Lowry, J. K., and H. E. Stoddart, 1989. The scopelocheirid genus *Aroui* (Crustacea: Amphipoda: Lysianassoidea) with notes on the association between scopelocheirid amphipods, cassid gastropods and spatangoid echinoids. *Records of the Australian Museum* 41(2): 111–120. [22 September 1989].

doi:10.3853/j.0067-1975.41.1989.139

ISSN 0067-1975

Published by the Australian Museum, Sydney

The Scopelocheirid Genus *Aroui* (Crustacea: Amphipoda: Lysianassoidea) with Notes on the Association between Scopelocheirid Amphipods, Cassid Gastropods and Spatangoid Echinoids

J.K. LOWRY & H.E. STODDART

Australian Museum
P.O. Box A285, Sydney South, NSW 2000, Australia

ABSTRACT. Formerly *Aroui* was a monotypic scopelocheirid genus known only from the Mediterranean Sea. The type species, *Aroui setosus* Chevreux, is redescribed. It is shown that a neotype, recently established for this species, is invalid, and a lectotype is selected from syntype material in the Muséum National d'Histoire Naturelle, Paris. A second species, *Aroui hamatopodus*, is described, based on widespread collections from the Australian continental shelf and slope. The genus is rediagnosed and distinguished from all other scopelocheirids by two autapomorphic character states. Evidence is presented which suggests that scopelocheirids are very primitive scavengers, and that there is a three-way association between cassid gastropod predators, scopelocheirid amphipod scavengers and their common prey, spatangoid echinoids. An hypothesis is presented which suggests that scopelocheirid scavengers may have evolved by the early Tertiary and that the association involving cassid gastropods and spatangoid echinoids may date from this time.

LOWRY, J.K. & H.E. STODDART, 1989. The scopelocheirid genus *Aroui* (Crustacea: Amphipoda: Lysianassoidea) with notes on the association between scopelocheirid amphipods, cassid gastropods and spatangoid echinoids. Records of the Australian Museum 41(2): 111-120.

Aroui setosus Chevreux, 1911 is well known from the works of Chevreux (1911) and Stroobants (1976). It is the type species of the genus *Aroui* Chevreux which until now was known only from the Mediterranean Sea. Although *Aroui* has been recognised by Stroobants (1976) and Bellan-Santini (1985) as closely related to *Scopelocheirus* Bate, the exact relationship has not been fully understood until now because *Aroui* has been monotypic. Among the extensive collections of lysianassoid amphipods from Australian waters we have found only one species of scopelocheirid lysianassoid, a new species of *Aroui*, which is described below. This has allowed us to rediagnose *Aroui* and consider its relationship to *Scopelocheirus* and other scopelocheirid genera.

Stroobants apparently believed that *A. setosus* was represented by a holotype because she reported being unable to find "la type" in either the Muséum National d'Histoire Naturelle, Paris, (MNHN) or the Musée

Océanographique, Monaco (MOM). She subsequently established a neotype for *A. setosus* from new material collected by E. Dupont in southern Sardinia (Stroobants, 1976:239). However, we believe that all specimens of *A. setosus* from Chevreux's original collection should be regarded as syntypic material, as has always been done by the institutions which hold this material. The designation of a neotype of *A. setosus* by Stroobants is invalid for two reasons. It is contrary to article 75(b)(ii) of the Code of the International Commission on Zoological Nomenclature. *Aroui* is a monotypic genus. Although the species had not been recollected until Stroobants obtained new material from Sardinia, there had been no question concerning its identity. It is easily distinguished from *Scopelocheirus hopei*, its closest relative, and Stroobants apparently had no difficulty identifying *A. setosus* and *S. hopei* in her collections. Thus there were no "exceptional circumstances" or complex zoological problem to justify the establishment of a neotype.

It is contrary to article 75(d)(iii). Stroobants failed to provide reasons for believing the types of *A. setosus* to be lost; syntypes were present at the time in three major institutions, those in the British Museum (Natural History), London and the Musée Océanographique having been reported in the recent literature (Belloc, 1960; Thurston & Allen, 1969).

In 1984 we examined the syntype material of *A. setosus* in the Museum National d'Histoire Naturelle. These specimens are in good condition. We have designated a lectotype, which is registered as Am 3995, from the MNHN Am 900 collection. This specimen is redescribed and illustrated below to allow comparison with the new species. The remaining syntypes (93 in the Museum National d'Histoire Naturelle, Am 900 and 901, 3 in the Musée Océanographique, 3 in the British Museum (Natural History), 1912:4:4:5-7 and 2 in the Australian Museum, Sydney, P35541) become paralectotypes. In accordance with Article 75(h) of the ICZN we referred this matter to the Commission for a ruling and received a reply (P.K. Tubbs, *in litt.*) confirming our interpretation.

Specimens of the new species are deposited in the Australian Museum, Sydney (AM) and the Western Australian Museum, Perth (WAM).

Aroui Chevreux

Aroui Chevreux, 1911: 169.-Barnard, 1969: 328.

Type species. *Aroui setosus* Chevreux, 1911, by monotypy.

Diagnosis. Antenna 1 with well-developed flagellum. Epistome not extending beyond the border of the upper lip; mandibular molar small, cylindrical, triturating; palp article 2 broad proximally, tapering distally. Maxilla 1, outer plate with 11 spine-teeth; inner plate with plumose setae along entire medial margin. Maxilla 2, outer plate half length of inner with long slender, distally barbed setae. Maxilliped outer plate with fully developed apical setae, medial spines and submarginal setae. Coxae 1-4 with setal fringe along ventral margin. Peraeopod 4, coxa with well-developed posteroventral lobe. Peraeopod 5, basis expanded posteriorly, merus expanded posteriorly.

Remarks. We consider scopelocheirids to be very primitive lysianassoids, and *Aroui* and *Scopelocheirus* appear to be the most primitive of the scopelocheirid genera which includes *Bathycallisoma* Dahl, 1959, *Eucallisoma* Barnard, 1961, *Paracallisoma* Chevreux, 1903, *Paracallisomopsis* Gurjanova, 1962 and *Scopelocheiropsis* Schellenberg, 1926. The evidence for this is mainly in the mouthparts. *Aroui* has the following combination of plesiomorphic mouthpart character states which is rarely found among the lysianassoids, but is common in outgroups such as *Valettiopsis* and eusiroids. The lacinia mobilis is a stemmed serrate blade. Plumose setae line the entire margin of the inner plate on maxilla 1. There is little displacement of the spine-teeth on the outer plate of maxilla 1. The outer plate of the maxilliped retains apical plumose setae, well-developed spines along the medial margin and well-developed submarginal setae.

Aroui and *Scopelocheirus* are very closely related as emphasised by Stroobants (1976) and Bellan-Santini (1985). They share two character states, considered to be synapomorphies not found in other scopelocheirid genera: a reduced triturating molar and a proximally broadened article 2 on the mandibular palp. *Aroui* is distinguished from all other scopelocheirid genera by two autapomorphic character states - the reduced outer plate of maxilla 2 with long slender distally barbed setae, and the setal fringe on coxae 1 to 4.

Aroui setosus Chevreux

Fig. 1

Aroui setosus Chevreux, 1911: 170, fig. 3, pl. 7, figs 14-27.-Stroobants, 1976: 239, figs 1-11.-Vader, 1978: 127.

Material examined. Lectotype female, 8.0 mm, ovigerous (8 eggs), MNHN Am 3995; paralectotype female, 7.6 mm, paralectotype male, 5.8 mm, AM P35541 (ex MNHN Am 900); off Bône, north-east of Cap de Garde, Algeria, Mediterranean Sea, [approx. 35°55'N 7°47'E], trawl, on urchins (*Spatangus* sp.), 65 m, E. Chevreux on the yacht *Melita*, 12 June 1904, Stn 726.

Diagnosis. Maxilla 1 palp with 8 terminal spines, 1 flag spine and 1 large subterminal seta. Maxilliped, outer plate with many apical plumose setae. Gnathopod 1 coxa with anterior margin concave, posterior margin straight and ventral margin convex. Gnathopod 2 carpus 3.5 times as long as deep, propodus 2.0 times as long as deep. Peraeopod 6 merus without hooked spines along the posterior margin.

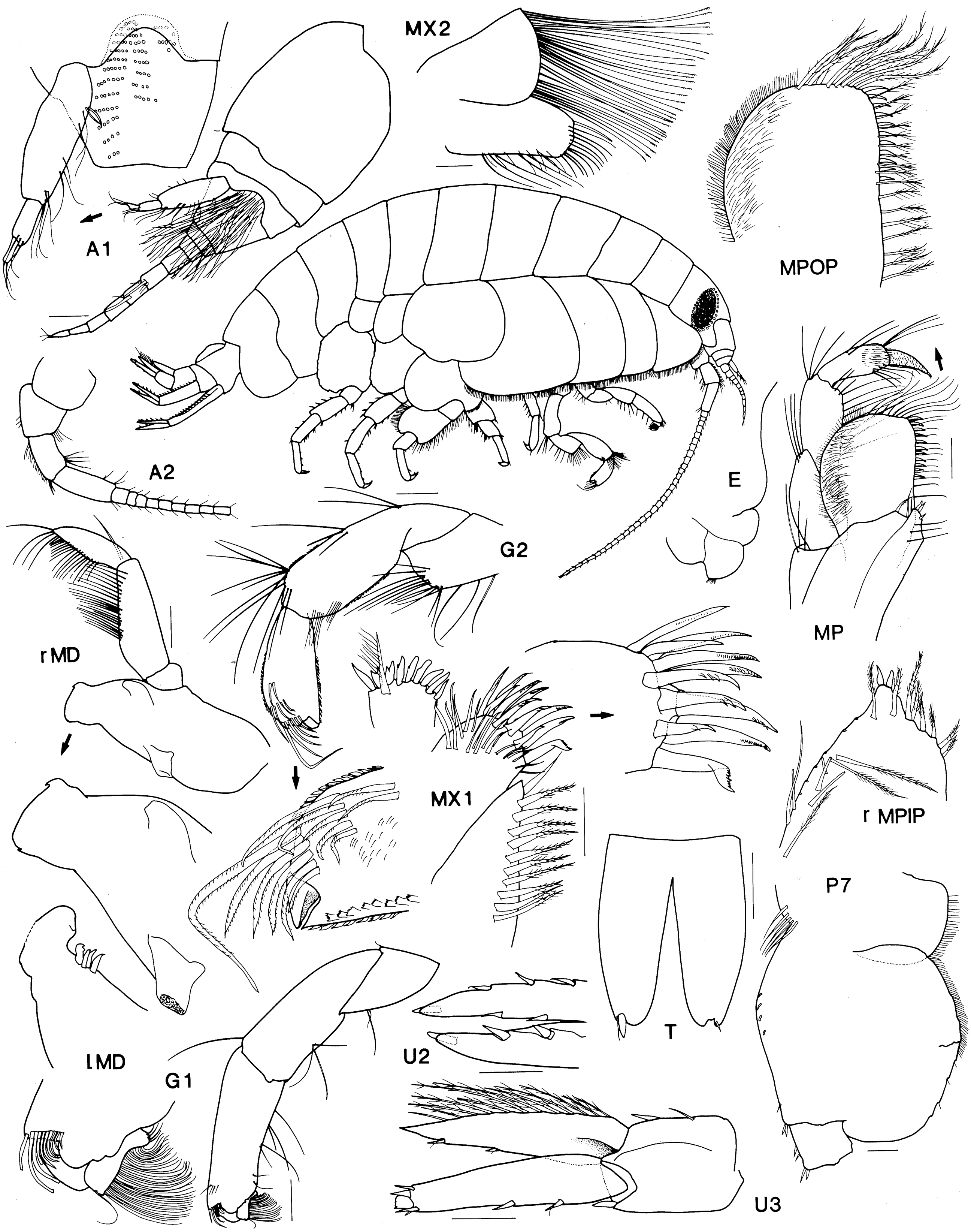

Fig.1. *Aroui setosus* Chevreux, lectotype, female, 8.0 mm, MNHN Am 3995, off Bône, Mediterranean Sea. Scales represent 0.1 mm.

Description. Based on female lectotype, 8.0 mm; dimorphic characters based on male paralectotype, 5.8 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broad, distally truncated; rostrum absent; eyes oval, not enlarged in reproductive male. *Antenna 1*: short, about 0.15 times as long as body, 0.33 times as long as antenna 2; peduncular article 1 short, 1.15 times as long as deep; without midmedial tooth; accessory flagellum 3-articulate, fused proximally to form cap partially covering callynophore; callynophore, well developed 2-field in female and male; flagellum short, 11-articulate; calceoli present in reproductive male. *Antenna 2*: peduncle with brush setae in reproductive male, peduncular articles 4 and 5 not swollen in female or male; flagellum as long as body in reproductive male; calceoli present in reproductive male.

Mouthpart bundle: subquadrate. *Epistome and upper lip*: separate, subequal. *Mandible*: incisors symmetrical, both with slightly convex margins; left lacinia mobilis present, a stemmed serrate blade; accessory spine row, left with 3 stout spines; right with 3 spines (obscured); molar with narrow column, weak triturating surface; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, broadened proximally, tapering distally, with 22 setae along 0.7 of distal medial margin; article 3 weakly falcate with 4 E-setae, 18 D-setae along most of posterior margin, and 1 B-seta. *Maxilla 1*: inner plate tapering distally, inner margin with 11 plumose setae along entire inner margin; outer plate narrow, with 11 spine-teeth in 2 rows, outer row with 7 spine-teeth, large, slender, distally multicuspidate, inner row with 4 spine-teeth, spine-tooth 1 large, slender, smooth, spine-teeth 2-3 large, slender, 3- and 2-cuspidate, spine-tooth 4 short, slender, with 1 cusp; palp large, 2-articulate, with 8 terminal spines, 1 flag spine and 1 subterminal seta. *Maxilla 2*: outer plate broad, half length of inner plate, with long slender distally barbed setae. *Maxilliped*: inner plate large, subrectangular, with 2-3 well-developed nodular spines, oblique setal row well developed, with 12 plumose setae and a submarginal row of 6 plumose setae; outer plate large, subovate, with 9 apical plumose setae, apical spines absent, 11 medial spines present, 17 marginal setae present; palp well developed, dactylus well developed, unguis present, terminal setae absent.

Gnathopod 1: simple; coxa 1 large, anterior margin concave, forming anteroventrally produced corner, posterior margin straight, ventral margin setose; carpus subrectangular, 3.0 times as long as deep, posterior margin straight, subequal in length to propodus; propodus large, subrectangular, 3.0 times as long as deep, margins subparallel; posterior margin smooth, subtly sinuate, without spines; dactylus extremely reduced and covered in sensory setae. *Gnathopod 2*: minutely chelate; coxa large, subequal in size to coxa 3, ventrally setose; carpus elongate, 3.5 times as long as deep, posterior margin straight; propodus subrectangular, short, 2.0 times as long as deep; palm obtuse, with straight margin; posterodistal corner with 1 medial spine.

Peraeopods 3-7: with short, stocky dactyli. *Peraeopod 3*: coxa large. *Peraeopod 4*: coxa with well-developed posteroventral lobe, anterior and posterior margins subparallel; male merus/carpus without setal brushes. *Peraeopod 5*: coxa bilobate, posterior lobe not produced ventrally; basis broadly expanded with posterior margin rounded; merus broadly expanded and posteriorly setose. *Peraeopod 6*: merus slightly expanded, posterior margin without setae; propodus, posterior margin without hooked spines. *Peraeopod 7*: basis, posterior margin slightly rounded with rounded posteroventral corner and rounded posteroventral margin; merus slender, not expanded posteriorly. *Oostegites:* from gnathopod 2 to peraeopod 5. *Gills*: from gnathopod 2 to peraeopod 7, smooth, gill on peraeopod 7 not reduced.

Epimeron 3: with broadly rounded posteroventral corner.

Uropod 1: rami subequal in length. *Uropod 2*: rami subequal in length, outer ramus without constriction. *Uropod 3*: peduncle short, 1.3 times as long as deep, without lateral flange; rami lanceolate; outer ramus 2-articulate; rami subequal in length; plumose setae present in female and male. *Telson*: longer than broad, deeply cleft (80%), without dorsal spines, distal margins rounded, with 1 simple seta and 1 spine apically on each lobe.

Remarks. *Aroui setosus* and *A. hamatopodus* are very similar. They differ mainly in the shape of coxa 1 which has a concave anterior margin in *A. setosus* and is convex in *A. hamatopodus*, and in the presence of hooked spines on the propodus of peraeopod 6 in *A. hamatopodus*.

Distribution. Apparently *Aroui setosus* is confined to the Mediterranean Sea.

Aroui hamatopodus n.sp.

Figs 2-4

Scopelocheirus sp. McNamara & Henderson, 1984: 410.

Type material. HOLOTYPE, male, 7.8 mm, AM P38460; PARATYPE female, 8.0 mm with oostegites, AM P38461; 9 PARATYPES AM P38462; from the stomach of a jackass fish, *Nemadactylus macropterus*, New South Wales waters, 73-183 m, A.C.S., July 1939.

Additional material examined. NEW SOUTH WALES: 1 specimen, AM P38463, east of Long Nose Point, 33°42'S 151°55'E, 620 m, 11 Dec. 1978, RV *Kapala* Stn K78-27-02. VICTORIA: 1 specimen, NMV J15062, South of Point Hicks, 38°17.7'S 149°11.3'E, coarse sand, gravel, mud, many sponges, 400 m, 24 July 1986, RV *Franklin* Slope Stn 40. WESTERN AUSTRALIA: 14 specimens, AM P38465, 129 specimens, WAM 38-84, north-east of Rowley Shoals, 16°56'S 120°06'E, feeding on a recently killed test of a large spatangoid, *Taimanawa mortenseni* Henderson & Fell, 431 m, 20 Aug. 1983, FV *Courageous*. QUEENSLAND: 10 specimens, AM P38464, North-east of Lady Elliot Island, 24°03.7'S 152°49.9'E, rubble bottom with many small disk corals, 150 m, 4 July 1984, HMAS *Kimbla* Stn 3.

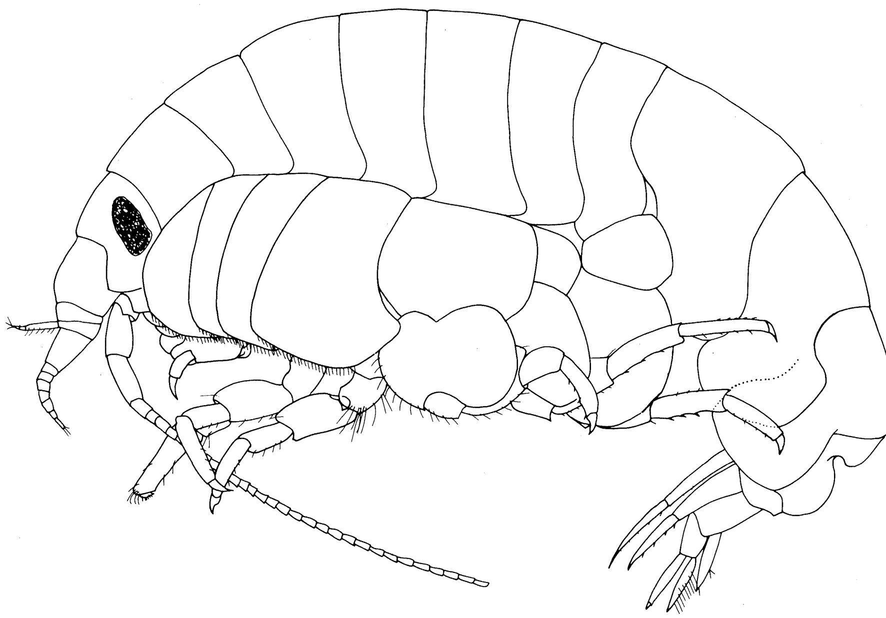

Fig.2. *Aroui hamatopodus* n.sp., holotype, male, 7.8 mm, AM P38460, New South Wales, Australia.

Diagnosis. Maxilla 1 palp with 6 terminal spines, 1 flag spine and 1 subterminal seta. Maxilliped, outer plate with 2 apical plumose setae. Gnathopod 1 coxa with anterior margin convex, posterior margin straight and ventral margin convex. Gnathopod 2 carpus 2.5 times as long as deep, propodus 1.6 times as long as deep. Peraeopod 6 merus with 6 hooked spines along the posterior margin.

Description. Based on holotype male (AM P38460), 7.8 mm and a paratype female (AM P38461), 8.0 mm. *Head*: slightly deeper than long, lateral cephalic lobe well developed, broad, distally rounded; rostrum absent; eyes oval, not enlarged in reproductive male. *Antenna 1*: short, about 0.17 times as long as body, 0.3 times as long as female antenna 2; peduncular article 1 short, 0.87 times as long as deep; without midmedial tooth; accessory flagellum 3-articulate, fused proximally to form cap partially covering callynophore; callynophore, well-developed 2-field in female and male; flagellum short, 9-articulate; calceoli present in reproductive male. *Antenna 2*: peduncle with brush setae in reproductive male, peduncular articles 4 and 5 not swollen in female or male; flagellum about half as long as body in reproductive male; calceoli present in reproductive male.

Mouthpart bundle: subquadrate. *Epistome and upper lip*: separate, subequal. *Mandible*: incisors symmetrical, both with slightly convex margins; left lacinia mobilis a stemmed serrate blade; accessory spine row, left and right each with 3 stout spines; molar with narrow column, weak triturating surface; mandibular palp attached midway; article 1 short, about as long as broad; article 2 elongate, broadened proximally, tapering distally, with 18 setae along 0.66 of distal medial margin; article 3 weakly falcate with 4 E-setae, 11 D-setae along most of posterior margin, and 1 B-seta. *Maxilla 1*: inner plate tapering distally, with 11 plumose setae along entire inner margin, outer plate narrow, with 11 spine-teeth in two rows, outer row with 7 spine-teeth (spine-tooth 1 slightly displaced onto inner row), large, slender, distally multicuspidate, inner row with 4 spine-teeth, spine-teeth 1-2 large, slender, multicuspidate, spine-tooth 3 large, slender, 2-cuspidate, spine-tooth 4, small, with 1 cusp; palp large, 2-articulate, with 6 terminal spines, 1 flag spine and 1 subterminal seta. *Maxilla 2*: outer plate broad, half length of inner plate, with long, slender, distally barbed setae. *Maxilliped*: inner plate large, subrectangular, with 3 well-developed nodular spines, oblique setal row well developed, with 12 plumose setae; outer plate large, subovate, 2 apical plumose setae present, 11 submarginal plumose setae present, 12 medial spines present, palp well developed, dactylus well developed, unguis present, terminal setae absent.

Gnathopod 1: simple; coxa 1 large, anterior margin convex, posterior margin straight, ventral margin convex, setose; carpus subrectangular, 2.5 times as long as deep, posterior margin straight; 0.86 times as long as propodus; propodus large, subrectangular, 3.0 times as long as deep, margins subparallel; posterior margin smooth, subtly sinuate, without spines; dactylus extremely reduced and covered in sensory setae. *Gnathopod 2*: minutely subchelate; coxa large, subequal in size to coxa 3, ventrally setose; carpus elongate, 2.5 times as long as deep, posterior margin straight; propodus subrectangular, short, 1.6 times as long as deep; palm obtuse, with rounded margin; posterodistal corner with 1 lateral and 1 medial spine.

Peraeopods 3-7 with short, stocky dactyli. *Peraeopod 3*: coxa large, ventrally setose. *Peraeopod 4*: coxa ventrally setose with well-developed posteroventral lobe, anterior and posterior margins subparallel; male merus/carpus without setal brushes. *Peraeopod 5*: coxa bilobate, posterior lobe not produced ventrally; basis broadly expanded with posterior margin rounded; merus broadly expanded and posteriorly setose. *Peraeopod 6*: merus slightly expanded without posteriorly setose margin;

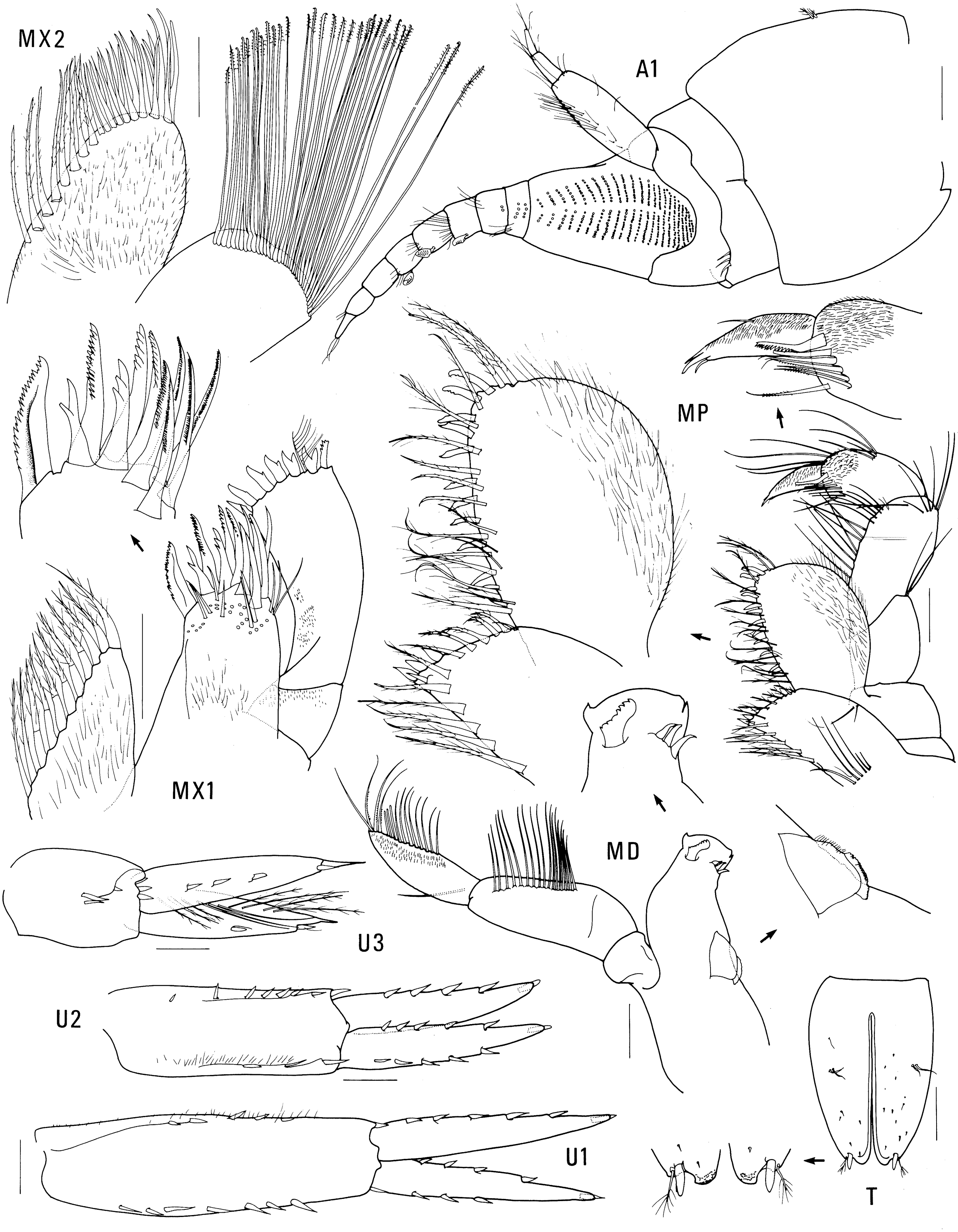

Fig.3. *Aroui hamatopodus* n.sp., holotype, male, 7.8 mm, AM P38460, New South Wales, Australia. Scales represent 0.1 mm.

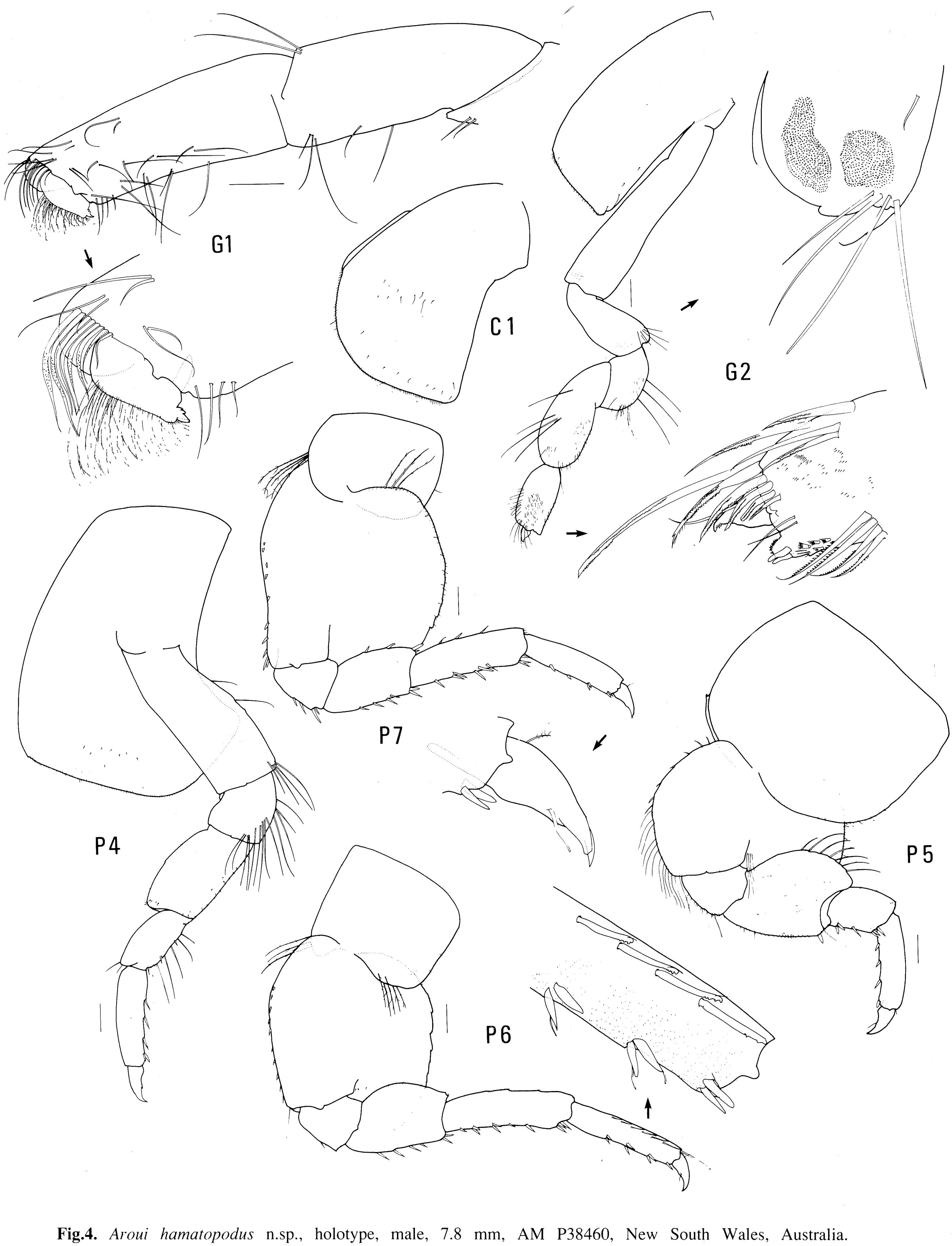

Fig.4. *Aroui hamatopodus* n.sp., holotype, male, 7.8 mm, AM P38460, New South Wales, Australia. Scales represent 0.1 mm.

propodus, posterior margin with 6 hooked spines. *Peraeopod 7*: basis, posterior margin slightly rounded with rounded posteroventral corner and rounded posteroventral margin; merus slender, not expanded posteriorly. *Oostegites*: from gnathopod 2 to peraeopod 5. *Gills*: from gnathopod 2 to peraeopod 7, smooth, gill on peraeopod 7 not reduced.

Epimeron 3: with a broadly rounded posteroventral corner.

Uropod 1: rami subequal in length. *Uropod 2*: rami subequal in length, outer ramus without constriction. *Uropod 3*: peduncle short, 1.3 times as long as deep, without lateral flange; rami lanceolate; outer ramus 2-articulate; rami subequal in length; plumose setae present in female and male. *Telson*: longer than broad, deeply cleft (80%), distal margins rounded, without dorsal spines, with 1 simple seta and 1 spine apically on each lobe.

Etymology. The specific name alludes to the peculiar hooks on the propodus of peraeopod 6.

Remarks. For the relationship of *Aroui hamatopodus* to *A. setosus* see the remarks for the latter species.

Distribution. *Aroui hamatopodus* is known from the outer continental shelf of north-western Australia, and the continental shelf and slope from north-eastern to south-eastern Australia.

The Association between Scopelocheirid Amphipods, Cassid Gastropods and their Common Prey, Spatangoid Echinoids

Scopelocheirids, spatangoid scavengers. Chevreux's (1911) original material of *A. setosus* was collected on a spatangoid echinoid *Spatangus* sp. Stroobants (1976) reported two large collections of *A. setosus*, each inside the test of *Spatangus purpureus* O.F. Muller. McNamara & Henderson (1984) reported *A. hamatopodus* (as *Scopelocheirus* sp.) feeding inside the test of the spatangoid *Taimanawa mortenseni* Henderson & Fell. Stroobants also recorded *A. setosus* from the sponge *Suberites* covering a gastropod shell which housed a hermit crab, *Paguristes oculatus* (Fabricius).

Species of *Scopelocheirus*[1] have also been reported in association with spatangoids. Costa (1852) reported *Scopelocheirus hopei* Costa, sometimes in extraordinary numbers in the tests of spatangoids in the Gulf of Naples. Wrzesniowski (1874) reported *S. branickii* Wrzesniowski in the clypeasteroid *Clypeaster* sp. (almost certainly misidentified and possibly a spatangoid: Rowe, personal communication), from Nice. Metzger (1875) reported *S. kroyeri* (Bruzelius) in great numbers within a dead specimen of the spatangoid *Echinocardium cordatum* (Pennant) among collections from the Firth of Forth, Scotland. Robertson (1888) reported *S. crenatus* Bate in a partly broken test of *Brissopsis lyrifera* (Forbes) from Liverpool Bay, England, a phenomenon he observed more than once. Chumley (1918) also reported *S. crenatus* from *Brissopsis lyrifera* in the Clyde Sea area. Chevreux & Fage (1925) recorded *S. hopei* from *Spatangus* sp. in the Mediterranean Sea. Stephensen (1935) cited a report of *S. hopei* inside the empty tests of *Echinocardium cordatum* from Plymouth, England. Stroobants (1976) recorded *S. hopei* and *A. setosus* inside the same test of *S. purpureus* from collections made off Cape Ferrato and Torre Corallo, Sardinia, Mediterranean Sea. Moore (1984) recorded *S. hopei* from tests of dead *Brissopsis lyrifera* in the Clyde Sea area.

Species of *Scopelocheirus* have also been recorded as scavengers on other food sources. Sars (1890) reported *S. crenatus* as plentiful in Trondheimsfjord from dead fish fastened to fishermen's lines. Monod (1923) found *S. hopei* swarming in thousands on the carcasses of fish taken off Cap d'Ail in the Mediterranean. Chevreux (1895) recorded *S. hopei* attacking specimens of the lysianassoid amphipod *Ichnopus affinis* Heller taken in traps off Monte-Cristo, and noted that they also voraciously attacked fish in the nets of fishermen becalmed at sea. Chevreux noted that *S. hopei* attacked *I. affinis* from the ventral part of the thorax and gained entry by a break made between the fifth and sixth segments. This may explain Stroobants' (1976:256) observation of seven instances where a juvenile of *S. hopei* was found in the "poche incubatrice" of *A. setosus*. It seems highly probable that the young *S. hopei* were actually attacking and eating individuals of *A. setosus*. Scott (1900) reported *S. crenata* burrowing into the flesh of the tope shark *Galeus canis* Bonaparte (= *Galeorhinus galeus* Linnaeus) taken off Aberdeen, Scotland. Similar occurrences have been reported by Williams (1938) and Moore (1984). Williams found *S. hopei* eating the gills, eye muscles and associated nerves of the dogfish *Acanthias vulgaris* (= *Squalus acanthias* Linnaeus) taken on long lines off the north-eastern coast of Ireland. Moore found large numbers of *S. hopei* attacking dead dogfish *Scyliorhynus cunicula* Linnaeus on baited lines in the Clyde Sea area, and also from traps baited with crab meat. Sekiguchi & Yamaguchi (1983) reported *S. hopei* collected from deep water off east central Japan in traps baited with fish.

Vader (1978) suggested that *Aroui setosus* was a scavenger on *Spatangus* and that species of *Scopelocheirus* were more generalised scavengers with a preference towards spatangoids. We consider that species of *Aroui* are likely to be exclusive scavengers of spatangoids and that species of *Scopelocheirus* behave as suggested by Vader.

McNamara & Henderson (1984) have explained a mechanism by which scopelocheirids may gain access to the inside of echinoids. In their specimen of *Taimanawa mortenseni* and in another specimen of *T. pulchella* Henderson & Fell there was "...a prominent circular hole in the anterior of the adoral surface of the test." They suggested that both specimens "...were probably attacked and killed by predatory gastropods..." and that the amphipods "...were probably scavenging a recently killed

[1]Because of the uncertainty concerning the taxonomic status of species in the genus *Scopelocheirus* we are using species names as given in the original reports.

individual." This observation indicates one way in which amphipods can enter a spatangoid test and may explain some earlier records where large numbers of scopelocheirids were found inside spatangoid tests.

Cassids, spatangoid predators. The mesogastropod family Cassidae feeds almost exclusively on echinoids (Hughes & Hughes, 1981). They drill a hole in the wall of the prey, insert the proboscis and eat everything but the gut. The hole is indistinguishable from the hole observed by McNamara & Henderson (1984) in their specimen of *Taimanawa mortenseni* the same specimen from which *Aroui hamatopodus* was taken. Cassids live predominantly on sandy substrates in tropical or warm temperate environments (Hughes, 1986). However species in the genus *Galeodea* tend to occur in deep cool water (O'Riordan, 1966, 1971; Ponder, 1983). Hughes (1986) has described in detail the feeding mechanisms of *Galeodea echinophora* (Linnaeus) on *Echinocardium cordatum*, both of which occur together in the Mediterranean Sea. *Scopelocheirus kroyeri* and *S. crenatus* have both been recorded from inside *Echinocardium cordatum* (Metzger, 1875; Stephensen, 1935). Ponder (1983) has recently described *Galeodea maccamleyi* from off the Queensland coast in depths of 220 to 365 m. Several large species of *Phalium*, another cassid genus known to feed on burrowing echinoids, are present in the collections of the Australian Museum and the Western Australian Museum from deep water (350 to 500 m) in Queensland and Western Australian. Thus there are several potential cassid predators of *Taimanawa mortenseni* in Australian waters.

However this may not be the only way in which species of *Aroui* and *Scopelocheirus* subsist. Hughes (1986) reported that when a *Galeodea* abandons an *Echinocardium* "...the test is stripped of all tissues except the gut, which was often burst and showed signs of lysis." In one species, *Aroui setosus*, the amphipod is identical in colour to the echinoid with which it is associated. It is possible that the scopelocheirids live in some other capacity among the spines of the echinoid host and scavenge it when the echinoid dies or is killed by a predator such as a cassid.

Fossil evidence. The majority of records report *Aroui* and *Scopelocheirus* associated with the spatangoid genera *Brissopsis*, *Echinocardium*, *Spatangus* and *Taimanawa*. These records are widespread geographically - the North Atlantic Ocean, the Mediterranean Sea and the eastern Indian Ocean - and imply a Tethyan distribution with post Tethyan speciation. All of the spatangoid genera associated with scopelocheirids are known from the fossil record (Mortensen, 1951; Henderson & Fell, 1969). *Spatangus* and *Taimanawa* are known from the Eocene, *Echinocardium* is known from the Oligocene and *Brissopsis* is known from the Miocene. Related spatangoid genera are known from the Mesozoic. Cassids first appear in the Cretaceous and there is evidence of cassids preying on echinoids in the Eocene (Sohl, 1969).

There is no lysianassoid fossil record, but based on the peracaridan fossil record amphipods may have arisen in the Carboniferous (Bousfield, 1978). Scopelocheirids have many plesiomorphic character states and may be among the earliest known lysianassoid scavengers. The potential for an association with spatangoids therefore extends back to the early Tertiary.

A possible origin of scavenging. It is possible that a commensal lysianassoid similar to an *Aroui* began to eat its host when the host died. Probably it gained access through the mouth or the anus and fed on the relatively soft tissue without highly modified mouthparts. Subsequent lysianassoids remained associated with the host, also feeding on it when it died. But these animals began to scavenge on other kinds of dead animals. Eventually some lysianassoids became free living and began to scavenge on a variety of dead animals. In these lysianassoids the mouthparts became highly modified for cutting the firm tissue of animals such as fish (Thurston, 1979).

There has been a proliferation of scavenging lysianassoids, particularly in cooler seas and in the deep sea. Genera such as *Alicella*, *Anonyx*, *Eurythenes*, *Ichnopus*, *Orchomene* and *Podoprion* belong in various, yet to be defined, lysianassoid family groups; but all have species reported as scavengers. Most of these animals are free living and all have some degree of modification in the mouthparts. The phylogenetic relationships between these groups and the scopelocheirids are unknown.

Conclusions. We suggest that scopelocheirids are specialised scavengers on spatangoid echinoids; that cassid gastropods provide one means by which scopelocheirids gain access to spatangoid tests; that there is a three-way association between the cassid predator, the spatangoid prey and the scopelocheirid scavenger; that the association may extend back at least to the Tertiary; and that the association between *Aroui* and the spatangoids may give us an indication of how scavenging evolved.

ACKNOWLEDGEMENTS. We thank Professor Forest and Dr Crosnier for the generous gift of *Aroui setosus* syntypes; Dr Frank Rowe for help with the echinoid literature and Dr Bill Rudman for help with the cassid literature; Mr Roger Springthorpe for composing and inking the plates; and Dr R.N. Hughes, Dr Winston Ponder, Dr Frank Rowe and Dr Bill Rudman for reading and making many useful comments on the manuscript. This work was supported in part by a grant from the Australian Research Council.

References

Bellan-Santini, D. 1985. Amphipodes profonds de Mediterranee (Campagnes Biomede I, Polymede I et II). Bollettino del Museo Civico di Storia Naturale, Verona 10: 263-313.

Belloc, G., 1960. Catalogue des types d'amphipodes du Musée Océanographique de Monaco. Bulletin de

l'Institut Oceanographique, Monaco 57: 1-28.
Barnard, J.L., 1961. Gammaridean Amphipoda from depths of to 6000 meters. Galathea Report 5: 23-128.
Bousfield, E.L., 1978. A revised classification and phylogeny of amphipod crustaceans. Transactions of the Royal Society of Canada, Series IV, 16: 343-390.
Chevreux, E., 1895. Les amphipodes des premières campagnes de la *Princesse-Alice*. Mémoires de la Société Zoologique de France 8: 424-435.
Chevreux, E., 1903. Campagnes scientifiques de S.A. le Prince Albert Ier de Monaco. Note préliminaire sur les amphipodes de la famille des Lysianassidae recueillis par la *Princesse-Alice* dans les eaux profondes de l'Atlantique et de la Méditerranée. Bulletin de la Société Zoologique de France 28: 81-97.
Chevreux, E., 1911. Campagnes de la *Mélita*. Les amphipodes d'Algérie et de Tunisie. Mémoires de la Société Zoologique de France 23: 145-285, pls 6-20.
Chevreux, E. & L. Fage, 1925. Amphipodes. Faune de France 9: 1-488.
Chumley, J., 1918. The Fauna of the Clyde Sea Area. Glasgow: University Press. 200 pp.
Costa, A., 1857. Ricerche sui crostacei Anfipodi del regno di Napoli. Memorie della Reale Accademia de Scienze di Napoli 1: 165-235 pls I-IV.
Dahl, E., 1959. Amphipoda from depths exceeding 6000 meters. Galathea Report 1: 211-241.
Gurjanova, E., 1962. Bokoplavy severnoi chasti Tixogo Okeana (Amphipoda-Gammaridea) chasti'1. Akademiya Nauk SSSR, Opredeliteli po Faune SSSR 74: 1-440.
Henderson, R.A. & H.B. Fell, 1969. *Taimanawa*, a new genus of brissid echinoids from the Tertiary and Recent Indo-West Pacific with a review of the related genera *Brissopatagus* and *Gillechinus*. Breviora 320: 1-29.
Hughes, R.N., 1986. Laboratory observations on the feeding behaviour, reproduction and morphology of *Galeodea echinophora* (Gastropoda: Cassidae). Zoological Journal of the Linnean Society 86: 355-365.
Hughes, R.N. & H.P.I. Hughes, 1981. Morphological and behavioural aspects of feeding in the Cassidae (Tonnacea, Mesogastropoda). Malacologia 20(2): 385-402.
Hurley, D.E., 1963. Amphipoda of the family Lysianassidae from the west coast of North and Central America. Occasional Papers of the Allen Hancock Foundation 25: 1-160.
McNamara, K.J. & R.A. Henderson, 1984. A redescription of the rare echinoid *Taimanawa mortenseni* Henderson and Fell (Spatangoida: Brissidae). Records of the Western Australian Museum 11(4): 403-410.
Metzger, A., 1875. Zoologische Ergebnisse der Nordseefarht. 10. Crustaceen aus den Ordnungen Edriophthalmata und Podophthalmata. Jahresbericht der Commission zur wissenschaftlichen Untersuchung der Deutschen Meere in Kiel 2/3: 277-310. [not seen]
Monod, T., 1923. Notes carcinologiques. (Parasites etcommensaux). Bulletin de l'Institut Océanographique, Monaco 427: 1-23.
Moore, P.G., 1984. The fauna of the Clyde Sea area. Crustacea: Amphipoda. University Marine Biological Station Millport, Occasional Publication 2: 1-84.
Mortensen, T., 1951. A Monograph of the Echinoidea. Vol. 5 Part 2. Spatangoida II. Copenhagen, 593 pp., 64 pls.
O'Riordan, C.E., 1966. Two interesting Mollusca from the Kerry Coast. Irish Naturalists' Journal 15: 296-298.
O'Riordan, C.E., 1971. Further interesting fauna from the Dingle area. Irish Naturalists' Journal 17: 12-14.
Ponder, W.F., 1983. A new species of *Galeodea* (Cassidae, Gastropoda) from Queensland, Australia, Australia. Journal of the Malacological Society of Australia 6: 91-97.
Robertson, D., 1888. A contribution towards a catalogue of the Amphipoda and Isopoda of the Firth of Clyde. Proceedings of the Natural History Society, Glasgow 2: 9-99.
Sars, G.O., 1890. An Account of the Crustacea of Norway, with short descriptions and figures of all the species. Vol. 1. Amphipoda. Part 1 Hyperiidae; Part 2 Orchestiidae and Lysianassidae (part); Part 3 Lysianassidae (continued). Christiania and Copenhagen (Cammermeyers): pp. 1-68 pls 1-24.
Schellenberg, A., 1926. Die Gammariden der Deutschen Südpolar-Expedition 1901-1903. Deutsche Südpolar-Expedition, 18, Zoology 10 : 235-414.
Scott, T., 1900. Notes on some crustacean parasites of fishes. Report of the Fishery Board for Scotland 18(3): 144-188, pls 5-8.
Sekiguchi, H. & Y. Yamaguchi, 1983. Scavenging amphipods from the deep-sea floor. Bulletin of the Faculty of Fisheries, Mie University 10: 1-14.
Sohl, N.F., 1969. The fossil record of shell boring by snails. American Zoologist 9: 725-734.
Stephensen, K., 1935. The Amphipoda of N. Norway and Spitzbergen with adjacent waters. Tromso Museums Skrifter 3(1): 1-140.
Stroobants, G., 1976. Description nouvelle d'*Aroui setosus* Chevreux 1910 (Crustacea Amphipoda) et comparaison de l'evolution morphologique des *Aroui setosus* et *Scopelocheirus hopei*. Bollettino del Museo Civico di Storia Naturale, Verona 3: 239-268.
Thurston, M.H., 1979. Scavenging abyssal amphipods from the north-east Atlantic Ocean. Marine Biology 51(1): 55-68.
Thurston, M.H. & E. Allen, 1969. Type material of the families Lysianassidae, Stegocephalidae, Ampeliscidae and Haustoriidae (Crustacea: Amphipoda) in the collections of the British Museum (Natural History). Bulletin of the British Museum (Natural History) (Zoology) 17(9): 347-388.
Vader, W., 1978. Associations between amphipods and echinoderms. Astarte 11: 123-134.
Williams, G., 1938. On the occurrence of *Scopelocheirus hopei* and *Cirolana borealis* in living *Acanthias vulgaris* (spiny dogfish). The Irish Naturalists' Journal 7: 89-91.
Wrzesniowski, A. 1874. On *Callisoma Branickii*, a new species from Nice. Annals and Magazine of Natural History, Series 4, 14: 15-16.

Accepted 29 March 1989