaku* is derived from the Rapa Nui word for supernatural beings who sometimes assumed animal shapes (Blixen 1993). The name is used an a noun in apposition.

Remarks.—The pleopodal formula of the female, the attenuated width of the pleonites of the male as compared with the pereonites, and the presence of uniramous pleopods in the male, clearly place this taxon in *Pseudionella*. Additionally, females of all species of *Pseudionella* possess small

lobes on the ventral surface of each pereonite mesial to the pleopods. The nature of these lobes is unknown but, as pointed out by Shiino (1949), they cannot be reduced pleopods as they occur alongside fully biramous pleopods. A comparison with the other three species now placed in this genus shows several important differences between the taxa. *Pseudionella akuaku* n. sp. has a "trilobed" appearance in the pleotelson of the female (i.e., a partly fused sixth pair of lateral plates), very broad uropods of the female, pronounced lateral lobes (fused sixth lateral plates) on the pleotelson

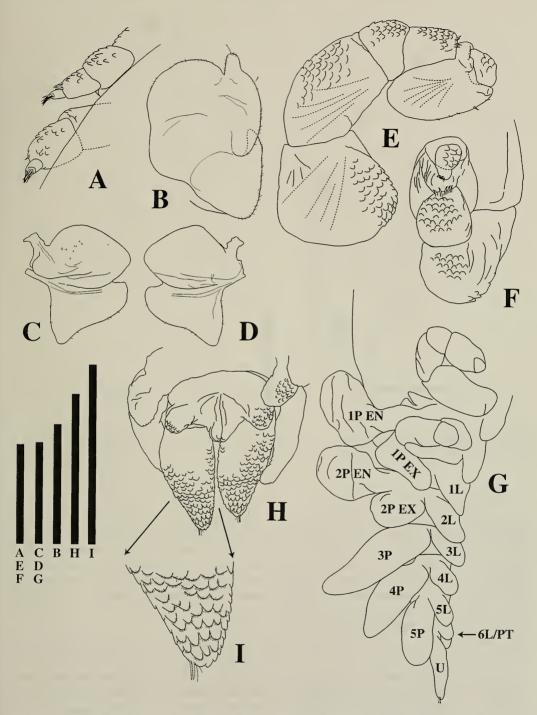


Fig. 2. *Pseudionella akuaku*, new species. Female, 1.75 mm, AMNH 18203, paratype (A–F): Female, 1.44 mm, AMNH 18201, holotype (G–I). A, left antenna and antennule; B, right maxilliped, external; C, right oostegite 1, external; D, right oostegite 1, internal; E, right percopod 1; F, right percopod 7; G, posterolateral view, left side; H, pleotelson and uropods; I, uropod detail (EN = endopod; EX = exopod; L = lateral plate; P = pleopod; PT = pleotelson; U = uropod; numbers indicate pleonite). Scale = 150 μ m (I), 200 μ m (A, E, F), 225 μ m (H), 250 μ m (G), 300 μ m (B), and 500 μ m (C, D).

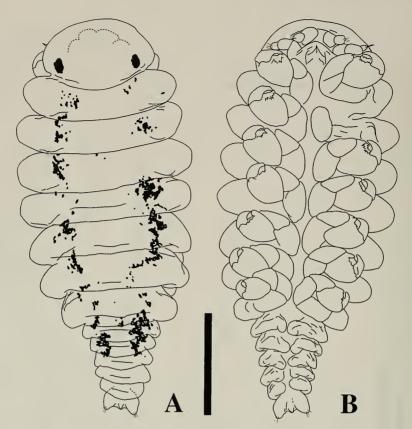


Fig. 3. *Pseudionella akuaku*, new species. Male, 0.91 mm, AMNH 18202, allotype. A, dorsal view; B, ventral view. Scale = 250μ m.

of the male, and flap-like pleopods. In contrast, both P. attenuata and P. deflexa have slender uropods on the female, no lateral lobes on the pleotelson of the male, and tuberculiform pleopods. The pleotelson of P. deflexa does have a "trilobed" appearance, but it is less pronounced than that of P. akuaku n. sp. Pseudionella markhami possesses both flap-like pleopods on the male and broad uropods on the female, while the male has only weakly produced lateral lobes on the pleotelson. The antennae and antennules of female P. deflexa, P. markhami, and P. akuaku n. sp. are each composed of three articles, while those of P. attenuata are 2 and 3 segmented, respectively (Shiino 1949).

Female and male specimens of *Pseudi*onella spp. possess plate-like scales bearing setae on the distal margins of the antennae, antennules, and pereopods. Such scales have been noted in other bopyrids and their fine structure has been examined by SEM in *Heterocepon marginatum* Shiino, 1936, by Janssen & Brandt (1994), who suggested that these scales may aid in attachment to host crabs (for females) or female bopyrids (for males).

The shape of the female pleotelson in all of the nine species of *Pseudione* found on hermit crabs is nondescript, typically being a small rounded or slightly pointed lobe, as is true of *Pseudionella attenuata*. In marked contrast, the female pleotelsons of *Pseudionella deflexa*, *P. markhami*, and *P. akuaku* n. sp. are large and trifid with pronounced and rounded median and lateral lobes. These lateral lobes represent poorly devel-

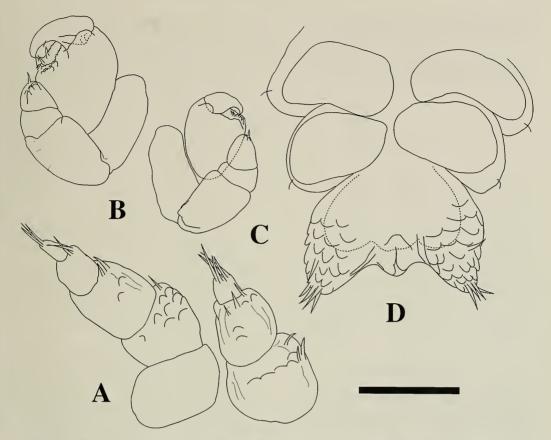


Fig. 4. *Pseudionella akuaku*, new species. Male, 1.26 mm, AMNH 18203, paratype (A); Male, 0.91 mm, AMNH 18202, allotype (B–D). A, right antenna and antennule; B, left percopod 1; C, right percopod 7; D, ventral view of posterior pleonites and pleotelson. Scale = $50 \mu m$ (B, C), $100 \mu m$ (A, D).

oped lateral plates partly fused with the pleotelson and are quite different from the lateral plates found on pleonites 1–5. *Pseudionella attenuata* may represent a transitional form between the hermit crab-infesting *Pseudione* and the other species of *Pseudionella*.

Ecology.—A total of 81 hermit crabs were collected from intertidal and subtidal locations on Easter Island from 22–31 August 1999. Examples of both previously known shallow water hermit crabs from the island were present in the collection: *Calcinus pascuensis* Haig (18 specimens) and *C. imperialis* (65 specimens), as well as a newly recorded species, *C. vachoni* Forest (1 specimen). Only two male hermit crab specimens of *C. imperialis* were found to have bopyrid parasites (2.4% overall prevalence). This is the first report of a member of *Pseudionella* on a species of *Calcinus*, the other three species being known from *Pagurus* spp. (Shiino 1949, Adkinson & Heard 1978, Bourdon 1979).

Key to females of the species of *Pseudionella*

1.	Pleotelson simple P. attenuata
_	Pleotelson "trifid" (with lateral plates)
2.	Medial pereonite segmentation entire
	P. deflexa
	Medial pereonite segmentation indistinct

- 3. Pleotelson lateral plates subacute, extending well beyond apex of pleotelson P. markhami
- Pleotelson lateral plates rounded, subequal to apex of pleotelson
 P. akuaku n. sp.

Key to males of the species of *Pseudionella*

1.	Pleotelson with lateral projections 2
	Pleotelson simple, without lateral projec-
	tions 3
2.	Pleotelson lateral projections large, dis-
	tinct P. akuaku n. sp.
-	Pleotelson lateral projections small, in-
	distinct P. markhami
3.	Pleotelson minute, shorter than pleonite
	5 <i>P. deflexa</i>
-	Pleotelson elongate, longer than pleonite
	5 <i>P. attenuata</i>

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Literature Cited

- Adkinson, D. L., & R. W. Heard. 1978. Description of a new genus and species of Pseudioninae (Isopoda: Bopyridae) parasite of the hermit crab *Pagurus annulipes* (Stimpson) from North Carolina.—Proceedings of the Biological Society of Washington 91:408–417.
- Blixen, O. 1993. The concept of akuaku. Pp. 138–142 in S. R. Fischer, ed., Easter Island Studies. Contributions to the History of Rapanui in Memory of William T. Mulloy. Oxbow Monograph 32.
- Bourdon, R. 1979. Crustacés isopodes: Bopyridae parsites de pagures.—Annales de l'Institut Océanographie, n.s. 55 (suppl.):139–144.
- Codreanu, R. 1967. Classificarea evolutivă a bopirienilor, isopode parazite ale crustaceelor decapode și importanta lor biologică generală.—Studii și Cercetări de Biologie 19:203–211.
- Janssen, H., H., & A. Brandt. 1994. *Heterocepon marginatum* Shiino, 1936, (Crustacea: Isopoda: Epicaridea: Bopyridae) a new hyperparasite from the Philippines, and a short review of the biology of the Bopyridae.—The Philippine Scientist 31:5–31.
- Kossman, R. 1881. Studien über Bopyriden. I, Gigantione moebii und Allgemeines über die Mundwerkzeuge der Bopyriden. II, Bopyrina virbii, Beiträge zur Kenntnis der Anatomie und Metamorphose der Bopyriden.—Zeitschrift für Wissenschaftliche Zoologie, Leipzig 35:652–680.
- Markham, J. C. 1972. Parasitic bopyrid isopods of the amphi-Atlantic genus *Stegophyrxus* Thompson with the description of a new species from California.—Bulletin of the Southern California Academy of Sciences 73:33–41.
- ———. 1978. Bopyrid isopods parasitizing hermit crabs in the northwestern Atlantic Ocean.—Bulletin of Marine Science 28:102–117.
- . 1982. Bopyrid isopods parasitic on decapod crustaceans in Hong Kong and southern China. Pp. 325–391 in B. S. Morton & C. K. Tseng, eds., The Marine Flora and Fauna of Hong Kong and Southern China, vol. 1. Hong Kong University Press.
- . 1988. Descriptions and revisions of some species of Isopoda Bopyridae of the north western Atlantic Ocean.—Zoologische Verhandelingen Uitgegeven Door Het Rijksmuseum van Natuurlijke Historie te Leiden 246:63 pp.
- Nierstrasz, H. F., & G. A. Brender à Brandis. 1931. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. LVII. Epicaridea II.—Videnskabelige Meddedelser fra den Dansk Naturhistoriske Forening i København 91:147–226, 1 plate.
- Rafinesque-Schmaltz, C. S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. Palermo, 224 pp.

- Shiino, S. M. 1933. Bopyrids from Tanabe Bay.— Memoirs of the College of Science, Kyoto Imperial University Series B 8:249–300.
- . 1936. Bopyrids from Shimoda and other districts.—Records of Oceanographic Works in Japan 8:161–176.
- —. 1949. On two new genera of Bopyridae found in Japan.—Bulletin of the Biogeographical Society of Japan 14:57–63.
- ——. 1958. Note on the bopyrid fauna of Japan.— Report of Faculty of Fisheries, Prefectural University of Mie 3:29–74, pl. 3.