AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Thomas, James Darwin, 1997. Systematics, ecology and phylogeny of the Anamixidae (Crustacea: Amphipoda). *Records of the Australian Museum* 49(1): 35–98. [4 July 1997].

doi:10.3853/j.0067-1975.49.1997.298

ISSN 0067-1975

Published by the Australian Museum, Sydney

Records of the Australian Museum (1997) Vol. 49: 35–98. ISSN 0067-1975

Systematics, Ecology and Phylogeny of the Anamixidae (Crustacea: Amphipoda)

JAMES DARWIN THOMAS

Nova University, Oceanographic Center, 8000 N Ocean Drive, Dania, FL 33004, USA
thomasjd@ocean.nova.edu

ABSTRACT. Thirteen new species and one new genus are described in the commensal amphipod family Anamixidae, bringing the total to 33 species in three genera. Thirteen species are recorded from the Pacific Ocean, eight from the Indian Ocean and four from the Caribbean. Developmental stages are documented in four species of *Anamixis* Stebbing, 1897 and one species of *Nepanamixis* n.gen. Developmental stages in *Nepanamixis* are profoundly different from those of *Anamixis* and *Paranamixis* Schellenberg, 1938. All new taxa are fully described and figured. Previously described taxa are reviewed and illustrated where necessary.

The cryptic Anamixidae are found in coral reefs and other hard-bottomed, shallow, tropical waters. An unusual tropical relic, *A. tangaroa* n.sp., is described from cold waters in the Bass Strait, Australia. Current species distributions and information probably reflect collecting bias as many areas remain uncollected.

Cladistic analysis of the Anamixidae proved informative in the *Nepanamixis–Anamixis* group where adequate specimens of new and existing species were available for examination. Results were less informative for *Paranamixis*.

THOMAS, JAMES DARWIN, 1997. Systematics, ecology and phylogeny of the Anamixidae (Crustacea: Amphipoda). Records of the Australian Museum 49(1): 35–98.

Amphipods of the family Anamixidae are commensals in sponges and ascidians and occur throughout the world's tropical and subtropical marine systems. They exhibit an unusual life history pattern involving two highly dissimilar developmental stages that occur simultaneously in the host (Thomas & Barnard, 1983). These two stages are so different they were previously assigned to separate families. Initial, or, "leucomorph" developmental stages (male and female) of different anamixid species are nearly identical, while the transformed, or "anamorph" stage (always male) is distinct for each species. In a remarkable transformation, leucomorph males pass via a single moult to anamorph males. This transformation is accompanied by a number of extreme morphological changes that explain their placement in separate families prior to this discovery. Leucomorphs outnumber anamorphs in the host approximately 10:1. Nearly all leucomorph females are ovigerous. It is not known which male stage (or both) interacts reproductively with the female. The fate of post-brood females remains unknown.

Background

Most of what we know of amphipod taxonomy, ecology and community structure shows a strong temperate bias. Tropical marine systems offer promising avenues of research, but advances are often highly unpredictable because so little is known. Coral reefs are geographically discrete, widespread biological systems that exist within a narrow range of biological and physical conditions. Coral reefs present a complex mosaic of macro and microhabitats (Hay, 1981) e.g., live coral, coral rubble, turf algae, sessile invertebrates, and reef-derived sediments, that allow ecological comparisons to be made. However, the small size of tropical amphipods (2–4 mm) combined with difficulties in obtaining representative collections from reef sites has hindered taxonomic and systematic progress within the group.

Cryptic and commensal reef species form highly localised populations, further minimising dispersive capabilities. For this reason, the author has chosen to focus research efforts primarily on cryptofaunal and commensal amphipods, with the assumption that their morphologies and distributions more clearly reflect evolutionary events than do epifaunal forms that can be widely dispersed and exhibit high phenotypic plasticity (Schram, 1986; Conlan, 1988).

Adequate representative samples of amphipods can be procured only by *in-situ* collection from specific substrates with the use of SCUBA techniques. To obtain representative samples of smaller benthic crustaceans, specific collecting programs must be undertaken. This habitat-intensive approach to collecting has opened a new era in the systematic study of shallow-water marine amphipods and other small invertebrates and has provided much new and exciting material for study.

Review of the Anamixidae

Prior to this research there were 13 described species of anamixids, in two genera, *Anamixis* and *Paranamixis*. These two genera were distinguished by the presence (*Anamixis*), or absence (*Paranamixis*), of first gnathopods. The majority of what is known of anamixid biology and ecology has been reported by the author and co-workers (Thomas, 1979, 1981; Thomas & Taylor, 1981; Thomas & Barnard, 1983). Prior to the discovery of the unique transformation process in anamixids (Thomas & Barnard, 1983), leucomorph stages of anamixids were assigned to a separate family, the Leucothoidae. Anamorphs are characterised by having extremely reduced and fleshy mouthparts, in having coxa 1 reduced or vestigial, and in having greatly enlarged second gnathopods and coxae 2–4 that act as a lateral shield to enclose the animal during feeding. Leucomorphs also show various modifications and reductions in structure, but possess only slightly reduced, spinose mouthparts and morphologically unique second gnathopods. Investigations by the author have shown that the transformation moult is not terminal and can be followed by several instars. Before discovery of the transformational process leucomorphs had been assigned to a number of species in the genus *Leucothoides* Shoemaker, 1933 in the Leucothoidae. Leucomorph stages of major anamixid groups are, in most instances, nearly identical and cannot be readily separated at the species level with the exception of the more primitive groups where both stages have morphologically distinct first and second gnathopods. In cases where the transformation process has been documented, or both stages collected *in-situ* from their invertebrate hosts, specific identifications can be made. These combinations of circumstances have produced an extremely tangled taxonomy.

Documentation of the transformation process in anamixids created a sizeable taxonomic problem, because there were now a dozen described species of *Leucothoides* with no possibility to associate them with their anamorph counterparts. This can only be accomplished by collecting the stages *in-situ* from their specific hosts, or by confirmation through rearing experiments that document the transformation process (Thomas & Barnard, 1983). To date, the author has documented the transformation process or confirmed host specificity for four species of anamixids. For detailed explanations regarding rearing methodologies and host confirmation procedures, see Thomas & Barnard (1983). Developmental information on all other taxa is lacking. It must be emphasised that occurrence of both stages in the same general collection does not necessarily confirm taxonomic relationships because most reef areas contain several anamixid species. Problems in the family with unassociated morphologies restrict primary taxonomic emphasis within anamixids to anamorphs, but because leucomorphs represent early developmental stages, they can be highly informative in determining generic limits and relationships from an ontogenetic perspective.

Distribution

The genus *Paranamixis* appears confined to the Pacific and Indian Ocean basins, while *Anamixis* is widespread, with representatives in all tropical oceans. Members of the more plesiomorphic *Nepanamixis* n.gen., are distributed as possible Gondwanaland relicts across the Indian and Pacific Oceans and the Caribbean Sea (Newman, 1991).

Ecology

Host associations for anamixids (when known) are the interior of small asconoid sponges and the branchial cavity of solitary and compound tunicates where the amphipods utilise host-generated currents to filter fine particulates. Where associations are known, anamixids appear highly specific in the choice of host and are either restricted to a particular host species, or in the case of multiple host species, are restricted to similar-sized interior feeding chambers. Unfortunately, host and ecological data are only available for a handful of species (Thomas & Barnard, 1983).

Information from host data, feeding behaviour, and distribution patterns can be valuable sources of information in phylogenetic studies. Observations from

natural history studies and in-situ observations can aid in interpreting convergent morphologies in certain structures. An example of this approach are attempts by the author to evaluate the presence of similar lateral ridges on the cephalic margin of anamixid species in different genera such as *A. vanga* and *P. kanu*. Ecological studies have shown these ridges are present only in those species inhabiting large solitary ascidian hosts, thus, this character probably reflects convergent adaptations to similar feeding strategies and not similar evolutionary histories. Such ecological information can assist in hypotheses addressing the evolutionary significance of a given morphology. In this regard the author agrees strongly with Brusca (1984) who stated similar views regarding isopods.

Selected taxonomic characters

The following characters are some of the more important for taxonomic purposes in the Anamixidae:

Head region: The presence or absence of a lateral keel on the head that serves to align the head against coxa 2 when the head is flexed ventrally during feeding. The morphology and microstructure of the ventral keel located in the mid-region on the ventral portion of the head. The relative length of antennae 1 and 2, and enlargement of the first peduncular segment of antenna 1.

Mouthparts: Standard light microscopy provides limited information on the microstructure of the mouthpart field, except in the case of the elongate and hyper-developed maxilliped palp and prominent ventral keel. Except for the maxilliped palp and ventral keel, the remaining mouthparts are reduced, fleshy and transparent in anamorph stages and are best observed by SEM or differential interference contrast microscopy. The maxilliped, enlarged and modified for food-handling, exhibits various reductions and degrees of fusion in the inner plates, while the outer plates bear vestigial inner lobes in the more plesiomorphic taxa.

Coxal morphology: The general size and dominance of various coxae, their shape and ornamentation can be important features. The morphology and amount of reduction in coxa 1 are important at the generic level. The morphology and ornamentation of the margins of the relatively larger coxae 2–4 are important at the species level, as is the relative dominance of coxae 2–4.

Gnathopods: Gnathopod 1 is present and reduced in most species of *Anamixis*, except for *A. jebbi* n.sp., where it is vestigial in transformed males. In *Paranamixis*, gnathopod 1 is lacking in all post-transformational anamorphs. However, the author has documented tiny vestiges of gnathopod 1 in 2 species of *Paranamixis*, assumed to persist at the transformational moult itself, a remnant of the leucomorph stage. All subsequent stages of *Paranamixis* are characterised by the complete lack of gnathopod 1 in post-transformational anamorphs. When gnathopod 1 is present, the general morphology and dimensions of article 5 (carpus) are important at the generic and specific levels. Patterns of armament and terminal ornamentation of article 6 are informative at the specific level. Anamorphs of *Nepanamixis* n.gen., possess a distinct gnathopod 1 with a basally-expanded carpus, and a linear gnathopod 2 with a geniculate carpal lobe, differing from all other species and underscoring the taxonomic importance of these appendages. Leucomorphs of *Nepanamixis* n.gen., also exhibit a unique configuration of gnathopods 1 and 2, further distinguishing them from all other juvenile anamixid morphs, providing a means of identifying the presence of *Nepanamixis* n.gen., in collections, even when anamorphs are lacking. Gnathopod 2 is greatly enlarged and modified for filter feeding and possesses a number of morphological and morphometric characters of value such as accessory ornamentation (spines, cusps, ridges, long setae) of article 2 (basis); the presence or absence of a serrate carpal ridge (either lateral or medial) on article 5 (carpus); the shape, armament, and morphometrics of article 6 (propodus); the shape, morphology and armament of the dactyl (article 7). The large second gnathopods bear mediofacial setae on the propodus that are used in filter feeding. *Nepanamixis* has two rows of this specialised seta, while *Anamixis* and *Paranamixis* both have a single row. Leucomorph stages possess unique second gnathopods that differ substantially from anamorph forms, being relatively smaller in size and having a prominent transverse palm.

Uropods: Anamorphs differ from leucomorphs in having the outer rami of uropods 2 and 3 reduced to about half the length of the inner ramus. Two species of *Paranamixis* have uropods and peduncles completely lacking spines. All other taxa have spines on the rami and peduncles of uropods 1–3.

Some characters may be especially difficult to observe under normal light microscopy and previous descriptions may be deficient in many cases in enumerating these features. For example, the lateral serrate ridge on the basis of gnathopod 2 in *P. clarkae* is hard to distinguish without Nomarski or phase contrast microscopy. The condition of the apices of the inner plates of the maxilliped is another situation that requires careful examination to accurately assess. Caution must be used in the analysis and interpretation of minute or hard to observe structures. This is especially true in constructing character transformation series for cladistic analysis. There is no substitute for careful and thorough examination of material, however, there are times when specimens are not available for examination and existing descriptions and illustrations lack the minute detail now required in taxonomic descriptions. In these circumstances, the taxonomist must make the best use of available character data.

Methodology

1. Thirteen new species and one new genus are described based on detailed character analysis.

2. Available type material are reviewed in cases where original species descriptions and figures were not adequate to interpret important taxonomic characters.

3. When type material was not available, comparative materials of extant species were used in efforts to resolve taxonomic problems. Material of several species, notably *A. stebbingi, P. bocki* and *P. madagascarensis*, was unavailable for analysis and use of character information was limited to the original descriptions of these species.

4. A detailed study of morphological characters was undertaken to more clearly define selected characters of primary taxonomic importance that would help in the development and interpretation of character state transformation series.

5. Ecological studies of host preference relationships were carried out in an effort to determine whether particular types of associations demonstrated any relationship(s) to selected morphological characters exhibited by the amphipods.

6. Attempts to associate leucomorphs with anamorph counterparts by rearing and/or host confirmation studies have confirmed four leucomorph stages.

7. A complete monographic treatment of the Anamixidae (primarily anamorphs) is presented, with revised family, generic, and specific diagnoses, with keys to all groups. This treatment includes an estimation of anamixid phylogeny generated by the computer program HENNIG86.

Holotypes of all new species have been deposited in the U.S. National Museum (USNM) and the Australian Museum (AM), except where prior arrangements were made with other institutions. Excess specimens will be distributed to interested museum departments that currently house substantial amphipod collections.

Computerised numerical phylogenetic programs were used to produce several trees that were most parsimonious and well resolved. There were no existing cladistic hypotheses to test, either of marine amphipods in general, or tropical amphipods in particular. Distribution patterns represented in the tree(s) (e.g., taxon-area cladograms) were used to infer ancestor-descendant relationships and distribution patterns.

Figure abbreviations (used in specimen drawings). Capital letters in figures refer to parts; lower case letters to the left of capital letters refer to specimens cited in legends and voucher material in the text; lower case letters to the right of capital letters refer to adjectives described below. A—antenna, B—body, C—head, D—dactyl of gnathopod or pereopod, E—coxa, F—accessory flagellum, G—gnathopod, H—peduncle, I—inner plate/ramus, K—ventral keel, M—mandible, O—outer plate/ramus, P—pereopod, R—uropod, T—telson, U—urosome, V—palp, W—pleon, X—maxilliped.

Lower case letters on the left side of labels denote specimens cited in the legends and voucher material in the text; lower case letters on the right side of the labels (or affixed to the drawings as is often the case) indicate the following: c—carpus, d—dorsal, e—broken, f—flat, h—half, i—medial, l—lateral, ll—lower lip, m—medial, n—oblique, o—opposite, p—distal, r—proximal, s—setae removed, t—right, u—left, v—ventral y—enlarged.

Letters in quotation marks are redrawn from previous figures, the drawing using the first letter of the species name.

Taxonomy

Anamixidae Stebbing, 1897

Diagnosis. Accessory flagellum minute, 1–2 articulate, or lacking. Pereonite 1 with lateral locking ridge. Mouthparts reduced in size and complexity, especially in terminal males. Mandible lacking molar. Inner plates of maxilliped reduced, partially to completely fused; outer plates with inner lobes reduced or absent. Coxa 1 much smaller than coxa 2. Coxae 2–4 enlarged; coxa 2 usually subequal to or dominant to coxae 3–4, coxa 3 occasionally dominant. Margins of coxae 2–4 smooth, anterior margin variously expanded, produced, or cuspate, usually with subapical setae. Gnathopod 1 reduced, vestigial, or absent; carpochelate. Gnathopod 2 greatly enlarged, carpochelate.

Description. Based on transformed males: Body laterally compressed, smooth, slick and shiny. Rostrum small to large and thick; lateral cephalic lobes weak, eyes ommatidial. Antenna 1 slender, often partially attached to rostrum, peduncle long, article 2 often as long as 1, main flagellum sparsely articulate, accessory flagellum vestigial or absent, rarely 2-articulate. Antenna 2 slender, feeble.

Mouthparts in terminal males (anamorphs) as follows: Epistome strongly produced anteriorly, front of head with midventral keel; labrum asymmetrically incised. Mouthparts except maxilliped extremely reduced, fleshy and vestigial, dominated by midventral keel. Mandibular palp vestigial, represented by setae; upper and lower lips, maxillae 1 and 2, lacking any spination or ornamentation. Maxilliped enlarged, inner plates reduced, partially or completely fused; outer plates reduced with inner lobes present or absent, when present represented by small medial process; palp 4-articulate, articles 1 and 2 with medial setae; articles 3 and 4 with multiple rows of parallel setae giving rugose appearance, palp article 4 elongate.

Mouthparts in females and non-transformed males (leucomorphs) as follows: Mandibles lacking molar, raker row long, incisors broad, toothed, wavy or with only one lateral notch, palp slender, feeble, 1- or 3-articulate, article 3 short, setae sparse. Labium with inner lobes discrete or fused to outer, gape moderate to absent, mandibular lobes well developed. Inner plates of maxilla 1 small, naked or sparsely setose, outer plate with 5–9 spines, palp 1- or 2-articulate. Maxilla 2 feeble, inner plate broad, medial setae sparse but thick and short, spine-like outer plate much more slender and sparsely setose. Outer plates of maxillipeds moderately developed to absent, inner plates small, small and discrete or mostly fused together or vestigial, palp of maxilliped long, thin, 4-articulate.

Coxa 1 hidden by shield-like coxae 2–4; coxa 2 (or 3) largest, 4 scarcely larger or smaller than 3, weakly excavate or not, ventral margin produced or not; coxae 5–6 smaller, bilobed, hind margin of 6 deeper than 5; coxa 7 entire. Gnathopod 1 small, vestigial, or absent, carpochelate, often 6-articulate. Gnathopod 2 very large and often strongly carpochelate; carpus furnished with dense tufts of medial feeding setae; hand large in males and some females, elongate, oval, weakly to strongly sculptured, palm transverse, oblique, or absent, with 1 or 2 dense rows of mediofacial setae; dactyl long, overlapping hand and carpal process.

Pereopods 3–4 slender, reaching same extent. Pereopods 5–7 alike, short, bases expanded, 7 often lobate or serrate. Pleopods biramous, multiarticulate.

Uropods 1–3 slender, reaching same extent or outer ramus shortened, uropod 3 often breaking; rami lanceolate, outer ramus on 1–2 strongly shortened, on 3 moderately shortened, ramal spines absent to moderate. Telson short to long, ovate, entire.

Gills present on gnathopod 2 to pereopod 6, small, simple, ovate.

Sexual dimorphism. Largely seen in transformed males. Mouthparts except maxillipeds becoming reduced or vestigial, dominated by ventral keel; inner plates of maxilliped becoming severely reduced and partially or completely fused; inner lobes of outer plates becoming reduced or absent. Female gnathopod 2 relatively smaller than non-transformed males, with moderate carpal lobe, distinct palm, and recurved dactyl fitting palm. Oostegites present on pereopods 3–5, typical, with marginal setae. Transformed males with reduced coxa 1 and enlarged gnathopod 2, with carpal process and dactyl immense.

Remarks. The Anamixidae and some Leucothoidae have been assumed in the past to be piercing and sucking inquilines, usually found in warm shallow waters on sessile invertebrates, particularly sponges, tunicates, coral, and perhaps hydroids. However, Thomas & Taylor (1981) found *A. cavatura* to be filter feeders, inhabiting the interior cavities of the hosts where they utilise host-generated currents to filter out food particles on the carpal lobes of the enlarged second gnathopods. The presence of the "piercing stylet" (ventral keel) is not used to pierce host tissue in a parasitic feeding mode, but is instead used to align the large antennal peduncles when they are folded down for feeding, allowing the antennal flagella to be freely articulate during feeding. Thomas & Barnard (1983) also found leucomorphs to be filter feeders, occupying the host in larger numbers with their anamorph counterparts.

Taxonomy. The discovery of the remarkable transformation process by Thomas & Barnard (1983) created sizeable taxonomic confusion because females and non-transformed males had been placed in the genus *Leucothoides* in the Leucothoidae. By redefining the Anamixidae to include only leucothoid-like taxa with reduced coxa 1, *Leucothoides* became a synonym of *Anamixis*. This left a number of anamixids known only from brief descriptions, only one of which allowed specific assignment to an anamorph counterpart (*L. pottsi* = *A. cavatura*). While the transformed males are distinctive, females and non-transformed females of different species exhibit only minute differences and can only be placed to species with certainty by rearing or host confirmation studies. It cannot be assumed that unassigned leucomorphs belong to the common anamorph in an area because extensive collecting efforts by the author have shown that most localities yield multiple species of anamixids, each with their own specific leucomorph.

Investigations by the author show leucomorphs of *Anamixis* and *Paranamixis* to be similar, whereas leucomorphs of *Nepanamixis* are quite distinct. Because of the lack of complete information regarding leucomorphs, taxonomy of anamixids is, of necessity, based primarily on anamorphs. However, because leucomorphs represent developmental stages, consistent morphological differences exhibited at this stage can provide valuable information on evolutionary relationships. For instance, the morphological differences between leucomorphs of *Nepanamixis* and those of *Anamixis* and *Paranamixis* provide strong evidence for *Nepanamixis* as a plesiomorphic genus, ancestral to both *Paranamixis* and *Anamixis*.

Keys to Genera of Anamixidae

(Terminal Males)

KEY I

1. Gnathopod 1 present, article 5 basally inflated ..... *Nepanamixis* n.gen.

—— Gnathopod 1 present, absent, or vestigial. If present, article 5 basally thin 2

2. Gnathopod 1 present, occasionally vestigial ..... *Anamixis*

—— Gnathopod 1 absent ..... *Paranamixis*

KEY II

1. Eyes with 9 ommatidia; maxilliped with inner plates cleft more than one-half, outer plates with inner lobes; carpus of gnathopod 1 basally expanded; coxa 1 moderately reduced, approximately one-half the width of coxa 2; gnathopod 2 with serrate ridge on carpal lobe, propodus with 2 rows of mediofacial feeding setae; ventral margin of coxa 4 crenulate or emarginate; telson triangular ..... *Nepanamixis* n.gen.

—— Eyes normally with 12–20+ ommatidia, occasionally 7; maxilliped, inner plates fused or with apical notch or cleft, outer plates lacking inner lobes; coxa 1 greatly reduced, approximately one-quarter or less the width of coxa 2; gnathopod 2 with carpal lobe smooth or serrate, propodus with 1 row of mediofacial feeding setae; ventral margin of coxa 4 rounded; telson ovate 2

2. Gnathopod 1 present (vestigial in *Anamixis jebbi*) ..... *Anamixis*

—— Gnathopod 1 absent ..... *Paranamixis*

Anamixis Stebbing

Anamixis Stebbing, 1897: 35.
Leucothoides Shoemaker, 1933: 249.

Type species. *Anamixis hanseni* Stebbing, 1897 by monotypy; *Leucothoides pottsi* Shoemaker, 1933, by monotypy.

Diagnosis. In terminal males: Antennae long; anterior margin of head oblique or transverse, with or without anteroventral cusp; eyes with ommatidia compact and numerous, or reduced in number and diffuse; inner plates of maxilliped fused into apically rounded process, or with apical notch, outer plates lacking inner lobes in most taxa. Coxa 1 greatly reduced, remainder of gnathopod 1 present, small, occasionally reduced to fleshy remnant; carpus not inflated basally. Gnathopod 2, propodus with single row of mediofacial feeding setae. Telson 1.1–1.6 longer than wide.

Variables. Head, differing in morphology on lateral, anterior and ventral margins; morphology of ventral keel; in shape and morphology of coxae 2–4; in shape and ornamentation of gnathopods 1 and 2.

Relationships. Differing from *Paranamixis* in the apically fused inner plates of the maxilliped and in presence of gnathopod 1 in post-transformational anamorphs. Differing from *Nepanamixis* in the relatively longer antennae, more numerous ommatidia, smaller coxa 1, in the carpus of gnathopod 1 thinner and lacking prominent cusps; in having gnathopod 2 with single row of mediofacial feeding setae, and the shorter telson.

Leucomorphs of *Anamixis* and *Paranamixis* are distinguished at the specific level by minute characters. *Anamixis* leucomorphs differ from *Nepanamixis* leucomorphs in having fewer ommatidia, a longer carpal lobe with only 2 embedded spines in gnathopod 1, and a more transverse palm in gnathopod 2. However, due to the present inadequate knowledge regarding leucomorphs of all three anamixid genera, characters of the few known leucomorphs cannot be construed as all-inclusive. While some leucomorph characters are highly informative, taxonomy of anamixids must be weighted toward morphological characters exhibited in all taxa. Thus, gnathopod 1, while of possible contradictory value, is retained as an important descriptive character until more complete character information becomes available.

Species: *Anamixis aldabra* n.sp.; *A. barnardi* Sasidharan, 1983; *A. bazimut* n.sp.; *A. cavatura* n.sp.; *A. excalibur* n.sp.; *A. falarikia* J.L. Barnard, 1965; *A. hanseni* Stebbing, 1897 (not Thomas 1979, 1981, 1983); *A. jebbi* n.sp.; *A. kateluensis* n.sp.; *A. mahe* n.sp.; *A. moana* here designated, J.L. Barnard, 1970 (*A. stebbingi*); *A. nedcampensis* n.sp.; *A. ningaloo* n.sp.; *A. pacifica* J.L. Barnard, 1955, 1969, 1979 (= *A. linsleyi*); *A. papuaensis* n.sp.; *A. stebbingi* Walker, 1904 (?Nayar, 1967) not Barnard, 1965, 1970, 1971; *A. tangaroa* n.sp.; *A. torrida* J.L. Barnard, 1974, (anamorph unknown); *A. vanga* n.sp.; *A. yarrega* (J.L. Barnard, 1974).

Other records. Recorded as leucomorphs: species V (Loggerhead Key) J.L. Barnard, 1974; species Q (Albatross) J.L. Barnard, 1974; species 2 from Micronesia, J.L. Barnard, 1974; species, J.L. Barnard, 1974; species (*A. pottsi* of Hirayama, 1983).

Distribution. Marine, Indo-Pacific, Micronesia, Caribbean, Western Atlantic, primarily warm shallows, especially coral reefs, endocommensals with sponges and ascidians, 0–89 m, 19 species as anamorphs, otherwise 18 species.

Key to the Species of *Anamixis*

(*Anamixis stebbingi* excluded because character data unavailable)

1. Article 2 of gnathopod 2 with 3 or more long setae on anterior margin 2

—— Article 2 of gnathopod 2 lacking long setae on anterior margin 3

2. Gnathopod 1 geniculate, reduced in size, but of normal proportions for genus, articles distinct; gnathopod 2, coxa produced into a sharp process midapically, article 2 with 10 or more numerous long setae on anterior margin ..... *A. aldabra* n.sp.

—— Gnathopod 1 greatly reduced, barely visible as a shrivelled appendage, articles indistinct; gnathopod 2, coxa rounded midapically, article 2 with 3 long setae on anterior margin ..... *A. jebbi* n.sp.

3. Carpal lobe of gnathopod 2 with thumb-like process 4

—— Carpal lobe of gnathopod 2 lacking thumb-like process 6

4. Gnathopod 1, articles 5 and 6 with 2 and 1 long apical setae respectively ..... *A. mahe* n.sp.

—— Gnathopod 1, articles 5 and 6 lacking long apical setae 5

5. Coxa 4, ventral margin convex; gnathopod 1, article 5 longer than article 6, apex dilated; gnathopod 2, mesoproximal border of carpus smooth ..... *A. nedcampensis* n.sp.

—— Coxa 4, ventral margin concave; gnathopod 1, article 5 subequal to article 6 in length, apex tapered; gnathopod 2, mesoproximal border of carpus denticulate ..... *A. barnardi*

6. Gnathopod 1, articles 5 and 6 each with long terminal seta, or article 6 with terminal spine 7

—— Gnathopod 1, articles 5 and 6 lacking terminal ornamentation 10

7. Gnathopod 1, articles 5 and 6 each with long terminal seta, 0.5 times the length of each article 8

—— Gnathopod 1, article 5 lacking ornamentation, article 6 with terminal spine, 0.3 times the length of article ..... *A. pacifica*

8. Lateral margins of head rounded, ventral keel sharp 9

—— Lateral margins of head excavate; ventral keel truncate ..... *A. vanga* n.sp.

9. Anterior margin of head oblique, lacking any defining process; anterior margin of ventral keel with small teeth; article 6 of gnathopod 2 elongate, 3.0–3.1 times longer than wide, inner margin of dactyl smooth ..... *A. hanseni*

—— Anterior margin of head transverse, defined by cusp at anteroventral corner; anterior margin of ventral keel smooth; article 6 of gnathopod 2 not elongate, 2.1–2.2 times longer than wide; inner margin of dactyl tuberculate ..... *A. cavatura* n.sp.

10. Head enlarged, anteroventral corner defined by large process; first peduncular segment of antenna 1 enlarged; palp article 4 of maxilliped elongate, 1.9 times length of article 3 11

—— Head not enlarged, anteroventral corner defined by small cusp or process; palp article 4 of maxilliped, 1.1 –1.8 times the length of article 3 13

11. Ventral keel a wide triangular process; gnathopod 2, coxa immense, greatly exceeding coxa 3–4 in size, carpal lobe less than one-half of propodus, hindmargin of propodus oblique with numerous serrations or teeth 12

—— Ventral keel sabre-shaped, extending well below ventral margin of head; gnathopod 2, coxa narrow, smaller than 3 or 4, carpal lobe reaching end of propodus, hindmargin of propodus rectilinear with 3 major teeth ..... *A. excalibur* n.sp.

12. Gnathopod 2: carpal lobe serrate; propodus with large cuspate basomedial process; hindmargin of propodus with small serrations; dactyl with 2 processes on inner margin, apex excavate ..... *A. papuaensis* n.sp.

—— Gnathopod 2: carpal lobe smooth; propodus lacking basomedial process; hindmargin of propodus with 5 major teeth; inner margin of dactyl smooth, apex bifid ..... *A. falarikia*

13. Gnathopod 2: carpal lobe straight, blunt, reaching to end of propodus; propodus rectilinear, hindmargin straight, unarmed; inner margin of dactyl unarmed. Inner plates of maxilliped apically notched or broadly truncate 14

—— Gnathopod 2: carpal lobe either long and recurved, or if short, blunt; propodus not rectilinear, hindmargin with oblique palm, with teeth or excavations; inner margin of dactyl armed. Inner plates of maxilliped apically rounded or cleft 16

14. Antenna 2 shorter than 1; coxa 3, ventral margin tapering posteriorly, anterior margin expanded; ventral keel small, anterior margin oblique, posterior margin defined by ventral tooth ..... *A. kateluensis* n.sp.

—— Antenna 2 subequal to 1; coxa 3, ventral margin quadrate, anterior margin straight; ventral keel a broad process, lower margin projecting well below ventral margin of head 15

15. Entire anterior margin of ventral keel perpendicular and parallel to anterior margin of head, distal margin with small anterior-directed tooth; ventral margin of coxa 2 with distinct angular projection ..... *A. bazimut* n.sp.

—— Anterior margin of ventral keel tapering posteriorly into a ventrally projected triangular tooth; ventral margin of coxa 2 with slight midventral angle ..... *A. moana* n.sp.

16. Inner plates of maxilliped apically rounded; coxa 2 ventrally produced; telson 1.3–1.4 times longer than wide 17

—— Inner plates of maxilliped cleft one-third; coxa 2 ventrally excavate; telson 1.7 times longer than wide ..... *A. tangaroa* n.sp.

17. Ventral keel large, sharp, with 3 small anterodistal teeth; gnathopod 2, carpal lobe short and blunt, hindmargin of propodus tapering with 2 major and 2 minor teeth, inner margin of dactyl with 2 processes, the innermost serrate, the outermost with paired setae ..... *A. ningaloo* n.sp.

—— Ventral keel small, truncate, lacking teeth; gnathopod 2, carpal lobe long, recurved, hindmargin of propodus convex, with 1–2 minor cusps, inner margin of dactyl evenly tuberculate ..... *A. yarrega*

Anamixis aldabra n.sp.

Fig. 1

Type material, HOLOTYPE, male "A", 2.52 mm, USNM 235727, forereef slope, Picard Island, Aldabra, Seychelles, formalin wash of coralline algae encrusted coral head, 2.5 m, J.D. Thomas, 17 April 1983, JDT-Ald-19. 1 PARATYPE, male "B", 2.58 mm, USNM 235728, Picard Island, Aldabra, Seychelles, formalin wash of rubble from forereef, 2.5 m, J.D. Thomas, 3 April 1983, JDT-Ald-5a.

Diagnosis. Anterior margin of head transverse. Gnathopod 1, article 6 geniculate. Anteroventral margin of head quadrate. Gnathopod 2, coxa produced into sharp process midventrally; basis with numerous long setae on lower anterior margin; carpus bearing weakly rounded, bifid process near apex. Coxae 3–4 tapering ventrally, anterior margin of coxa 3 expanded.

Description. Head, anteroventral margin quadrate, lacking cusps or other process; antenna 1 ratio 21:15:13; ventral keel scarcely extending below head margin, broadly rounded with slight ventral protuberance; eyes red in 7-year formalin, ommatidia with 16–18 coloured facets, and 2 clear facets at posterior margin of eye. Lower lip lobes not readily visible from lateral view. Antenna 1, article 3 of peduncle much thinner than articles 1–2; flagellum 10-articulate, aesthetascs on articles 8–9. Antenna 2, flagellum 4- or 5-articulate. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.8 times length of article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa rounded anteroventrally, bearing 2 small apical setae; propodus exceeding carpus in length, slightly recurved at apex, inner margin serrate with small embedded setae. Gnathopod 2, coxa subequal in size to 3 and 4, lower margin produced into sharp midventral projection, several small setulae embedded submarginally; basis expanded distally, with 12 long setae on anterior and medial surface; carpus inflated and slightly recurved, anterior surface irregular and indented, bearing several small setae, distal portion with an indentation and weakly rounded process near apex bearing a seta, apex furnished with 5 apical and 2 subapical setae; Posterior margin of propodus narrowed posteriorly, row of mediofacial setae extending nearly one half the length of palm, posterior margin with scattered setae, ventral margin defined by quadrate process laterally, medial margin oblique; dactyl straight, unarmed, bearing 2 setae on small rounded process. Pereopod 3, coxa with anterior margin expanded, apex broadly rounded and tapering posteriorly, with 5–6 submarginal setae; posterior margin defined by small cusp; remainder of pereopod normal. Pereopod 4, coxa rounded ventrally, tapering posteriorly, 5–6 submarginal setae present, posterior margin expanded at midpoint, then tapering forward to pereonite; remainder of pereopod similar to pereopod 3. Pereopods 5–6 similar, coxae bilobed; basis spinose anteriorly, evenly rounded posteriorly. Pereopod 7, coxa entire; basis spinose anteriorly, posterior margin with several notches bearing setae. Uropods 1 and 2, outer ramus about one-half the length of inner ramus. Uropod 3 missing. Telson 1.9 times longer than wide, with 2 apical setae and two pairs of dorsofacial setae.

Etymology. Named for the type locality, Aldabra Atoll, a noun in apposition.

Relationship. *Anamixis aldabra* is distinct in bearing numerous long setae on the basis of gnathopod 2, and in having a geniculate propodus on the first gnathopod. *Anamixis aldabra* appears to show no clear affinities to its nearest geographic neighbour, *A. mahe*. While both species have a process on the carpal lobe of gnathopod 2, *A. aldabra* lacks the serrations found along the proximal carpal margins found in other species of Indian Ocean *Anamixis*, *A. mahe, A. stebbingi* and *A. barnardi*. *Anamixis aldabra* also differs from *A. mahe* in the reduced peduncular article 3 of antenna 1; the quadrate lower margin of the head; the geniculate propodus of gnathopod 1; the morphology of coxae 2–4; the straight dactyl of gnathopod 2; a deeper hind lobe on coxa 6; and a relatively narrower telson. The sharp ventral process found in coxa 2 is widespread in both Indian Ocean and South Pacific taxa. The relative taxonomic value of this character is unclear.

Remarks. Leucomorphs of *A. aldabra* are not confirmed. Leucomorphs have been recorded from Aldabra, but until specific hosts are documented, or rearing experiments confirm relationships, assignment of this material to *A. aldabra* is premature. Colour in freshly preserved material: Antenna 1 and pereonites 1–7 with dorsal and lateral blotches of red; red eye colour persisting in formalin and alcoholated specimens.

Habitat. Specific habitat or host unknown, general habitat preference shallow coral rubble.

Distribution. Indian Ocean, presently known only from the type locality, Aldabra Atoll, coral reefs, 2–3 m.

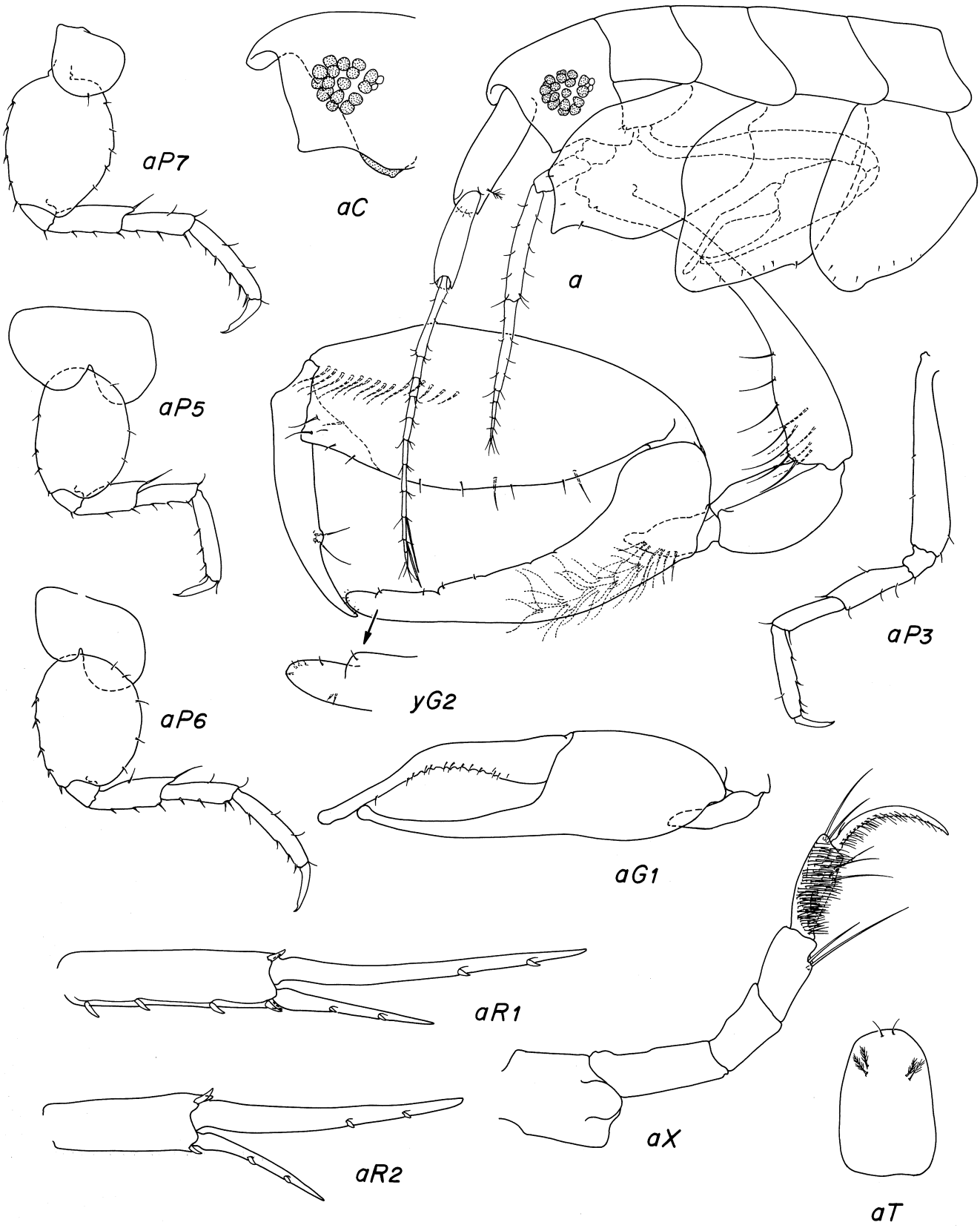

Fig. 1. *Anamixis aldabra* n.sp., holotype, anamorph male "A", 2.52 mm.

Anamixis barnardi Sasidharan, 1983

Anamixis barnardi Sasidharan, 1983: 195–199, figs 1–14.

Diagnosis. Ventral keel rounded; gnathopod 1, articles 5 and 6 with apical setulae; gnathopod 2, carpus bifid laterally, denticulate on proximal margin; coxa 4 emarginate ventrally.

Description. Head, lateral margin rounded, anterior margin transverse, defined ventrally by small cusp, eye composed of compact ommatidia; ventral keel obliquely rounded. Antenna 1, 1.28 the length of head to second pereonite segment, ratio of peduncle segments 1–3, 10:9:6; flagellum subequal to peduncle, 9-articulate. Antenna 2, 1.0 the length of head to second pereonite segment, flagellum short, 4-articulate. Gnathopod 1 lacking terminal setae on articles 5 and 6. Gnathopod 2, coxa subequal to 3–4, rounded, with anterior cusp; lateral margin of carpus with tooth at distal one-third, proximal margin denticulate. Telson, lateral margins slightly expanded, apically rounded, 1.52 times longer than wide.

Relationship. *Anamixis barnardi* forms part of a species complex including *A. mahe* and *A. stebbingi*, all Indian Ocean species that share the following characters: transverse anterior margin of the head defined by a small cusp, a rounded ventral keel; coxae 2–4 subequal in size; carpal lobe of gnathopod denticulate; and coxa 4 ventrally emarginate. *Anamixis mahe, A. barnardi* and *A. nedcampensis* have a prominent carpal tooth on gnathopod 2, however, the proximal denticulations on the carpus occur laterally in *A. mahe*, while they are found on the medial margin in *A. barnardi* and *A. stebbingi*, lacking in *A. nedcampensis*. *Anamixis mahe* also has a much larger and more recurved dactyl than is found in either *A. stebbingi* or *A. barnardi*. Both *A. stebbingi* and *A. barnardi* lack the long terminal setae of articles 5 and 6 of gnathopod 1, a feature apparently unique to *A. mahe*. See *A. stebbingi* for discussion of Nayar's report of *A. stebbingi* from the region.

Habitat. From sponges in littoral waters.

Distribution. Indian Ocean, Krusadi Island, Gulf of Manaar, South India, littoral.

Anamixis bazimut n.sp.

Fig. 2

Type material. HOLOTYPE, anamorph male "A", 2.87 mm, USNM 243318, Tab Anchorage, Madang, Papua New Guinea, gully in south Dam Awan (Rasch Passage), rubble and sediment, 3 m, J.D. Thomas, 22 February 1990, JDT-PNG-57g. PARATYPES, USNM 239493; anamorph male "B", 2.68 mm, Tab Anchorage, Madang, Papua New Guinea, reef flat on south end of Wongad Island, 4–6 m, J. Thomas, 2 May 1991, JDT-PNG 85b; anamorph males "C", 2.80 mm, and "D", 2.31 mm, Madang Harbour, Papua New Guinea, coral rubble and debris in front of Madang Reef Resort, taken from small asconoid sponges, 1 m, 28 February 1990, J. Thomas, A. Myers and J.L. Barnard, JDT-PNG 68a.

Diagnosis. Anterior margin of head transverse, with or without cusp; ventral keel large, projecting well below head, anterior margin transverse, parallel to anterior margin of head, ventral margin defined by anteroventrally directed tooth, anterior margin coxae 2–4 subequal in size, coxa 2, midventral margin produced.

Description. Holotype "A". Head, anterior margin transverse, with small anteroventral cusp; ventral keel broad, anterior margin transverse, extending well below ventral margin of head, anterior margin parallel with anterior margin of head, ventral corner defined by anteroventrally directed tooth; eyes with 18 scattered ommatidia. Antennae: Antenna 1, ratio of peduncle articles 1–3, 28:20:13; flagellum 8-articulate; antenna 2 scarcely shorter than 1; flagellum short, 3- or 4-articulate. Maxilliped, inner plates reduced, tapering, with small apical cleft; outer plates lacking inner lobes; palp article 4, 1.5 times article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apically bifid; article 5 geniculate, inner margin unarmed; article 6 recurved, inner margin tuberculate with submarginal setae. Gnathopod 2, coxa thinner than 3, more or less subequal to 4, ventral margin produced, angular, bearing 4–5 submarginal setae; carpal lobe long, blunt reaching to end of propodus, apex curved slightly forward; hindmargin of propodus smooth, linear, unadorned, with 5–7 submarginal setae; dactyl with paired setae on inner distomedial margin. Pereopod 3, coxa rectangular, with 4–5 submarginal setae. Pereopod 4, coxa tapering posteriorly, posteroventral margin with slight excavation, bearing 4 submarginal setae. Pereopods 5–6 similar, coxae bilobed, basis spinose anteriorly, posterior margin slightly expanded. Pereopod 7, coxa entire, with 2 submarginal setae in small notches on posteroventral corner. Uropods 1–2, outer rami reduced approximately one-half of inner, spinose. Uropod 3, outer ramus scarcely shorter than inner, spinose. Telson broad, entire, with 2 dorsofacial plumose setae and 2 apical setae.

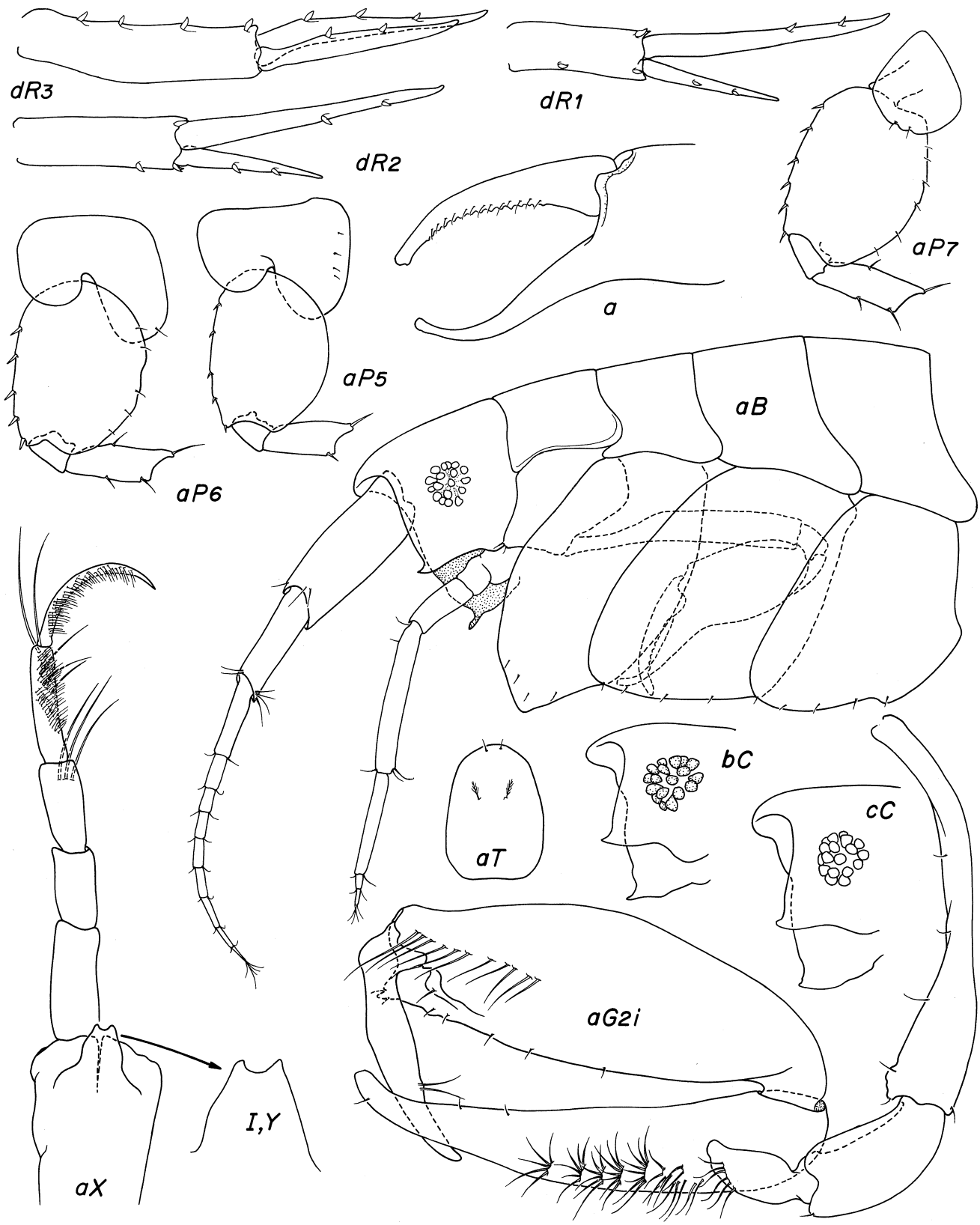

Fig. 2. *Anamixis bazimut* n.sp., holotype anamorph male "A", 2.87 mm; "B", 2.68 mm; "C", 2.80 mm; "D", 2.31 mm.

Leucomorphs. Recorded from small asconoid sponges, undescribed.

Etymology. Pidgin English; named after the Bazimut clan, Riwo District, Madang, who own much of the waters and reefs of Tab Anchorage.

Relationship. *Anamixis bazimut* forms part of a triad of closely related species, including *A. kateluensis* and *A. moana*. These species share the following characters: coxa 2 subequal to 3–4, broad ventral keels extending well below the ventral margin of the head, and general shape and morphology of gnathopod 2. *Anamixis bazimut* and *A. kateluensis* both have apical processes on the inner plate of the maxilliped, whereas *A. moana* exhibits an apically truncate inner plate on the maxilliped. This morphological clade suggests a closer relationship between *A. bazimut* and *A. kateluensis* than either species has to *A. moana*.

Remarks. The *bazimut–kateluensis–moana* clade shows little variation over wide expanses of ocean and may eventually prove to be morphoclines of a previously widespread palaeoendemic of the Pacific Plate. Additional sampling and analysis of specimens are needed to resolve this situation. Application of molecular systematic techniques may also prove informative.

This species has also been collected by the author from Australian coral reefs, Lizard Island south to Orpheus Island, off Townsville.

Habitat. Small asconoid sponges in rubble areas.

Distribution. Bismarck Sea of northern Papua New Guinea to the Coral Sea of northern Queensland, coral reefs, 1–5 m.

Anamixis cavatura n.sp.

Figs 3,4

Anamixis hanseni Thomas, 1979: 107–109; Thomas & Taylor, 1981: 462–467, figs 1–5; Thomas & Barnard, 1983: 154–157 (not *A. hanseni* Stebbing, 1897).

Type material. HOLOTYPE, anamorph male "D", 2.39 mm, USNM 253729, Carrie Bow Cay, Belize, coral rubble from reef flat just behind reef crest near north-east corner of South Water Channel, 1–2 m, J.D. Thomas, 3 July 1987, JDT-Bel-115a; 1 PARATYPE, anamorph male "C", 4.60 mm, USNM 253730, Carrie Bow Cay, Belize, formalin wash of rubble from backreef area of reef bordering South Water Channel, 1 m, J.D. Thomas, 14 July 1987, JDT-Bel-126; 2 PARATYPES, leucomorphs, male "A", 4.41 mm, USNM 253732, and female "B", 3.28 mm, USNM 253733, Carrie Bow Cay, Belize, JDT-Bel-126.

Additional material examined. Anamorph male "K", 4.85 mm, USNM 253731, Coupon Bight, Big Pine Key, Florida Keys, from branchial chamber of the colonial ascidian *Ecteinascidia turbinata* Herdman, 2 m, J.D. Thomas, 1 November 1981.

Diagnosis. Head, rounded laterally, anterior margin oblique, defined by small cusp; ratio of antenna 1 peduncle segments 1–3, 14:12:10; ventral keel prominent, extending beneath head, triangular, slightly recurved anteriorly, ventrally sharp; gnathopod 2, palm with 3–5 distinct cusps, largest near insertion of dactyl, others progressively smaller, dactyl tuberculate. Leucomorph males and females: head angle truncate, nearly 90 degrees, ventral keel produced beneath head, subrectangular; gnathopod 1, coxa tapered, seta present at apex and near notch along posterior margin, carpus, inner margin finely serrate, apex with 2 serrate spines, the larger bifid distally; gnathopod 2, palms transverse.

Description. Transformational anamorph, holotype "D". Head, lateral margins rounded, anterior margin broadly rounded and lacking cusp; eye composed of numerous compact ommatidia. Antenna 1 and 2, 0.37 and 0.28 as long as body. Antenna 1, flagellum with 8-articulate. Antenna 2, flagellum 3-articulate. Lower lip lobes not readily visible from lateral view. Maxilliped, inner plates fused into apically produced process; outer plates lacking inner lobes; palp article 4, 1.2 times length of article 3. Pereonite 1 with prominent lateral locking ridge. Gnathopod 1, coxa reduced, distally bifid; carpus, upturned distally, inner margin lacking serrations, apex with long setae; propodus, apex not quite reaching terminus of carpus, inner margin unevenly serrate, apex with long setae. Gnathopod 2, coxa larger than 2 or 3, rounded ventrally, anterior and posterior margins defined by small cusp; basis with small triangular locking process distally; carpus recurved; propodus with 3 teeth; dactyl slightly recurved, with two tubercles on inner margin. Pereopod 3, coxa rounded ventrally, anterior margin with small cusp; remainder of pereopod normal for genus; Pereopod 4, coxa rounded ventrally, posterior margin expanded; remainder of pereopod similar to pereopod 3. Pereopod 5, coxa bilobed, hind margin not produced; basis, spinose anteriorly, posterior margin expanded. Pereopod 6, coxa bilobed, hind margin slightly rounded; basis, anterior margin spinose, posterior margin expanded. Pereopod 7, coxa entire; basis spinose anteriorly, posterior margin expanded. Epimera normal. Uropods 1 and 2 with outer ramus reduced. Outer ramus of uropod 3 relatively longer than rami of uropods 1 and 2, not reaching apex of inner ramus. Telson entire, apex produced, 1.46 times longer than wide.

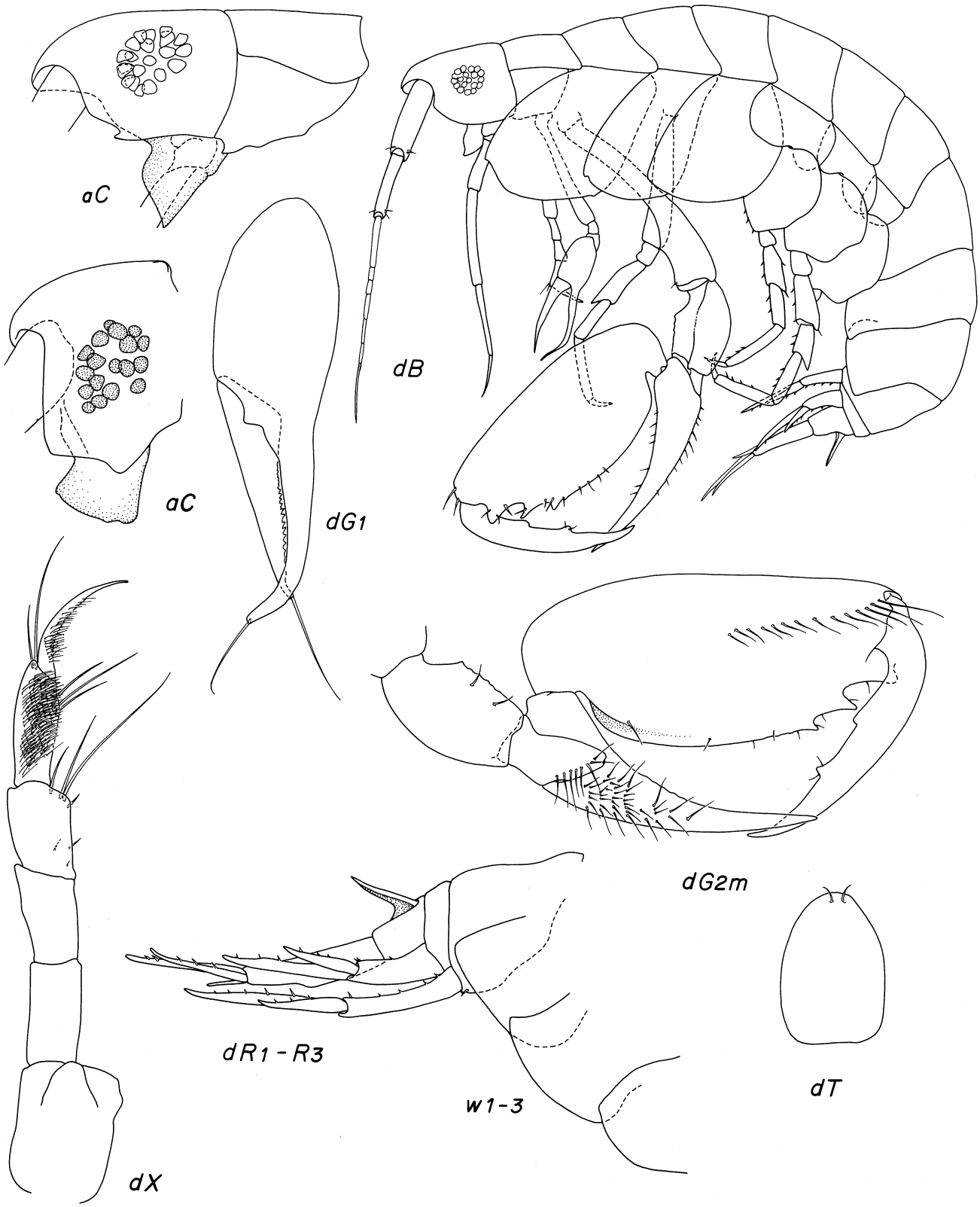

Fig. 3. *Anamixis cavatura* n.sp., holotype, anamorph male "D", 2.39 mm; "A", leucomorph male, 4.41 mm.

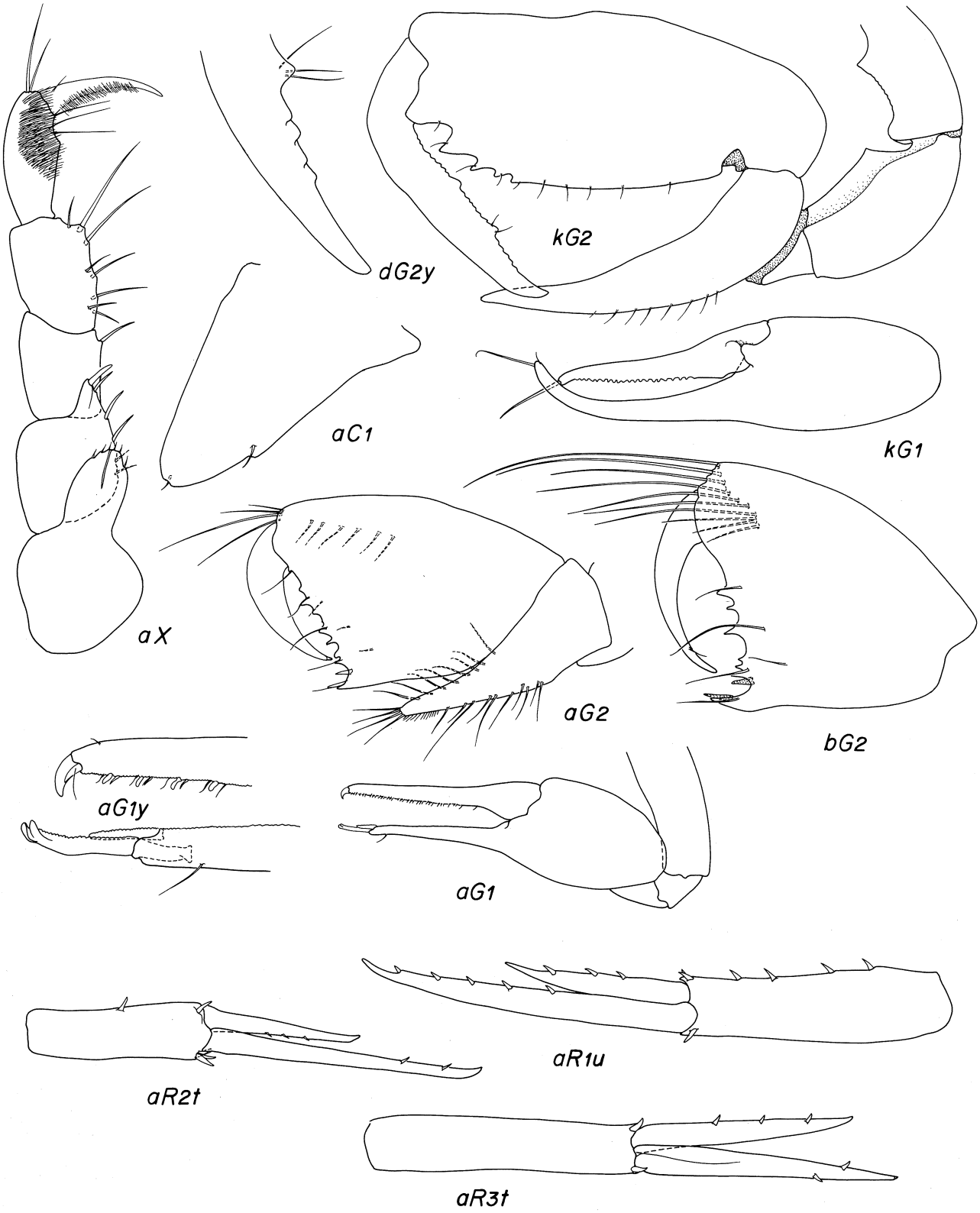

Fig. 4. *Anamixis cavatura* n.sp., holotype, anamorph male "D", 2.39 mm; "A", leucomorph male, 4.41 mm; "B", leucomorph female, 3.28 mm; "K", anamorph male, 4.85 mm.

Leucomorphs. Known from hosts, small asconoid sponges and colonial ascidians. Following description based on male "A", and female "B" from type locality: male, head margin acute, forming sharp angle; ventral keel adze-shaped and slightly extended forward, eye with 18 ommatidia. Mouthparts normal for genus. Gnathopod 1, coxa tapering, with two widely separated small setae, one at apex and one near small posterior cusp; propodus, inner margin finely serrate, apex with 2 embedded spines, inner margins serrate, larger spine bifid distally; propodus, inner margin finely serrate and armed with a series of grouped seta, and small spine surrounding a thicker spine of equal length. Gnathopod 2, palm nearly transverse and bearing approximately 6 short and dispersed feeding setae. Females similar to males except for a relatively smaller second gnathopod, with a more excavate palm, and inner margin of propodus with a dense series of 9 long feeding setae.

Variations. Anamorph specimens from the Florida Keys are consistently larger than specimens from other parts of the Caribbean. This may be due in part to the increased availability of hosts and the relatively greater particulate and nutrient loads that occur in Florida Keys waters compared to other parts of the Caribbean. Morphological variations are documented primarily in the development of a head cusp in post-transformational anamorphs; and in gnathopod 2, where increased size produces the characteristic 5 teeth on the propodus, and tuberculations on the inner margin of the dactyl.

Etymology. From the Latin "cavatura", meaning a hollow or cavern, referring to the interior cavities of hosts.

Remarks. Colour in live material: anamorphs, prominent dorsal and lateral banding of a brilliant reddish-pink colour, coxae 2–4 with a diffuse scattering of this same colour; eyes are a brilliant red. The large second gnathopods have a shiny appearance and are white in colour. Leucomorphs, exoskeleton transparent, gonadal tissue usually visible as brownish dorsal mass; eggs deep green in colour.

Thomas & Taylor (1981) first documented the existence of vestigial mouthparts and the feeding ecology in anamorphs of this species from the host ascidian *Ecteinascidia turbinata*. The normal complement of specimens within the host is 1–2 anamorphs and 5–8 leucomorphs. Methods of reproduction in this and other species are undocumented.

Anamixis cavatura was incorrectly referred to as *A. hanseni* by the author in earlier publications (Thomas, 1979). Considering collected materials and examination of type material, *A. hanseni* appears limited to its type locality, stated as "West Indies" in the original description, but reported to be St. Croix in the Virgin Islands (Dr Jan Stock, Netherlands, personal communication).

Anamixis cavatura differs from *A. hanseni* in the cuspate margin of the head, morphology of the ventral keel, a coxa 2 without marginal cusps, and the shorter propodus of gnathopod 2. Stebbing (1897) shows a series of teeth on the anterior margin of the ventral keel. Unfortunately, the type borrowed from the Copenhagen Museum was missing the head, so that this feature cannot be definitely confirmed. No other specimens from the type locality or its environs are known to exist. *Anamixis cavatura* differs form *A. vanga* in the relatively shorter antennae, cuspate margin of head, lack of a hollowed lateral margin of the head, shape of the ventral keel, in having 5 teeth on the propodus of the second gnathopod (larger specimens), and a shorter row of mediofacial feeding setae. Leucomorphs of the *A. cavatura* are easily distinguished from those of *A. vanga* by the more angular head margin and truncate ventral keel; in gnathopod 1, the tapering coxa with widely separated setae, in having serrations on the apical spines of the carpus, the larger apical spine being bifid, in lacking the larger serrations on the inner margin of the carpus; and in the more transverse palm of gnathopod 2.

Habitat. Internal cavities of small asconoid sponges and colonial ascidians, especially *Ecteinascidia turbinata* Herdman.

Distribution. Western Atlantic Ocean, Ft. Pierce Florida to Biscayne Bay; Gulf of Mexico, Key West to Tampa; Florida Keys, Caribbean Sea, Yucatan, Belize, Honduras, Jamaica, The Bahamas, Greater and Lesser Antilles, 1–5 m.

Anamixis excalibur n.sp.

Fig. 5

Type material. HOLOTYPE, male "A", 2.75 mm, USNM 253734, Banana Reef, Tab Anchorage, Madang, Papua New Guinea, from formalin wash of "penny coral" *Diaseris fragilis*, 30–34 m, J.D. Thomas, 8 February 1990, JDT-PNG-38b; 1 PARATYPE, male "B", USNM 253735, JDT-PNG-38b; 1 PARATYPE, USNM 253744, Padoz Natun reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of attached rubble, 2–3 m, J. D. Thomas, 27 January 1990, JDT-PNG-24a; 3 PARATYPES, USNM 253737, Wongad Reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble on forereef slope, 12–15 m, J.D. Thomas, 28 January 1990, JDT-PNG-25a; 1 PARATYPE, USNM 253738, Mizegwadan (Tripod) reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble from 50 m south of marker, bottom mostly rubble and soft corals, 3–4 m, J.D. Thomas, 2 February 1990, JDT-PNG-32a; 1 PARATYPE, USNM 253739, Wongad Reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble from forereef slope, 34 m, J.D. Thomas, 6 February 1990, JDT-PNG-36a; 1 PARATYPE, male "C", USNM 253736, Barracuda Point, East of Tab Island, Madang, Papua New Guinea, formalin wash of rubble from

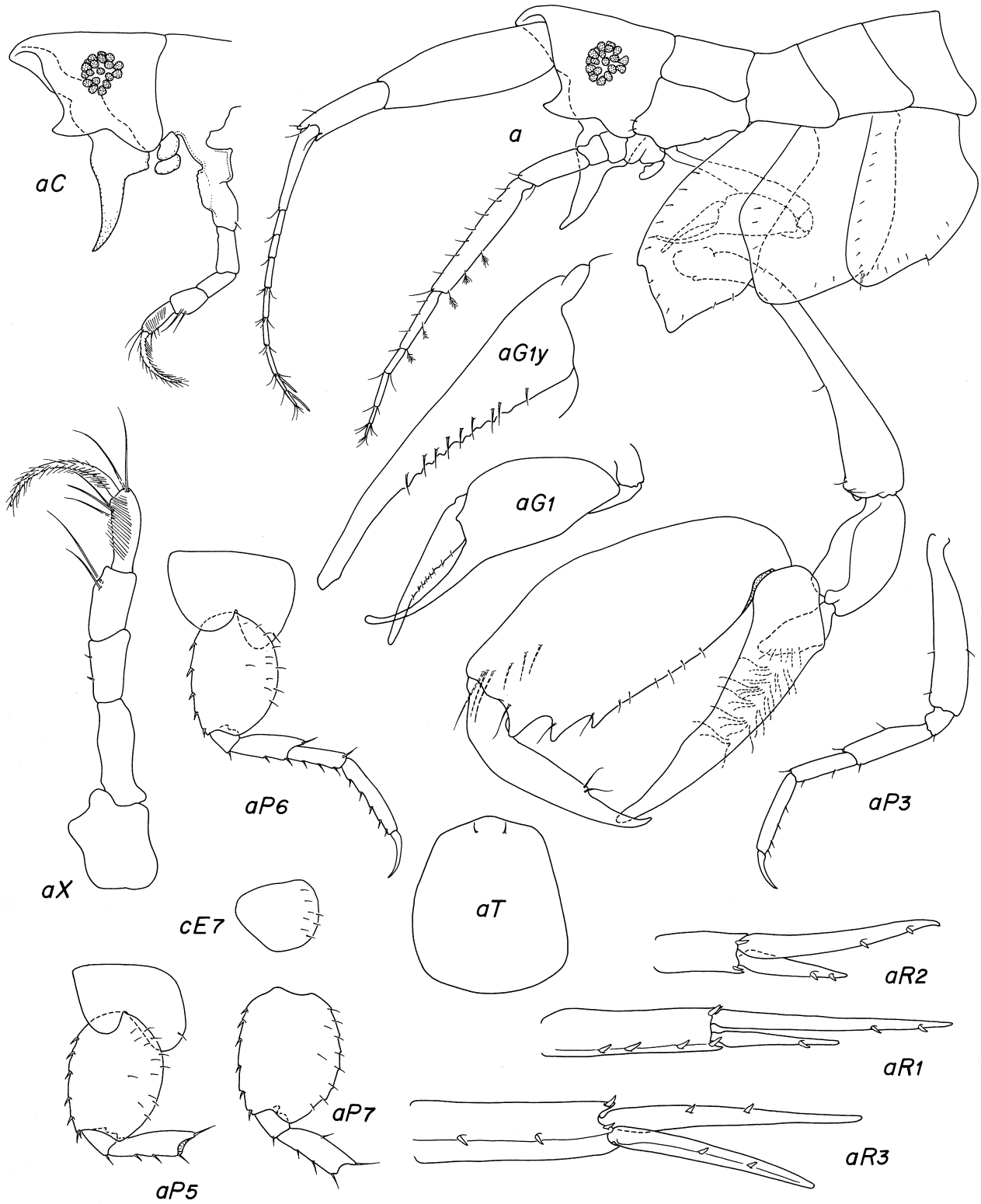

Fig. 5. *Anamixis excalibur* n.sp., holotype, anamorph male "A", 2.75 mm.

forereef slope, 30–33 m, J.D. Thomas, 8 February 1990, JDT-PNG37a; 2 PARATYPES, USNM 253740, Mizegwadan (Tripod) reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble, 3–4 m, J.D. Thomas, 16 February 1990, JDT-PNG-48a; 1 PARATYPE, USNM 253741, gully in south Dam Awan (Rasch Passage), Tab Anchorage, Madang, Papua New Guinea, formalin wash of dead *Acropora* samples, 4–6 m, J.D. Thomas, 22 February 1990, JDT-PNG-57f; 2 PARATYPES, USNM 253742, Wongad Reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of *Acropora* rubble, 40–55 m, J.D. Thomas, 24 February 1990, JDT-PNG-59a.

Diagnosis. Head enlarged, anteroventral corner defined by a large upturned cusp. Antenna 1, first peduncular segment enlarged, ratio of peduncle segments 1–3, 30:17:16; antenna 2 inserted near posterior margin of eye. Ventral keel prominent, recurved, extending well below margin of head; terminal article of maxilliped palp elongate. Coxa 2 narrow, linear, distally produced; coxa 3 wider than 2 or 4.

Description. Head, anterior margin transverse, anteroventral margin defined by large cuspate process, ventral margin excavate; eye with 20 ommatidia; ventral keel elongate, slightly recurved anteriorly. Antenna 1, article 1 enlarged, equal to articles 2 and 3 in length, flagellum with 8 articles, aesthetascs present on articles 7–8. Antenna 2, peduncle normal, flagellum with 5 articles. Fleshy lobes of lower lip readily visible from lateral view. Maxilliped, inner plates fused into an apically rounded plate; outer plates lacking; palp article 4, 1.9 times length of palp article 3. Pereonite 1 with prominent lateral locking ridge. Gnathopod 1, coxa reduced, rounded anteriorly bearing 2 small setae; carpus slightly recurved; propodus serrate and setose on inner margin. Gnathopod 2, coxa narrow, 2.28 times deeper than wide, apically produced, anterior margin defined by distinct cusp, margins bearing numerous small embedded setulae; basis, anterior margin bearing 2 short setae; carpal lobe with dense tuft of medial setae; propodus with 3 large distal teeth, ventral and posterior margins with short to medium setae, medial surface with short row of long feeding setae near anteroventral margin; dactyl straight, with small process bearing 2 medium setae. Pereopod 3, coxa broad, anterior margin expanded, ventral margin tapering distally, anterodistal margin slightly excavate, posterior margin defined by small cusp, numerous small setulae embedded along margins, remainder of pereopod normal. Pereopod 4, anterior margin of coxa straight, ventral margin rounded distally, posterior margin defined by small cusp, numerous setulae embedded along margins, remainder of pereopod 4 similar to pereopod 3. Pereopods 5–6, coxae bilobed, bearing a single posterior seta; bases, anterior margins spinose, posterior margins evenly rounded bearing numerous small setae. Pereopod 7, coxa small, entire, with numerous small setae; anterior margin of basis spinose, posterior margin weakly serrate, bearing marginal and submarginal setae. Epimera normal for genus. Outer rami of uropods 1 and 2 shortened, outer ramus of uropod 3 only slightly shortened, all rami with 2 spines each, except for the outer ramus of uropod 1 which bears a single spine. Telson broad, 1.2 times longer than wide, apical margin only slightly produced, 2 apical setae.

Etymology. Named for the sword of King Arthur, the mythical mediaeval ruler of Camelot, referring to the elongated ventral keel.

Relationship. *Anamixis excalibur* is distinct in the size and shape of the head, prominent ventral keel, and elongate coxa 2. *Anamixis excalibur* from Papua New Guinea resembles *A. falarikia* from Micronesia in the elongate maxilliped palp article 4, enlarged first peduncular segment on antenna, 1 and large process defining the anteroventral margin of the head; but differs in the linear coxa 2, and in having a more transverse palm with fewer teeth on gnathopod 2, and a longer carpal lobe.

Remarks. Colour of freshly collected material: pereonites 1–7 with faint orange dorsal band, and with a small, prominent orange dot laterally near insertion of coxae; Gnathopod 2 with distinct orange blotch along distal portion of propodus; dactyl with orange bands at base and tip. Colour fading rapidly in preserved material to translucent white. Leucomorphs of this species are currently unknown.

Habitat. Specific host or habitat unknown. General habitat preference algae-covered coral rubble, becoming more common at depths below 12 m.

Distribution. Bismarck Sea, from coral reefs in the Madang region along the north coast of Papua New Guinea, 3–55 m.

Anamixis falarikia J.L. Barnard, 1965

Fig. 6

Anamixis falarikia J.L. Barnard, 1965: 485–488, fig. 3.

Diagnosis. Head large, anterior margin oblique, defined by sharp, ventrally-projecting process, ventral keel toothed anteriorly. Antenna 1, article 1 of peduncle enlarged; antenna 2 attached well behind eye. Maxilliped, palp article 4 elongate. Gnathopod 2, coxa greatly enlarged, serrate anteriorly, expanded posteriorly, with sinuous ventral margin; carpus shortened; propodus inflated, palm oblique, with 6 major teeth; dactyl long, recurved, apex bifid.

Description. Head, lateral margins rounded, anterior margin oblique, defined by sharp ventral process, eye small relative to head size, composed of approximately 10 ommatidia, ventral keel a broad, toothed projection extending below margin of head. Antenna 1, 1.38 times length of head to posterior margin of pereonite segment 4; article 1 enlarged, articles 1–3, 29:15:10, flagellum subequal to peduncle, 9-articulate. Antenna 2, 0.89 times the length of head to pereonite 4; flagellum short, 3- to 5-articulate. Maxilliped, palp article 4 very elongate, 1.95 times length of palp article 3. Gnathopod 2, coxa enlarged, greatly exceeding coxae 3–4; carpal process shortened, propodus inflated, palm oblique, with 6 major teeth separating major indentations; dactyl elongate, recurved, reaching near

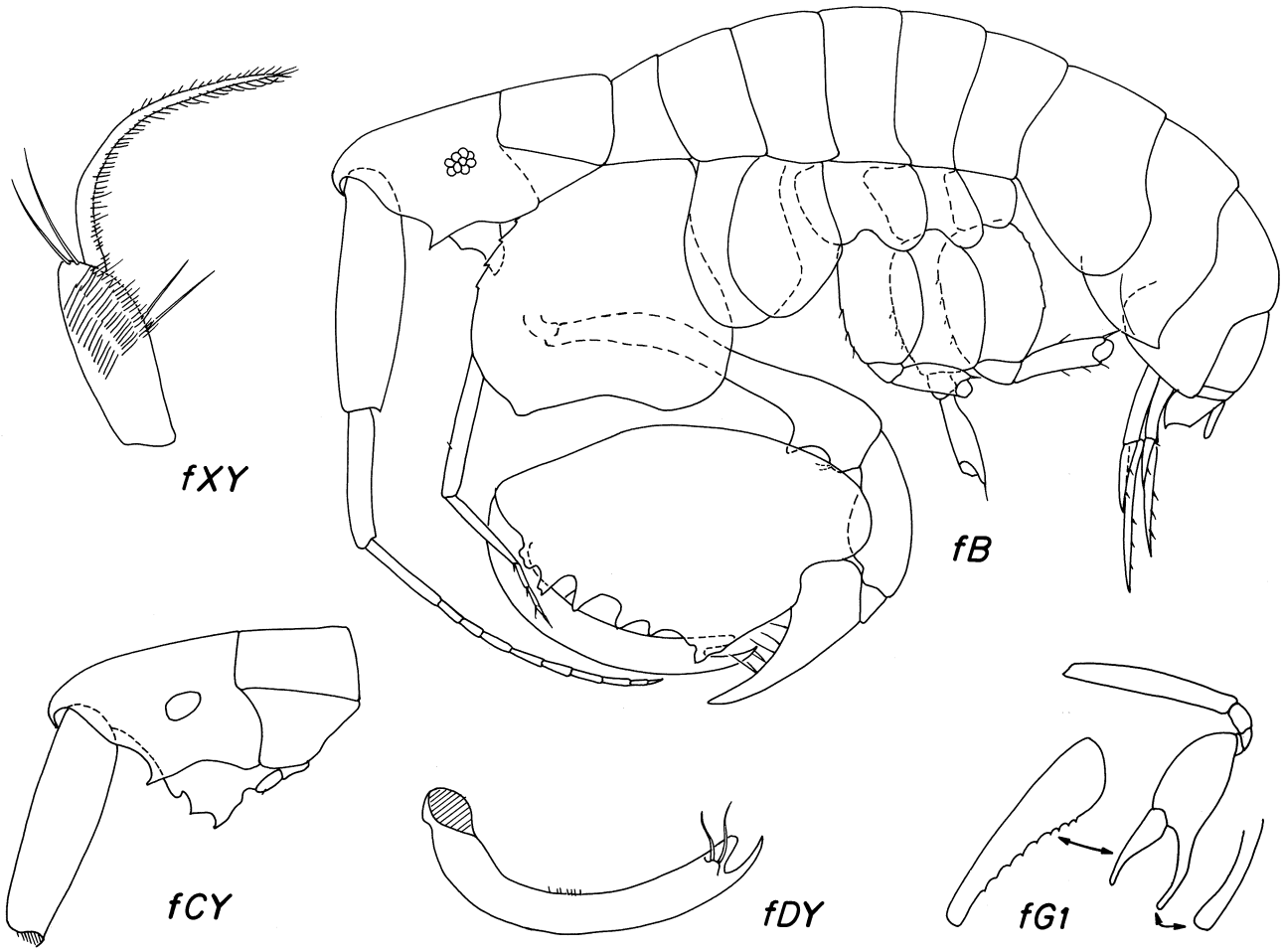

Fig. 6. *Anamixis falarikia*, anamorph male "F".

mid-region of carpus, apex bifid. Uropod 3 missing. Telson apically rounded.

Relationship. *Anamixis falarikia* resembles *A. papuaensis* in the enlarged coxa 2 and aberrant palm of gnathopod 2. *Anamixis falarikia* resembles *A. excalibur* in the enlarged first peduncular segment of antenna 1 and in the elongate palp article 4 of the maxilliped. *Anamixis falarikia* differs from *A. excalibur* in the more oblique head angle and ventrally projecting process; in the dominance of coxa 2; in having gnathopod 2 with a shortened carpal process, inflated propodus with oblique, 6-toothed margin; and in the bifid apex of the dactyl.

Remarks. This remarkable specimen is known from the original description from the type locality.

Habitat. Coral reefs, algal covered coral rubble.

Distribution. Pacific Ocean, Ifaluk Atoll, Caroline Islands, 0–1 m.

Anamixis hansensi Stebbing, 1897

Fig. 7

Anamixis hanseni Stebbing, 1897: 36–38, fig. 11; 1906: 170–171, fig. 42–43.

Diagnosis. Head angle oblique, lacking any defining cusps; anterior margin of ventral keel with microscopic teeth; gnathopod 2 with terminal setae; coxa 2 enlarged, broadly rounded, margin smooth; propodus of gnathopod 2 elongate, 3.05 times deeper than wide, with 3 teeth; dactyl with 2 slight projections on inner margin.

Description. Head, lateral margin rounded, anterior margin oblique; antenna 1, ratio of segments 1–3, 32:25:14; eyes compact, large, composed of numerous ommatidia, ventral keel projecting as truncate process, with anterior microscopic teeth and excavate bottom margin, anteroventral corner defined by small, sharp projection; maxilliped, article 4, 1.25 times article 3. Antenna 2 attached near posterior margin of eye. Gnathopod 2, coxa larger than 3–4, margins smooth;

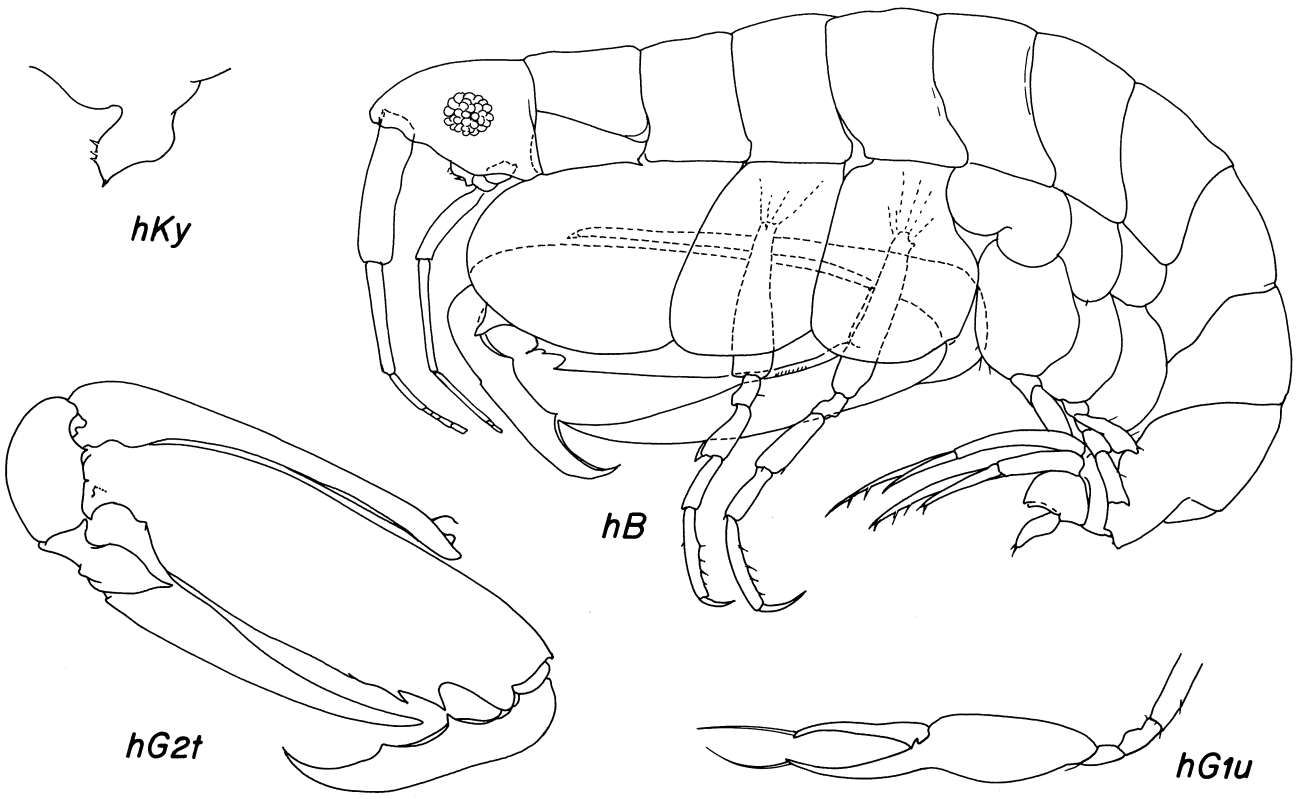

Fig. 7. *Anamixis hanseni*, anamorph male "H".

carpus elongate; propodus very elongate, with 3 major teeth; dactyl with 2 small projections in inner margin. Coxa 3 smaller than 4, both with smooth margins. Uropod 3 missing. Telson apically rounded, 1.28 times longer than wide.

Relationship. *Anamixis hanseni* is most closely related to *A. cavatura* but differs from this species in the following characters: the oblique head angle lacking any defining process; the smooth margins of coxa 2; in gnathopod 2, the elongate propodus with 3 teeth, and dactyl with two small projections on the inner surface. It differs from *A. vanga* in lacking the laterally excavate margins of the head, the apically produced ventral keel with microscopic teeth, smooth margins on coxa 2, and the elongate propodus of gnathopod 2.

Remarks. In the past, this author has confused this species with *A. cavatura* (Thomas, 1979; Thomas & Taylor, 1981; Thomas & Barnard, 1983). A loan of the type specimen was requested from the Copenhagen Museum to confirm specific characters, but unfortunately the head was missing. Thus, minute details of head margins and ventral keel cannot be discerned. However, Stebbing's excellent original description clearly sets this species apart from *A. cavatura*.

Habitat. Stebbing lists *A. hanseni* as collected from the coral *Goniastraea varia*, which is not a valid specific name for the genus. In addition, *Goniastraea* is not a Caribbean coral but rather an Indo-Pacific genus. It is the author's suspicion that the coral may have been misidentified by the original collector, J.H. Hansen. A more remote possibility is that the name of the coral is correct and the collecting locality is incorrect and may in fact not be in the Tropical Atlantic as depth, specific location, and other collecting particulars remain unknown.

Distribution. Tropical Atlantic, West Indies (no specific location given by Stebbing in his description, but reported to possibly be St. Croix, J. Stock, personal communication).

Anamixis jebbi n.sp.

Figs 8,9

Type material. HOLOTYPE, anamorph male "A", 2.54 mm, USNM 253745, Padoz Natun reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of cemented rubble in centre of reef, 1–2 m, J.D. Thomas, 28 February 1990, JDT-PNG-67; 1 PARATYPE, anamorph male, "C", USNM 253746, 2.50 mm, overturned and partially cemented *Acropora cytherea* rubble, 2–3 m, J.D. Thomas, 10 February 1990, JDT-PNG-40; 2 PARATYPES, leucomorph male "D", 1.92 mm, USNM 253747, leucomorph female "E", 1.62 mm, USNM 253748, and 5 other unmeasured leucomorphs, USNM

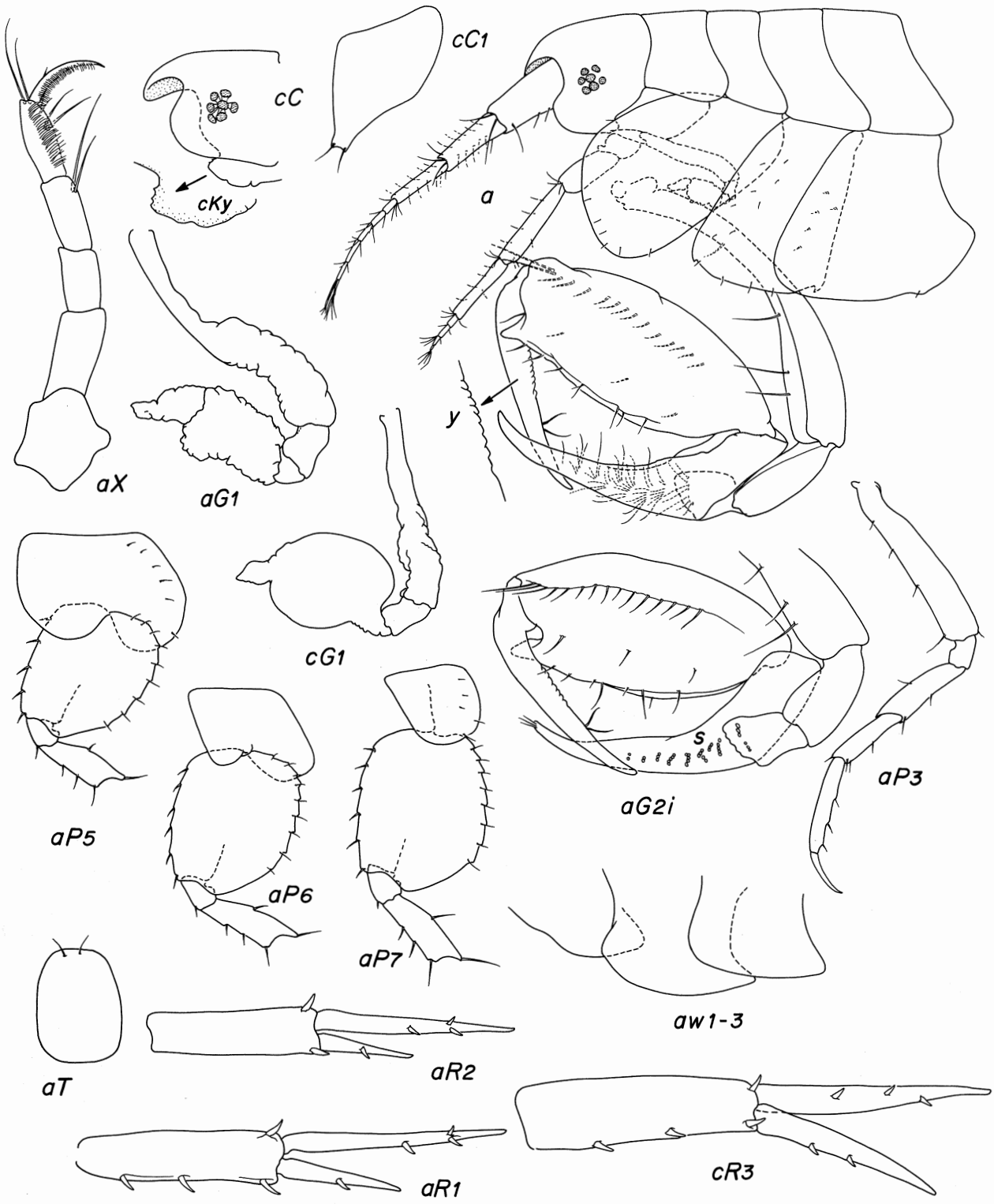

Fig. 8. *Anamixis jebbi* n.sp., holotype, male, 56 "A", 2.75 mm; "C", anamorph male, 2.50 mm.

253749, and 3 unmeasured anamorphs, USNM 253750, Padoz Tinan reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of overturned plates of *Acropora cytherea* 3 m, J.D. Thomas, 15 February 1990, JDT-PNG-46; 4 PARATYPES, 3 anamorphs and 1 leucomorph, USNM 243313, Padoz Natun reef, Tab Anchorage, Madang, Papua New Guinea, heavily cemented rubble from centre of reef, 1 m, J.D. Thomas, 18 February 1990, JDT-PNG-50a,b; 2 PARATYPES, 1 anamorph and 1 leucomorph, USNM 243314, Guzem reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of *Acropora* rubble, 2.5 m, J.D. Thomas, 12

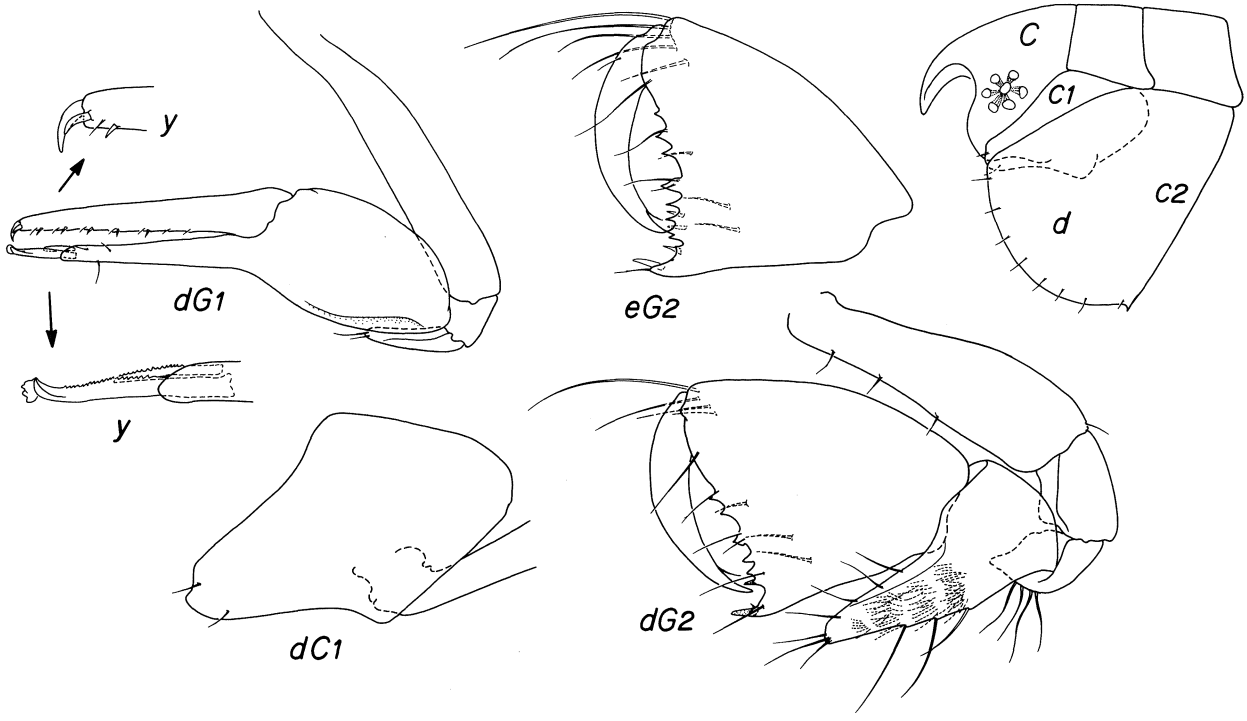

Fig. 9. *Anamixis jebbi* n.sp., "D", leucomorph male, 1.92 mm; "E", leucomorph female, 1.62 mm.

February 1990, JDT-PNG-44a; 2 PARATYPES, 1 anamorph and 1 leucomorph, USNM 243315, Tab Anchorage, Madang, Papua New Guinea, patch reef bearing 210° from Wongad Island, rubble from 3 m, J.D. Thomas, 13 February 1990, JDT-PNG-45a.

Diagnosis. Gnathopod 1 vestigial, persisting in post-transformation anamorphs as minute fleshy appendage; eyes reduced, composed of 7 ommatidia in both anamorph and leucomorph stages. Ventral keel rounded, anterior margin with two small cusps. Gnathopod 2, basis with 3 long setae anteriorly; carpus projecting above attachment with ischium, proximolateral margin weakly serrate; propodus with long line of mediofacial feeding setae near anterior margin and, a second, posterior row composed of 3 widely spaced setae.

Description. Head margin broadly rounded, lacking any defining processes; ventral keel rounded, sinuous, anterior margin cuspate; eyes reduced, bearing 7 scattered ommatidia. Antenna 1, ratio of segments 1–3, 15:12:11, peduncle segment 2 and 3 with 5–6 pairs of setae each; flagellum 6-articulate, articles 5 and 6 with aesthetascs. Antenna 2, flagellum short, 4-articulate. Lower lip lobes not readily visible from lateral view. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.1 times length of article 3. Pereonite 1 with lateral locking ridge. Gnathopod 1, coxa apically bifid, bearing 2 small setae; remainder of appendage extremely reduced, remaining wrinkled and fleshy, and persisting in subsequent post-transformational moults. Gnathopod 2, coxa scarcely larger than 3 or 4, evenly rounded, bearing approximately 6 submarginal setae; basis with 3 long setae along anterior margin; carpus slightly recurved, vaulting above attachment of ischium, lateral ridge weakly serrate from midpoint; propodus with double row of mediofacial feeding setae, anterior row 70 per cent of propodus, posterior row composed of 3 widely spaced setae; dactyl straight, inner surface margin nodulose proximally, paired setae inserted toward apex. Pereopod 3, coxa subrectangular, anterior and posterior margins straight, defined by small cusp, ventral margin furnished with 3–4 submarginal setae, mediofacial surface with scattered small setulae; remainder of pereopod normal. Pereopod 4, coxa equal to or slightly larger than 2, posteroventral margin expanded distally, ventral margin with small posterior indentation, anterior margin with several small mediofacial setulae; remainder of pereopod similar to pereopod 3. Pereopods 5, coxa bilobed, posterior margin with 6 submarginal setae; basis suboval, anterior margin spinose, posterior margin with series of indentations, each bearing a single seta; remainder of pereopod missing. Pereopod 6, coxa bilobed, relatively smaller than coxa 5; articles 5–7 missing; remainder of articles similar to pereopod 5. Pereopod 7, coxa entire, posterior margin with single posterior seta, medial surface furnished with several small setulae; articles 5–7 missing. Epimera normal for genus. Outer rami of uropods 1 and 2 shortened, approximately 50 per cent of inner ramus. Uropod 3, outer ramus 85 per cent of inner ramus. Telson 1.3 times longer than wide; bearing 2 apical, and two pairs of dorsofacial setae.

Leucomorphs. Description of male leucomorph "D": head, margin rounded, eyes with seven scattered ommatidia. Gnathopod 1, coxa reaching ventral margin of head, apically rounded and bearing 2 setae; carpus, inner margin bare, apex with 2 serrate spines, the larger spine 1.8 times longer than the shorter and bearing a

vertical terminal flake or blade; propodus, finely denticulate and furnished with a series of paired small spines and setae, dactyl possibly represented at apex by short hook. Gnathopod 2, coxa rounded, ventral margin expanded, bearing 8 submarginal setae, posterior margin defined by small cusp; second article with 3 anterior setae; palm of propodus more or less transverse, palmar margin defined by series of sharp cusps and 4 large embedded spines, corner of palm not produced forward; dactyl reaching next to last embedded palmar spine. Leucomorph female "E" similar to male except for a relatively smaller second gnathopod. Palm of female gnathopod 2 slightly excavate, hind margin tapering; dactyl not reaching next to last embedded palmar spine.

Etymology. Named for Matthew Jebb, Director, Christensen Research Institute in Madang, whose enthusiastic support of our amphipod biodiversity project and untiring good humour has made our efforts in Papua New Guinea most rewarding.

Relationship. *Anamixis jebbi* does not appear to share close affinities with any other known anamixid. The small, vestigial first gnathopod that persists in post-transformational anamorphs is unique and suggests an evolutionary link to *Paranamixis* where gnathopod 1 has been lost in post-transformational moults, but persists as a tiny vestige in transformational anamorphs. Until additional material of a variety of *Paranamixis* species are available for dissection and detailed observation, the fused inner plates of the maxilliped place *A. jebbi* in *Anamixis*. *Anamixis jebbi* also has an unusual attachment of the carpus to the ischium, with the attachment being significantly further down the carpus than is exhibited in other taxa. Articles 2 and 3 of antenna 1 are unusually setose for an anamixid, and few other taxa have such a long row of feeding setae on the medial surface of gnathopod 2. Because the second gnathopods and antennae are used in conjunction with the maxilliped in feeding, these unusual features may be attributable to a different feeding ecology than is found in other species. The variable form and surface texture of gnathopod 1 probably results from preservation procedures. Leucomorphs of *A. jebbi* are readily separated from other species by the reduced (and seemingly consistent) number of ommatidia, 7, and, in fresh material, by the pale pinkish colour.

Remarks. Colour of freshly preserved anamorphs and leucomorphs a pale, translucent pink, fading rapidly in preservative.

Habitat. Specific habitat or host is unknown, but specimens of *A. jebbi* were always collected from deep within rubble accumulations, indicating a preference for highly cryptic habitats. The reduced number of ommatidia also suggest a cryptofaunal existence and low ambient light conditions.

Distribution. Bismarck Sea, shallow coral reefs in the Madang region of Papua New Guinea, 1–3 m.

Anamixis kateluensis n.sp.

Fig. 10

Anamixis stebbingi J.L. Barnard, 1965: 488–489, fig. 4.

Type material. HOLOTYPE, anamorph male "K", 1.98 mm, USNM 106914, Caroline Islands, Katelu area of south-west Falarik Islet, wash from algae growing on dead coral, 25 m from shore, 0–1 m, D.P. Abbott, 21 October 1953, 145-C-2.

Diagnosis. Antenna 2 shorter than antenna 1, reaching only 0.69 on antenna 1; ventral keel large, tapering posteriorly, ventral margin defined by sharp, vertical tooth; gnathopod 2, coxa 2 apically produced, with slight anterior and posterior emarginations; gnathopod 2, propodus with subdistal indentation near base of dactyl; coxa 3 slightly larger than 2 or 4, anterior margin expanded, posterior margin tapering; coxa 4, posterior margin tapering.

Description. Holotype "K". Head, anterior margin transverse, corner defined by small upturned cusp, eye with 16 ommatidia. Antennae: antenna 1, ratio of segments 1–3, 15:11:8; flagellum 8-articulate; antenna 2, shorter than 1, apex reaching articles 5–6 on flagellum of antenna 1, flagellum 4-articulate. Maxilliped, inner plates with small apical cleft; outer plates lacking inner lobes; palp article 4 missing. Gnathopod 1, opposing chelae recurved and crossing on closure, apices slightly bulbous; article 6 with toothed inner margin. Gnathopod 2, coxa slightly smaller than 3; basis unadorned with setae or spines; carpal lobe thickened, straight, tapering evenly to apex, distal portion with small subapical swelling, apex reaching end of propodus; palm unexpanded, hindmargin slightly excavate, adjacent to small subdistal cusp; dactyl with elevated truncate projection near base, inner margin with small process bearing paired setae, remainder smooth. Coxa 3, slightly larger than 2 or 4, anterior margin expanded. Coxa 4 smaller than 2 or 3, posteroventral margin oblique. Pereopods 5–6 similar, coxae bilobed; basis spinose anteriorly, posterior margin expanded, submarginal setae present. Pereopod 7, coxa entire, ovate. Uropods 1–2, outer rami shortened, approximately one-half of inner rami. Uropod 3 missing. Telson apically rounded.

Leucomorphs. Unknown.

Etymology. Named for the Katelu area of south-west Falarik, Ifaluk, the type locality.

Relationship. *Anamixis kateluensis* closely resembles *A. bazimut* from Papua New Guinea and *A. moana* from Hawaii in the transverse margin of the head, the broad and enlarged ventral keel, the apically notched inner plates of the maxilliped and in the long, non-geniculate carpal lobe and similar propodus of gnathopod 2. *Anamixis kateluensis* differs from both *A. bazimut* and *A. moana* in the relatively shorter antenna 2; the more

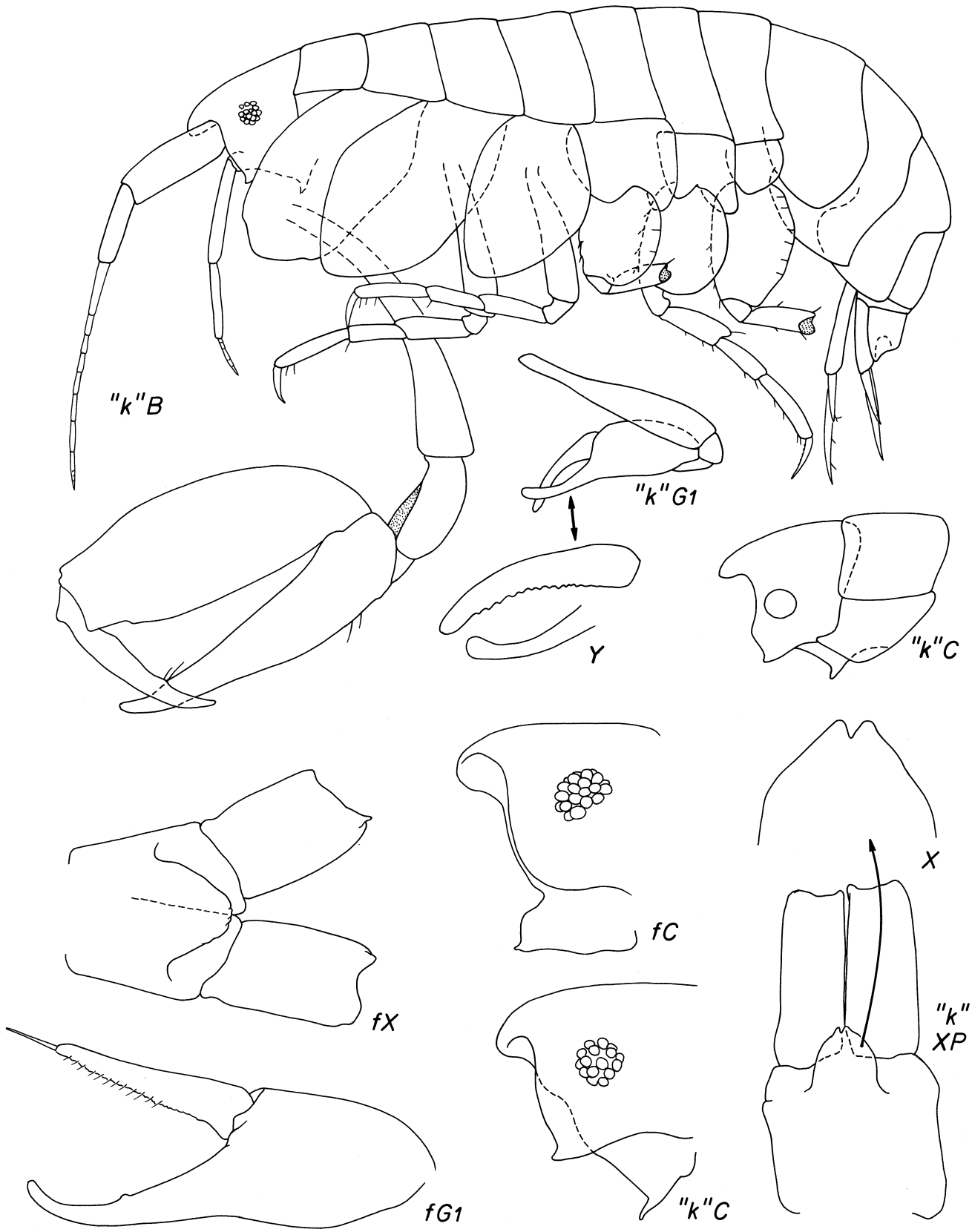

Fig. 10. *Anamixis kateluensis* n.sp., holotype, anamorph male "K", 1.98 mm. *Anamixis pacifica*, anamorph male "F", 5.87 mm.

oblique ventral keel; the expanded anterior margin of coxa 3; and in having coxa 2–4 of differing morphology and size. Based upon examination of the original specimen, the second gnathopod of *A. kateluensis* also exhibits several minor features not found in *A. moana* or *A. bazimut*: a relatively straighter carpal lobe with a slight swelling on the inner margin near the apex and the presence of a subdistal cusp on the palm.

Remarks. Barnard (1965) reported this species as *A. stebbingi*, but his description and drawings were adequate to establish significant character differences found in this species. Examination of Barnard's figured specimen confirmed the specific differences.

Habitat. From coral rubble, assumed to be commensal.

Distribution. Central Pacific Ocean, Ifaluk Atoll, Falarik Island, Caroline Islands, 0–1 m.

Anamixis mahe n.sp.

Fig. 11

Type material. HOLOTYPE, male "A", 2.66 mm, USNM 243316, rubble and stones among algal turf in current-swept channel, sheltered embayment near Mahe Beach Motel, Mahe, Seychelles, 0.5 m, J. Clark, 29 April 1984, J-Sey-2; 1 PARATYPE, male "B", 2.56 mm, 243317, J-Sey-2.

Diagnosis. Anterior margin of head transverse, defined by small cusp; anterior margin of ventral keel denticulate. Gnathopod 1, carpus with geniculate apical seta; propodus with one geniculate and one straight seta apically. Gnathopod 2, lateral margin of carpus bifid near apex, proximal margin serrate; dactyl elongate, recurved; anterior margin of coxae 3–4 oblique.

Description. Head, anterior margin transverse, anteroventral corner defined by small cusp; antenna 1, first peduncular segment scarcely exceeding articles 2 and 3; ratio of articles 1–3, 15:14:13; ventral keel rounded, barely projecting below margin of head, anterior surface with 3–4 irregular projections, posterior margin evenly rounded; eye with 18–20 ommatidia; accessory flagellum a minute scale with 2 apical setae; flagellum 9-articulate, aesthetascs on articles 6–8. Antenna 2 normal for genus; fifth peduncular article with long seta; flagellum short, 5-articulate. Lower lip lobes not readily visible from lateral view. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.3 times length of article 3. Coxae 2–4 subequal in size. Pereonite 1 with prominent lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, anteroventral margin rounded and bearing 2 apical setae; carpus, recurved apically, bearing a single geniculate seta, inner margin smooth; propodus, inner margin finely serrate with embedded short setae, bearing one geniculate, and one straight seta apically. Gnathopod 2, coxa subequal to 3 and 4 in size, 1.70 times deeper than wide, evenly rounded, bearing 2–3 small setulae and defined by a small cusp at the posteroventral margin; basis unarmed, with 3 short setae along anterior margin; carpus with prominent bifid process at Mark 0.77, with 3 small setulae, lateral ridge with irregular serrations on proximal portion; propodus, hind margin with 6 short setae, distal margin excavate, lacking sharp cusps or teeth, medial surface with row of 10–12 long feeding setae; dactyl long and recurved, inner margin smooth, 2 setae present on inner margin. Pereopod 3, coxa 1.5 times deeper than wide, anteroventral margin slightly excavate, posteroventral margin with small cusp, small setulae present along ventral margin; remainder of pereopod normal for genus. Pereopod 4, coxa 1.2 times deeper than wide, projecting midventrally, posteroventral margin defined by rounded process, small setulae along ventral margin; remainder of pereopod similar to pereopod 3. Pereopod 5, coxa bilobed; basis spinose anteriorly, posterior margin evenly rounded with small submarginal setulae. Pereopod 6, coxa bilobed, posterior lobe much deeper than anterior; basis spinose anteriorly, posterior margin evenly rounded with small submarginal setulae. Pereopod 7, coxa entire, bearing a single posterior seta; basis spinose anteriorly, posterior margin with small serrations, each with small setule. Uropods 1 and 2, outer rami about half the length of the inner. Uropod 3 missing. Telson subquadrate, 1.5 times longer than wide, apical margin rounded with two setulae, dorsal surface bearing two pairs of double setulae.

Etymology. Name refers to the type locality Mahe, in the Seychelles.

Relationship. *Anamixis mahe* is the only anamixid from the Pacific and Indian Oceans that bears long apical setae on gnathopod 1, this character being previously restricted to Caribbean *Anamixis*. *Anamixis mahe* is related to *A. barnardi* in having a rounded ventral keel, bifid distal process on the carpus of gnathopod 2, and in having coxa 4 emarginate ventrally. *Anamixis mahe* differs from *A. barnardi* in having an apically setose carpus and propodus on gnathopod 1, and a more quadrate telson. *Anamixis stebbingi* also has an emarginate ventral margin on coxa 4. Both *A. barnardi* and *A. stebbingi* have a serrate proximal ridge on the medial margin of the carpus on gnathopod 2, whereas *A. mahe* exhibits this character on the lateral margin of the carpus. The denticulate anterior margin of the ventral keel of *A. mahe* resembles the condition seen in *A. jebbi* from Papua New Guinea.

Leucomorphs. Unknown.

Remarks. Leucomorphs of *A. mahe* are undocumented.

Habitat. Specific host(s) or habitat(s) unknown, general habitat is shallow algal turf in coral reef rubble zones.

Distribution. Indian Ocean, Mahe, Seychelles.

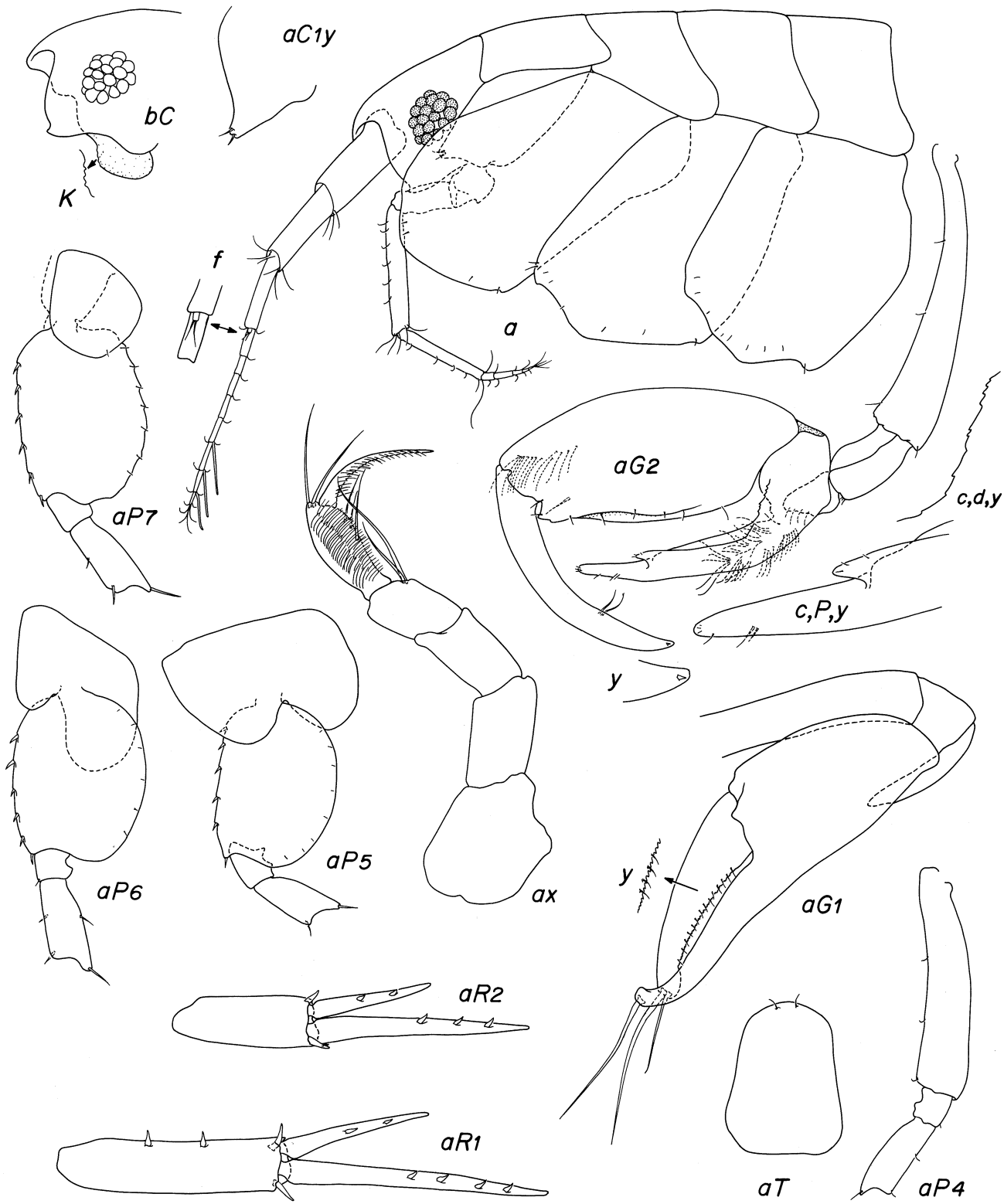

Fig. 11. *Anamixis mahe* n.sp., holotype, anamorph male "A", 2.66 mm; "B", anamorph male, 2.56 mm.

Anamixis moana n.sp.

Fig. 12

Anamixis stebbingi Barnard, 1970: 64, fig. 27.

Type material. HOLOTYPE, anamorph male "M", 2.40 mm, BPBM 58650, heads of *Pocillopora meandrina*, 2 m, Sampan Pass, Kaneohe Bay, Oahu, divers Kruschwitz and Bowers, 23 Feb. 1967, JLB Haw 10.

Diagnosis. Anterior margin of head transverse, with or without cusp; ventral keel large, oblique, projecting well below ventral margin of head, anteroproximal margin parallel to anterior margin of head, anterodistal and posterior margins oblique, tapering to broad, ventrally directed triangular process beneath eye; maxilliped inner plates fused, apically subtruncate, coxae 2–4 subequal in size, ventral margin of coxa 2 slightly expanded, angular, anteroventral and posteroventral corners smooth, 3 and 4 not expanded ventrally.

Description. Holotype "M". Head, anterior margin transverse, sometimes with small cusp. Antennae: antenna 1, ratio of articles 1–3, 12:8:6; flagellum 4- or 5-articulate; antenna 2 barely shorter than 1; flagellum 3- or 4-articulate. Eyes with approximately 17 loosely packed ommatidia, ventral keel massive, anteroproximal margin vertical, anterodistal margin oblique, tapering posteriorly to a broad triangular projection beneath eye. Maxilliped inner plates fused, subtruncate; outer plates lacking inner lobes; article 4 of maxilliped 1.6 times longer than article 3. Gnathopod 1 carpochelate, apex of article 5 slightly bulbous. Gnathopod 2, coxa with angular midventral projection; carpal lobe thick, elongate, reaching almost to end of propodus, apex blunt, slightly recurved; propodus slightly expanded, lacking any significant teeth or cusps. Pereopods 3–4 similar, ventral margins of coxae linear. Pereopods 5–6 similar, coxae bilobed. Pereopod 7, coxa entire, oval. Uropods 1–3, outer rami of 1 and 2 shortened to one-half of inner; of uropod 3, two-thirds. Telson entire, broad, apically rounded, 1.3 times longer than wide.

Leucomorphs Unknown.

Etymology. From the Hawaiian "moana", meaning ocean.

Relationship. *Anamixis moana* appears most closely related to *A. kateluensis* from Micronesia and *A. bazimut* from Papua New Guinea in the large ventral keel, subequal coxae 2–4, and general morphology of gnathopod 2. *Anamixis moana* differs from both *A. kateluensis* and *A. bazimut* in having the inner plates of the maxilliped apically truncate. *Anamixis kateluensis* differs from *A. moana* in having shorter second antenna; a more oblique ventral keel with distoventral projection; in various features of gnathopod 2; in having an expanded anterior margin of coxa 3; and in having coxae 3–4 with ventral margins not tapered. *Anamixis bazimut* has a vertical anterior margin on the ventral keel; an angular expansion on the ventral margin of coxa 2, and virtually straight hindmargin of gnathopod 2 propodus.

Remarks. Collecting from intermediate locations may provide additional information on the distribution and variation among the clade to which *A. bazimut* belongs. All members of this clade appear to be relatives of a previously widespread palaeoendemic that may have subsequently given rise to numerous species as ancestors became isolated in island archipelagos. Representative collections of amphipods from reef systems in the Central and South Pacific are limited, but additional collecting efforts in isolated island areas are sure to provide a wealth of new anamixid species.

Habitat. Coral rubble, specific host(s) unknown.

Distribution. Hawaiian Islands, coral rubble, 2–30 m.

Anamixis nedcampensis n.sp.

Fig. 13

Type material. HOLOTYPE, anamorph male "L", 3.02 mm, AM P41033, green and brown algae, inshore limestone reef south of Ned's Fish Camp, Ningaloo Reef, Cape Range National Park, Western Australia, 21°59'S 113°55'E, 1 m, R.T. Springthorpe, 2 January 1984, WA-373. PARATYPES, anamorph males "C" 2.95 mm; "M" 2.87 mm.

Diagnosis. Article 5 of gnathopod 1 distally dilated. Gnathopod 2, carpus with distal bifid process; propodus narrow, hindmargin straight, smooth, anterior margin not expanded.

Description. Holotype "L". Head, anterior margin transverse, anteroventral corner with small cusp; ventral keel rounded; eyes with 16 compact ommatidia. Antennae: antenna 1, peduncular ratio 23:18:12; accessory flagellum minute, 1-segmented; flagellum 10-articulate. Antenna 2, flagellum short, 4- or 5-articulate. Maxilliped, inner plates fused into apically rounded process bearing 2 nipple-like processes, outer plates lacking inner lobes; palp article 4, 1.2 times length of article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apically bifid; article 5 distally dilated; article 6 geniculate, inner margin with few weak serrations. Gnathopod 2, coxa subequal to 3 and 4, anterior margin with small cusp, ventral margin rounded; carpus with distal bifid process; propodus, hindmargin smooth, sparsely setose, anterior margin straight; dactyl long, slightly recurved, with paired distomedial setae. Pereopod 3, anteroventral of coxa margin defined by moderate cusp, ventral margin slightly expanded. Pereopod 4, anteroventral margin of coxa

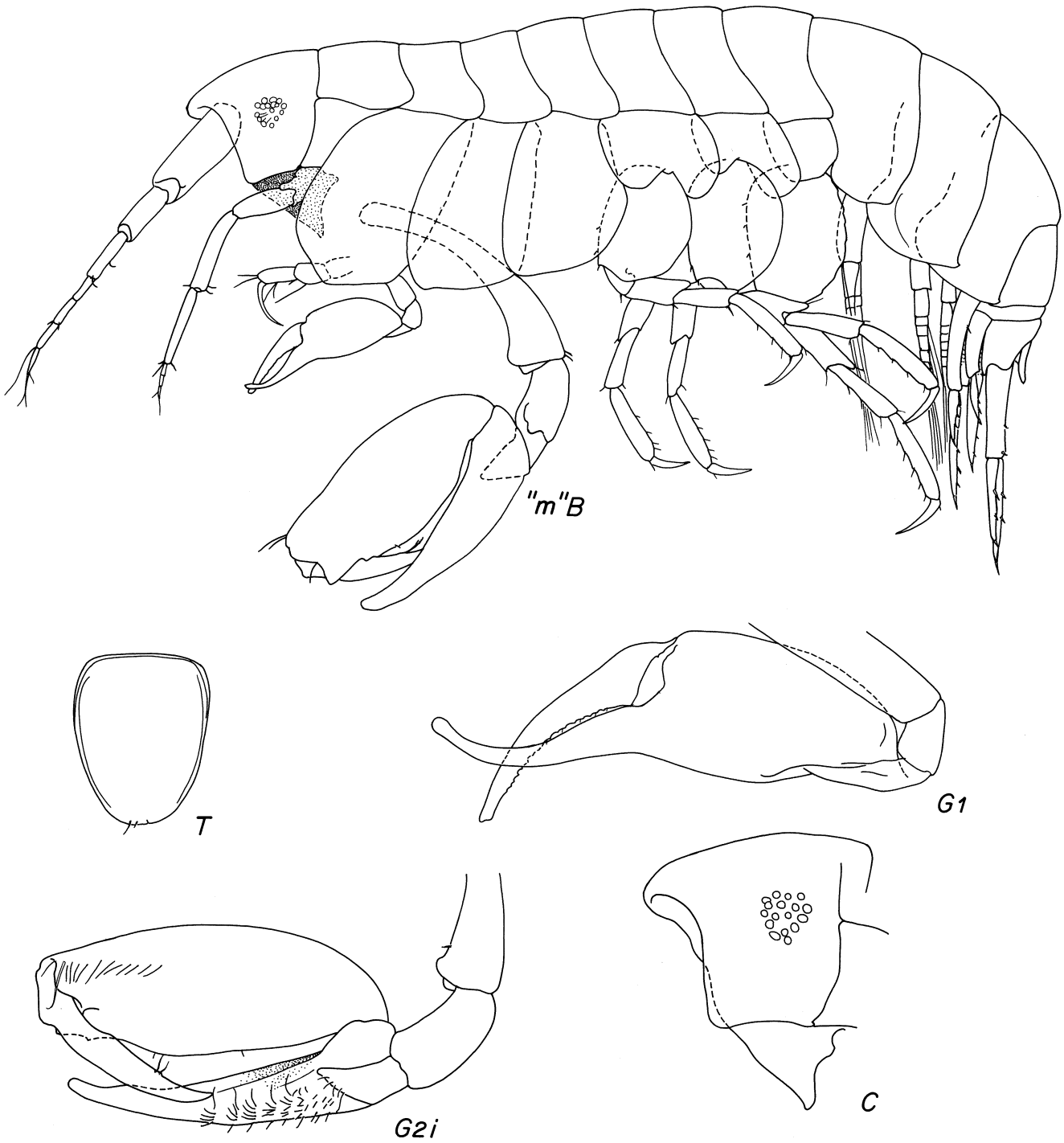

Fig. 12. *Anamixis moana* n.sp., holotype, anamorph male "M".

defined by moderate cusp, ventral margin expanded, crenulate, posterior margin slightly expanded. Pereopods 5–6 similar, coxae bilobed; basis spinose anteriorly, posterior margin evenly rounded and furnished with 6–9 submarginal setae. Pereopod 7, coxa entire, with single posteroventral seta; basis spinose anteriorly, posterior margin ovorectangular, ventral margin produced along article 4. Uropods 1 and 2, outer rami one-half length of inner. Uropod 3 missing. Telson entire, broad, 1.2 times longer than wide, with two groups of paired dorsofacial setae, distal margin with pair of apical setae.

Leucomorphs. Unknown.

Etymology. Named for Ned's Fish Camp, a popular camping area near Ningaloo Reef, Western Australia.

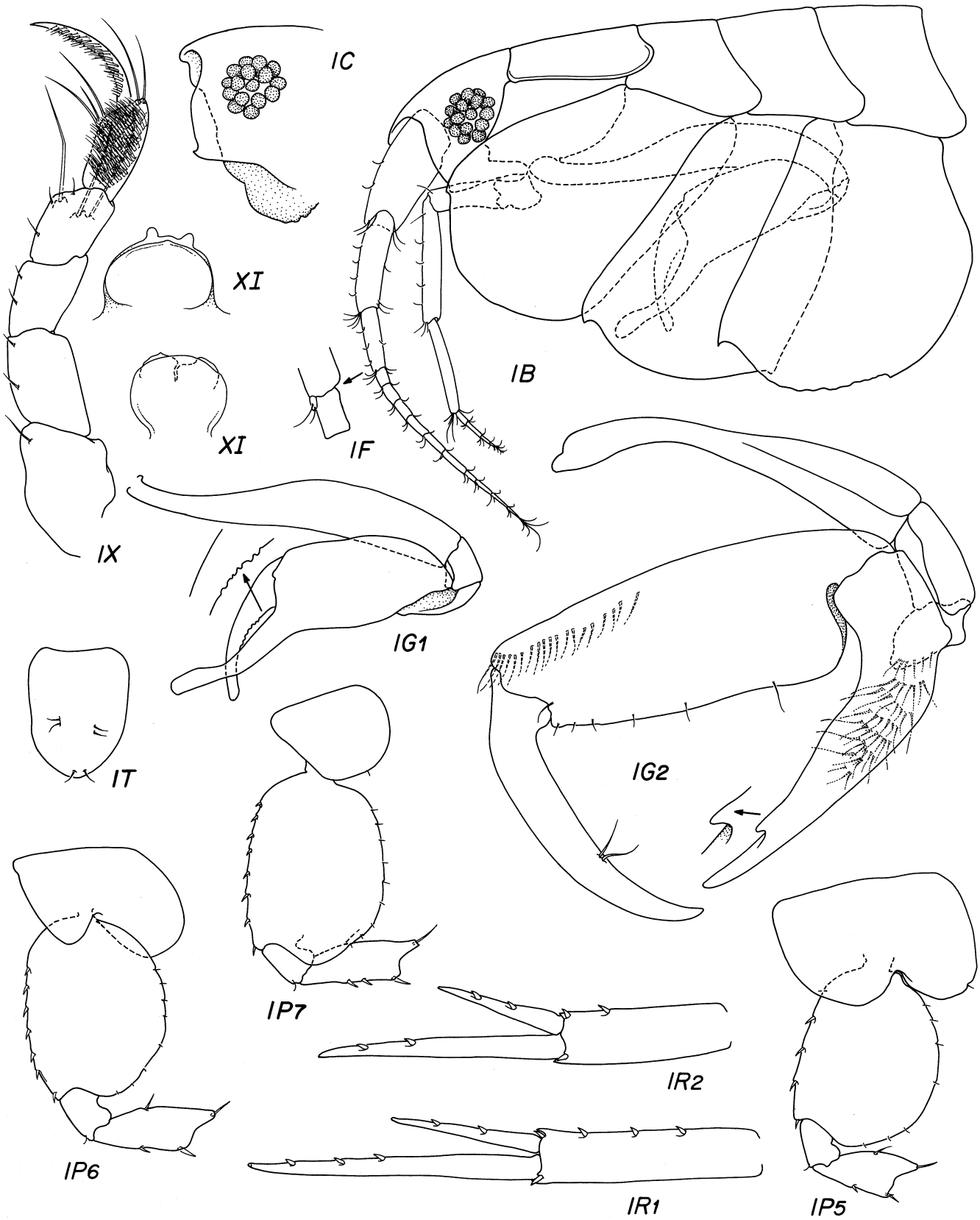

Fig. 13. *Anamixis nedcampensis* n.sp., holotype, anamorph male "L", 3.02 mm; "C", 2.95 mm; "M", 2.87 mm.

Relationship. *Anamixis nedcampensis* is part of a triad of Indian Ocean species, (*A. nedcampensis, A. mahe, A. barnardi*), of anamixids having a rounded ventral keel; subequal coxae 2–4, and in having gnathopod 2 with a bifid process on the carpus, and an elongate, unarmed dactyl. The lack of a serrate proximal ridge on the carpus of the second gnathopod further distinguishes *A. nedcampensis* from *A. barnardi* and *A. mahe*.

Remarks. Superficially, *A. nedcampensis* most closely resembles *A. mahe* and *A. barnardi* in the bifid process on the carpal lobe of gnathopod 2. However, *A. nedcampensis*, and all other Indo-Pacific anamixids differ from *A. mahe* in lacking terminal setae on gnathopod 1. The other Indian Ocean anamixid, *A. stebbingi*, lacks an apically dilated article 5 of gnathopod 1, and has a serrate carpal lobe, and a denticulate inner margin on the dactyl of gnathopod 2.

Habitat. Presumed commensal, specific host(s) unknown, general habitat shallow limestone reefs among algae.

Distribution. Eastern Indian Ocean, Western Australia, coral reefs, 1 m.

Anamixis ningaloo n.sp.

Fig. 14

Type material. HOLOTYPE, anamorph male "W", 2.63 mm, AM P41031, inside outer reef off Ned's Fish Camp, Ningaloo Reef, Cape Range National Park, Western Australia, 21°59.5'S 113°54.5'E, 2 m, airlift from living *Acropora* sp., R.T. Springthorpe and J.K. Lowry, 1 January 1984, station WA-346.

Diagnosis. Antenna 1, peduncle article 1 enlarged. Gnathopod 1, article 5 thin and attenuate relative to article 6. Gnathopod 2, coxa not greatly enlarged, anteroventral and posteroventral corners each defined by a single cusp, ventral margin expanded; carpal lobe of moderate length, thickened; ventral margin of propodus oblique, defined by a tooth and a truncate process; dactyl inflated, inner margin with denticulate proximal process and smaller distal process bordered by paired setae.

Description. Holotype "W". Head, anterior margin transverse, anteroventral corner defined by small cusp; ventral keel, anterior margin oblique, bearing 3 small teeth on anterodistal margin, ventral margin defined by anteroventral tooth; eyes with 15 loosely bundled ommatidia. Antennae: antenna 1 peduncular ratio 35:25:17; article 1 enlarged, 2.1 times thicker than article 2; flagellum 10-articulate, aesthetascs on articles 3–10; antenna 2 apex reaching to flagellar article 4 of antenna 1, flagellum short, 4-articulate. Maxilliped, inner plates fused into apically rounded process with slightly sinuous anterior margin; outer plates lacking inner lobes; palp article 4, 1.6 times length of article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apically bifid; article 5 feeble, distally attenuate; article 6 straight, inner margin with complexly serrate inner margin, apical pore present. Gnathopod 2, coxa scarcely larger than 3 or 4, ventral margin expanded, defined by cusp at anterior and posterior margins; carpus thickened, unarmed, 0.85 the length of propodus, hindmargin smooth, ventral margin oblique, defined by posterior tooth and anterior truncate process; dactyl with denticulate proximal ridge, with smaller distal process bearing paired setae. Pereopod 3, coxa subrectangular, slightly larger than coxa 4, ventral margin rounded. Pereopod 4, anterior margin of coxa straight, posterior margin tapering. Pereopod 5–6 similar, coxae bilobed; basis spinose anteriorly, posterior margin expanded, with 6–7 submarginal setae. Pereopod 7, coxa entire, submarginal setae lacking; basis spinose anteriorly, posterior margin expanded, with 6 serrations, each with a submarginal seta. Epimera typical. Uropods 1 and 2, outer rami shortened, spinose, approximately one-half length of inner. Uropod 3 missing. Telson broad, subrectangular, 1.3 times longer than wide, with 4 dorsofacial and 2 apical setae.

Leucomorphs. Unknown.

Etymology. Named for the type locality, Ningaloo Reef, Cape Range National Park, Western Australia.

Relationship. The more or less subequal coxae 2–4 and the thickened carpal lobe of gnathopod 2 of *A. ningaloo* are reminiscent of the *A. moana, A. kateluensis* and *A. bazimut* clade, but *A. ningaloo* lacks the apically notched inner plates of the maxilliped found in these central and south Pacific species.

Remarks. The single holotype specimen of *A. ningaloo* seems to show a slight apical indentation of the inner plate of the maxilliped that may represent incomplete fusion, natural malformation, or damage in dissection and mounting. Additional specimens must be examined before the value of this character is established.

Habitat. Presumed to be commensal, specific host(s) unknown, general habitat is shallow coral reef environments. It is worth noting here that this species was taken in an airlift sample from live coral (*Acropora*). Corals of the genus *Acropora* include 54 species from Western Australia. The complex branching growth pattern of *Acropora* provides a multitude of microhabitat and a number of commensals, including crustaceans, have been reported associated with *Acropora* corals. It is assumed that the habitat of *A. ningaloo* is the typical host ascidian or asconoid sponge. However, since *Acropora* inhabits shallow, wave washed reef flats, it

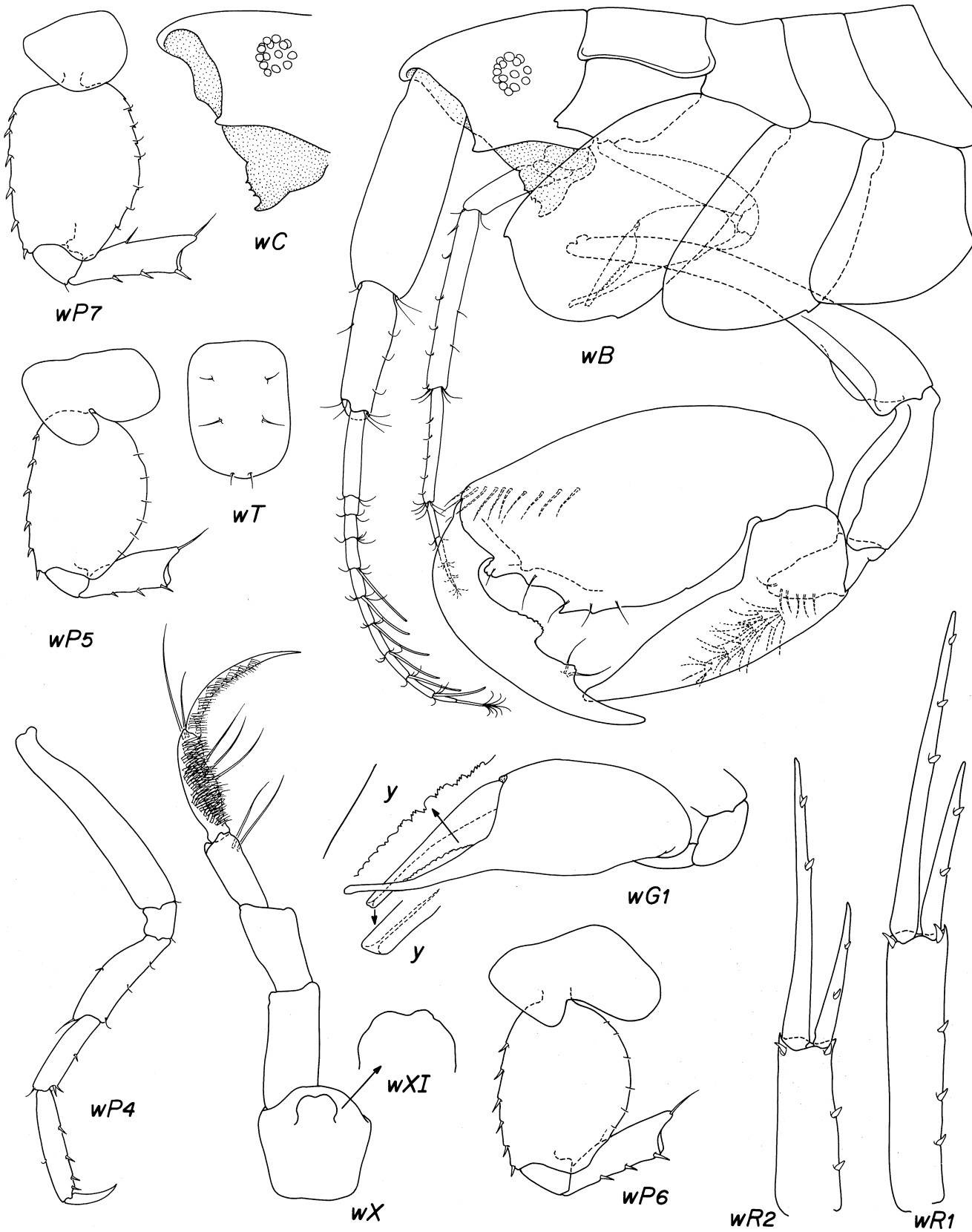

Fig. 14. *Anamixis ningaloo* n.sp., holotype, anamorph male "W", 2.63 mm.

is possible that anamorphs and leucomorphs of *A. ningaloo* could be found in secondary chambers, such as coral galls. The bases of *Acropora* colonies are frequently dead and overgrown with fouling communities that could support typical anamixid hosts. Further ecological studies are needed to resolve this issue.

Distribution. Eastern Indian Ocean, Western Australia, coral reefs, 2 m.

Anamixis pacifica (Barnard, 1955)

Fig. 10 (in part)

Leucothoides pacifica Barnard, 1955: 26–28, fig. 1a–k.
Anamixis linsleyi Barnard, 1955: 28–30, fig. 2a–d.

Material. Newport Beach, California; January, 1954; depth 15 m; J.L. Barnard and D.L. Reish.

Diagnosis. Propodus of gnathopod 1 with apical spine; palm of gnathopod 2 with several cusps, the distal one the longest.

Description. Head, anterior margin transverse, lower margin evenly rounded, ventral keel with low, sharp process. Antenna 1, ratio of articles 1–3, 14:10:7. Details of maxilliped unknown. Gnathopod 1, carpochelate, carpus recurved and blunt at apex; propodus with serrate inner edge and apical spine scarcely extending beyond carpus. Gnathopod 2, coxa ventrally expanded, lower margin demarcated by two small indentations; carpal lobe recurved, tapering; propodus, palm not distinct from hind margin, armed with several cusps, the distal one the longest; inner edge of dactyl with 3 cusps, the distal one armed with 2 spinules. Telson rounded apically, 1.5 times longer than wide, with several groups of marginal setae.

Leucomorphs. Unknown.

Relationship. *Anamixis pacifica* is unique in having a single terminal spine on the propodus of gnathopod 1. The second gnathopod appears intermediate in ornamentation between *A. cavatura* and *A. vanga* of the Caribbean.

Remarks. The anamorph was originally described as *A. linsleyi*. However, *A. pacifica*, initially described as *Leucothoides*, is assumed to be the leucomorph stage of *A. linsleyi* and takes page priority. This assumption is based on association of the two stages from the same localities and may prove problematic in the future if other anamixids are discovered from California waters. Until such time as confirmation can be obtained through rearing experiments, taxonomic decisions incorporating leucomorph characteristics of *A. pacifica* into *A. linsleyi* are to be avoided.

Habitat. From sponges found growing on floating docks.

Distribution. Eastern Pacific Ocean, Newport Bay, California, fouling communities.

Anamixis papuaensis n.sp.

Fig. 15

Type material. Anamorph male "A", 2.92 mm, AM P41032, *Galaxaura* algae from base of coral reef, east of Manunouha Island, Bootless Bay, Papua New Guinea, 9°30'S 147°07'E, 10 m, J.K. Lowry, 26 October 1980, station PNG-14.

Diagnosis. Head angle transverse. Ventral keel large, projecting will below head, bearing apically constricted tooth. Coxa 2 greatly enlarged; anterior margin expanded, with 4 small truncate cusps; ventral margin sinuous with midventral tooth. Gnathopod 2, carpus shortened, anterolateral margin serrate; propodus, hindmargin tapering, serrate, bearing a complex cuspate process on medial margin; distal portion with 2 large teeth; dactyl denticulate near insertion of propodus, distal margin with 2 blunt medial processes.

Description. Holotype "A". Head, anterior margin transverse, corner sharp; ventral keel enlarged, projecting will below ventral margin of head, bearing ventrally projecting tooth; eyes with 16 compact ommatidia. Lower lip lobes not readily visible from lateral view. Antennae: antenna 1, peduncle ratio 30:18:12; flagellum 10-articulate, aesthetascs on articles 8–9. Antenna 2, flagellum 4-articulate. Maxilliped, inner plates fused, small apical notch present; outer plates lacking inner lobes; palp article 4 elongate, 1.8 times length of article 3. Pereonite one with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apically bifid; article 6 finely serrate on inner margin. Gnathopod 2, coxa greatly enlarged over coxae 3–4, anterior margin with 4 cusps, expanded, ventral margin sinuous with midventral tooth; medial margin of basis with distal triangular locking process; carpus short, anterolateral margin serrate; hindmargin of propodus tapering ventrally, serrate, mesoproximal region bearing large cuspate process; dactyl reaching to cuspate process of propodus, proximally denticulate, distomedial margin with blunt process, apex excavate. Pereopods 3 and 4, coxae subequal. Pereopod 5–6, coxae bilobed; second articles slightly rounded posteriorly. Pereopod 7, coxa entire, oval, article 2 similar to pereopod 5 and 6. Uropods 1 and 2, outer rami one-half length of inner. Uropod 3 missing. Telson broad, entire, 1.3 times longer than wide, bearing 2 small subapical setae.

Leucomorphs. Unknown.

Etymology. Named for the Papuan region of the South Pacific.

Relationship. *Anamixis papuaensis* appears most closely related to *A. falarikia* in the elongate palp

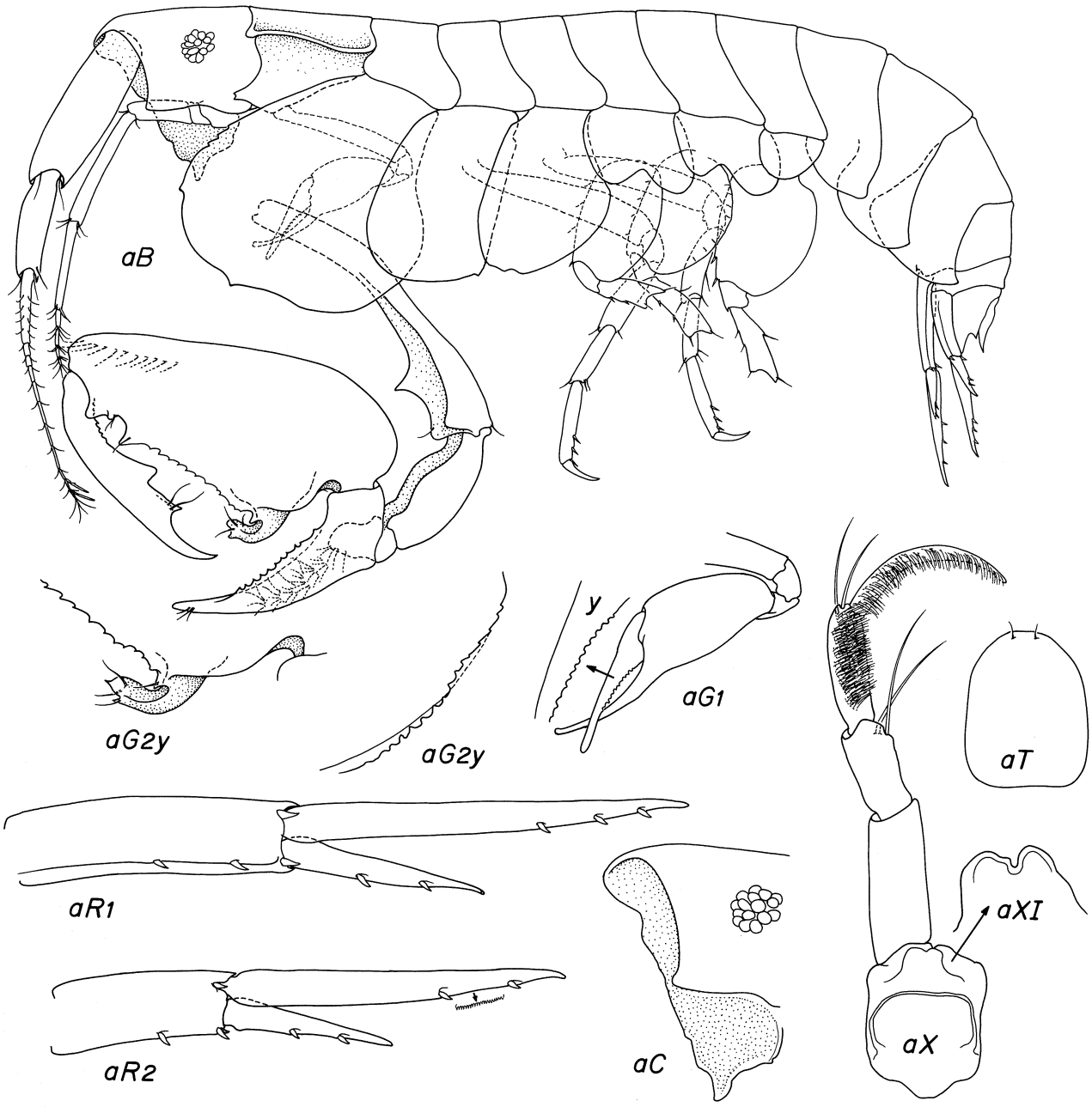

Fig. 15. *Anamixis papuaensis* n.sp., holotype, anamorph male "A", 2.92 mm.

article 4 of the maxilliped and features of the second gnathopod including an enlarged coxa with anterior cusps, a sinuous ventral margin with a midventral tooth, and an apically excavate dactyl. *Anamixis papuaensis* resembles *A. excalibur* in the elongate palp article 4 of the maxilliped.

Remarks. *Anamixis papuaensis* is clearly related to *A. falarikia* and *A. excalibur* by the elongate palp article 4 of the maxilliped. The similarities of *A. papuaensis* and *A. falarikia* including the morphology of coxa 2, the generally aberrant nature of the carpus, propodus, and dactyl of the second gnathopod indicate unusual variation along a common theme. The unique medial process on the inner margin of the second gnathopod of *A. papuaensis* may be an adaptation for a suspected commensal existence. *In-situ* behaviour studies of *A. papuaensis* and *A. falarikia* may elucidate the function of the atypical gnathopod 2 found in these two species.

Habitat. Unknown, suspected to be commensal in small asconoid sponges and ascidians.

Distribution. Coral Sea; south-eastern New Guinea, Papua New Guinea, coral reefs, 10 meters.

Anamixis stebbingi Walker, 1904

Anamixis stebbingi Walker, 1904: 259–261, fig. 18; ?Nayar, 1967: 44, fig. 6.

Diagnosis. Gnathopod 2, carpus denticulate near base, middistal portion with 2 raised processes.

Description. Gross morphology of most characters known only from original drawings, details on specific characters lacking in most instances.

Leucomorphs. Unknown.

Remarks. Walker's description of *A. stebbingi* from India was based on a single imperfect specimen, and only gnathopods 1 and 2 were partially figured. It now appears that there are several species from littoral coastal waters of India, all of which are closely related. All three species found in the region have the base of the carpal lobe on gnathopod 2 denticulate. *Anamixis barnardi, A. mahe* and *A. nedcampensis* exhibit a distinct thumb-like process on the carpus of gnathopod 2. Neither Walker's figure nor text description of gnathopod 2 mention such a process. Nayar (1967: 144, fig. 6) reported *A. stebbingi* from coastal India, his description also based on a damaged specimen. Nayar shows the carpus of gnathopod 2 with a small but distinct thumb-like process. However, he also shows a denticulate inner margin on the dactyl that is lacking in *A. barnardi*, but was figured by Walker in his description of *A. stebbingi*. Until additional material from the type localities are available for examination, *A. stebbingi* and *A. barnardi* will continue as distinct species, with Nayar's report of *A. stebbingi* problematical, falling intermediate between the two. It is probable that Nayar's material is an undescribed species. Considering distribution patterns in anamixids from other localities, it would not be unreasonable to expect another distinct species to occur in this region. Future species descriptions must include even the most minute details if subsequent authors are to sort out the species occurring within a given region.

Habitat. Oyster reefs.

Distribution. Indian Ocean, Sri Lanka (formerly Ceylon), sublittoral.

Anamixis tangaroa n.sp.

Fig. 16

Type material. HOLOTYPE, anamorph male "A", 3.58 mm, NMV 19742, Bass Strait, VIMS, cruise 81-T-1, NZOI RV *Tangaroa*, station 158, 13 November 1981, 39°49.5'S 146°18.5'E, 82 m, sediment: bryozoa mud, S-M grab. PARATYPES, anamorph males "B" 3.75 mm, and "C" 3.26 mm, NMV 19743, Bass Strait, Station 160, 13 November 1981, 39°43.7'S 147°19.6'E, 59 m, sediment: muddy shell, epibenthic sled.

Diagnosis. Inner plates of maxilliped, separate, incompletely fused; outer plates with vestigial inner lobes. Gnathopod 2, coxa ventrally excavate, inner margin of dactyl strongly tuberculate. Telson elongate.

Description. Holotype "A". Head, anterior margin transverse, anteroventral corner defined by small cusp; ventral keel truncate, barely extending below ventral margin of head, anterior margin oblique, straight, anterodistal region with several minute serrations; eyes with 14 compact ommatidia. Antennae, antenna 1, peduncular ratio 35:24:17, flagellum 12-articulate, aesthetascs on articles 10–12; antenna 2 approximately subequal to antenna 1, flagellum 4-articulate. Maxilliped, inner plates partially fused, outer plates with vestigial inner lobes; palp article 4, 1.2 times article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1, coxa reduced, apex bifid; article 5 recurved apically, inner margin bare; article 6 straight, inner margin with minute, uneven serrations and setae, apex with accessory nail. Gnathopod 2, coxa somewhat larger than 2–4, anterior margin expanded smooth, ventral margin with broad excavation; carpus long, slightly recurved; propodus, hindmargin with several widely spaced setae, distal portion with 3 small teeth; dactyl, inner margin grossly tuberculate to paired setae. Pereopod 3, coxa smaller than 2 or 4, ventral margin rounded. Pereopod 4, coxa tapering posteriorly. Pereopods 5 and 6, coxae bilobed; basis spinose anteriorly, posterior margin expanded and furnished with 6–8 submarginal setae. Pereopod 7, coxa entire, posterior margin with 3 submarginal setae; basis spinose anteriorly, posterior margin with 14–15 submarginal setae. Uropods 1 and 2, peduncles and rami spinose, outer ramus one-half length of inner. Uropod 3 missing. Telson entire, elongate, 1.7 times longer than wide, with two pairs of dorsofacial, and one pair of apical setae.

Leucomorphs. Unknown.

Etymology. Named for the New Zealand Research Vessel, RV *Tangaroa*.

Relationship. The presence of incompletely fused inner plates on the maxilliped distinguish *A. tangaroa* from

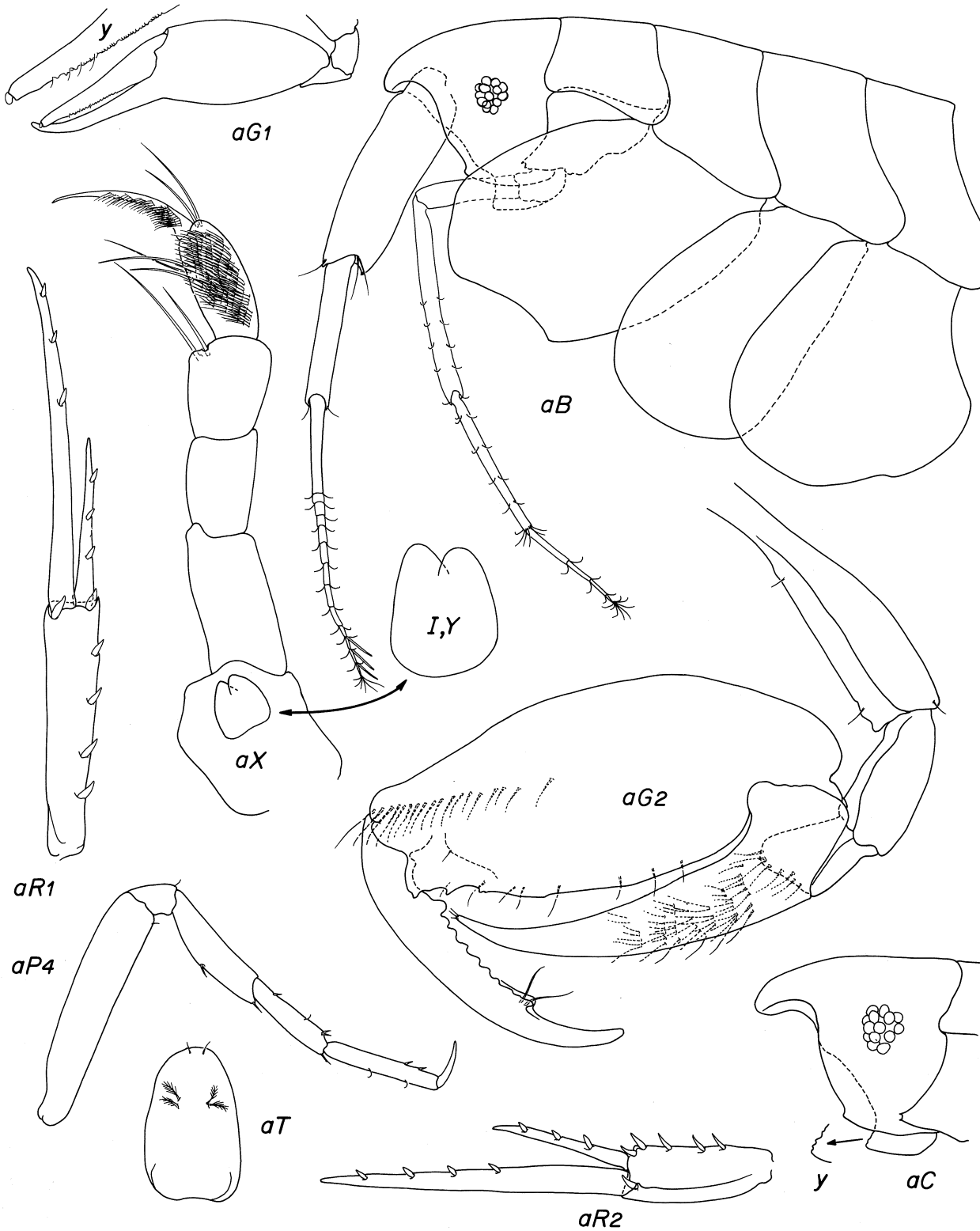

Fig. 16. *Anamixis tangaroa* n.sp., holotype, anamorph male "A", 3.58 mm.

all other members of the genus *Anamixis*, placing it in proximity with the genus *Nepanamixis* in this regard. The ventrally excavate second coxa and the strongly tuberculate inner margin of the dactyl of gnathopod 2 separate this species from other *Anamixis* species.

Remarks. The collection of *A. tangaroa* from depths over 80 meters in the cold waters of the Bass Strait (10°C) significantly extends the range of this typically tropical, shallow water family. *Anamixis tangaroa* may be a tropical relic (Newman, 1991) either from previous

sea level lowering, or, by prior tropical transgressions into lower latitudes. In either scenario, the plesiomorphic nature of *A. tangaroa* offers an interesting benchmark in the evolutionary history of the Anamixidae. The challenge will be to accurately integrate this information into the overall phylogeny of the group. On the other hand, it may that when we begin to adequately sample the deeper tropical waters, more of these unusual "relic" species will come to light.

Habitat. Presumed commensal, specific host(s) unknown.

Distribution. Tasman Sea, Bass Strait, coarse muddy sediments, 59–82 m.

Anamixis torrida Barnard, 1970

Anamixis torrida Barnard, 1970: 103, fig. 65a.
Leucothoides pottsi.–Schellenberg, 1938: 26–28, fig. 13.–J.L. Barnard, 1965: 492–493.–1970: 211–213, fig. 138 (not *A. pottsi* Shoemaker, 1933).–Ledoyer, 1984: 82 (as *L. torrida*).

Remarks. This species is based on a leucomorph and *A. torrida* should not be considered valid until it is connected with its anamorph counterpart. It is highly doubtful that the references to *A. torrida* by J.L. Barnard are valid and probably represent several species of possibly *Anamixis* and *Paranamixis*.

Anamixis vanga n.sp.

Figs 17,18

Type material. HOLOTYPE, anamorph male "E", 4.85 mm, USNM 243319, Carrie Bow Cay, Belize, rubble on reef slope, from the branchial basket of *Ascidia interrupta* Heller, 1878, 13.3 m, J.D. Thomas, 14 July 1988, JDT-Bel-132c; 1 PARATYPE, anamorph male "F", 4.34 mm, USNM 243320, JDT-Bel-132c; 3 PARATYPES, leucomorph male "G", 3.14 mm, USNM 243321, leucomorph female "H", 2.65 mm, USNM 243322, leucomorph female "I", 3.14 mm, USNM 243323, JDT-Bel-132c; 11 PARATYPES, 10 leucomorphs, 1 anamorph, USNM 243324, JDT-Bel-132c.

Additional material examined. USNM 243324, Carrie Bow Cay, Belize, rubble zone in backreef area north of Carrie Bow Cay, taken from the branchial basket of *A. interrupta*, located on the underside of coral rubble, 1 m, J.D. Thomas, 29 June 1987, JDT-Bel-112b; Carrie Bow Cay, Belize, rubble from patch reef near south-east corner of South Water Cut, 2 m, J. D. and S. Thomas, 24 July 1988, JDT-Bel-140.

Diagnosis. Anamorphs: head, lateral margins excavate, lacking any defining process; ventral keel subrectangular, scarcely projecting below head. Gnathopod 1, carpus and propodus each bearing a single terminal seta, inner margin of propodus dentate and setose. Gnathopod 2, propodus elongate, distal portion defined by 3 major teeth; dactyl without ornamentation. Leucomorphs: anterior margin of head broadly rounded; ventral keel projecting beneath head as a broadly rounded V-shaped process. Gnathopod 1, coxa subquadrate, bearing 2 apical setae; carpus, inner margin with minute serrations separated by larger serrate processes, apex with 2 embedded spines without ornamentation, the larger of the two with an accessory blade or flake; propodus, inner margin denticulate, armed with short spines and setae. Gnathopod 2, males, palm oblique, reaching Mark 0.65 on anterior margin of propodus.

Description. Based on holotype, male, "G", and paratype, male, "H". Head, lateral margin with prominent ridge, deeply excavate below, anterior margin oblique, lacking any defining processes; ventral keel projecting as a subrectangular process borne on posterior lamina; eyes composed of numerous ommatidia, bisected by lateral ridge. Antenna 1 elongate, ratio of segments 1–3 37:42:21; flagellum 12-articulate. Antenna 2 elongate, inserted well behind eye, flagellum 4-articulate. Lower lip lobes not readily visible from lateral view. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.2 times the length of article 3. Pereonite 1 with prominent lateral locking ridge continuous with lateral ridge on head. Gnathopod 1, coxa with small apical process; carpus slightly recurved distally, inner margin unarmed, apex with long seta; propodus straight, not quite reaching the end of the carpus, inner margin denticulate, furnished with series of paired blunt spines and short setae, apex with long seta. Gnathopod 2, coxa much larger than 3 or 4, anterior margin with small cusp, ventral margin rounded, posterior margin straight, posteroventral corner with small cusp; carpus slightly recurved, bearing numerous mediofacial setal tufts; propodus long, hindmargin smooth, distal portion defined by a series of 3 teeth, the largest near insertion of dactyl, the remaining teeth becoming progressively smaller, inner surface with long row of mediofacial setae; dactyl nearly straight, bearing a seta on a small process. Pereopod 3, coxa slightly narrower than 2, rounded ventrally, posteroventral corner defined by small cusp. Pereopod 4, ventral margin of coxa emarginate posteriorly, posterior margin slightly expanded. Pereopods 5–6 similar, coxae bilobed, second articles with setose posterior lobe excavate ventrally. Pereopod 7, coxa entire, article 2 similar to pereopods 5 and 6. Epimera typical for family. Uropods 1 and 2, outer rami reduced. Uropod 3, outer ramus nearly as long as inner, spinose. Telson, suboval, 1.4 times longer than wide, bearing 2 small apical setae.

Description of leucomorphs. Based on male paratype "G", and female paratypes "H" and "I". Males similar to females in most aspects except for the relatively smaller second gnathopods and the presence of brood plates in females. Head, anterior margin broadly rounded,

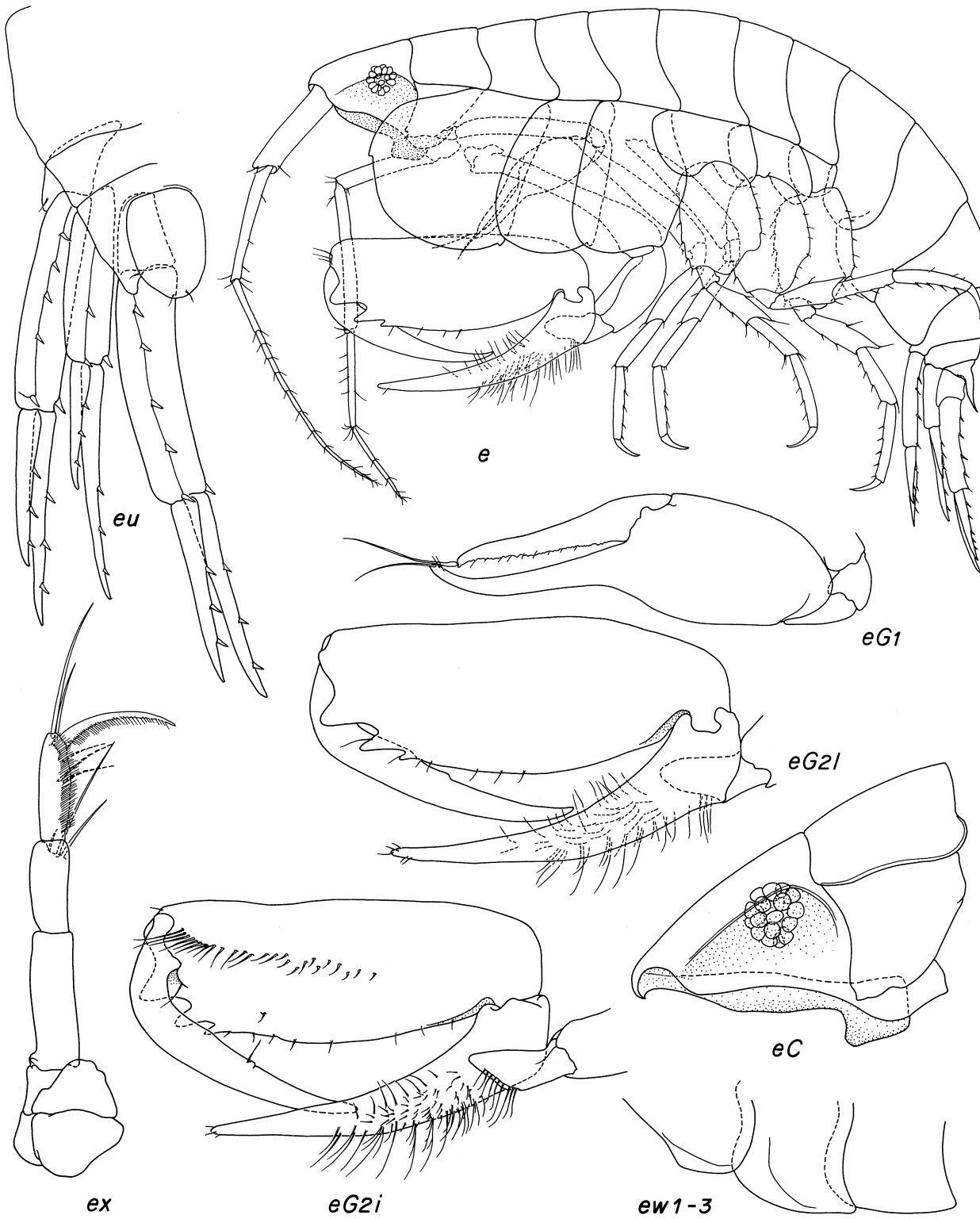

Fig. 17. *Anamixis vanga* n.sp., holotype, anamorph male "A", 4.85 mm.

lacking any defining processes; ventral keel oblique, subtruncate, anterior margin nearly vertical. Mouthparts normal for genus, left mandible with broad incisor and large lacinia mobilis; right mandible, incisor with hooked anterior margin, lacinia mobilis lacking. Gnathopod 1, coxa apically rounded with 2 closely spaced apical setae; carpus straight, inner margin finely serrate, with minute serrations separated by 9–12 elevated serrations, apex bearing 2 large spines embedded at Mark 0.77 of propodus, both spines lacking serrations, the larger spine with terminal flake; propodus, inner margin finely serrate, furnished with series of short

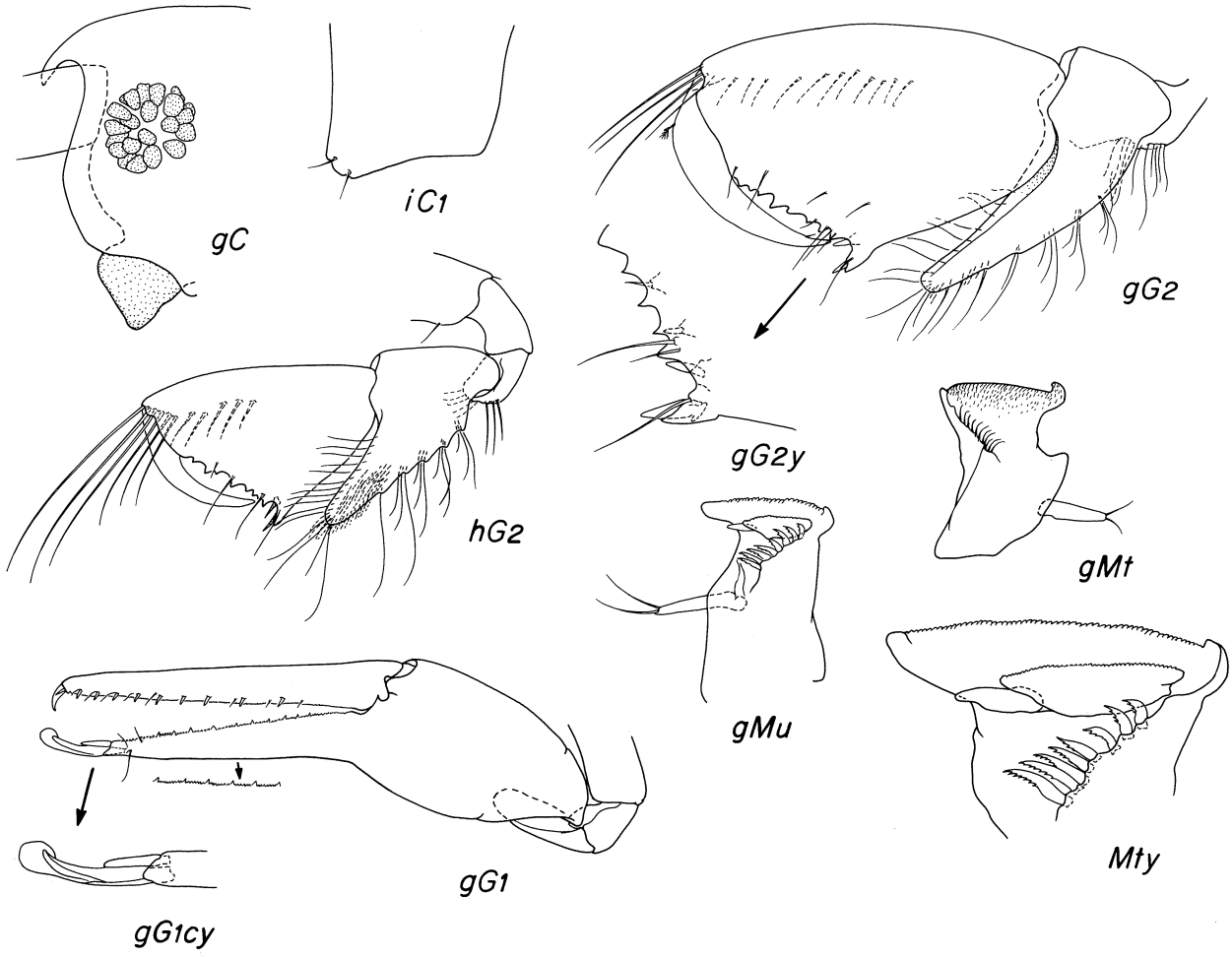

Fig. 18. *Anamixis vanga* n.sp., "G", leucomorph male, 3.14 mm; "H", leucomorph female, 2.65 mm; "I", leucomorph female, 3.14 mm.

spines and setae; dactyl represented with stout recurved spine. Gnathopod 2, in males, article 6 subquadrate, palm oblique, reaching Mark 0.65; in females, relatively smaller than males, article 6 subtriangular, palm oblique, reaching Mark 0.58, carpal setae numerous, and longer than in males.

Etymology. From the Latin, "vanga", meaning spade or mattock, referring to the appearance of the lateral margins of the head, noun in apposition.

Relationship. *Anamixis vanga* is readily separated from its nearest relative, *A. cavatura*, by the shape of the head and ventral keel, longer antennae; and the presence of 3 teeth on the propodus of gnathopod 2. Leucomorphs of these two species are separated on the basis of head margins, ventral keels, and general shape and armament of gnathopods 1 and 2.

Remarks. Colour in life and freshly preserved material: anamorphs, translucent pink, lacking any other significant coloration or patterns; leucomorphs, lacking any coloration and appearing transparent, internal organs readily visible through the exoskeleton.

All three Caribbean species of *Anamixis* have 2 long setae on gnathopod 1. The only other species of anamixid having long setae on gnathopod 1, *A. mahe*, from the Seychelles, differs in having an additional long seta on the propodus. The occurrence of this condition in such widely separated taxa could be attributed to convergence, possibly due to similar feeding adaptations or requirements. A similar argument could also be made for excavate lateral margins of the head exhibited by *A. vanga* and *Paranamixis kanu* from Papua New Guinea. Because anamixids are known or assumed commensals, the occurrence of convergent characters is not unusual. Such convergent morphologies can prove especially dangerous to the unwary taxonomist using cladistic methodologies. Great care must be taken to analyse and develop transformations series that incorporate those characters that will ultimately prove most informative in such analyses. The limited number of representative collections of amphipods from a wide variety of localities and the resulting inability to resolve details of specific character morphologies continue to be a hindrance in this regard.

Habitat. *Anamixis vanga* is most frequently collected from large, solitary tunicates in shallow coral reef or hard bottom areas. While occasionally taken from small asconoid sponges, the preferred host appears to be *Ascidia interrupta* Heller, 1878. The author has collected up to 4 anamorphs and 23 leucomorphs from the branchial basket of a single specimen of *A. interrupta*. Observations of *A. vanga* feeding within the host show that during feeding, *A. vanga* lowers the head ventrally, the lateral ridge on the head contacting the anterior margin of the large second coxa. The lateral ridge of the head thus may be used to "lock" the head in this position during feeding. The author speculates that this morphology may represent an adaptation found in species inhabiting larger hosts such as *A. interrupta* where the amphipods are subject to the relatively stronger current flow. For those species living in relatively smaller hosts, the locking ridge on the first pereonite appears sufficient to stabilise the head during feeding.

Distribution. Western Atlantic and Caribbean, from off Georgia to the Florida Keys, Belize; 2–20 m.

Anamixis yarrega (Barnard, 1974)

Leucothoides yarrega J.L. Barnard, 1974: 103; 1979: 130.
Anamixis yarrega.–Moore, 1987: 240–245, figs 1–4.

Diagnosis. Chelae of gnathopod 1 straight; dactyl of gnathopod 2 tuberculate on inner margin; coxa 4 concave posterodistally.

Description. Head, anterior margin transverse, defined by small cusp, eyes consisting of about a dozen scattered facets, ventral keel subrectangular, small. Antennae subequal in length. Antenna 1, ratio of articles 1–3 unknown, accessory flagellum minute, armed with 3 setae, flagellum 10-articulate. Antenna 2, slender, article 4 longer than 5; flagellum shorter than article 5, 4-articulate. Maxilliped, palp article 4, 1.30 times longer than article 3. Gnathopod 1, basis very elongate; carpus distally blunt, slightly upturned, with small terminal spine; propodus not quite reaching end of carpus, inner margin armed with short setae. Gnathopod 2, coxa large, margins smooth, 4 setae on anterior margin; carpus produced for 80 per cent of propodus length; propodus, hindmargin slightly expanded, merging into palm which is armed with several cusps, of which the anterior is the largest; dactyl straight to paired setae, then recurved, proximal margin denticulate. Uropods 1 and 2, outer ramus reduced to half the length of inner; uropod 3 missing. Telson suboval, entire, 1.38 times longer than wide. For a more detailed discussion of this species, see Moore (1987).

Leucomorphs. Unknown.

Remarks. Colour in life orange, with red eyes. This species is difficult to separate from other taxa as it possesses no striking characteristics. The ventral keel, of potential informative value, is unobservable in the holotype due to artefacts in the permanent slide preparation. Superficially, this species resembles *A. moana* but is distinguished by the subrectangular keel, the straight chelae on gnathopod 1, and the recurved carpal lobe and tuberculate inner margin of the dactyl on gnathopod 2. Moore's designation of a leucomorph for this species is premature and circumstantial.

Habitat. *Ecklonia radiata* and *Caulerpa trifaria* holdfasts.

Distribution. Tasman Sea, Tinderbox, Tasmania, 3–4 m.

Nepanamixis n.gen.

Type species. *Nepanamixis dianthus* n.sp.

Diagnosis. Terminal males: antennae relatively short, eyes with 9 scattered ommatidia, head margins rounded. Maxilliped, inner plates only partially fused, outer plates with inner lobes present or reduced to a small process. Coxa 1 moderately reduced. Gnathopod 1, carpus basally inflated, inner margin cuspate; when armed, apex of propodus with terminal spine or bulbous process. Coxae 2 dominant or subequal to 3 and 4; margins of coxae 2–3 smooth, sparsely setose submarginally; ventral margin of coxae 4 distally produced or crenulate. Gnathopod 2, propodus with 2 rows of mediofacial setae, each row with 4 or more seta, hindmargin straight or sinuous. Coxa 4 ventrally crenulate or excavate. Telson long, 1.80–2.10 or longer than wide, tapering apically.

Variables. Shape and armament of gnathopod 1 carpus and propodus; occurrence of tuberculations on anterior margin of the basis of gnathopod 2; extent of serrate lateral ridge on carpus of gnathopod 2; ventral margin of coxa 4.

Relationship. Differing from *Anamixis* and *Paranamixis* with the characters of the genus. Leucomorphs of *Nepanamixis dianthus* are unique in having a shortened carpus with 4 successively shortened, recurved spines on gnathopod 1; in having a more oblique palm in gnathopod 2. Leucomorphs currently known only from the type species of the genus, characters of other *Nepanamixis* species unknown at present.

Species. *Nepanamixis dianthus* n.sp.; *N. grossimana* (Ledoyer, 1978) as *Anamixis grossimana*; *N. torreanus* n.sp.; and *N. vectoris* n.sp.

Distribution. Marine, Indo-Pacific, Eastern Pacific, Western Caribbean, Mauritius to Belize, coral reefs, 1–10 m, 4 species.

Key to the Species of *Nepanamixis*

1. Gnathopod 2 of thick form, length 2.1–2.3 times width; apex of article 6, gnathopod 1 with bulbous process 3

—— Gnathopod 2 of thin form, length 2.8–3.0 times width; apex of article 6, gnathopod 1 lacking bulbous process 2

2. Gnathopod 1, apex of articles 5 and 6 with embedded spines, palm with 1 prominent tooth ..... *N. grossimana*

—— Gnathopod 1, apex of articles 5 and 6 lacking spines, palm with 2 prominent teeth ..... *N. dianthus* n.sp.

3. Article 5 of gnathopod 1 with stout spine at apex; coxa 4 emarginate ventrally ..... *N. vectoris* n.sp.

—— Article 5 of gnathopod 1 with small seta at apex; coxa 4 crenulate ventrally ..... *N. torreanus* n.sp.

Nepanamixis dianthus n.sp.

Figs 19,20

Type material. HOLOTYPE, anamorph male "A", 2.44 mm, USNM 243334, "Sand bores", Carrie Bow Cay, Belize, formalin wash of shallow rubble, 1–2 m, J.D. Thomas, 21 July 1984, JDT-Bel-105a. 1 PARATYPE, anamorph male "B", 2.39 mm, USNM 243335, Carrie Bow Cay, Belize, formalin wash of rubble in patch reef, south-west of reef crest on south side of South Water Cut, 1–2 m, J.D. Thomas, 5 July 1984, JDT-Bel-117; 1 PARATYPE, leucomorph male "C", 2.52 mm, USNM 243336, Carrie Bow Cay, Belize, formalin wash of *A. palmata* rubble, patch reef inside reef crest on South Water Cut, 1–2 m, J. D. Thomas, 9 June 1987, JDT-Bel-121a; 1 PARATYPE, leucomorph male "D", 2.00 mm, USNM 243337, JDT-Bel-121a; 1 PARATYPE, female leucomorph "E", 1.93 mm, USNM 243338, JDT-Bel 121a.

Additional material examined. Leucomorph, male, "F", 2.18 mm, (uncatalogued), Sand Bores, Carrie Bow Cay, Belize, formalin wash of rubble, 1–2 m, J.D. Thomas, 14 July 1988, JDT-Bel-133c.

Diagnosis. Gnathopod 1, carpus dilated, inner margin with 2 major and several minor cusps. Gnathopod 2, carpal lobe with prominent serrate lateral ridge, apex tapering; propodus elongate, 1.25 times longer than wide. Pereopod 4, coxa ventrally crenulate.

Description. Based on anamorph male: head, lateral margins rounded, anteroventral margin without defining cusps or processes, eye composed of 9 loosely scattered ommatidia; ventral keel projecting below margin of head, truncate. Antennae reduced in length; antenna 1 and 2, 0.61 and 0.59 the length of head to pereonite 4 respectively; antenna 1, ratio of articles 1–3 12:11:8, flagellum 4-articulate, of antenna 2, 3-articulate. Maxilliped, inner plates present, cleft; outer plates with distinct inner lobes; palp article 4, 1.1 times longer than article 3. Lower lip lobes not readily visible from lateral view. Pereonite 1, locking ridge present, scarcely produced posteriorly. Gnathopod 1, coxa reaching ventral margin of head, broadly rounded anteriorly; carpus, posterior margin inflated, inner surface with 2 prominent lateral cusps and 4 minor processes medially; propodus straight, inner margin with setae only, apex lacking ornamentation. Gnathopod 2, coxa larger than 3 or 4, margins smooth, broadly rounded with 3 ventral setae; basis unarmed; carpal lobe with pronounced serrate lateral ridge flared outwards, distal portion of carpus attenuate, apex with several small setae; propodus elongate, 3.12 times longer than wide, hindmargin sinuous, apex truncate and lacking defining ornamentation, secondary row of 5 mediofacial setae present; dactyl elongate, recurved distally, with 2 small paired setae, tip of dactyl nearly reaching entire length of palm. Pereopod 3, coxa smaller than 4, margins not expanded, with 2 ventral setae; remainder of pereopod normal. Pereopod 4, coxa 4 crenulate ventrally, with 3 setae; remainder of pereopod similar to pereopod 3. Pereopods 5 and 6 similar except for deeper hind lobe on coxa 6; bases spinose anteriorly, posterior margins uneven, tapering ventrally and setose. Pereopod 7, coxae entire, basis slightly more expanded than 5 or 6, otherwise similar to 5 and 6. Epimera normal for genus. Uropods 1 and 2, outer rami reduced, outer ramus of uropod 1 lacking spines and styliform. Uropod 3, outer ramus nearly subequal to inner. Telson, elongate, subovate, 1.87 times longer than wide, apex evenly tapered and bearing 2 setae.

Leucomorphs. Confirmed from rearing experiments. However, selected leucomorph males apparently undergo a terminal transformation, persisting as leucomorphs

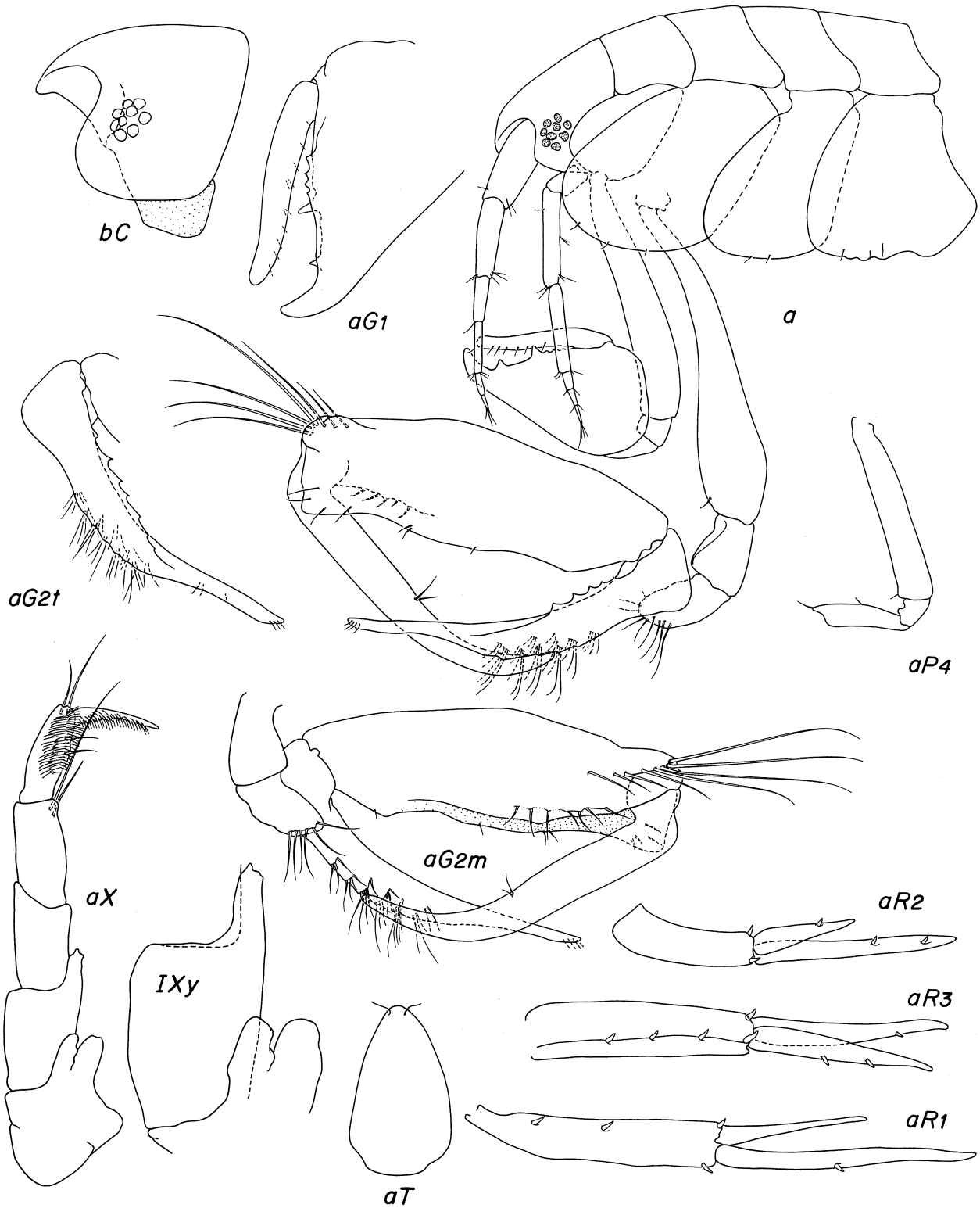

Fig. 19. *Nepanamixis dianthus* n.sp., holotype, anamorph male "A", 2.44 mm; "B", anamorph male, "B", 2.39 mm.

that are larger in size than their anamorph counterparts. Such males are characterised by large second gnathopod with a more oblique palm than smaller male leucomorphs (see leucomorph male "C").

Description of sub-adult male and female leucomorphs: head, anterior margins rounded, eye composed of 9 loosely packed ommatidia. Maxilliped, inner plates separate, apices with 3 marginal spines; outer plate

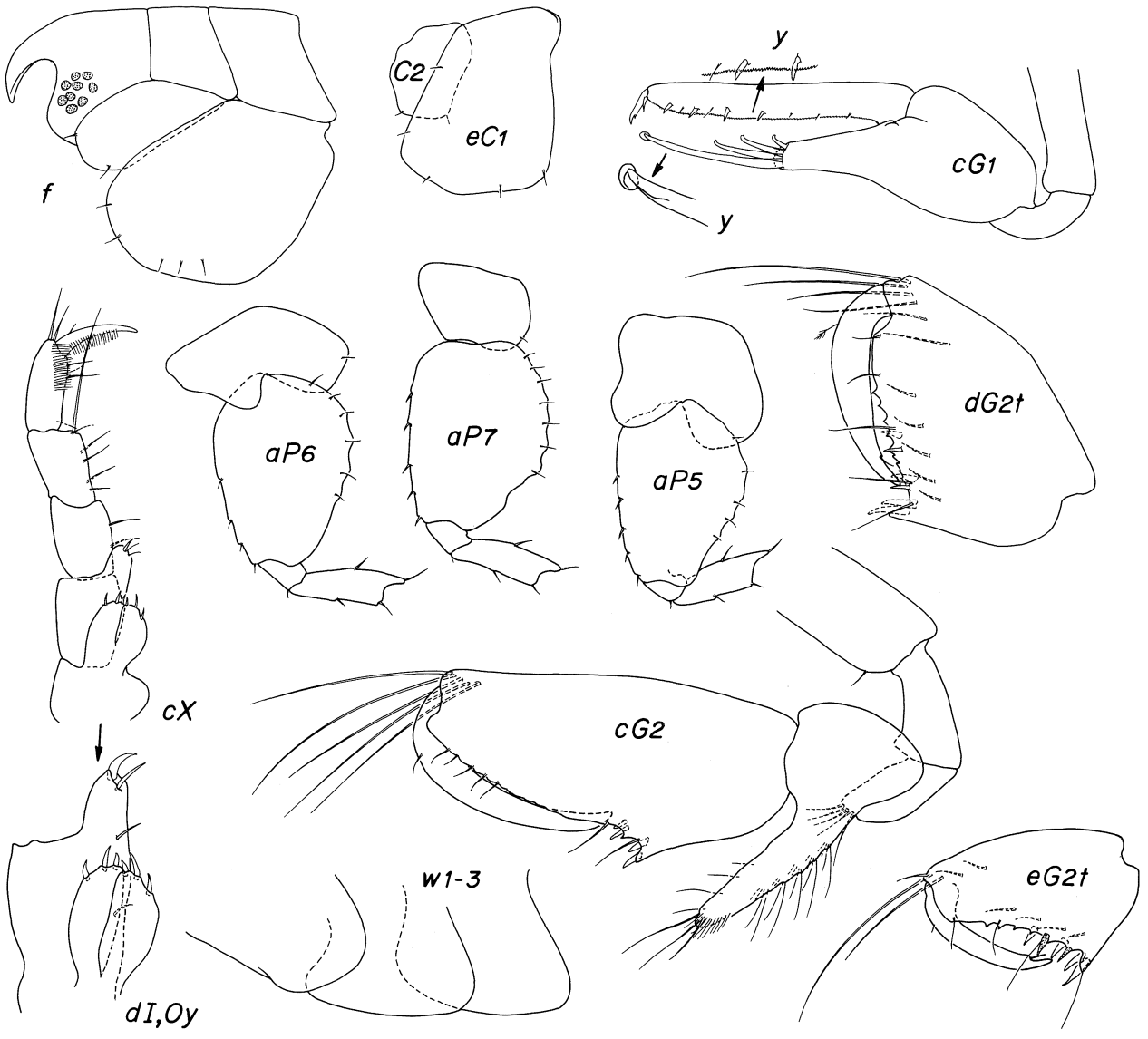

Fig. 20. *Nepanamixis dianthus* n.sp., holotype, anamorph male "a", 2.44 mm; "c", leucomorph male, 2.52 mm; "d", leucomorph male, 2.00 mm; "e", leucomorph female, 1.93 mm; "f", leucomroph male, 2.18 mm.

produced medially, apex with 1 large and 1 medium spine. Gnathopod 1, coxa reduced, rounded, extending below margin of head; carpus shortened, apex only reaching to midpoint of propodus, apex with 4 embedded spines, the largest reaching apex of propodus and bearing terminal flake, the three remaining spines successively shortened; propodus minutely serrate on inner margin with 4 equally spaced submarginal spines and setae, apex with stout spine. Gnathopod 2, coxa large, evenly rounded; carpus, palm multidentate, inner margin with 6 embedded spines, the largest defining the palm; palm oblique, inner margin with two rows of feeding setae; dactyl slightly recurved, reaching to second pair of embedded spines.

Sexual dimorphism. Non-transformed, non-terminal males and females are similar in all aspects except for the relatively smaller gnathopod 2 of females, the palm of which is more oblique than males and slightly excavate. Terminal male leucomorphs develop a greatly elongated carpus of gnathopod 2, the palm becoming even more oblique and bearing two groups of embedded spines near the palmar margin. Gnathopod 1 is essentially similar in all respects. It is currently not known whether this stage is a separate terminal leucomorph state, or, whether this stage, non-transformed males, or both, are capable of transforming into an anamorph stage. Because this hyper-developed male stage exists at a size larger than that recorded for some of the smaller anamorphs it may represent another terminal condition unique to this species. Leucomorph counterparts for other species of *Nepanamixis* are unknown, but their discovery could shed light on this interesting situation.

Relationships. *Nepanamixis dianthus* resembles *N. grossimana*, from the reefs of Mauritius, in the maxilliped,

the general shape of gnathopods 1 and 2. *Nepanamixis dianthus* differs from *N. grossimana* in the following characters: in having 2 major cusps in the inner margin of the propodus and in lacking an apical spine in both the carpus and propodus; in gnathopod 2 lacking the conspicuous serrate lateral carpal ridge and the sinuous margin of the palm; in uropod 1 with the outer ramus lacking spines (versus the inner ramus in *N. grossimana*); and in the apically pointed telson. Unfortunately, leucomorphs are undocumented for *N. grossimana*, but it is assumed that they would share similar qualities as those of *N. dianthus*. The unique juvenile morphology exhibited in *N. dianthus* provides strong evidence for the value of juvenile characters in helping to unravel the taxonomy of anamixids. Based on this evidence it can be postulated that the more plesiomorphic *Nepanamixis* is possibly an ancestral form from which both *Anamixis* and *Paranamixis* are derived. Additional specialised collecting efforts from reefs in Pacific Ocean and the Caribbean should reveal more representatives of *Nepanamixis* and provide additional information regarding the early evolution of this group.

Colour of anamorphs and leucomorphs in live and freshly preserved material is a translucent pink, fading rapidly in preservative to a nearly transparent condition.

Etymology. From the Latin "dianthus", meaning carnation pink, referring to the colour of live and freshly preserved specimens.

Habitat. Specific habitat unknown, all specimens have been taken from deep within coral rubble, assumed to be commensal, but it is possible that the unique morphologies in *N. dianthus* are adaptations to highly cryptic habitats are precursors to commensalism.

Distribution. Western Caribbean Sea; Belize, among coral rubble. 2–8 m.

Nepanamixis grossimana (Ledoyer, 1978)

Anamixis grossimana Ledoyer, 1978: 229, fig. 13(II).

Diagnosis. Gnathopod 1 with 1 major and 1 minor cusp on palm of carpus, carpus and propodus with apical spine; gnathopod 2, carpus serrate proximally, hind margin of propodus straight; bottom margin of coxa 4 with shallow emargination.

Description. Head, lateral margin rounded, ventral keel unknown. Antennae 1 and 2 subequal in length; antenna 1 with small, 1-articulate accessory flagellum; ratio of articles 1–3 of antenna 1, 7:10:5; flagella 7 and 4-articulate respectively. Maxilliped, inner plates consisting of 2 small lobes separated by evagination; outer plates with distinct inner lobes. Gnathopod 1, coxa half as deep as coxa 2, evenly rounded; basis thick, with 10–11 scattered tubercles along anterior margin; carpus with 1 major cusp and 9–10 small tubercles on palm, with thick apical spine; propodus, inner margin nodulose, apex with thick spine. Coxa 4 with slight ventral emargination. Bases of pereopods 5–7 narrow, hind margin of 7 with large serrations. Telson elongate, 1.88 times longer than wide, apically truncated, tridentate.

Relationship. *Nepanamixis grossimana* is most closely related to *N. dianthus* with which it shares several features: general shape of gnathopods 1 and 2; emarginate ventral margin of coxa 4; relatively narrower article 2 on pereopods 5–7; and an elongate telson. *Nepanamixis grossimana* differs from *N. dianthus* in small details of these same features: gnathopod 1, basis with small tubercles on anterior margin; in having only 1 major cusp on the palm; in having a nodulose inner margin on the propodus; and in having thick terminal spines on both carpus and propodus; in having the basis of gnathopod 2 with small anterior tubercles (not illustrated); in the carpal lobe having only the proximal portion scarcely denticulate; and in having a straight hind margin on the propodus.

Remarks. Ledoyer's original figures for *N. grossimana* clearly shows the distinct condition of the maxilliped that places this species in the genus *Nepanamixis*. Examination of the single type specimen in permanent slide mounts has revealed a number of characters not discussed or illustrated in the original description. Leucomorphs are unknown for this species, but examination of collections for leucomorphs similar to those of *N. dianthus* should reveal specimens with characters of the genus. *Nepanamixis dianthus* and *N. grossimana* are more closely related to each other than either is to the Eastern Pacific species *N. torreanus* and *N. vectoris*, indicating that *N. grossimana* and *N. dianthus* may have shared an ancestor with a wide geographical distribution and that the Eastern Pacific species may have arisen after the ancestral distribution experienced an isolating vicariant event. It is highly unlikely that these species came to exist in their present distributions by dispersal.

Habitat. Coral rubble, Balaclava Reef.

Distribution. Indian Ocean, Mauritius, coral reefs, especially shallow rubble areas.

Nepanamixis torreanus n.sp.

Fig. 21

Type material. HOLOTYPE, anamorph male "B", 2.52 mm, USNM 243340, Darwin Bay, Tower Island, Galapagos, shore collection of *Porites* at Seal Beach, 1 m, 22 February 1933, Alan Hancock Expedition, Station 94-33.

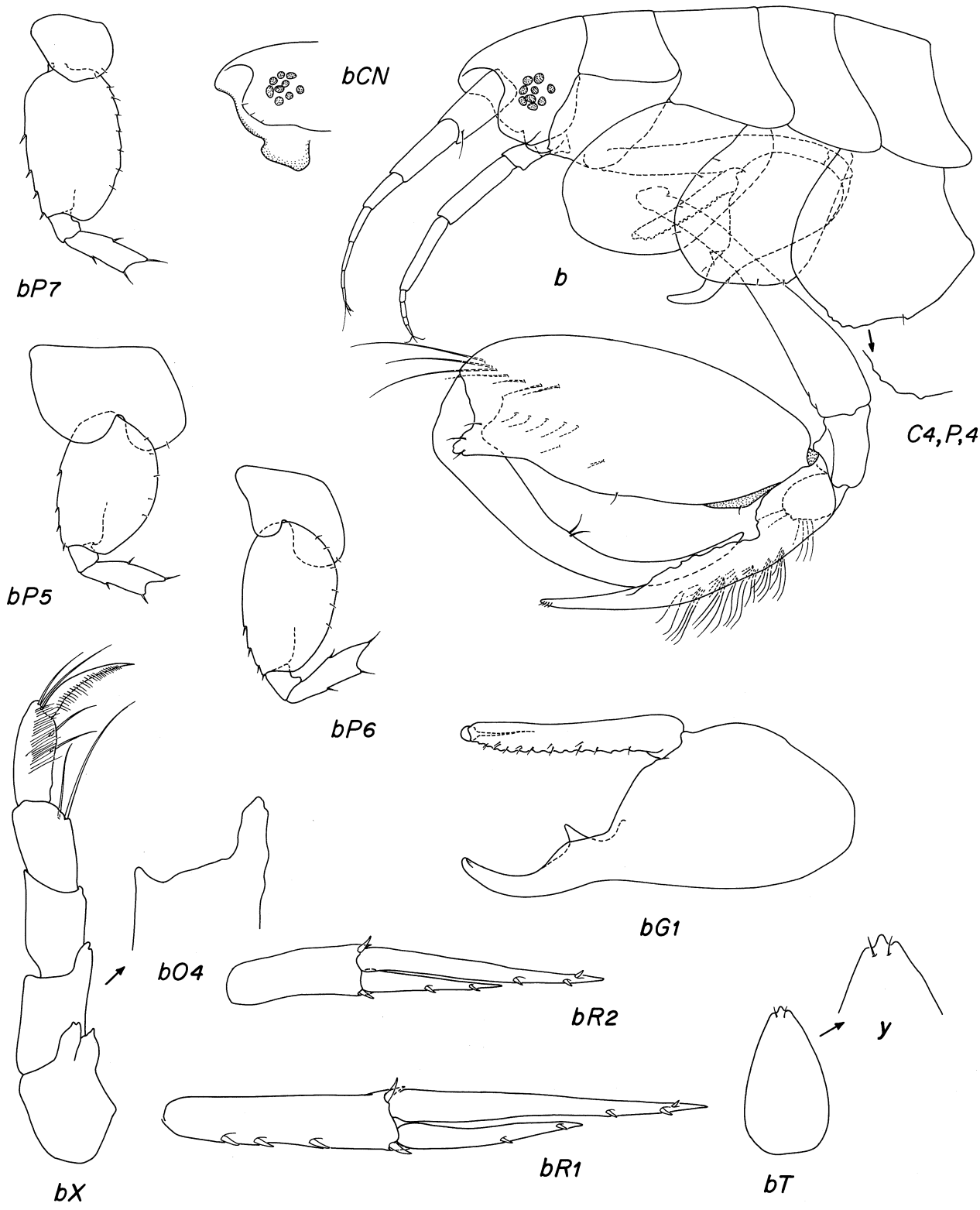

Fig. 21. *Nepanamixis torreanus* n.sp., holotype, anamorph male, "B", 2.52 mm.

Diagnosis. Coxa 4 crenulate ventrally; gnathopod 1, apex of carpus with minute setule; telson, with midapical projection.

Description. Head, lateral and ventral margins rounded; eyes composed of 9 diffuse ommatidia; ventral keel scarcely produced, rounded, subrectangular. Antenna 1 and 2, 0.60 and 0.53 the length of head to pereonite

4. Antenna 1, ratio of articles 1–3, 14:14:8; flagellum with 4 elongate articles. Antenna 2, flagellum composed of 4 shortened articles. Lower lip lobes visible in lateral and ventral view. Maxilliped, inner plates cleft, apices produced; outer plate prominent, apices produced, reaching 0.45 mark of palp article 1; palp article 4, 1.09 times as long as article 3. Pereonite 1 with small lateral locking ridge. Gnathopod 1, coxa reaching bottom margin of head, anteroventral apices bifid; carpus expanded basoproximally, inner margin bearing a large, sharp process, apex with small setae; propodus linear, inner margin with scattered tuberculations and setae, apex with fleshy bulbous process. Gnathopod 2, coxa subequal in size to 3 and 4, margins smooth, evenly rounded; carpus with proximolateral ridge scarcely serrate; propodus, hindmargin sinuous distally, posterodistal margin defined by large process, inner margin with secondary row of 5 mediofacial setae plus 2 additional isolated setae; dactyl elongate, recurved, nearly reaching to base of carpus, with 2 paired setae. Pereopod 3, coxa slightly smaller than coxa 2 or 4, ventral margins rounded, anterior and ventral margins with scattered submarginal setae, posteroventral corner with small cusp; remainder of pereopod normal. Pereopod 4, ventral margin of coxa produced and crenulate; remainder of pereopod similar to pereopod 3. Pereopod 5, coxa bilobed, hind lobe equal to front; basis evenly rounded, posterior margin with scattered submarginal setae. Pereopod 6, coxa bilobed, hind lobe larger and deeper than front lobe; basis evenly rounded. Pereopod 7, basis small, entire, with 2 posteroventral setae; coxa somewhat deeper than 5 or 6, hind margin acute and setose. Epimera normal for genus. Outer rami of uropods 1 and 2 reduced. Uropod 3 missing. Telson suboval, 1.82 times longer than wide, tapering distally, apical margin produced into a triangular projection with 2 subapical setae.

Leucomorphs. Unknown.

Etymology. From the Spanish "torreanus" meaning tower, referring to the type locality, Tower Island, Galapagos.

Remarks. *Nepanamixis torreanus* bears a strong superficial resemblance to *N. vectoris* but differs in the more deeply cleft inner plates and larger inner lobes of the outer plates of the maxilliped; in the apically bifid coxa and lack of a large embedded spine in the apex of the carpus of gnathopod 1; in the less pronounced serrations on the carpal lobe of gnathopod 2; the ventrally crenulate coxa 4, and the apical process on the telson. The fact that *N. torreanus* retains the plesiomorphic condition of the inner and outer plates of the maxilliped, while *N. vectoris* retains only the slightest remnant of this structure, supports the hypothesis that taxa from remote island archipelagos tend to retain plesiomorphic characters, while related taxa from continentally associated habitats tend to exhibit apomorphic trends in certain morphologies. While *N. grossimana, N. torreanus* and *N. dianthus* all retain, to some degree, the inner lobes of the outer plates of the maxilliped, the similarity of other characters between *N. grossimana* and *N. dianthus* argues for a closer relationship between these two species than either is to *N. torreanus* or *N. vectoris*.

Habitat. Unknown, assumed to be commensal.

Distribution. Pacific Ocean; Tower Island, Galapagos, among coral rubble, 1 m.

Nepanamixis vectoris n.sp.

Fig. 22

Type material. HOLOTYPE, anamorph male "A", 2.69 mm, USNM 131571, Pinas Bay, Panama, coral in South Bay, mainland side, 2–4 fathoms, Alan Hancock Expedition, 29 January 1935, Hancock-444-35.

Diagnosis. Anterior margin of basis of gnathopod 1 and 2 weakly tuberculate. Gnathopod 2, carpal process with elevated serrate ridge on lateral margin extending proximally to insertion of propodus. Gnathopod 1, carpus with large apical spine; propodus, apex with blunt, bulbous process.

Description. Head, rounded laterally, ventral margin evenly rounded with 4 submarginal setulae, eye composed of 9 slightly dispersed ommatidia, ventral keel scarcely extending below head, posterior portion subrectangular. Antenna 1 missing beyond peduncle segment 1. Antenna 2, 0.55 the length of head and first four pereonite segments; flagellum 4-articulate. Lower lip lobes visible from lateral and ventral view as 2 small fleshy processes. Maxilliped, inner plates partially fused, apically cleft one-third of length; outer plates with vestigial inner lobes, represented by minute process on inner margin; palp article 4, 1.23 times longer than article 3. Pereonite 1 with lateral locking ridge, not produced posteriorly. Gnathopod 1, coxa reduced, extending to ventral margin of head or below; anterior margin of basis weakly tuberculate; proximal portion of carpus expanded, inner margin with single large cusp, apex with large embedded spine; article 6 straight, reaching end of article 5, inner margin nodulose, apex with bulbous process. Gnathopod 2, coxa slightly larger than 3 or 4, margins smooth; basis dilated distally, anteroproximal margin with several small tubercules (not illustrated); carpus, elevated serrate lateral ridge extending to basal portion of carpal margin, apex with 4 setae; propodus with secondary row of 5 setae; ventral margin defined by a single large serrate process, hindmargin smooth; dactyl long, recurved, with 2 setae on inner margin. Pereopod 3, coxa smaller than 2 or 4, evenly rounded ventrally. Pereopod 4, coxa with

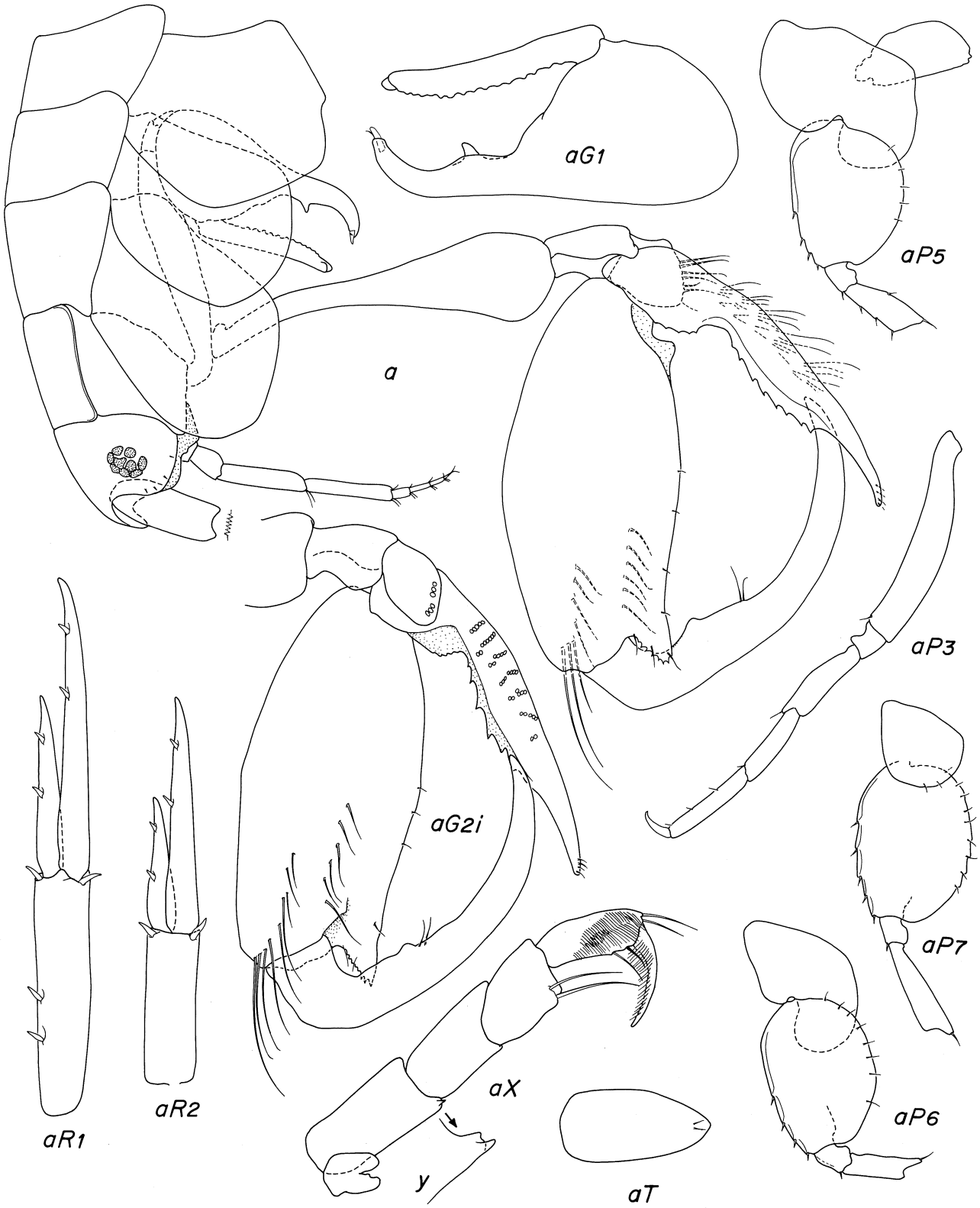

Fig. 22. *Nepanamixis vectoris* n.sp., holotype, anamorph male "A", 2.69 mm.

anterior, ventral and posterior margins produced, posterior portion of ventral margin tapering, with small cusp in midventral region, posterior margin slightly excavate. Pereopod 5, coxa bilobed, hind margin not produced; basis, posterior margin evenly expanded. Pereopod 6, hind margin of coxa produced ventrally; basis similar to pereopod 5. Pereopod 7, coxa entire, with 2 setae along posteroventral margin; basis expanded, small

indentations with small setae. Epimera normal. Uropods 1 and 2, outer ramus reduced; uropod 3 missing. Telson elongate, 2.08 times as long as wide, apex produced, 2 subapical setae.

Leucomorphs. Unknown.

Etymology. From the Latin "vecta" meaning passenger, referring to the commensal habits of anamixids.

Remarks. *Anamixis vectoris* shares a superficial resemblance to *A. torreanus* in the eyes, head margins, and gnathopods 1 and 2. *Anamixis vectoris* differs from *A. torreanus* in the following characters: outer plates of maxilliped with vestigial inner lobes; gnathopod 1, coxa apically rounded, basis with small tubercles along anterior margin; carpus with apical spine. Gnathopod 2, basis with small tubercles along anterior margin; carpus with more pronounced lateral serrations; propodus, large defining cusp serrate. Coxa 4, ventral margin with single cuspate process, lacking the crenulations of *A. torreanus*.

Habitat. Unknown, assumed to be commensal.

Distribution. Eastern Pacific Ocean, Panama, from coral reefs, 4–8 m.

Paranamixis Schellenberg

Paranamixis Schellenberg, 1938: 29.

Type species. *Paranamixis bocki* (Schellenberg, 1938), monotypy.

Diagnosis. In terminal males: antennae relatively long. Inner plates of maxilliped partially or completely fused, apically cleft or entire; outer plates lacking inner lobes. Coxa 1 greatly reduced, remainder of gnathopod 1 absent in post-transformational moults, occasionally represented by small vestige in transformational males. Article 2 of gnathopod 2 normally smooth, occasionally with serrate anteroproximal ridge. Telson 1.2–1.5 times longer than wide.

Relationship. Differing from *Anamixis* in lacking gnathopod 1 in post-transformational moults. Differing from *Nepanamixis* in the relatively longer antennae; more numerous ommatidia; in lacking inner lobes on the outer plates of the maxilliped; the lack of gnathopod 1; in having a single row of mediofacial feeding setae on the propodus of gnathopod 2; in having a ventrally rounded coxa 4; and in the relatively shorter telson.

Remarks. Leucomorphs are undocumented for any species in this genus. Detailed analyses are needed on the maxillipeds of all *Paranamixis* to determine the condition of the inner plates. Until such information is available, the genus is retained.

Species. *Paranamixis aberro* Hirayama, 1983; *P. bocki* Schellenberg, 1938; (?Ruffo, 1969; Ledoyer, 1978); *P. clarkae* n.sp.; *P. denticulus* Kim & Kim, 1991; *P. excavatus* Ledoyer, 1978; *P. fijiensis* n.sp.; *P. indicus* Sivaprakasam, 1968; (?Ledoyer, 1979); *P. kanu* n.sp.; *P. madagascarensis* Ledoyer, 1982; (?Myers, 1985 = *P. fijiensis*); *P. misakiensis* n.sp.

Distribution. Marine, Polynesia to Madagascar, coral reefs, 0–4 m, eight species.

Key to the Species of *Paranamixis*

1. Coxa 2, anterodistal margin with midventral projection(s), cusp(s), or serrations 8
—— Coxa 2, anterodistal distal margin evenly rounded 2
2. Coxa 2, anteroproximal margin evenly rounded 3
—— Coxa 2, anteroproximal margin expanded ..... *P. fijiensis* n.sp.
3. Head, anterior margin transverse or slightly produced, ventral margin horizontal, anteroventral corner defined by small upturned cusp 4
—— Head, anterior margin oblique, ventral margin lacking or oblique, anteroventral corner lacking upturned cusp 5
4. Anterior margin of head slightly produced; coxa 2, anterior margin smooth; uropods spinose ..... *P. madagascarensis*
—— Anterior margin of head transverse; coxa 2, anterior margin with 2 cusps; uropods without spines ..... *P. indicus*

5. Head, ventral oblique margin with mid lateral notch, lateral margins rounded 6

—— Head, ventral oblique margin continuous, lacking any defining notch or cusp, lateral margins with elevated ridge, head excavate below ..... *P. kanu* n.sp.

6. Gnathopod 2, anterior margin of coxa rounded, basis with serrate distomedial locking ridge, anterior margin of carpus minutely toothed, hindmargin of propodus finely serrate, inner margin of dactyl tuberculate 7

—— Gnathopod 2, anterior margin of coxa expanded forward, basis with triangular anteromedial locking ridge; anterior margin of carpus smooth, hindmargin of propodus smooth with scattered setae; inner margin of dactyl smooth ..... *P. aberro*

7. Gnathopod 2, coxa with anteroventral and posteroventral cusps, anterior margin of carpus toothed, inner margin of dactyl with 8–9 continuous tubercles ..... *P. misakiensis* n.sp.

—— Gnathopod 2, anterior margin of coxa smooth, inner margin of dactyl with 4–5 disjunct tubercles ..... *P. denticulus*

8. Eyes, ommatidia diffuse; anterodistal margin of coxa 2 with serrate process ..... *P. excavatus*

—— Eyes, ommatidia compact; anterodistal margin of coxa 2 lacking serrate process 9

9. Gnathopod 2, anterodistal margin of coxa rounded, ventral margin with sharp process; anteroproximal margin of article 2 of gnathopod 2 finely serrate; article 2 of pereopod 5 subquadrate on posterior margin ..... *P. bocki*

—— Gnathopod 2, anterodistal margin of coxa slightly excavate, ventral margin with a small, produced point; anteroproximal margin of article 2 of gnathopod 2 grossly serrate ..... *P. clarkae* n.sp.

Paranamixis aberro (Hirayama, 1983)

Paranamixis aberro Hirayama, 1983: 143–146, figs 36,37.

Diagnosis. Head margin oblique with distinct concavity near midsection; coxa 2, anterior margin expanded forward to middle of head, margins smooth; gnathopod 2, basis with thin triangular protrusion on anteromedial margin, posterodistal portion of propodus excavate, bearing 3 teeth.

Description. Ventral keel subtriangular, projecting beneath head, directed slightly anteriorly. Antennae subequal in length, shorter than half as long as body. Antenna 1, ratio of articles 1–3, 20:10:5; peduncular segment 1 stout, with several small setae, article 2 much thinner than 1, with many setae; accessory flagellum small, uniarticulate with apical pair of setae; flagellum 9-articulate. Antenna 2, flagellum 4-articulate. Gnathopod 2, coxa larger than 3 or 4, expanded forward, rounded, smooth marginally, lower margin setose; basis with thin triangular protrusion on anteromedial margin; carpus recurved; propodus, posterodistal margin with 3 teeth, gradually increasing in size distally; dactyl with pair of setae at distal third of article. Coxa 6, posterior lobe about twice the anterior lobe in width and depth. Telson broad, entire, 1.55 times longer than wide, distal margin rounded, with 2 minute setae, dorsal margin with two opposite rows of 2 single setae and 2 paired setae, all setae pinnate.

Leucomorphs. Unknown.

Relationship. *Paranamixis aberro* is separated from other *Paranamixis* species by the unique configuration of the head margin, otherwise it exhibits no clearly distinct group of characteristics.

Remarks. Hirayama's description and figures of *P. aberro* are complete and detailed, but comparison to other taxa is premature until more material becomes available for examination. Detailed analysis of the

maxillipeds of all *Paranamixis* species are required to confirm the condition of the inner plates.

Habitat. Unknown.

Distribution. East China Sea, Shijiki Bay, west Kyushu, Japan.

Paranamixis bocki Schellenberg, 1938

Paranamixis bocki Schellenberg, 1938: 29–30, fig. 14; ?Ruffo, 1969: 13. (not) Ledoyer, 1978: 231–232, fig. 14; and 1967: 125.

Diagnosis. Gnathopod 2, coxa with sharp anteroventral projection; basis serrate proximally; pereopod 5, basis quadrate.

Description. Schellenberg originally described this species from reefs in the Gilbert Islands, but his description and figures are limited and not adequate to distinguish this species from other material in hand. Until material is available from, or near, the type locality, distinguishing characteristics for this species are limited to those of the diagnosis.

Leucomorphs. Unknown.

Remarks. The author has in hand a single damaged specimen of *Paranamixis* from Truk Lagoon in the Carolines that closely resembles *P. bocki* in several features. However, due to the poor quality of this specimen and that these two regions are separated by more than 2,000 miles, they cannot be assumed to be equivalent until comparisons can be made with material collected at or near the type locality.

Habitat. Coral reefs.

Distribution. Pacific Ocean, Gilbert Islands.

Paranamixis clarkae n.sp.

Fig. 23

Type material. HOLOTYPE, anamorph male "R", 3.06 mm, USNM 243342, Mahe, Seychelles, near Mahe Beach Hotel, sheltered embayment, rubble and stones among algal turf in current swept channel, 0.5 m, J. Clark, 29 April 1984, J.Sey-2; 1 PARATYPE, anamorph male "P", 3.15 mm, USNM 243343, J.Sey-2; 1 PARATYPE, anamorph male "S", 2.69 mm, USNM 243344, J.Sey-2.

Diagnosis. Head with ventral cusp; ventral keel bifid; gnathopod 2, coxa with sharp anteroventral tooth, basis with proximolateral and mesodistal serrate ridges.

Description. Lateral margin of head rounded, anterior margin rounded, ventral margin with cusp, eyes composed of 16 compact ommatidia; ventral keel sharp, bifid, projecting anteriorly. Antennae 1 and 2, 0.94 and 0.87 as long as head to posterior margin of pereonite 4. Antenna 1, ratio of articles 1–3, 55:38:28; article 3 thin; flagellum with 8-articulate, aesthetascs on articles 4–8. Antenna 2, flagellum short, 5-articulate. Lower lip lobes visible from lateral view. Maxilliped, inner plates fused basally, but with apical notch; outer plates lacking inner lobes; palp article 4, 1.4 times length of article 3. Pereonite 1 with lateral locking ridge. Gnathopod 1, coxa not reaching bottom margin of head, anteroventral corner rounded, bearing 2 small setae; remainder of gnathopod lacking in holotype. Gnathopod 2, coxa larger than either 3 or 4, with sharp midventral projection, scattered submarginal setae; basis, locking ridge serrate on both lateroproximal and mediodistal margins; carpus basally thick, tapering toward apex; propodus, apex defined by single sharp process lacking cusps or serrations, hindmargin nearly straight; dactyl tuberculate on inner margin. Pereopods 3 and 4 similar, coxa 4 larger than 3, posterior margin slightly expanded. Pereopods 5–6 similar, coxa 6 with deeper hind lobe than coxa 5; bases with distal portion of posterior margin excavate. Pereopod 7, coxa entire; posterior margin of basis with small serrations. Epimera normal for genus. Outer ramus of uropods 1–3 reduced, styliform and spinose; uropod 3 with small subapical spine near distal ramal spine. Telson subrectangular, tapering distally, 1.2 times longer than wide, with 2 apical setae.

Leucomorphs. Unknown at this time. Because there are at least two species of anamixids from the same locality in the Seychelles, specific designations cannot be made. Confirmation must be made through rearing experiments or through host confirmation.

Variations. Paratype "P" with shrunken vestiges of gnathopod 1, assumed to be transformation stage. Post-transformational males lack this appendage entirely. Occurrence of a vestigial first gnathopod may be a common feature of in transformational moults of *Paranamixis* as more collections are made from tropical areas. A similar condition has been noted on *P. kanu* and is probably due to the availability of more material for examination from tropical collecting efforts.

Etymology. Named in appreciation of Janice B. Clark of the National Museum of Natural History, whose untiring assistance on reefs of the Caribbean and South Pacific has been greatly appreciated.

Remarks. *Paranamixis clarkae* most closely resembles *P. excavatus* from Madagascar in the following characters: serrate locking ridges of the basis and tuberculate inner margin of the dactyl of gnathopod 2. The configuration of the basis of pereopod 5 also appears similar to that of *P. excavatus*. *Paranamixis excavatus* differs from *P. clarkae* in the more transverse anterior margin of the head, in having compact ommatidia, in lacking the prominent serrate anteroventral process on coxa 2 and in possessing ramal spines on uropods 1–3. *Paranamixis*

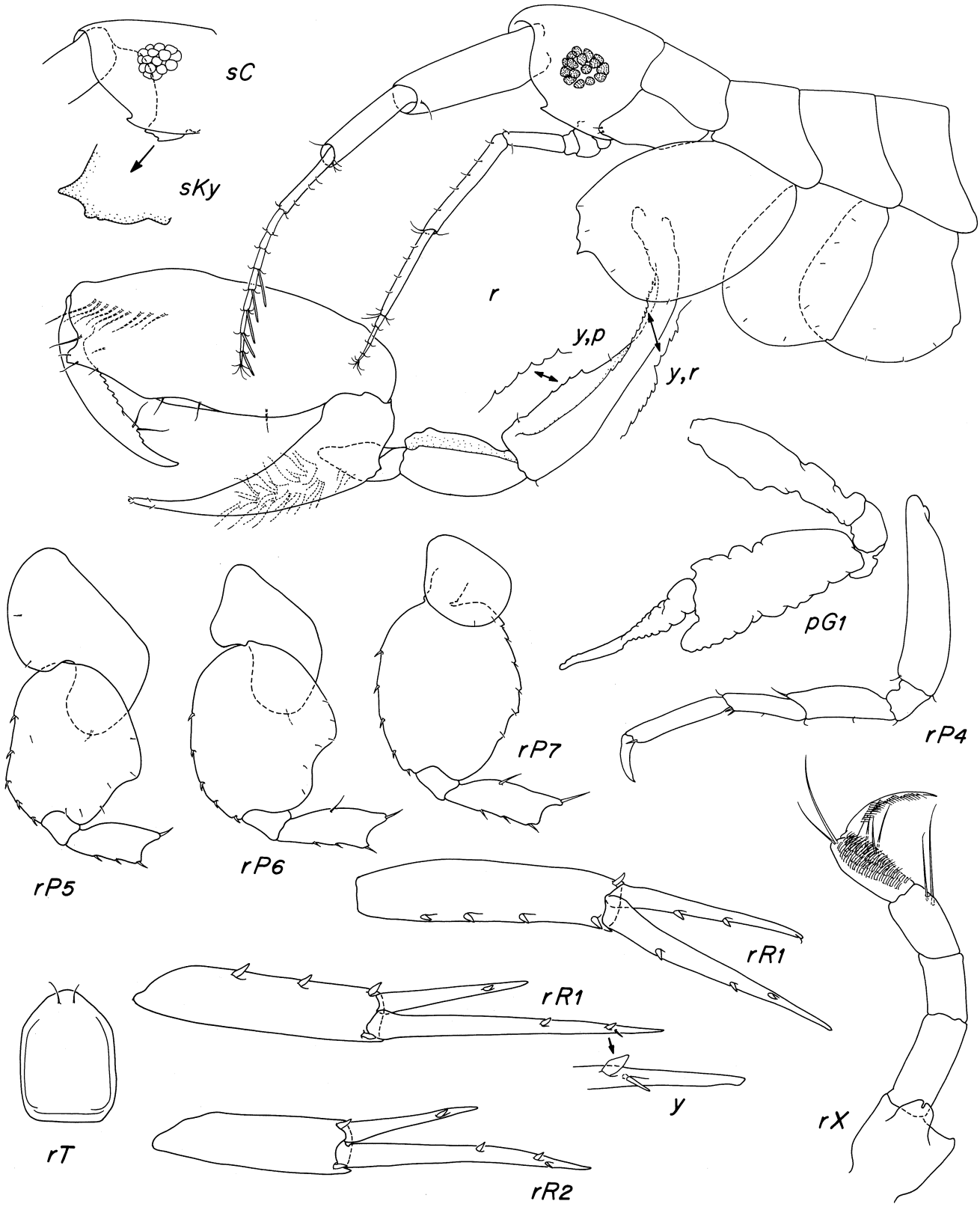

Fig. 23. *Paranamixis clarkae* n.sp., holotype, male "R", 3.06 mm; "P", anamorph male, 3.15 mm; "S", anamorph male, 2.69 mm.

clarkae is distinguished from its other nearest geographic relative *P. madagascarensis* by the following: in gnathopod 2, by the ventral projection on the coxa, the presence of serrate locking ridges on the basis, and the palm of the propodus lacking 2 additional processes. *Paranamixis indicus* from coastal India has a transverse anterior head margin and a rounded coxa 2 lacking ventral cusps or projections. *Paranamixis bocki*, the only other species in the genus with serrations on the basis of gnathopod 2, has much more apically produced cusp on coxa 1, and the basis of pereopod 5 is nearly square. Like *P. clarkae, P. indicus* from sponges in the Gulf of Manaar, India, lacks spines on the peduncles and rami of uropods 1–3, but otherwise apparently shares no close relationship to *P. clarkae*.

Habitat. Shallow coral rubble and algal turf, 1–2 m, assumed to be commensal.

Distribution. Indian Ocean; Mahe, Seychelles, 1–2 m.

Paranamixis denticulus Kim & Kim, 1991

Paranamixis denticulus Kim & Kim, 1991: 15–16, figs 2–3, depth unrecorded.

Diagnosis. Anterior margin of head oblique, with midventral notch. Gnathopod 2, anterior margin of coxa smooth, lacking cusp(s) or tooth, inner margin of dactyl with 4–5 distinct tubercles.

Remarks. The midventral notch on the head and finely denticulate margin of the propodus of gnathopod 2 place *P. denticulus* among the other Asian taxa exhibiting these features, *P. misakiensis* and *P. aberro*. Differences among these taxa are generally found on the anterior margin of coxa 2 and the presence and type of tubercles on the inner margin of the dactyl of gnathopod 2.

Habitat. Coral rubble and rocky bottoms, shorelines and harbours.

Distribution. Sea of Japan, Ulreung Island.

Paranamixis excavatus Ledoyer, 1978

Paranamixis excavatus Ledoyer, 1978: 233, fig. 14 (I).

Diagnosis. Anterior margin of head nearly transverse, anteroventral margin defined by small cusp, ommatidia reduced in number, scattered and diffuse, ventral keel subtriangular, projecting beneath head. Gnathopod 2, anteroventral margin of coxa produced into sharp process, proximal margin linear, serrate; basis with serrate lateral ridge and serrate distal locking ridge; propodus elongate and thin, with single large tooth near dactyl. Rami and peduncles of uropods lacking spines; telson ovate.

Remarks. There is little additional information available from Ledoyer's description of *P. excavatus*. The description is only three sentences in length and the figures consist of nine separate drawings. Nonetheless, this unusual species is readily distinguishable from all other *Paranamixis* by the scattered and diffuse ommatidia; ventral process and serrations on coxa 2; and the complete loss of spines on the peduncles and rami of the uropods. The outer ramus of uropod 1 is reduced to half of the inner ramus. Detailed examination of this species is certain to provide additional taxonomic characters overlooked in the original description. Specialised collecting efforts in the waters or Mauritius may also be expected to provide additional undescribed anamixid species.

Habitat. Unknown.

Distribution. Indian Ocean, Mauritius, coral reefs, to 5 m.

Paranamixis fijiensis n.sp.

Fig. 24

Type material. HOLOTYPE, anamorph male "A", 2.87 mm, USNM 266410, *Halimeda* in lagoon, Nanaui Ra, Fiji, 6 October 1979, Alan Myers, station 53. PARATYPES, anamorph males "B", 2.92 mm, USNM 266411, and "C", 2.72 mm, USNM 266412.

Diagnosis. Gnathopod 2, coxa enlarged, anteroproximal margin expanded; basis with weakly denticulate anterodistal locking ridge, propodus extending proximally beyond insertion of carpus. Maxilliped, inner plates fused, apically rounded. Telson elongate, 1.9 times longer than wide.

Description. Holotype "A". Head, anterior margin more or less transverse, somewhat expanded, anteroventral corner defined by small cusp; ventral keel scarcely extending beneath ventral margin of head, triangular; eyes with 21 compact ommatidia. Antennae: antenna 1 peduncular ratio 25:20:14; flagellum 7-articulate, aesthetascs on articles 5–7; antenna 2, flagellum 4-articulate. Maxilliped, inner plates fused into apically rounded process; outer plates lacking inner lobes; palp article 4, 1.6 times article 3. Pereonite 1 with lateral locking ridge, expanded posteriorly. Gnathopod 1 lacking, coxa reduced, apically bifid. Gnathopod 2, coxa larger than 3 or 4, anteroproximal expanded, ventral margin evenly rounded, posterior margin with small cusp; basis with serrate anterodistal locking ridge on medial margin; carpus recurved, tapering distally, unarmed; propodus, proximal margin extending beyond insertion of carpus, hindmargin unarmed, furnished with approximately 7 submarginal setae, distal margin with small serrations;

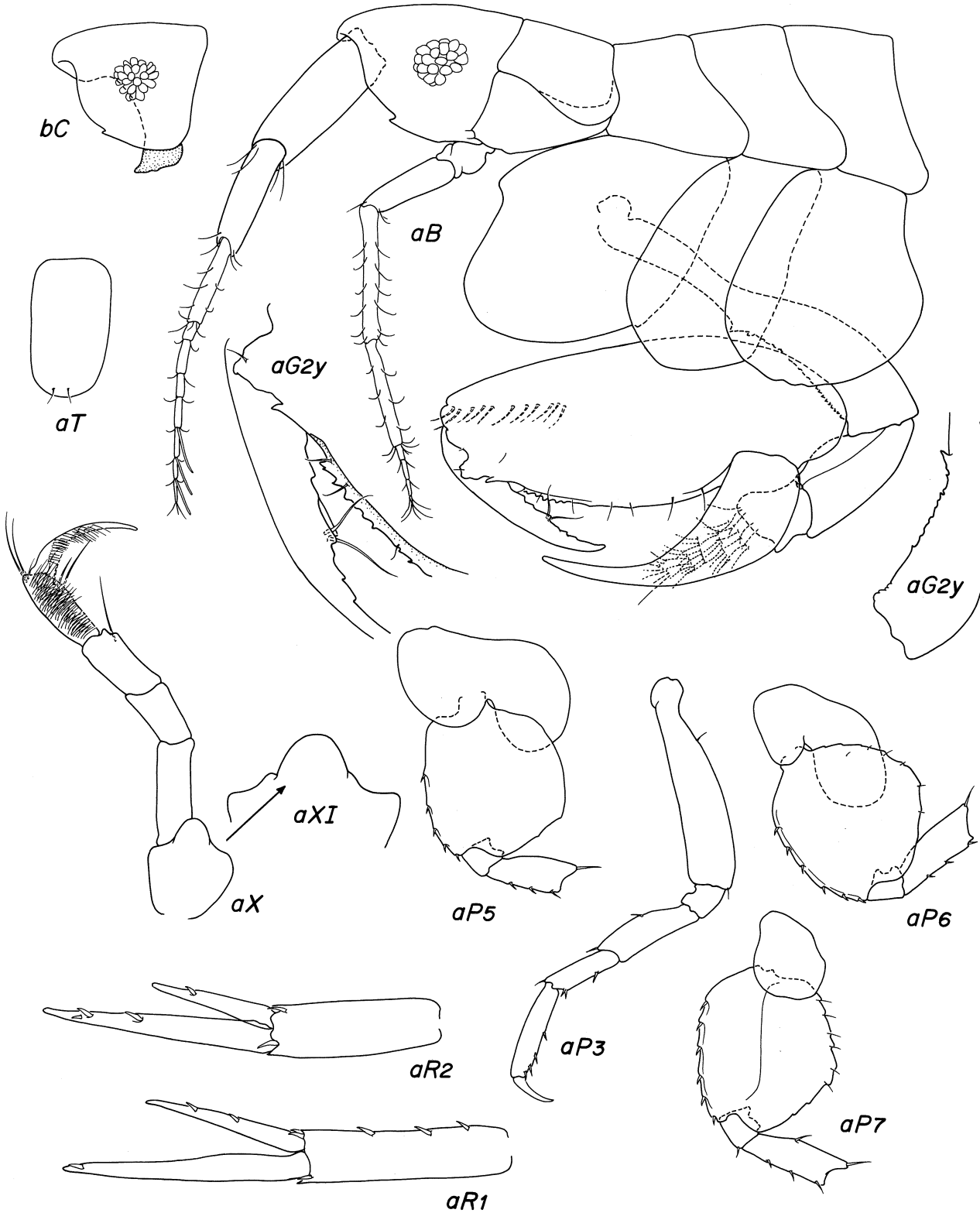

Fig. 24. *Paranamixis fijiensis* n.sp., holotype, anamorph male "A", 2.87 mm; "B", 2.92 mm.

dactyl with 4–5 widely spaced serrations on inner margin. Pereopod 3, coxa smaller than 4, ovorectangular, ventral margin expanded. Pereopod 4, ventral margin of coxa expanded, with 2 small emarginations. Pereopods 5–6 similar, coxae bilobed; basis spinose anteriorly, posterior margin expanded, with widely separated serrations bearing submarginal setae. Pereopod 7, coxa oval. Uropods 1–2, outer rami shortened, two-thirds and one-half of inner rami respectively. Uropod 3 missing. Telson entire, elongate and subrectangular, 1.9 times longer than wide, apical margin rounded, with pair of apicodistal setae.

Leucomorphs. Unknown. The report by Myers (1985) of a leucomorph from Fiji cannot be attributed to *P. fijiensis* until a more thorough survey of the anamixid fauna is made.

Etymology. Named for the Island nation of Fiji.

Relationships. *Paranamixis fijiensis* appears to be similar in several respects to *P. madagascarensis*, including the general shape of the head, gnathopod 2, and coxae 3–4. *Paranamixis fijiensis* is distinguished within *Paranamixis* by the anteroproximal expansion of coxa 2 and the apically fused inner plates of the maxilliped.

Remarks. Until the discovery of *P. fijiensis*, all previously examined species of *Paranamixis* had apically cleft or partially fused inner plates of the maxilliped. The elongate telson of *P. fijiensis* is morphometrically identifiable with the genus *Nepanamixis*, however, it is ovorectangular in *P. fijiensis*, not apically tapered as is typical in *Nepanamixis*. These apparent anomalies are examples of mosaic characters that seem to arise in isolated or relict anamixid species, such as *A. aldabra* and *N. torreanus*. Isolation appears to contribute to this unusual mix of plesiomorphic and apomorphic traits. Again, the cautionary note of incomplete collections, taxonomies and analysis, must be invoked, reflecting our incomplete understanding of the group. In the case of *P. fijiensis* the apically fused inner plates of the maxilliped present two possibilities: (1) a species of *Paranamixis* with fused inner plates on the maxilliped, or (2) a form of *Anamixis* that has lost gnathopod 1. The vestigial first gnathopod of *A. jebbi* may be a transitional example of how this appendage is lost, by gradual reduction rather than immediate developmental loss. Further investigations may resolve whether loss of gnathopod 1 may have arisen in multiple anamixid lineages.

Habitat. Unknown, presumed to be commensal.

Distribution. South Pacific Ocean, Nananui, Fiji, coral reefs, lagoonal.

Paranamixis indicus Sivaprakasam, 1968

Paranamixis indicus Sivaprakasam, 1968: 131–136, figs 1–3; (not Ledoyer, 1978: 233).

Diagnosis. Ventral keel truncate; propodus of gnathopod 2 with deep sinus near articulation with carpus; peduncles and rami of uropods lacking spines.

Description. Head, anterior margin transverse, lower margin defined by small upturned tooth; eyes with 20–22 ommatidia; ventral keel a truncate process angled forward. Antenna 1, ration of articles 1–3, 11:12:6. Gnathopod 2, coxa larger than 2 or 3, rounded, anterior margin with 2 teeth; propodus, palm undefined and continuous with hindmargin, with flat-topped tooth near base of dactyl, followed by a small, pointed tooth with a seta, followed by a shallow sinus and then a small and a minute tooth, remainder of hindmargin straight with 5 equidistant setulae, base with a narrow sinus; dactyl about half as long as propodus, curved near the base and near the pointed tip, the middle portion being straight; proximal two-thirds stout, inner margin with small tooth at curve near the base, followed by a series of eight teeth gradually increasing in size with 2 setae on teeth 7 and 8; distal one-third of dactyl half as thick as the rest, with 4 teeth on inner margin. Coxa 4 larger than 3, posterior margin expanded. Telson entire, apex broadly rounded, 1.33 times longer than wide.

Leucomorphs. Unknown.

Relationship. *Paranamixis indicus* and *P. excavatus* both have uropods completely lacking spines, but share virtually no other similarities. The truncate ventral keel of *P. indicus* is also unusual for this genus, the process being triangular in those species where it has been described.

Remarks. It is doubtful that the loss of spines on the uropods of *P. indicus* link it to *P. excavatus* in an evolutionary perspective, because each species may have evolved this condition independently. A similar convergence is seen in the laterally excavate head margins of *P. kanu* and *A. vanga*.

Habitat. Occurring in sponges, leucomorphs undocumented.

Distribution. Indian Ocean, Appa Island in the Gulf of Manaar, Madras, India, littoral.

Paranamixis kanu n.sp.

Fig. 25

Type material. HOLOTYPE, anamorph male "A", 3.77 mm, USNM 243345, Mizegwadan (Tripod) reef, Tab Anchorage, Madang, Papua New Guinea, formalin wash of rubble 50 m south of reef marker, 3–4 m, J.D. Thomas, 2 February 1990, JDT-PNG-32b; 1 PARATYPE, anamorph male "B", 3.70 mm, USNM 243346, JDT-PNG-32b; 8 PARATYPES, USNM 243347, JDT-PNG-32b; 15 PARATYPES, USNM 243348, JDT-PNG-50c; 11 PARATYPES, JDT-PNG-51a, USNM 243349

Diagnosis. Lateral margin of head excavate, anterior margin oblique; inner plates of maxilliped cleft, apically sharp. Coxae 2 larger than 3 or 4; margins of coxae evenly rounded, bearing submarginal setae. Propodus of gnathopod 2, hindmargin with serrate subdistal process followed by 2 smaller projections; inner margin of dactyl tuberculate.

Description. Head, lateral margin excavate below prominent lateral ridge, ventral margin oblique, eye with 23 compact ommatidia, ventral keel barely extending

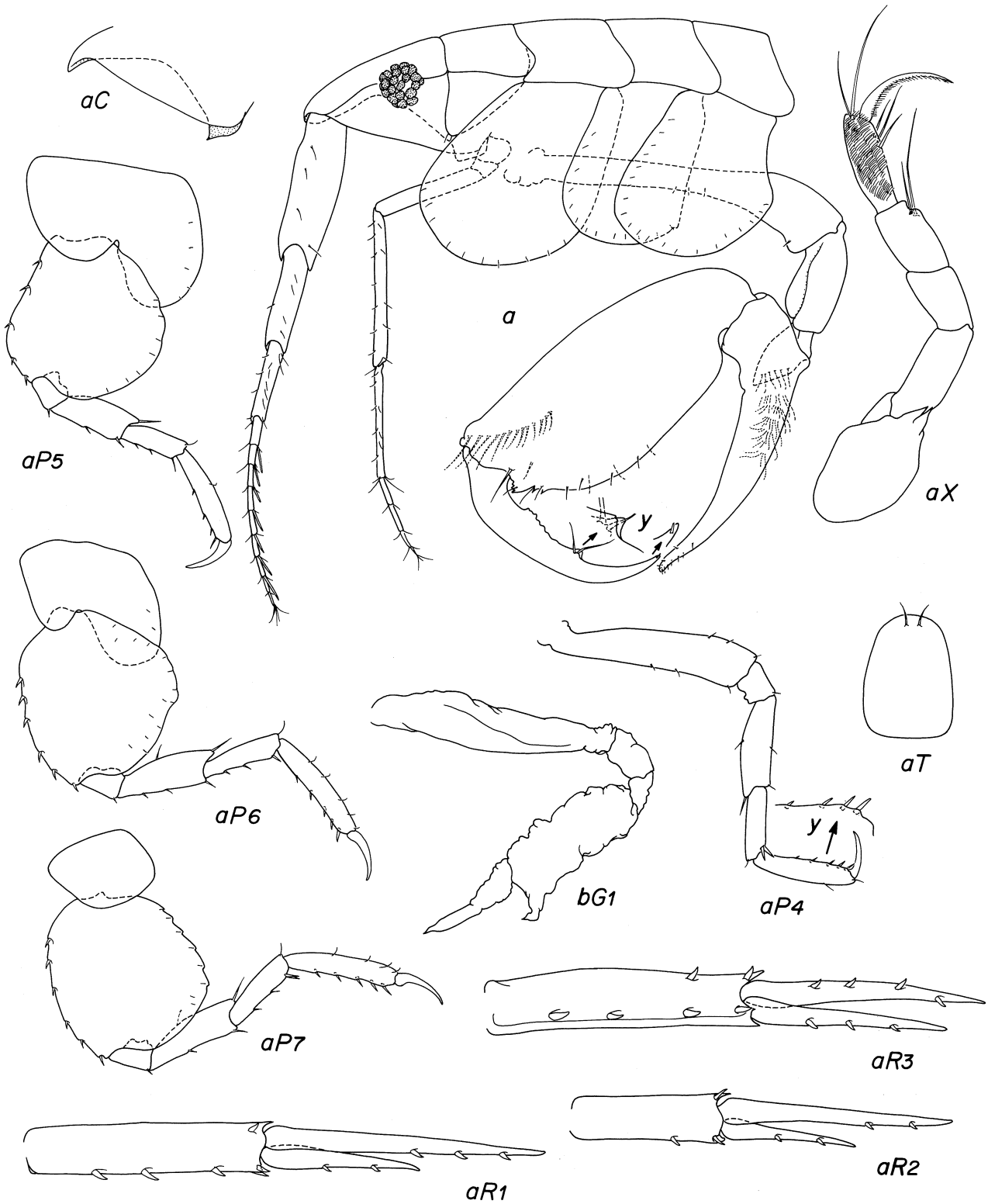

Fig. 25. *Paranamixis kanu* n.sp., holotype, male, "A", 3.77 mm; "B", anamorph male, 3.70 mm.

below head, anterior margin apically pointed. Antennae long, antennae 1 and 2, 1.0 and 1.03 as long as head to pereonite segment 4. Antenna 1, ratio of articles 1–3, 48:35:26; flagellum 9-articulate, aesthetascs on articles 1–7. Antenna 2, flagellum short, 4-articulate. Maxilliped, inner plates partially fused, apices sharp; outer plates lacking inner lobes; palp article 4, 1.05 times longer than article 3. Pereonite 1, prominent lateral locking ridge present. Gnathopod 1, coxa reduced, not reaching bottom margin of head, apex rounded with 2 setae;

remainder of gnathopod absent. Gnathopod 2, coxa larger than 2 or 3, margins smooth, ventral margin expanded, with numerous submarginal setulae; basis with 3 short setae near midpoint; carpus, apex slightly recurved, furnished with short setae on inner and outer margins; propodus, hindmargin slightly expanded, distal portion with large serrate process and 2 smaller posterior teeth; dactyl recurved, proximal portion with raised tuberculate ridge, distal third with paired setae between 2 projections. Pereopod 3, coxa smaller than 4, margins not expanded, with numerous posterior and ventral submarginal setulae. Pereopod 4, coxa with ventral and posterior margins slightly expanded, smooth, with numerous anterior and ventral submarginal setulae. Pereopod 5, coxa with hind margin slightly produced; basis subcircular, posterior margin smooth. Pereopod 6, coxa with hind lobe greatly produced; basis subcircular with slight excavation below mid-posterior margin. Pereopod 7, coxa entire, basis subcircular, posterior margin with series of notches. Epimera normal. Uropods 1 and 2, outer rami shortened, spinose. Uropod 3, outer ramus slightly shortened. Telson subrectangular, apically rounded, 1.4 times longer than wide, with pair of apical setae.

Leucomorphs. Unknown.

Variations. Anamorph male "B": gnathopod 1 present as small shrivelled appendage on what is assumed to be a transformational moult, otherwise, gnathopod 1 lacking in all post-transformational moults.

Relationship. *Paranamixis kanu* bears no close resemblance to other species of *Paranamixis* due to the oblique anterior angle, and midlateral ridge of the head.

Etymology. The word kanu, is Riwo pidgin for canoe and it refers to the shape of the head that looks similar to the upturned bow of local outrigger canoes.

Remarks. A common species, host(s) unknown. Other anamixids with laterally excavate heads are known to inhabit larger solitary ascidians (sponges?) where the lateral ridge serves to anchor the head against the second coxa while feeding in the increased current velocities generated by larger hosts.

Habitat. Coral rubble.

Distribution. South Pacific Ocean; north and south coasts of Papua New Guinea; northern Queensland, to 5 m.

Paranamixis madagascarensis Ledoyer, 1982

Paranamixis madagascarensis Ledoyer, 1982: 141–142, fig. 49. Not Myers, 1985: 42–44, fig. 31.

Diagnosis. Rami of uropods 1 and 2, one-half the length or less than inner rami. Gnathopod 2, basis with denticulate distolateral ridge; dactyl deeply excavate near base, inner margin denticulate to apex.

Description. Head, anterior margin produced, then tapering to small cusp. Antenna 1, ratio of articles 1–3, 12:7:4; accessory flagellum minute, 1-articulate, tipped with a seta; flagellum 9-articulate. Antenna 2, flagellum 4-articulate. Gnathopod 2, coxa larger than 3 or 4, rounded, lacking cusps, anterior margin slightly produced; propodus, palm undefined, hind margin with 1 large and 2 small teeth; dactyl nearly straight, deeply incised near base. Coxa 3 smaller than 4. Telson subrectangular, apex more or less truncate, 1.33 times longer than wide.

Leucomorphs. Unknown.

Relationship. *Paranamixis madagascarensis* differs from its closest relative *P. indicus* in lacking anteroproximal teeth on coxa 2, the presence of a denticulate distolateral ridge on the basis of gnathopod 2, and the more reduced outer rami with spines on uropods 1 and 2.

Remarks. Myers report of *P. madagascarensis* from Fiji is *P. fijiensis*.

Habitat. Coral rubble.

Distribution. Indian Ocean, Madagascar to Mauritius, coral reefs, 0–4 m.

Paranamixis misakiensis n.sp.

Fig. 26

Type material. HOLOTYPE, anamorph male "M", 4.41 mm, CRU1575, deposited in the Zoological Museum, Copenhagen, Denmark, Misaki Coast, Sagami Bay, Japan, on *Corallina*, littoral collections and dredging to 20 fathoms, Th. Mortensen, 26 May 1914.

Diagnosis. Head, anterior angle oblique, bearing midlateral notch. Maxilliped, inner plates fused except for small apical notch. Gnathopod 2, anterior margin of coxa expanded, with small, truncate cusp; basis with toothed, distomedial locking ridge; carpus reaching half of propodus, anterior margin minutely toothed; hind margin of propodus expanded, evenly serrate; inner margin of dactyl tuberculate.

Description. Holotype "M". Head, anterior margin oblique, bearing midlateral notch; ventral keel a simple triangular process barely extending below ventral margin of head; eyes with 22 compact ommatidia. Antennae: antenna 1, peduncular ratio 22:13:9; accessory flagellum minute, 1-articulate; flagellum 10-articulate, aesthetascs on articles 2–10; antenna 2, subequal or slightly longer than antenna 1, peduncle article 3 elongate, 0.87 as long as article 4; flagellum 4-articulate. Maxilliped, inner plates almost completely fused, apical margin minutely cleft; outer plates lacking inner lobes; palp article 4, 1.1 times article 3. Pereonite 1 with lateral locking ridge. Gnathopod 1 lacking, coxa reduced, apically bifid.

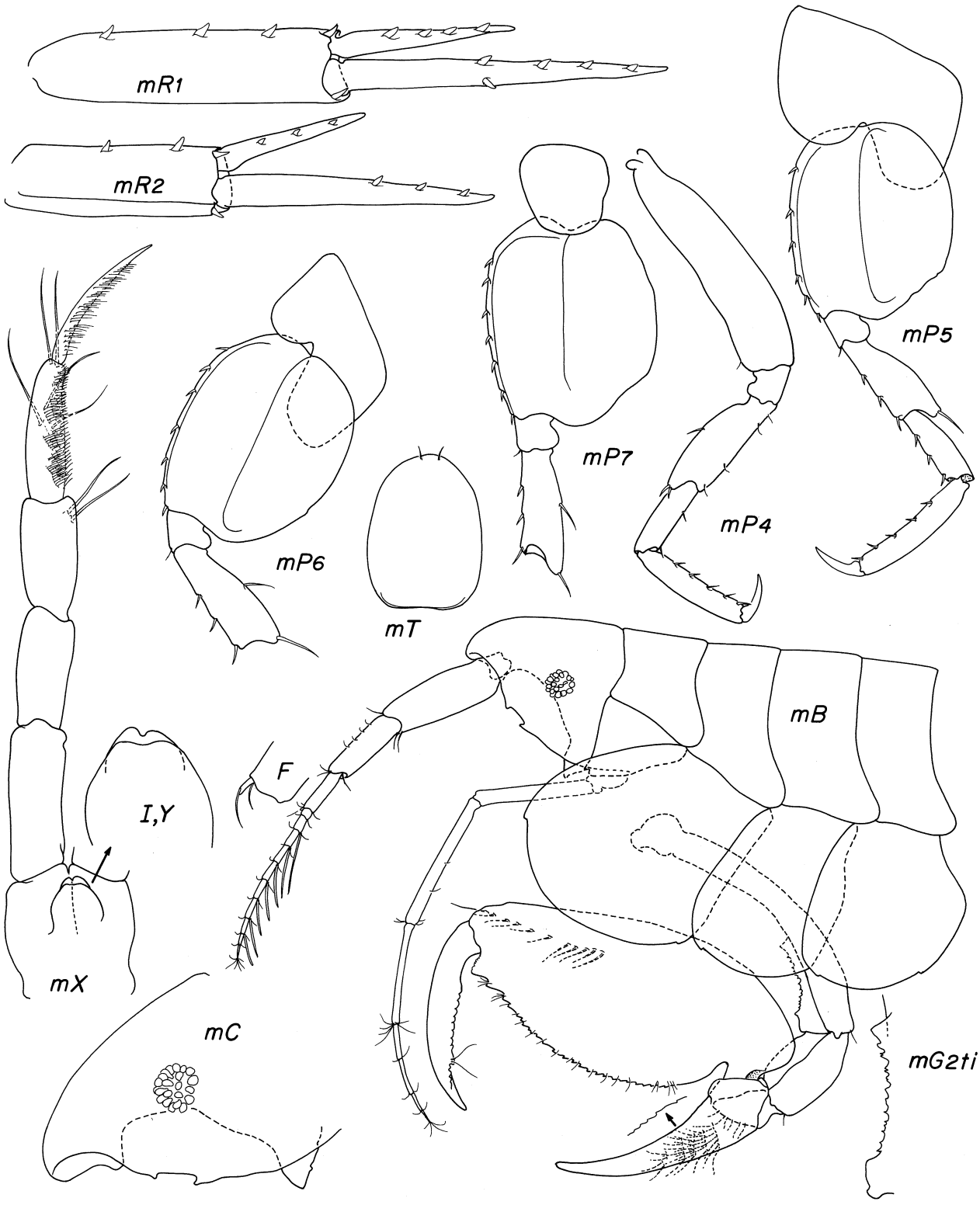

Fig. 26. *Paranamixis misakiensis* n.sp., holotype anamorph male "M", 4.41 mm.

Gnathopod 2, coxa much larger than 3 and 4, anterior margin rounded, with truncate cusp; basis with serrate distomedial locking ridge; carpus short, slightly recurved, reaching 0.50 of propodus, anterior margin with minute serrations; hindmargin of propodus expanded, evenly serrate, with scattered submarginal setae; inner margin of dactyl with small tubercles. Pereopod 3, coxa ovorectangular, subequal in size to 4, anteroventral

margin with cusp. Pereopod 4, ventral margin of coxa rounded, anteroventral and posteroventral corners with small cusp. Pereopod 5–6 similar, coxae bilobed; bases with spinose anterior margins, posterior margins without submarginal setae. Pereopod 7, coxa entire basis similar to pereopods 5 and 6. Uropods 1 and 2, outer rami reduced approximately one-half of inner. Telson broad, entire, distal margin rounded, 1.3 times longer that wide, single pair of apical setae.

Leucomorphs. Unknown.

Etymology. Name refers to the Misaki Coast, Japan.

Relationship. *Paranamixis misakiensis* is most closely related to *P. aberro* from Shijiki Bay, Japan in the transverse anterior angle of the head with a midlateral notch; the small, triangular ventral keel; and the elongate peduncle article 3 of antenna 2. *Paranamixis misakiensis* differs from *P. aberro* primarily in features of gnathopod 2, including a cusp on the anterior margin of the coxa; the presence of a serrate distomedial ridge on the basis; the shortened carpal lobe; and the serrate hindmargin of the propodus; and the tuberculate inner margin of the dactyl. *Paranamixis misakiensis* also lacks submarginal setae on the posterior margin of the basis on pereopods 5–7.

Remarks. *Paranamixis misakiensis* and *P. aberro* appear to be more similar to each other than either species is to any other species of *Paranamixis*, a relationship not confirmed by cladistic analysis. Examination of existing material, and the collection of new material from Japanese and Asian waters will expand the species diversity of anamixids in this region. The presence of minutely cleft inner plates of the maxilliped is significant in a taxonomic and evolutionary sense, but its relevance must await detailed examination of this character in other taxa.

Habitat. Presumed commensal, specific host(s) unknown.

Distribution. Sagami Bay, Pacific Ocean, on *Corallina*.

Phylogenetic analysis

Relationships among and within the genera *Anamixis, Paranamixis* and *Nepanamixis* were analysed using HENNIG86 by James Farris. Analyses of *Anamixis* and *Nepanamixis* were based on data presented in the character matrix, with 41 characters and 24 taxa. Kevin Nixon's CLADOS program was used to map and view characters on the resulting trees. The cladistic analysis was run using the genus *Leucothoe* as the outgroup. All multistate characters were treated as unordered and nonadditive. The analysis in HENNIG86 included a successive weighted option (XS W) and the M*BB* which incorporates branch swapping and uses all available tree space to store results. Initial analyses using all taxa resulted in 16 equally parsimonious trees with a consistency index of 0.81. Many of the characters used in the analysis could not be coded for the genus *Paranamixis* due lack of material for observation. Because the condition of the inner plates of the maxilliped are critical, and, except for *Paranamixis* species described herein, no material is available for analysis. The largest amounts of variability within the cladograms was due to *Paranamixis*. Since *Paranamixis* appeared to be obscuring a more succinct analysis, it was omitted and subsequent analyses were made with *Nepanamixis* and *Anamixis* for which most taxa were able to be completely scored, with the exception of *A. stebbingi* and *A. yarrega*. Analysis of *Anamixis* and *Nepanamixis* produced 12 equally parsimonious trees with a consistency index of 0.85 which were then used to generate a strict consensus tree. This cladogram is represented in Figure 27.

The discussion of generic and specific relationships is organised by nodes labelled in the cladogram, Figure 27. Supporting characters for each node are discussed, the character number is listed above the small rectangle, the character state below. Homoplastic characters are represented by a small dark rectangle below the box.

The character matrix used to score characters and character states is listed below.

Character matrix

1. Eyes: number of ommatidia
   0 = 10+
   1 = 9
   2 = 7
2. Antennae, relative to body length
   0 = both antenna 1, antenna 2 short, less than 1/2 body length
   1 = antenna 1, antenna 2 greater than 1/2 body length
3. Head size
   0 = head less than pereonites 1,2
   1 = head greater than pereonites 1–2
4. Head, anterior margin
   0 = rounded, no notch anteroventral corner
   1 = oblique, unadorned
   2 = oblique, with midlateral notch
   3 = transverse
   4 = oblique, with anteroventral notch
5. Head, lateral margin
   0 = evenly rounded
   1 = with prominent lateral ridge
6. Ventral keel, shape
   0 = sharp
   1 = rounded/truncate
   2 = sharp, with anterior serrations/teeth
   3 = rounded, with anterior teeth
7. Maxilliped, inner plates
   0 = inner plate spinose, lobes separate
   1 = inner plate without spines, cleft to base; outer plate with inner lobes
   2 = inner plate without spines, cleft 1/2–1/3; outer plate with vestigial inner lobes

3 = inner plate without spines, cleft 1/2–1/3; outer plate without inner lobes
4 = inner plate without spines, apically notched or truncate; outer plate without lobes
5 = inner plate without spines, apically rounded; outer plate without lobes

8. Maxilliped, palp article 4
0 = short, not recurved
1 = recurved, 1.0–1.8 × article 3 (normal)
2 = recurved, 1.9+ × article 3 (elongate)

9. Coxa 1
0 = coxa 1 subequal to coxae 2–4, apically rounded
1 = coxa 1 one-half of coxa 2, apically rounded
2 = coxa 1 less than one-quarter coxa 2, apically bifid

10. Gnathopod 1 (revised)
0 = carpochelate, article 6 greater than 5
1 = carpochelate, article 6 not equal to 5; no terminal seta(e)/spine
2 = carpochelate, article 6 not equal to 5; with terminal setae/spine
3 = article 5 basally inflated
4 = article 5 distally attenuate
5 = article 5 distally expanded
6 = gnathopod 1 vestigial
7 = gnathopod 1 absent (*Paranamixis*)
8 = article 5 moderately inflated, with terminal spine

11. Antennae 1, peduncle
0 = peduncle article 1 of normal thickness, width less than 2.0 × article 2.
1 = peduncle article 1 substantially enlarged/thickened: width greater than 2.0 × article 2

12. Antennae, relative length of antenna 1–2
0 = antenna 1 = antenna 2
1 = antenna 1 greater than antenna 2

13. Coxa 2: relative size versus coxa 3–4
0 = coxa 2 = coxa 3–4
1 = coxa 2 (occasionally 3) enlarged greater than 3 or 4, moderately enlarged
2 = coxa 2 greatly enlarged, 2.0 × coxa 3 or 4

14. Coxa 2, anterior margin
0 = small, evenly rounded
1 = with small cusps/teeth
2 = with large cusps/processes
3 = medial portion broadly expanded

15. Gnathopod 2, ornamentation of basis
0 = unarmed
1 = tuberculate proximal ridge
2 = serrate distal ridge (*Paranamixis*)
3 = numerous long setae present

16. Gnathopod 2, carpal lobe
0 = short, less than one-half of palm
1 = long, straight, wide at base; reaching apex of propodus
2 = medium, thickened basally, blunt, not reaching apex of propodus
3 = long, recurved, depth greater than one-half of palm, thin reaching 2/3 of propodus
4 = long; geniculate, reaching nearly to end of propodus.

17. Gnathopod 2, carpus, ornamentation
0 = unornamented
1 = bifid process or denticles
2 = serrate lateral ridge

18. Gnathopod 2, mediofacial setae on propodus
0 = 1 long row of mediofacial setae
1 = 2 long rows of mediofacial setae
2 = 2 rows of mediofacial setae; 1 long, 1 sparse

19. Gnathopod 2, general morphology
0 = Type I =carpus short, grooved, palm oblique, dactyl less than one-half of palm
1 = Type II =carpus short, palm oblique, dactyl recurved, reaching one-half along palm
2 = Type III =carpus long, straight, propodus 2.5 × longer than wide, dactyl straight, one-half length of palm
3 = Type IV =carpus long, recurved, propodus thin, greater than 3.4 × longer than wide; dactyl long, geniculate
4 = Type V =carpus short, palm oblique, with major teeth, dactyl reaching end of propodus

20. Gnathopod 2, ornamentation on propodus
0 = oblique, generally lacking significant ornamentation
1 = truncate, no teeth or cusps
2 = few teeth/cusps, shape variable
3 = major teeth/excavations
4 = entire hindmargin with small serrations
5 = with medial cusps/process

21. Gnathopod 2, dactyl
0 = medium length, recurved, unarmed
1 = medium length, recurved, with serrations, tubercles or ridges
2 = long, evenly recurved
3 = long, geniculate
4 = long, apically bifid
22. Coxa 3, anterior margin
0 = straight, evenly rounded
1 = expanded anteriorly

23. Coxa 4, ventral margin
0 = evenly rounded
1 = crenulate/produced
2 = excavate

24. Uropods, length
0 = rami equal
1 = outer ramus of uropods 2–3 one-half of inner

25. Uropods, spination
0 = spinose
1 = lacking spines

26. Telson, length
0 = 2.5 × width (long)
1 = 1.8–2.0 × width (intermediate)
2 = less than 1.7 × width (short)

27. Coxa 2, ventral margin
0 = rounded
1 = produced; rounded or angular
2 = sinuous; with large cusp
3 = small cuspate process
4 = excavate
5 = anteroventral corner produced

28. Gnathopod 2, proximal margin of carpus
0 = smooth, unarmed
1 = denticulate/serrate

29. Gnathopod 1, article 6
0 = normal, curved (absent in *Paranamixis*)
1 = geniculate

30. Telson shape
    0 = triangular
    1 = broad, ovate
31. Juvenile morphology
    0 = juveniles and females similar to adult males
    1 = juveniles and females dissimilar to adult males
32. Juvenile, gnathopod 1
    0 = carpochelate, 7 articulate
    1 = chelate, carpus less than 1/2 length of propodus, with 3 long, spoon-shaped spines, 6-articulate
    2 = chelate, carpus with single (occasionally double) spine(s)
33. Maxilliped, outer plate, palp article 1
    0 = outer plate with inner lobes, produced
    1 = outer plate without inner lobes, unproduced
34. Maxilliped, length of outer plate
    0 = prominent, reaching to end of palp article 1
    1 = reduced; reaching less than one-half of palp article 1
    2 = vestigial; scarcely produced
    3 = absent
35. Maxilliped, shape of inner plate
    0 = inner plates cleft; one-half to base
    1 = inner plate entire (apically truncate/rounded, or with small apical processes)
36. Maxilliped armament on inner plates
    0 = small spines
    1 = no spines
37. Maxilliped, apical ornamentation of inner plate
    0 = apical margin unarmed
    1 = apical margin with small projections
    2 = apical margin sharp, lobes deeply cleft
38. Gnathopod 1, apical ornamentation on dactyl
    0 = none
    1 = long seta(e)
    2 = swollen knob, small nipple
39. Gnathopod 1, gross morphology (transformed males)
    0 = carpochelate
    1 = chelate
    2 = vestigial
    3 = absent
40. Gnathopod 1, shape of dactyl
    0 = linear
    1 = geniculate
41. Gnathopod 2, insertion point article 5
    0 = insertion point at a more proximal margin of article 6
    1 = insertion point at one-third of article 6 (verticalised)

Node A: *Nepanamixis*.—This genus is supported by ten apomorphic characters, four of which demonstrate some degree of homoplasy. Characters 1,7,9,10,18,32 and 38 provide unambiguous support, while characters 17,21 and 37 are ambiguous. Character 32 has been documented only in *N. dianthus* and is inferred in the remaining taxa of the clade. Clearly while there is homoplasy within this node, there are clearly apomorphic characters that unite these taxa into a monophyletic clade.

Character 1: number of ommatidial facets in the eyes.—The genus *Nepanamixis* is unique in having nine ommatidial facets (state 1). This character is also documented in the only described juvenile morphology, *N. dianthus*. For the other members of the genus, this character is known only from adults.

Character 7: inner plates of maxilliped.—All taxa in this group have the inner plates of the maxilliped cleft one-half or more to the base (state 1).

Character 9: relative size of coxa 1 to coxae 2–4.—The apomorphic condition of coxa 1 being approximately one-half the size of coxae 2–4 (state 1) is unequivocal for these taxa.

Character 10: shape of gnathopod 1.—The basal portion of gnathopod 1 is inflated in *Nepanamixis*, (state 3) providing a distinct morphology for this appendage.

Character 17: ornamentation of carpal lobe, gnathopod 2.—The presence of a serrate lateral ridge (state 2) along the carpal margin distinguishes three of the four taxa in this group.

Character 18: rows of mediofacial setae on propodus of gnathopod 2.—The presence of a double row of long mediofacial setae on the propodus (state 1) is unique to *Nepanamixis*. Other taxa either have a single long row of such setae, or a second row consisting of only a few setae.

Character 21: gnathopod 2, length and shape of dactyl.—The long, evenly recurved condition of the dactyl (state 2) is equivocal, showing much homoplasy throughout all taxon groups. The strength of this character in diagnosing relationships appears to be minimal.

Character 23: ventral margin of coxa 4.—The crenulate or produced ventral margin of coxa 4 (state 2) is a synapomorphy for two species, *N. torreanus* and *N. vectoris*.

Character 26: telson length.—All four taxa in this clade have telsons of intermediate length-versus-width ratio of 1.8–2.0 (state 1).

Character 29: telson shape.—The triangular telson (state 0) is unequivocal for all *Nepanamixis*.

Character 32: juvenile morphology of gnathopod 1.—The unusual chelate condition of juvenile gnathopod 1 with three embedded, spoon-shaped spines in article 6 is known only from *N. dianthus* from Belize, and hypothesised for the sister species *N. grossimana* and eastern Pacific taxa, *N. torreanus* and *N. vectoris*. Whether other members of this group have similar juvenile morphologies remains to be resolved.

Character 37: apical ornamentation of inner plate of the maxilliped.—The rounded apical margins of the inner plates and the deeply to moderately cleft nature of the inner plates (state 3) uniquely defines *Nepanamixis*.

Character 38: gnathopod 1, apical ornamentation of dactyl.—The presence of a small knob-like process at the terminus of the dactyl (state 3) is an apomorphic condition that defines the taxa at this node.

Node B: the *grossimana–dianthus* clade.—These two taxa both have long, geniculate dactyls on gnathopod 2 (character 16, state 4) and an excavate ventral margin on coxa 4 (character 23, state 2). While *N. grossimana* and *N. dianthus* are sister species, their widespread distributions, Mauritius and Belize respectively, present a disjunct pattern that is difficult to evaluate in the absence of additional material from intermediate localities. It is probable future sampling efforts will reveal related taxa.

Node C: the *Anamixis* clade.—This node is supported by eight characters, three of which are homoplastic, 4, 7 and 34. Apomorphic character support is furnished by characters 9, 30, 32 and 39.

Character 4: shape of anterior margin of head.—The shape of the anterior margin of the head exhibits varying degrees

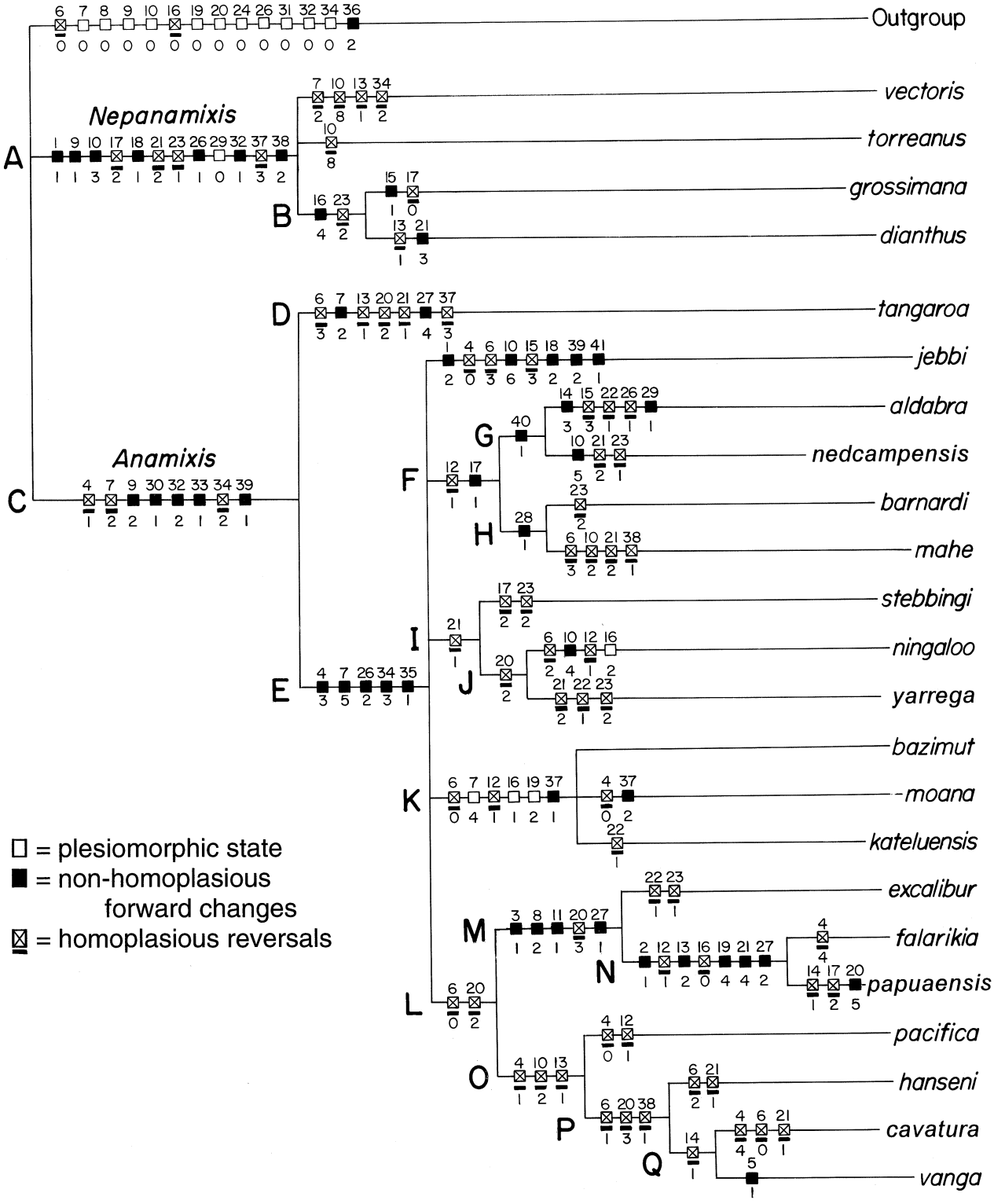

Fig. 27. Strict consensus tree of the Anamixidae.

of homoplasy and is equivocal for almost all taxa. Due to the nature and variety of homoplasy encountered, this character currently does not support monophyly.

Character 7: inner plates of the maxilliped.—With the exception of *A. tangaroa* that has cleft inner plates (state 2) and the *bazimut–moana–kateluensis* clade that has apically notched or indented inner plates (state 4), the remaining species all exhibit apically rounded plates (state 5). The ancestral condition of fully cleft inner plates (state 0) appears to be gradually lost as fusion of the inner plates results in decreasing amounts of separation.

Character 9: size of coxa 1 versus coxae 2–4.—The

synapomorphic character of coxa 1 reduced to one-quarter or less of coxae 2–4 (state 2) unequivocally defines all *Anamixis*. In all taxa that have been examined by the author the apex of the reduced coxa exhibits a small bifid process. In most cases where material was unavailable for examination and figures of extant taxa were relied upon, the bifid apex was not illustrated. It is probable that this condition was overlooked and most likely occurs in all *Anamixis* species.

Character 30: shape of telson.—The broad, ovate shape of the telson (state 1) unequivocally defines the *Anamixis* clade.

Character 32: juvenile morphology.—All *Anamixis* juveniles (leucomorphs) have chelate first gnathopods with a single embedded apical spine. This character is hypothesised for most *Anamixis* as the majority of the juvenile stages remain to be documented.

Character 33: palp article 1, outer plate of maxilliped.—Outer plates lack inner lobes in all *Anamixis*. This character is unequivocal for the node (state 1).

Character 34: maxilliped, length of outer plate.—The outer plate is absent in all *Anamixis* (state 3).

Character 39: gnathopod 1 morphology (transformed males).—Unequivocal for *Anamixis*, all anamorphs have thin, finely chelate first gnathopods (state 1) except for the vestigial gnathopod 1 of *A. jebbi*.

Node D: the "*tangaroa*" clade.—This unusual species from the cool, deep waters of the Bass Strait exhibits several characters that indicate its possible link with ancestral lineages. While seven characters that define this species, only two provide unequivocal support. Those characters are condition of the inner plates of the maxilliped (character 7) and the length of the telson (character 26).

Character 7: inner plate of maxilliped.—The inner plates of *A. tangaroa* are partially cleft, with fusion occurring along one-half to one-third the medial margin (state 2).

Character 26: telson length.—The telson is of the intermediate length (state 1). This condition is unequivocal and clearly relates *A. tangaroa* those taxa with more elongate telsons (Node A).

Node E.—This node contains the remaining members of the *Anamixis* group. In addition to the characters already discussed for *Node C* there are two characters that provide unequivocal support for this group. Telson length (character 26) and the shape of the inner plate of the maxilliped (character 35).

Character 26: telson length.—All remaining taxa in this group are united by the shortened condition of the telson (state 2). While there is some variation within this character all species have telsons 1.7X or less, width versus length.

Character 35: shape of inner plate of maxilliped.—All remaining taxa are supported unequivocally by having inner plates that are apically truncate or rounded. In the case of the Pacific Plate species (Node K), a slight emargination or projection of the apical margin is present.

Node F: Indian Ocean anamixids.—The four species in this clade, *A. aldabra, A. nedcampensis, A. barnardi* and *A. mahe* are defined by two synapomorphies, one of which, is homoplastic, the relative length of antenna 1 and 2; and the other unequivocal, the presence of a bifid process on the carpal lobe of gnathopod 2.

Node G: the *aldabra–nedcampensis* clade.—These sister species are defined by a single derived character state.

Character 40: morphology of gnathopod 1.—These species share the geniculate condition of gnathopod 1 (state 1).

Node H: the *barnardi–mahe* clade.—These two species are also defined by a single apomorphic character state.

Character 28: proximal margin of carpus, gnathopod 2.—These two taxa have a distinct serrate ridge along the proximal insertion of the carpus (state 1).

Nodes I and J.—These nodes are supported by a single homoplastic character each indicating that they may not be reliable indicators of relationships. Further analysis of material will allow character relationships to be more thoroughly investigated.

Node K: Pacific Plate clade.—The taxa within this clade are supported by six characters, two of which are homoplastic and four unequivocal. While they are similar in gross morphology, they are readily distinguished by a variety of features, including variations in the broad ventral keel, coxal morphology and condition of the inner plate of the maxilliped. Only unequivocal characters are presented.

Character 7: inner plates of the maxilliped.—Inner plates entire, occasionally apically emarginate or with slight projections (state 4).

Character 16: carpal lobe of gnathopod 2.—All taxa have carpal lobes that are straight, thickened and blunt at the base (state 1).

Character 19: general morphology of gnathopod 2.—All species have a Type III second gnathopod, with a quadrate propodus, 2.5X length versus width, the long blunt carpus and straight dactyl extending one-half the length of the palm (state 2).

Character 37: apical ornamentation of inner plate, maxilliped.—All three species have an unusual condition of the inner plate, with the apical margins being slightly to sharply produced (state 1). In *A. bazimut* and *A. kateluensis* this condition was originally interpreted as the inner plates being cleft. My phylogenetic hypothesis supports the condition of projections extending from apically rounded margins, rather than representing a cleft condition. Additional material from other locations will elucidate the full range of traits for this group.

Node L: the presence of a sharp ventral keel (character 6, state 0) and a propodus of gnathopod 2 with variable ratio of teeth and cusps defining the palm (character 20, state 2) support this node. Both characters are homoplastic and thus provide only equivocal support.

Node M: the *excalibur* clade.—This branch is supported by five apomorphies, four of which are unequivocal. The large size of the head (character 3, state 2), the elongate palp article 4 of the maxilliped (character 8, state 2) and the enlarged first antennal peduncular segment (character 11, state 1) provide strong synapomorphic support for this unusual group of taxa. The elongate palp article 4 of the maxilliped is used in feeding, and its unique morphology may indicate specialised feeding adaptations. Additional investigations on feeding and host preference(s) for these taxa may explain the elongation of the fourth article and other morphological apomorphies.

Node N: *A. falarikia* and *A. papuaensis*.—These sister taxa are defined by seven apomorphies, two of which are homoplastic.

Character 2: relative length of antennae to body length.—The length of antenna 1 and 2 are less than one-half the body length (state 1). Since the antennae are used in feeding (Thomas, 1981; Thomas & Taylor, 1981), the use of this character in strictly defining taxa may prove problematical as more species are described and additional ecological studies are undertaken.

Character 12: relative length of antenna 1 versus antenna 2.—This homoplastic apomorphy shows substantial variation among species and clades. Its use in supporting phylogenies is questionable.

Character 13: relative size of coxa 2 versus coxae 2–4.—The immensely enlarged second coxa (state2) is unequivocal for these two species. Because second coxae are involved in feeding of anamixids it is hypothesised that these taxa have undocumented feeding or host relationships that could account for the immense increase in size of this character.

Character 16: length of carpal lobe, gnathopod 2.—The shortened carpal lobe, less than one-half of the palm (state 0), is found elsewhere only in the outgroup. The use of this character in feeding activities may determine its ultimate morphology. The equivocal nature of this character precludes its use as a strong indication of phylogenetic relationships, however, its occurrence in other clades may aid in hypothesising feeding behaviour.

Character 19: morphology of gnathopod 2.—The Type IV second gnathopod, with a short carpus and an oblique palm with numerous teeth or serrations (state 4) is unequivocal for these species, occurring nowhere else within *Anamixis*.

Character 21: dactyl of gnathopod 2.—The apically bifid dactyl (state 4) is unequivocal for *A. falarikia* and *A. papuaensis*.

Character 27: ventral margin of coxa 2.—The sinuous margin and large cuspate processes of the second coxae in these species (state 2) is also unequivocal for these two species.

Node O: eastern Pacific–Caribbean clade.—This clade is defined by three homoplastic apomorphies. Two of these characters provide support for this clade.

Character 10: shape and ornamentation of gnathopod 1.—All members of this clade have either a terminal spine or setae at the apex of gnathopod 1, or are carpochelate, with moderate or no basal inflation of the propodus (state 2). The only other occurrence of this condition is in *A. mahe* from the Seychelles Islands.

Character 13: relative size of coxa 2.—The moderately enlarged second coxa (state 1) is unequivocal for this clade. The presence of this state in *A. tangaroa* and *N. dianthus* warrants further analysis and refinement. The amount of enlargement in *A. tangaroa* and *N. dianthus* is not equal to the enlargement to found in this clade.

Node P: Caribbean clade.—Three homoplastic apomorphies define this clade restricted to the Caribbean Sea.

Character 6: shape of ventral keel.—Character states vary in two of the three taxa of this clade, rendering it unreliable.

Character 20: ornamentation of propodus, gnathopod 2.—Members of this clade all have a rectolinear propodus with major teeth or excavations on the palmar margin (state 3). A convergent condition in *A. excalibur* is the only other occurrence of state 3.

Character 38: apical ornamentation of dactyl, gnathopod 1.—The presence of long, paired terminal setae uniquely define the three species of Caribbean anamixids.

Node Q.—*Anamixis cavatura* and *A. vanga* are sister taxa based on the anterior margin of coxa 2 which has small teeth or cusps (character 14, state 1). This character is equivocal and additional character support at this node is needed for further resolution of relationships.

Biogeography

Distribution patterns resulting from the cladistic analyses can be explained in part by: 1, geological history, especially interactions at plate boundary margins; 2, effects of sea-level change and 3, effects of depressed sea-surface temperatures due to upwelling.

Geological activity and events at the margins of plates (e.g., docking of allochthonous terranes, volcanic uplift, coalescence of island arcs into composite terranes) may help explain the composite nature of some distribution patterns. Scenarios detailing composite faunas and how they may have accumulated have been put forth by Pandolfi (1992). For the purposes of this discussion, composite areas are defined as those areas where faunal composition appears to bridge wide geographic gaps, and documented population structure is composed of taxa with diverse geographic and phylogenetic affinities.

Glacial effects of sea-level change could cause widespread populations to be isolated thus making them more susceptible to genetic drift and possibly modify habitat and niche requirements. Maximum effects of this process would be in the intricate island coastlines of the Indo-Malayan region, an area from which comprehensive amphipod collections are almost totally lacking.

Depression of sea-surface-temperature would eliminate and fragment widespread populations of tropical amphipods, however, the data are insufficient to speculate about the historical effects of temperature on amphipod populations. One apparent anomaly in amphipod distribution related to water temperature is the occurrence of *A. tangaroa* in waters of the Bass Strait off southern Australia. Collected in cool deep waters (10°C; 60–82 m) *A. tangaroa* could be a disjunct relict of tropical transgressions into the higher latitudes. The cleft inner plats of the maxilliped of *A. tangaroa* clearly link it to the plesiomorphic genus *Nepanamixis*. Whether the occurrence of this species is atypical, or represents a common relict pathway (Newman, 1991) in species once more widespread during periods of tropical expansions remains to be addressed.

Nepanamixis

Of the four species in this clade, two, *Nepanamixis torreanus* from the Galapagos and *N. vectoris* from Panama are sister taxa. Current distributions probably resulted from rifting of the Nazca and Cocos Plates from the South American Plate which would have separated and split ancestral populations to the west. *Nepanamixis torreanus* retains the plesiomorphic condition of the inner plates and outer lobes of the maxilliped, while *N. vectoris* exhibits the more derived condition. The remaining two taxa *N. grossimana* and *N. dianthus*, present a widely disjunct distribution from Mauritius (Indian Ocean) to Belize (Caribbean Sea). I can provide no hypothesis for this distribution pattern. Additional sampling of reef sites, especially along plate boundary margins may produce additional species of *Nepanamixis*. Juvenile morphologies that differ drastically from other anamixid juveniles are known only from *N. dianthus* from Belize. Information on the juvenile morphologies of the remaining species of *Nepanamixis* is lacking, but efforts to document juvenile morphologies will further elucidate relationships within this clade. Commensal habitats (if any) and ecological niches are also unknown for all species of *Nepanamixis*. Any information regarding

the ecology of *Nepanamixis* will undoubtedly provide further insight regarding their habitat requirements.

Within *Anamixis* there are several recognisable distribution patterns in the Central and South Pacific (Node K), Eastern Pacific/Western Caribbean (Node O), Indian Ocean (Nodes G and I) and the South Pacific (Node M).

Three species, *A. bazimut, A. kateluensis* and *A. moana*, are widely distributed on the Pacific Plate and immediate margins to the south (Node K). *Anamixis moana* is known only from the Hawaiian islands and the emarginate inner plate of the maxilliped is apparently plesiomorphic. *Anamixis kateluensis* from the Caroline Islands, and *A. bazimut* from northern Papua New Guinea and the northern end of the Great Barrier Reef, Australia, both have apical projections in the inner plate of the maxilliped, apparently a derived condition.

Widespread distribution of a group suspected of having limited dispersal capabilities can be explained only by a reliction scenario (Newman, 1991). One plausible explanation would be the reliction and speciation of a previously widespread ancestral species. The resultant distribution pattern would be a series of closely related species with consistent morphological features and widespread distributions. Scenarios involving active dispersal of host and commensal do not appear plausible at this time.

Four species comprise the Indian Ocean component, *A. stebbingi* from the northern Indian Ocean, *A. aldabra* and *A. mahe* from the Seychelles and *A. nedcampensis*, from Western Australia. The two clades with Indian Ocean distributions, *A. aldabra* from Aldabra Atoll and *A. nedcampensis* from Ningaloo Reef, Western Australia (Node G); and *A. barnardi* from the littoral of South India and *A. mahe* from Mahe Island, Seychelles (Node H) are supported by equivocal characters. Node G is defined by the presence of a geniculate gnathopod 1, while Node H is defined by a denticulate carpal margin near the insertion of the propodus. A possible explanation for Indian Ocean distribution patterns was presented by Springer (1988). Essentially, the northward movement of the Indian subcontinent through the region divided ancestral components into two portions: western Indian Ocean and eastern Indian Ocean-Pacific Ocean. While there are eastern and western components to the distribution patterns, detailed scenarios that might account for this are as yet undeveloped.

Three species that share unusual character morphologies are distributed in the South Pacific, *A. papuaensis* from the south coast of Papua New Guinea, *A. falarikia* from the Caroline Islands and *A. excalibur* from the north coast of Papua New Guinea. Distributions in this group are more confined than the previous group of Pacific Plate species (Node K), with two of the species occurring at the north edge of the Australian Plate. *Anamixis papuaensis* and *A. falarikia* are sister species based on five unequivocal apomorphies (Node N), while *A. excalibur* is a sister taxa to the other two (Node M). Character support for this clade is strong with four unequivocal apomorphies. While species in this clade share distinct character states, there is considerable variation in morphology within this group. *Anamixis papuaensis* has a recurved medial process on the propodus, a derived condition not found anywhere else in the Amphipoda. Natural history studies to document host relationships and feeding behaviour may explain how these morphologies are used by the amphipods.

Four species comprise the eastern Pacific-Caribbean clade, *A. pacifica* from southern California and *A. hanseni, A. cavatura* and *A. vanga* from the Caribbean. These species have either a terminal spine or setal ornamentation on the apices of gnathopod 1. Thomas and co-workers have conducted extensive studies on *A. vanga* and *A. cavatura* describing feeding behaviour and biology in addition to documenting juvenile morphologies in these two species (Thomas, 1979, 1981; Thomas & Taylor, 1981; Thomas & Barnard, 1983). *Anamixis vanga* and *A. cavatura* are sister taxa, found throughout the central Caribbean and into the Carolinas. They overlap in range distributions but are separated by niche preferences, *A. cavatura* preferring small asconoid and colonial ascidians in relatively shallow depths (1–5 m), while *A. vanga* prefers larger solitary ascidians and occurs to deeper waters (2–20 m). Barnard (1955) listed "ascidians" as the host for *A. pacifica*. *Anamixis pacifica* was probably separated from its Caribbean counterparts by geological processes related to the formation of the Central American isthmus about three million years ago (Woodring, 1966).

ACKNOWLEDGMENTS. The following individuals and institutions provided material for this study: Lou Eldridge, Bernice P. Bishop Museum; Jim Lowry, Australian Museum; Gary Poore, Museum of Victoria; Torben Wolff, Zoological Museum of Copenhagen; C.A. Childs, J.L. Barnard, and Brian Kensley, National Museum of natural History. Richard Heard, Michel Ledoyer, and Alan Myers provided material for study from their personal collections. This research was supported by grants from the National Science Foundation, BSR-891558, BSR-85-15186, and DEB-8121128; National Geographic Society; Smithsonian Institution; and the Christensen Research Institute, Madang, Papua New Guinea. For help in the field, I would like to thank Jerry Barnard (deceased), Mike Carpenter, Klaus Ruetzler, and Janice Clark, of the Smithsonian; Jim Lowry, Alan Myers, Deb Coulombe, Sharon Thomas, and my daughters Eryn and Debra Kelly. Matthew Jebb, Director of the Christensen Research Institute kindly provided funding for work in New Guinea. Linda Lutz inked the plates. This is contribution number 40 of the Christensen Research Institute.

References

Barnard, J.L., 1955. Two new spongicolous amphipods (Crustacea) from California. Pacific Science, 9: 26–30, figs 1–2.

Barnard, J.L., 1965. Marine amphipods of atolls in Micronesia. Proceedings of the United States National Museum, 117: 459–552, 35 figs.

Barnard, J.L., 1969. The families and genera of marine gammaridean Amphipoda. United States National Museum, Bulletin, 271. Pp. 535, figs 173.

Barnard, J.L., 1970. Sublittoral gammaridea (Amphipoda) of the Hawaiian Islands. Smithsonian Contributions to Zoology, 34. Pp. 286, figs 180.

Barnard, J.L., 1971. Keys to the Hawaiilan marine gammaridea, 0–30 meters, Smithsonian Contributions to Zoology, 58. Pp. 135, figs 68.

Barnard, J.L., 1974. Gammaridean Amphipoda of Australia, Part II. Smithsonian Contributions to Zoology, 139. Pp. 148, figs 83.

Barnard, J.L., 1979. Littoral gammaridean Amphipoda from the Gulf of California and the Galapagos Islands. Smithsonian Contributions to Zoology, 271. Pp. 149, figs 74.

Brusca, R.C., 1984. Phylogeny, evolution and biogeography of the marine isopod subfamily Idoteinae (Crustacea: Isopoda: Idoteidae). Transactions of the San Diego Society of Natural History 20: 99–134, figs 18.

Conlan, K.E., 1988. Phenitic and cladistic methods applied to a small genus (Corophoidea: Ischyroceridae: Microjassa) and a larger outgroup. Crustaceana Supplement 13: 143–166.

Hay, M.E., 1981. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. The American Naturalist 118(4): 520–540.

Hennig, W., 1966. Phylogenetic Systematics. University of Illinois Press, Urbana, Illinois.

Hirayama, A., 1983. Taxonomic studies on the shallow water gammaridean Amphipoda of West Kyushu, Japan. I. Acanthonotozomatidae, Ampeliscidae, Ampithoidae, Amphilochidae, Anamixidae, Argissidae, Atylidae and Colomastigidae. Publications of the Seto Marine Biology Lab 28(2): 75–150, figs 42.

Kim, Won, & Chang Bae Kim, 1991. The marine amphipod crustaceans of Ulreung Island, Korea: Part II. The Korean Journal of Systematic Zoology 7(1): 13–38, figs 20.

Ledoyer, M., 1978. Amphipodes gammariens (Crustacea) des biotopes cavitaires organogenes recifaux de l'ile Maurice (Ocean Indian). Bulletin of the Mauritius Institute 8(3): 197–331, figs 43.

Ledoyer, M., 1979. Les gammaraiens de la pente externe du grand recif de Tulear (Madagascar), (Crustacea: Amphipoda). Memorie del Museo Civico di Storia Natuale di Verona, 2. Pp. 149.

Ledoyer, M., 1982. Faune de Madagascar. 59(1), Crustaces amphipodes gammariens, familles des Acanthonotozomatidae a' Gammaridae. Centre National de la Recherche Scientifique. Pp. 598, figs 226.

Ledoyer, M., 1984. Les Gammariens (Crustacea, Amphipoda) des Herbiers de Phanérogames Marines de Nouvelle Calédonie (Région de Nouméa). Mémoires du Museum National d'Histoire Naturelle, Nouvelle Serie, serie A, Zoologie, 129. Pp. 113, figs 48, tables 4.

Moore, P.G., 1987. Taxonomic studies on Tasmanian phytal amphipods (Crustacea): the families Anamixidae, Leucothoidae and Sebidae. Journal of Natural History 21: 239–262, figs 15.

Myers, A.A., 1985. Shallow-water, coral reef and mangrove amphipoda (Gammaridea) of Fiji. Records of the Australian Museum, Supplement 5: 1–143, figs 109.

Nayar, K.N., 1967. On the gammaridean Amphipoda of the gulf of Mannar (sic), with special reference to those of the pearl and chank beds. Proceedings of a Symposium on Crustacea, Ernakulam 1: 133–168.

Newman, W.A., 1991. Origins of southern hemisphere endemism, especially among marine Crustacea. Memoirs of the Queensland Museum 31: 51–76.

Pandolfi, J.M. 1992. A review of the tectonic history of New Guinea and its significance for Marine biogeography. Pp. 718–728. **In** R. Richmond (ed.). Proceedings of the Seventh International Coral Reef Symposium, Guam, Vol. 2. University of Guam Press, Mangilao.

Ruffo, S., 1969. Terzo contributo alla consoscenza degli anfipodi del Mar Rosso. Memorie del Museo Civico di Storia Naturale, Verona 17: 1–77, figs 24.

Sasidharan, K.K., 1983. *Anamixis barnardi* sp. nov. a littoral amphipod from South India. **In** Selected Papers on Crustacea. The Aquarium Trivandrum. Pp. 195–199, fig. 1.

Schellenberg, A., 1938. Littorale amphipoden des Tropischen Pazifics. Kungliga Svenska Vetenskapsakademiens Handlingar 16(3): 1–105.

Schram, F.R., 1986. Crustacea. Oxford University Press, London.

Shoemaker, C.R., 1933. Two new genera and six new species of Amphipoda from Tortugas. Papers of the Tortugas Lab, Carnegie Institute of Washington 28: 245–256, figs 8.

Sivaprakasam, T.E., 1968. A new species of *Paranamixis* Schellenberg (Crustacea Amphipoda) from the Gulf of Manaar. Proceedings of the Zoological Society of Calcutta 21: 131–136, figs 3.

Springer, V.G., 1988. The Indo-Pacific Blennid fish genus *Ecsenius*. Smithsonian Contributions to Zoology, 465: 1–134, pls 1–14.

Stebbing, T.R.R., 1897. Amphipoda from the Copenhagen Museum and other sources. Transactions of the Linnaean Society of London, Zoology 7(2): 25–45, pls 9.

Stebbing, T.R.R., 1906. Amphipoda I: Gammaridea. Das Tierreich, 21. Pp. 806, figs 127.

Thomas, J.D., 1979. Occurrence of the amphipod *Leucothoides pottsi* Shoemaker in the tunicate *Ecteinascidia turbinata* Herdman form Big Pine Key, Florida. Crustaceana 37(1): 107–109.

Thomas, J.D., 1981. Mouthpart morphology and feeding behavior in the amphipod families Anamixidae and Leucothoidae. American Zoologist 21: 230.

Thomas, J.D., 1983. Discovery of a majid host for the commensal amphipod *Stenothoe symbiotica* Shoemaker, 1956. Bulletin of Marine Science 34(3): 484–485.

Thomas, J.D., & J.L. Barnard, 1983. Transformation of the *Leucothoides* morph to the *Anamixis* morph (Amphipoda). Journal of Crustacean Biology 3(1): 154–157.

Thomas, J.D., & G.W. Taylor, 1981. Mouthpart morphology and feeding strategies of the commensal amphipod *Anamixis hanseni* Stebbing. Bulletin of Marine Science 31(2): 462–467, figs 5.

Walker, A.O., 1904. Report on the Amphipoda collected by Professor Herdman, at Ceylon in 1902. Ceylon Perarl Oyster Fisheries Supplemental Report 17: 229–300, pls 8.

Woodring, W.P., 1966. The Panama land bridge as a sea barrier. Proceedings of the American Philosophical Society 110(6): 425–433.

Accepted 6 October 1995.