

The systematics and ecology of some sand beach isopods (Crustacea: Eurydicidae) from the coast of Kenya

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(Accepted 9 February 1971)

(With 13 figures in the text)

Quantitative collections from sand beaches and inshore waters at Watamu, Kenya, revealed eight species of eurydicid isopod, of which seven are new to science. Descriptions of these species are given together with details of their distribution, ecology and behaviour. Patterns of zonation shown by these isopods are compared with similar zonation patterns found elsewhere, and the use of these isopods as indicator species of zones on sand beaches is discussed.

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Introduction

Whilst the systematics of the marine isopods of South Africa are reasonably well known (Barnard, 1914, 1920, 1925, 1940; Nierstrasz, 1931; Stebbing, 1905, 1909), and those of North Africa perhaps less so (Monod, 1931, 1933; Stebbing, 1910), no work appears to have been carried out on the family Eurydicidae on the East African coast. The present collections were made during the University College of Bangor's marine biology expedition to Watamu (3° 0' S, 40° 0' E) in the summer of 1969.

Quantitative sampling of sand beaches, together with collections of tidal plankton and sublittoral plankton, made both with tow-nets and using a light at night, revealed a total of eight species of eurydicid isopod of which seven species are new to science. Physical conditions of the beaches sampled were measured and the bathy-metric distribution and ecological preference of each species was ascertained. Some preliminary experiments on their behaviour were conducted by measuring the swimming activity of a member of the genus *Excirolana*.

Methods

The coast of Kenya is characterized by a border of fringing reefs separated from the intertidal zone by shallow reef lagoons. The intertidal zone at Watamu consists of a line of sand beaches

interrupted at intervals by rock platforms which extend into the mangrove area of Mida Creek, a fully saline area in the south-west, and into Blue Lagoon in the north-east (Fig. 1). Five sites on these beaches were chosen for sampling (Fig. 1) as they reflect varying degrees of exposure and differ considerably both with regard to physical constitution and fauna and flora.

On each beach samples were taken at 7 equidistant stations along transects extending from 0 metres chart datum to M.H.W.S. (+3.5 m) (Admiralty tide table predictions for Kilindini 1969). A 25 cm² quadrant was taken to a depth of 15 cm in the sand for each sample and all the animals retained after washing through a 1 mm mesh sieve were preserved. Sublittoral collections of eurydicid isopods were made at night using a 45 W, 12 V spot lamp enclosed in a waterproof housing, when the isopods in their free-swimming phase (Jones & Naylor, 1970) were attracted to light. These collections were standardized by fishing for 20 minutes on each occasion.

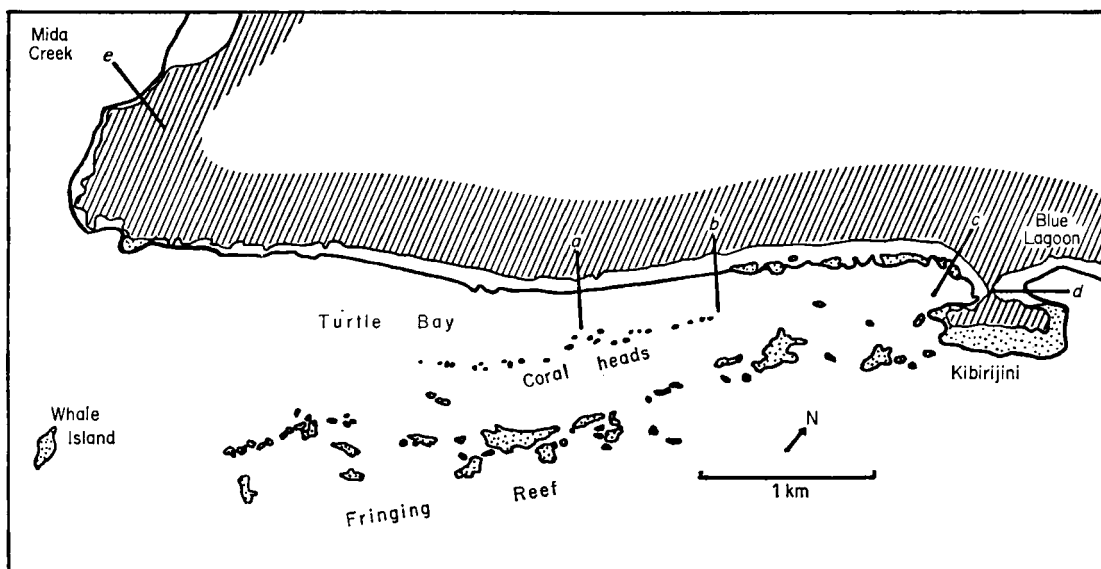


FIG. 1. Map of Watamu Marine Park, showing position of transect sites a-e.

To investigate the duration of the free-swimming phase of the intertidal species, quantitative plankton samples were taken from the water's edge at hourly intervals on both flood and ebb tides. The spontaneous swimming activity of *Exciorolana geniculata* sp. n. was recorded in the laboratory by counting the number of animals swimming above mid depth in a small aquarium at hourly intervals throughout the day and night. These experiments were conducted in a dark box with a temperature range of 22–26°C over a period of several days. The results have been analysed using the periodogram method (Williams & Naylor, 1967).

Systematics

FAM. EURYDICIDAE

Eurydicidae Stebbing, 1905: 10; Barnard, 1914: 350a; 1940: 387; Hale, 1925: 129. Cirolanidae Monod, 1930: 129.

Genus *Eurydice* Leach

Eurydice Leach, 1815: 370; Hansen, 1890: 362; 1905: 340; Richardson, 1905: 123; Stebbing, 1910: 95; Barnard, 1914: 350a, 1940: 387.

Eurydice agilis sp. n.

(Fig. 2)

Description of male holotype. Mouthparts not differing significantly from those of other members of the genus. *Antennule* short, reaching to centre of eye only; third peduncular article longest, just less than length of flagellum (Fig. 2(a)); fourth peduncular article as

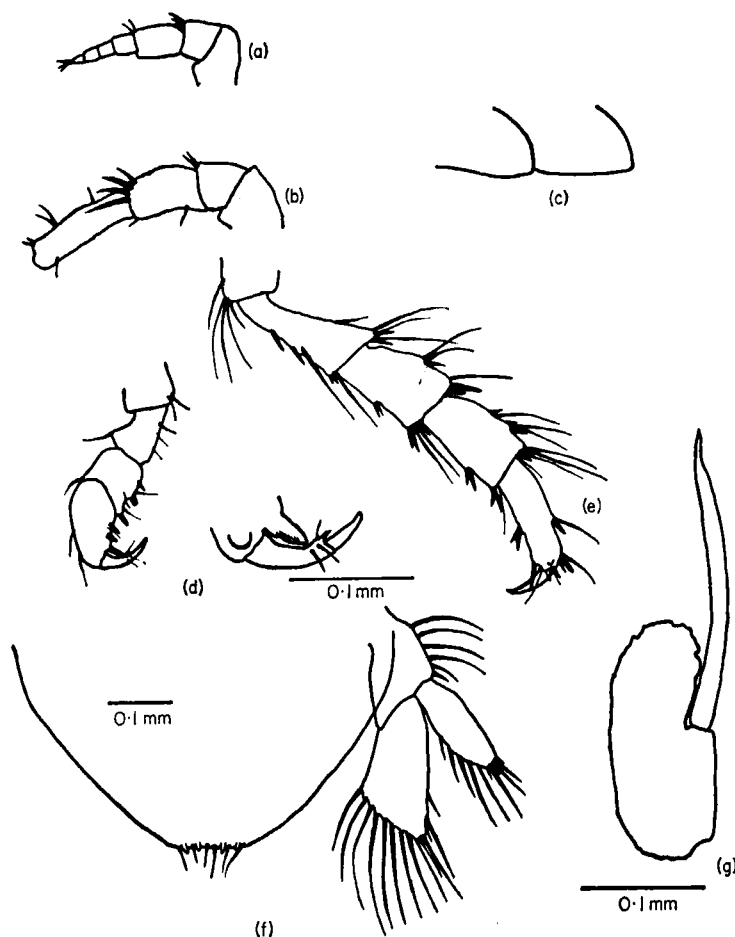


FIG. 2. *Eurydice agilis* sp. n.: (a) antennule; (b) peduncle of antenna; (c) epimera 6-7; (d) peraeopod 1, dactylus enlarged; (e) peraeopod 7; (f) telson and uropod; (g) appendix masculina.

broad as long, equal to half of peduncular article 3. *Antenna* with fourth peduncular article equal to combined length of articles 2 and 3 (Fig. 2(b)); third peduncular article greater than half the length of article 4, bearing 4 well developed setae on its outer margin. Antennal flagellum with 10 articles reaching to the middle of the fifth peraeon segment.

Thoracic epimera 6-7 non setose, with hind margins terminating in a blunt point (Fig. 2(c)).

Peraeopods 1–6, propodus with short terminal spine less than half the length of opposing dactyl, as is the more usual case in the genus (Fig. 2(d)).

Peraeopod 7 elongate, with articles 2 and 5 subequal and longer than articles 3 and 4 which are also subequal; hind margins sparsely setose, small groups of spines on anterior margins with three spines only on article 5; terminal dactyl curved (Fig. 2(e)).

Telson broad, width one third greater than length; hind margin narrow, almost straight, approximately one sixth of width of telson bearing two pairs of short marginal spines and 6 plumose setae (Fig. 2(f)).

Uropods short and slender not quite reaching hind margin of telson, posterior outer angles of exopod and endopod armed with a small group of strong spines. *Appendix masculina* (Fig. 2(g)) very elongate and slender, exceeding hind margin of pleopod 2 by two thirds of its length, tapering to a sharp point.

Colour in formalin, white with black and brown chromatophores on dorsal and ventral surfaces of the body, not on peraeopods.

Length: 2 mm.

Female. As the male except for absence of male sexual characters, all females non-ovigerous. Maximum size of female 3.5 mm.

Types. 1♂ Holotype B.M. (N.H.), registration number 1970: 230.

3♀ Paratypes B.M. (N.H.), registration number 1970: 231.

Type locality. Entrance to Mida Creek, Watamu, Kenya. 25.8.69.

Remarks. Superficially similar to *E. inornata* sp. n. (see p. 207) with which species *E. agilis* was first caught. However, the presence of two pairs of marginal spines on the telson of the latter species immediately distinguishes it from the former species. The extremely narrow hind margin of the telson separates *E. agilis* from all other known species in the genus.

Eurydice cavicaudata sp. n.

(Fig. 3)

Description of female holotype. Mouthparts not differing from those of other members of the genus; *Antennule* (Fig. 3(a)) slender, reaching the middle of the eye, third and fourth peduncular articles subequal; combined length of articles 1 and 2 equal to length of flagellum, but less than the combined length of peduncular articles 3 and 4; terminal flagellar article bears a tuft of short setae. *Antenna* (Fig. 3(b)) with fourth peduncular article equal to combined length of articles 2 and 3 and bearing 4 short setae on outer margin; third peduncular article equal to combined length of articles 1 and 2, bearing 5 stout spines on outer distal margin and a group of 3 long spines on inner distal margin. Antennal flagellum elongate with 17 articles reaching to the seventh paraeon segment.

Thoracic epimera (Fig. 3(c)) 1–4 and 7 with posterior free borders terminating in a point, epimera 5–6 with posterior free borders drawn out into pointed processes.

Peraeopods 1–6 (Fig. 3(d)) of typical appearance with terminal spine on propodus not greatly produced.

Peraeopod 7 (Fig. 3(e)) rather broad with articles 2 and 5 subequal, and article 3 shorter than 4 which is in turn shorter than article 5; dactyl straight; hind margins sparsely setose, anterior margins bearing few spines.

Telson (Fig. 3(f)) slightly broader than long with hind margin deeply indented, armed

with two pairs of marginal spines which are not produced beyond the posterior corners of the telson margin; a single pair of plumose setae present in a central position. *Uropods* broad, endopod triangular in shape not quite reaching hind margin of telson. Colour in formalin, heavily covered in black and brown chromatophores on both dorsal and ventral surfaces of the body and extending on to the pereopods.

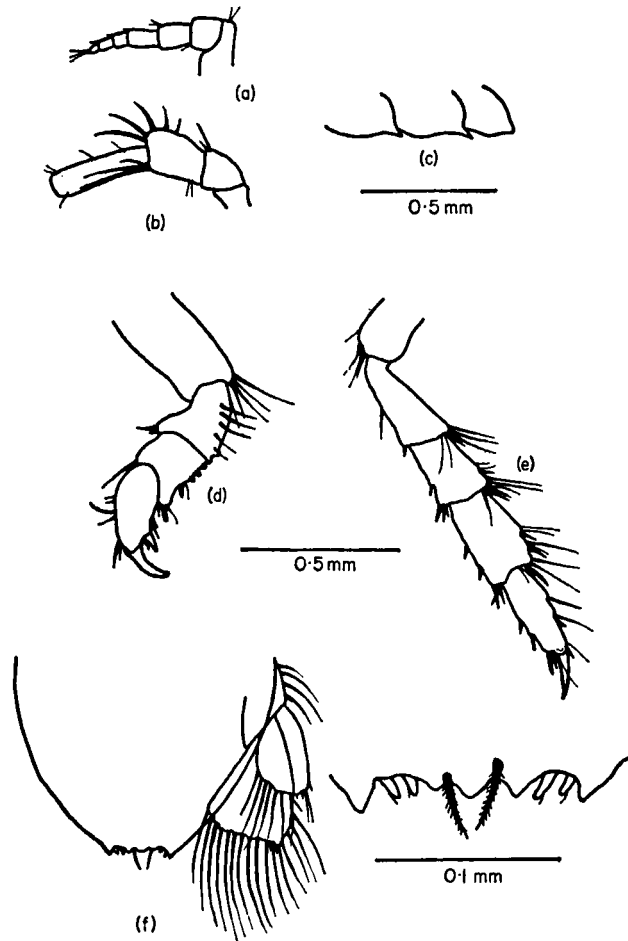


FIG. 3 *Eurydice cavicaudata* sp. n.: (a) antennule; (b) peduncle of antenna; (c) epimera 5-7; (d) pereopod 1; (e) pereopod 7; (f) telson and uropod with enlarged view of telson hind margin.

Length: 3.85 mm.

Male. Unknown.

Type. 1♀ Holotype B.M. (N.H.), registration number 1970: 232.

Type locality. Turtle Bay, Watamu, Kenya. 30.8.69.

Remarks. Although the above description is based upon a single adult female specimen the shape and armature of the telson hind margin serve to distinguish this species from all other species of *Eurydice*. Details of the epimera, antennule and antenna are also distinctive. The presence of chromatophores on the pereopods is of interest as this species

was captured below the low tide mark, supplying additional evidence that species with this character are sublittoral in distribution (Jones, 1969).

Eurydice chelifera sp. n.

(Fig. 4)

Description of male holotype. Mouthparts not differing significantly from other *Eurydice*; *Antennule* (Fig. 4(a)) extremely long and narrow, reaching to the middle of pereon segment 3; peduncular article 4 longest, much longer than combined length of peduncular

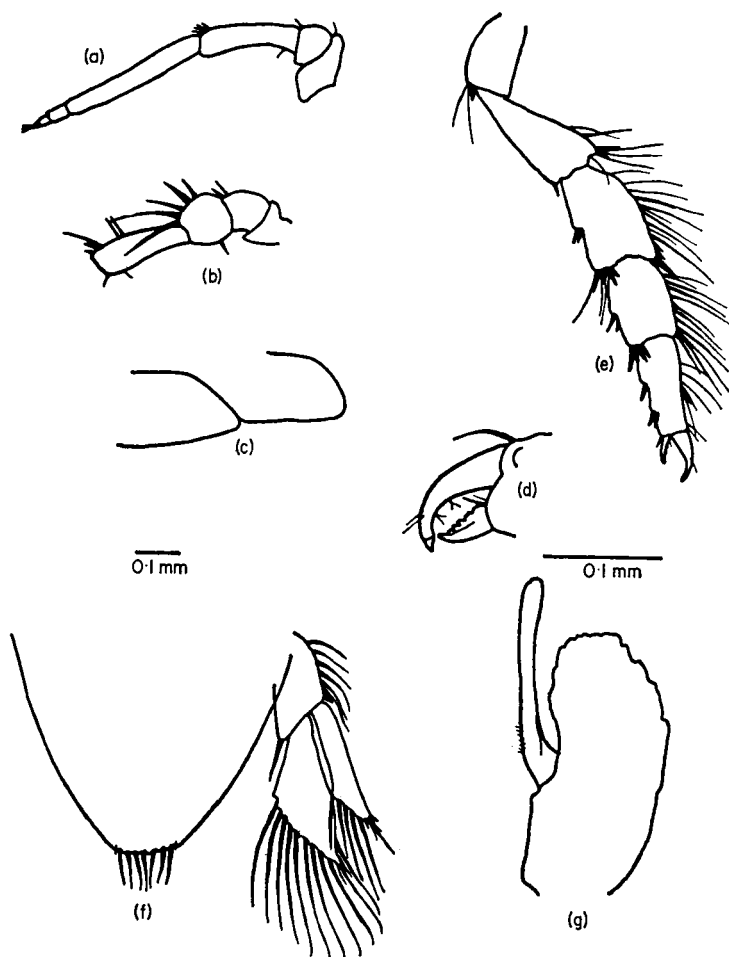


FIG. 4. *Eurydice chelifera* sp. n.: (a) antennule; (b) peduncle of antenna; (c) epimera 6-7; (d) dactyl peraeopod 1; (e) peraeopod 7; (f) telson and uropod; (g) appendix masculina.

segments 2 and 3 and nearly four times the length of the flagellum. Peduncular article 3 also elongate being longer than the combined length of peduncular articles 1 and 2, and bearing a small group of four spines distally on the anterior margin. First flagellar article

less than the combined length of flagellar articles 2 and 3, combined length of flagellar articles greater than that of peduncular article 2. *Antenna* (Fig. 4(b)) with peduncular article 4 shorter than the combined length of preceding articles, but greater than the combined length of articles 2 and 3; peduncular article 3 as broad as long bearing a row of 5 spines with the longest spine more than half the length of peduncular article 4. Antennal flagellum with 8 articles reaching to the middle of the fifth peraeon segment.

Thoracic epimera (Fig. 4(c)) 6 and 7 non setose, hind margins rounded and not produced into processes.

Peraeopods 1-7 chelate with terminal spine on the propodus approximately two thirds of the length of the opposing dactyl and bearing a serrated inner margin (Fig. 4(d)). *Peraeopod* 7 elongate and slender with articles 2 and 5 subequal, and article 4 shorter than article 5 (Fig. 4(e)); hind margins moderately setose, but spines on anterior margin sparse apart from 2 groups of 4 spines on the distal margins of articles 3 and 4; terminal dactyl curved and opposed to the terminal spine on the propodus.

Telson (Fig. 4(f)) elongate, as broad as long, with narrow convex hind margin measuring approximately one fourth of the telson breadth. No marginal spines present, hind margin armed with 7 plumose and 2 non-plumose setae, the latter inserted at either edge of the hind margin. *Uropods* narrow and elongate, reaching beyond the telson hind margin; angle between outer and hind margins of both endopod and exopod is acute.

Appendix masculina (Fig. 4(g)) elongate, extending beyond the hind margin of pleopod 2 for a quarter of its length, narrow with expanded, rounded, tip.

Colour: neither of the two specimens collected show any sign of pigmentation on the body or on the peraeopods, appearing quite transparent when alive.

Length: 2.55 mm.

Female. Unknown.

Types. 1♂ Holotype B.M. (N.H.), registration number 1970: 233.

1♂ Paratype B.M. (N.H.), registration number 1970: 234.

Type locality. Turtle Bay, Watamu, Kenya. 31.7.69.

Remarks. The presence of elongate antennules and chelate peraeopods separates *E. chelifera* from all other known species of the genus. Only *E. orientalis* Hansen possesses longer antennules than *E. chelifera*. However, in the former species it is the flagellar articles which are greatly produced (Hansen, 1890). The elongation of the terminal spine on the propodus of the peraeopods is a condition seen only in one other species, *E. longispina* Jones, but the spines are not serrated in *E. longispina* and are not found on the seventh peraeopod. Other distinguishing characters include the shape and armature of the telson and uropods, appendix masculina, antennal peduncle and absence of pigmentation.

Eurydice inornata sp. n.

(Fig. 5)

Description of male holotype. Mouthparts as in other members of the genus. *Antennule* (Fig. 5(a)) of medium length, not reaching hind margin of the eye, second and third peduncular articles subequal with fourth greater than third, but not equal to combined length of articles 2 and 3. First flagellar article equal to the combined length of articles 2 and 3, flagellum equal to length of fourth peduncular article. *Antenna* (Fig. 5(b)) peduncle of medium width, sparsely setose, with peduncular article 4 less than the combined length

of articles 1-3, but greater than twice the length of article 3; article 3 longer than broad and bearing a row of 5 spines on the outer margin. Flagellum with 10 articles reaching to the middle of the fifth pereaeon segment.

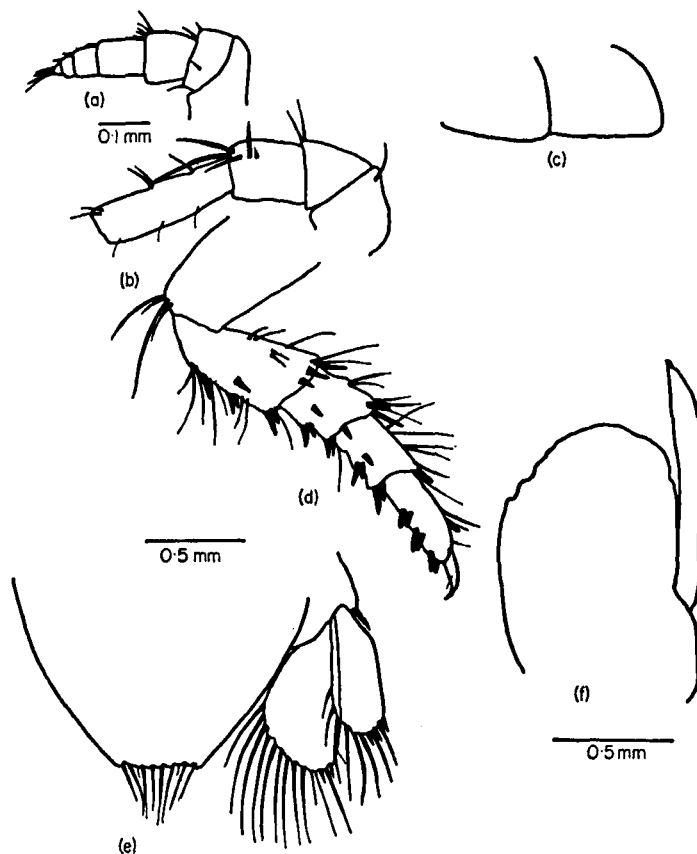


FIG. 5. *Eurydice inornata* sp. n.: (a) antennule; (b) peduncle of antenna; (c) epimera 6-7; (d) pereaeopod 7; (e) telson and uropod; (f) appendix masculina.

Thoracic epimera 6-7 (Fig. 5(c)) with hind margins terminating in a blunt point, non setose and not produced into processes.

Pereaeopod 7 (Fig. 5(d)) broad with fourth article longer than third, but shorter than fifth, all articles armed with 2-4 pairs of strong spines on the anterior margins, terminal dactyl curved.

Telson (Fig. 5(e)) broader than long; posterior margin slightly convex, narrow, about one fourth the width of the telson. No spines on hind margin of telson, but 8 plumose setae present together with one or two pairs of short non-plumose setae inserted between the second and third pairs of plumose setae.

Uropods of moderate width, projecting slightly beyond hind margin of telson, endopod with hind margin convex and bearing two short strong spines on the outer angle.

Appendix masculina (Fig. 5(f)) elongate, extending by less than a quarter of its length beyond the hind margin of pleopod 2, broad, tapering sharply to an acute point. Colour in

formalin, white with black chromatophores scattered on both ventral and dorsal body surfaces, not on peraeopods.

Length: 3 mm.

Female. As in the male with the following exceptions; male sexual characters absent; third and fourth peduncular articles of the antennule are sub-equal and longer than article 2; antennal peduncular article 4 is less than twice the length of article 3.

Maximum length female—5 mm, with marsupium containing 11 late stage embryos.

Types. 1♂ Holotype B.M. (N.H.), registration number 1970: 235.

7♀ Paratypes B.M. (N.H.), registration number 1970: 236.

Type locality. Turtle Bay, Watamu, Kenya. 16.7.69. also Kilife, Kenya, 1.9.69.

Remarks. The lack of articulated spines on the posterior margin of the telson immediately separates this species from most species in the genus, and of the remaining species which do not possess spines on the telson margin only *E. inermis* Hansen and *E. humilis* Stebbing have relatively narrow hind margins. However, *E. inornata* may be readily distinguished as the antennal flagellum of both the former species extends beyond the seventh peraeon segment. Other diagnostic features shown by *E. inornata* include the appendix masculina, relative proportions of the articles of the antennule and antenna, and finer details of the telson margin.

Eurydice longipes sp. n.

(Fig. 6)

Description of male holotype. Mouthparts as for other members of the genus; *antennule* (Fig. 6(a)) elongate, not quite reaching the first peraeon segment, fourth peduncular article longest, equal to combined length of peduncular articles 2 and 3 and more than twice the length of flagellar articles 2 and 3; flagellum equal to length of second peduncular article. *Antenna* (Fig. 6(b)) with peduncle narrow and hirsute, fourth peduncular article elongate, equal in length to articles 1–3 combined, and four times the length of article 2, bearing 2 rows of setae on upper margin. Peduncular article 3 with a row of well developed setae on outer margin; antennal flagellum with 16 articles reaching to the fifth peraeon segment.

Thoracic epimera (Fig. 6(c)) with hind margins pointed, epimera 4–6 with a marginal row of long setae. Peraeopods 4–6 broad and setose with greatly enlarged dactyls (Fig. 6(d)), the dactyl of paraeopod 6 being longer than the combined length of articles 3 and 4 (Fig. 6(e)). *Peraeopod* 7 (Fig. 6(f)) broad and strongly built with articles 4 and 5 subequal, terminal dactyl straight; posterior margin of the peraeopod strongly setose, anterior margin of each article armed with 3–6 strong spines.

Telson (Fig. 6(g)) with posterior margin convex, approximately one third of total breadth of telson, bearing two pairs of marginal spines.

Uropods broad, projecting just beyond hind margin of telson; endopod with hind margin straight, produced at right-angles to inner margin.

Appendix masculina (Fig. 6(h)) extending beyond hind margin of pleopod 2 by almost half its length, narrow, tapering to a blunt point. Colour in formalin, white with black chromatophores on both dorsal and ventral surfaces of the body, not on peraeopods.

Length: 5 mm (Maximum: 7 mm).

Types. 1♂ Holotype B.M. (N.H.), registration number 1970: 237.

9♀ Paratypes B.M. (N.H.), registration number 1970: 238.

Type locality. Blue Lagoon, Watamu, Kenya, 27.7.69.

Female. As for male, with exception of sexual characters; female with marsupium containing 30 late stage embryos.

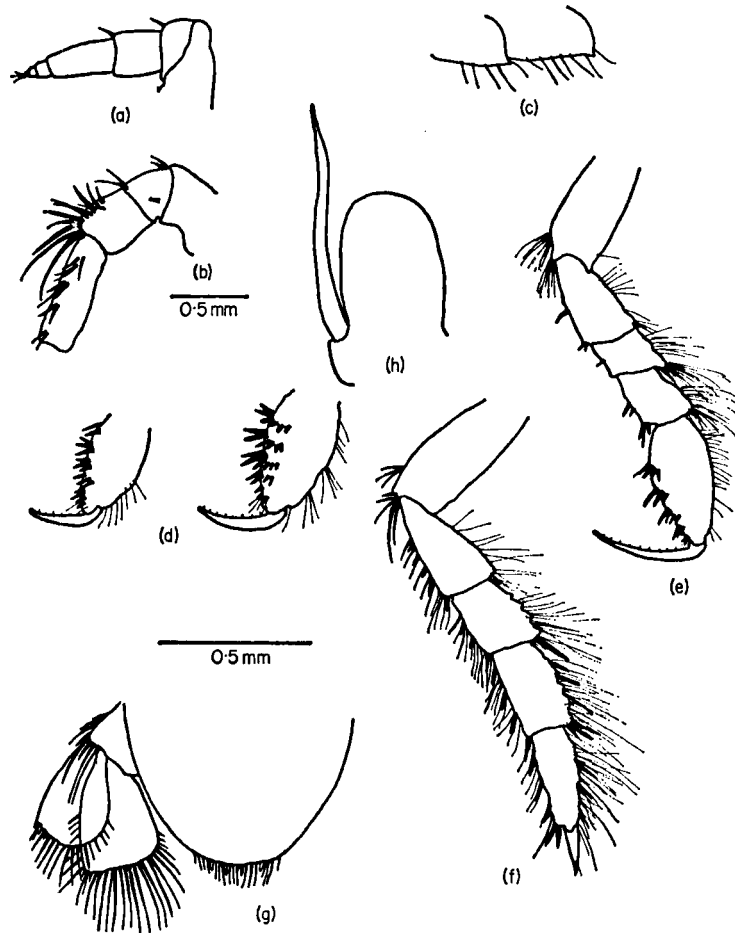


FIG. 6. *Eurydice longipes* sp. n.: (a) antennule; (b) peduncle of antenna; (c) epimera 6-7; (d) dactyls of peraeopods 4-5; (e) peraeopod 6; (f) peraeopod 7; (g) telson and uropod; (h) appendix masculina.

Remarks. *E. longipes* is easily distinguished from other members of the genus by the elongated dactyls on peraeopods 4-6. The only other species having any marked elongation of the dactyls in *E. humilis*. However, the maximum length of the dactyl in this species is equal only to the length of any one article of the peraeopod. Other diagnostic features shown by *E. longipes* are the shape and length of the appendix masculina, details of the uropods, and the relative lengths of the antennule and antenna articles.

Genus *Pontogeloides* Barnard

Pontogeloides Barnard, 1914: 355a; Monod, 1930: 174 (subgenus of *Excirolana*); 1931: 3 (subgenus of *Excirolana*); Nierstrasz, 1931: 149 (subgenus of *Excirolana*); Barnard, 1940: 389.

Pontogeloides affinis sp. n.

(Fig. 7)

Description of male holotype. Head with small median rostrum meeting the frontal lamina as described for *P. latipes* (Barnard, 1914). *Mandibles* with cutting edge tridentate, central tooth small; *mandibular* palp two jointed, second joint twice length of first, apex rounded with three long setae and bearing a row of four setae on outer margin; first and

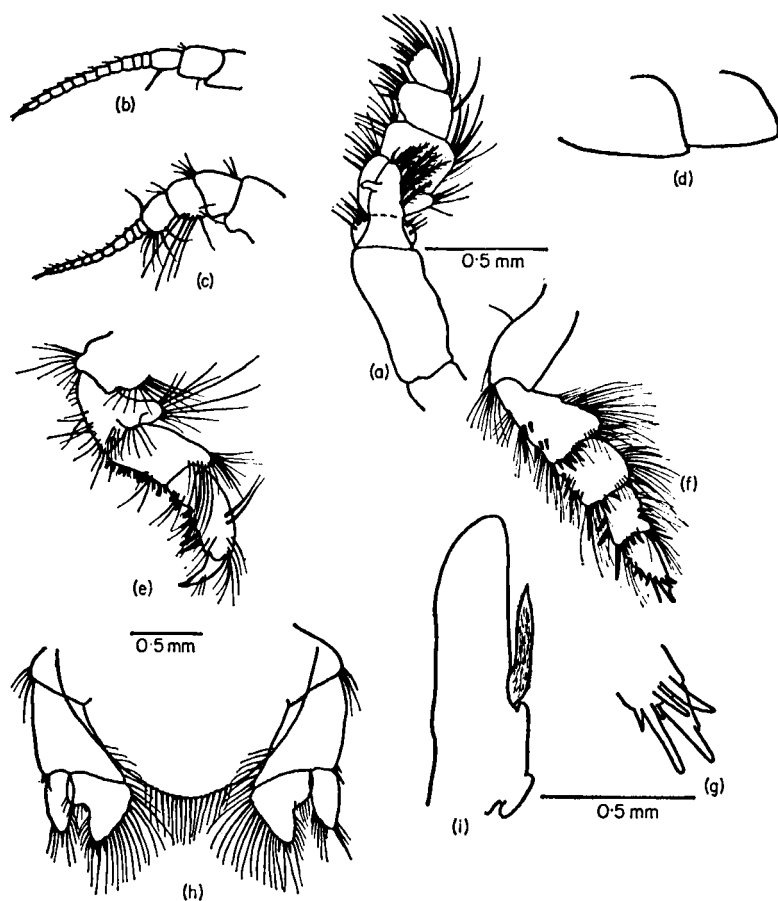


FIG. 7. *Pontogeloides affinis* sp. n.: (a) maxilliped; (b) antennule; (c) antenna; (d) epimera 6-7; (e) peraeopod 1; (f) peraeopod 7; (g) dactyl enlarged; (h) telson and uropod; (i) appendix masculina.

second *maxilla* as in type species. Maxilliped (Fig. 7(a)) with second article twice as long as broad, not setose, all other articles strongly setose; inner plate narrow, more than half the length of article 2, bearing 7 plumose setae on its outer margin and a small blunt protruberance on the inner margin. *Antennule* (Fig. 7(b)) reaching to the middle of second peraeon segment, third peduncular article shorter than second, bearing a single strong

spine on posterior margin; flagellum comprising 12 articles, less than twice the length of the peduncle. *Antenna* (Fig. 7(c)) broad, with 4 peduncular articles, second being slightly longer than the third, which is in turn longer than the fourth, articles 3 and 4 with hind margins strongly setose; flagellum short, not exceeding length of the peduncle and comprising 12 articles.

Thoracic epimera 6–7 (Fig. 7(d)) with postero-lateral angles rounded, that of peraeopod 6 somewhat produced into a blunt point. First *peraeopod* (Fig. 7(e)) with inner margins of third, fourth and fifth articles with *c.* 14, 3 and 5 closely set spines respectively. First article of *seventh peraeopod* (Fig. 7(f)) long and narrow with a single bunch of setae at outer apex, second article equal to combined length of articles 3 and 4, articles 3 and 5 subequal. Both anterior and posterior margins of articles 2–5 strongly setose, with apex of each article bearing groups of spines, article 2 *c.* 10, article 3, *c.* 6, article 4 *c.* 7; apex of article 5 bearing 3 long spines together with the dactyl which is straight (Fig. 7(g)).

Telson (Fig. 7(h)) bifoveolate, almost twice as broad as long with posterior margin denticulate and bearing *c.* 17 plumose setae.

Uropods, peduncle narrow and elongate reaching to the hind margin of the telson, outer apical angle with 2 spines, distal half of the inner margin fringed with plumose setae; rami short, not exceeding two-thirds of the length of the peduncle; endopod base occupying only two thirds of base of peduncle, apex subacute, inner margin and distal part of outer margin with long plumose setae, apex with 3 short spines, outer margin with very deep sub-terminal indentation extending to over half the length of the endopod. Exopod shorter than endopod approximately twice as long as broad, apex armed with plumose setae and a single spine.

Pleopods as for *P. latipes* with laminar expansions on outer margins of peduncle and lobes on inner rami of all pleopods.

Appendix masculina (Fig. 7(i)) arising one third along the inner margin of pleopod 2, medium length, almost equal to half the length of the pleopod, tapering to a fine point and covered with minute setae.

Colour in formalin white, almost transparent, with small brown chromatophores dotted over dorsal surface of the body only.

Length: 5.0 mm.

Female. As the male, both ovigerous and non-ovigerous females collected, maximum size 7.5 mm with 12 late stage embryos.

Types. 1♂ Holotype B.M. (N.H.), registration number 1970: 239.

5♀ Paratypes B.M. (N.H.), registration number 1970: 240.

Type locality. Blue Lagoon, Watamu, Kenya, 27.7.69.

Remarks. This species is very similar to *P. latipes* (Barnard, 1914), the type species, and only other species in the genus with possible exception of *Eurydice carangis* Van Name (see Monod, 1924, 1930, 1931; Barnard, 1940). However, *P. affinis* may be immediately distinguished from *P. latipes* on the shape and relative dimensions of the uropods (see Barnard, 1914, plate 30, Fig. c), details of the antennule and antenna and relative proportions and setation of the peraeopods. *P. affinis* is distinct from *E. carangis* (Van Name, 1920; 49, Figs. 1–5) as the latter species has elongate antennules.

Genus *Exciorolana* Richardson

Exciorolana Richardson, 1912: 201; Hale, 1925: 156; Nierstrasz, 1931: 148; Barnard, 1940: 387.

Exciorolana orientalis (Dana)

(Fig. 8(a))

Cirolana orientalis Dana, 1853: 773, pl. li, Fig. 7; Hansen, 1890: 353, pl. iv, Fig. 4; Stebbing, 1900: 633; Richardson, 1910: 4. *Exciorolana orientalis* Richardson, 1912: 201; Hale, 1925: 156, Fig. 14, a–j; Nierstrasz, 1931: 148.

Female. Agreeing closely with the detailed description by Hale (1925) with following exceptions; *Antennule*, third article of peduncle longer than articles 1 and 2 which are subequal, flagella unequal comprising 10–14 articles.

Length: 10–12 mm.

Male. As for female with exception of flagellum of antenna which comprises 19 articles. *Appendix masculina* (Fig. 8(a)) elongate, extending a short distance beyond apex of pleopod 2, broad, tapering to narrow blunt pointed tip.

Length: 7–0 mm.

Remarks. Despite the apparently small differences there can be no doubt of the identification of this species, the material agreeing closely in all other respects with the excellent description given by Hale (1925).

Distribution. Turtle Bay, Watamu, Kenya.

Previous records. Nicobar Islands, Malay Archipelago, New Guinea, Isle of Pines, North-eastern Australia.

Exciorolana geniculata sp. n.

(Figs 8 and 9)

Description of male holotype. Mouthparts not differing significantly from other members of the genus; anterior border of eyes with deep triangular indentation (Fig. 8(b)). *Antennule* (Fig. 8(c)) with first peduncular article longest and robust; second, third and fourth articles subequal, flagellum of 13 articles reaching hind margin of third peraeon segment. *Antenna* (Fig. 8(d)) with peduncular articles 1 and 3 subequal, article 4 longest bearing 2 groups of setae on apex; antennal flagellum of 15 articles reaching to the middle of fifth peraeon segment. First free *epimeral plate* (peraeon segment 2), length less than twice width (Fig. 8(b)), epimeron 6 (Fig. 8(e)) with postero-lateral angle drawn into a blunt point, lateral border with 6 fine setae; epimeron 7 narrow, triangular with posterolateral angle acute.

Peraeopod 1 (Fig. 9(a)) with articles 2 and 3 subequal, dactyl longer than either of these articles; anterior margin of article 3 with 6 spines, article 4 with 3 spines, article 5 with c. 9 spines; dactyl bearing a distal group of 4 short spines and 1 longer spine.

Peraeopod 7 (Fig. 9(b)) with article 2 less than the combined length of articles 3 and 4, article 3 shorter than article 5; joint between articles 3 and 4 "S" shaped, dactyl with base thickened, apex straight and pointed. Apical margin of article 2 armed with 4 stout spines, article 3 with 6 spines, article 4 with 8 spines and article 5 with 7 spines.

Telson (Fig. 9(c)) bifoveolate, length approximately three quarters of width, hind margin with c. 17 plumose setae and one pair of marginal spines. *Uropod*, peduncle twice as broad as long, inner apex slightly tapering bearing a terminal row of c. 8 plumose setae, outer apex with 3 blunt spines; endopod triangular with a small notch in the outer margin as in *E. natalensis* (Barnard, 1940) and 5 spines on postero-lateral angle. Exopod equal in

length to endopod, length five times breadth with a row of plumose setae on the inner margin and 3 spines on apex.

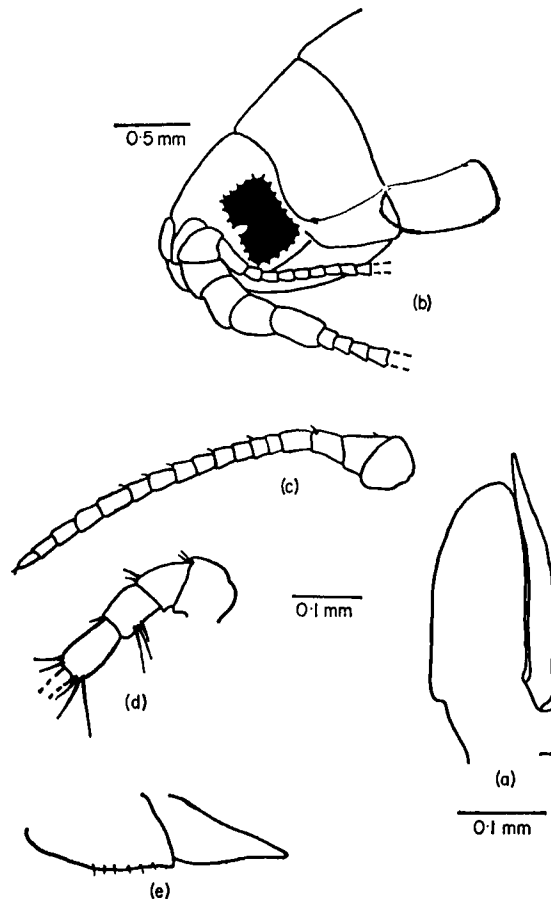


FIG. 8. *Excirolana orientalis* (Dana): (a) appendix masculina. *Excirolana geniculata* sp. n.: (b) head and anterior thorax; (c) antennule; (d) peduncle of antenna; (e) epimera 6-7.

Appendix masculina (Fig. 9(d)) mounted approximately one third along inner edge of pleopod 2, short, less than half the length of the pleopod, broad and straight, terminating in a blunt point and covered with rows of minute setae.

Colour in formalin white, with black chromatophores on dorsal and ventral body surfaces, none on peraeopods.

Length: 8 mm (maximum 9.0 mm).

Female. As the male excepting male sexual characters; all females collected non-ovigerous.

Types. 1♂ Holotype B.M. (N.H.), registration number 1970: 241.

1♂ and 2♀ Paratypes B.M. (N.H.), registration number 1970: 242.

Type locality. Turtle Bay, Watamu, Kenya, 11.8.69 also Kilife, Kenya, 30.8.69.

Remarks. This species resembles very closely the description of *E. natalensis* (Vanhöffen)

given by Barnard (1940). *E. geniculata* differs from this species and all other species in the genus in the length and shape of the exopod of the uropod, the relative dimensions of the articles of the first and seventh pereopods and the shape of the joint between the third and fourth article of the latter, and the shape and armature of the dactyls. Other diagnostic features are the relative dimensions of the telson, lengths of the peduncular segments of the antennule and antenna and number of flagellar articles. Probably the shape of the appendix masculina will also be diagnostic (not figured for *E. natalensis*).

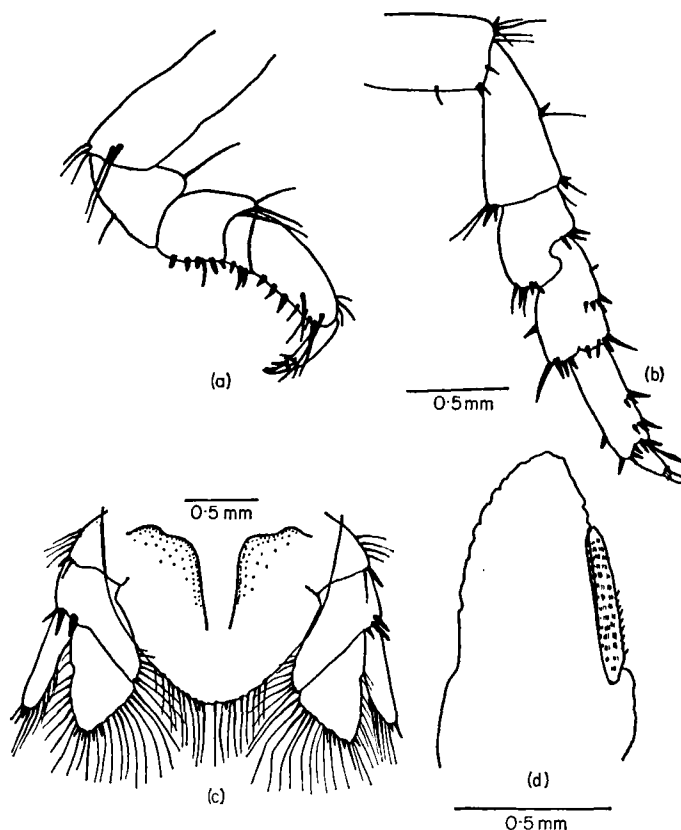


FIG. 9. *Excirrolana geniculata* sp. n.: (a) pereopod 1; (b) pereopod 7; (c) telson and uropod; (d) appendix masculina.

Ecology

Physical environment

Whilst there are seasonal variations in both sea temperature (Newell, 1957) and salinity (Newell, 1959) in East African coastal waters, these features, together with tidal range, remain relatively uniform at any one time on the beaches studied. The main difference between the beaches lies in their aspect and exposure to wind and wave action throughout the year. During the south east monsoon period (April–October), the main beach running

parallel to the inner reef in Turtle Bay (Fig. 1) receives the full force of wave action at high tide, as waves backed by the prevailing wind sweep in over the reef.

This beach (Fig. 10(a), (b)) had the shallowest angle measured from high water springs to mean tide level when compared with profiles taken on other beaches. This is in agreement with Shepard (1950) who has shown that a relationship exists between beach slope and wave action, high energy waves tending to be destructive and reducing steepness of beach slope. It is generally accepted that particle size is larger where wave energy is greater (Trask & Johnson, 1955; King, 1959). The beach in the region of profiles *a* and *b* was investigated, therefore by particle size analysis (Table I) which revealed a median diameter (md) of 0.396 mm at MTL for profile *a*. This is larger than that of any of the other profiles and confirms its exposed nature.

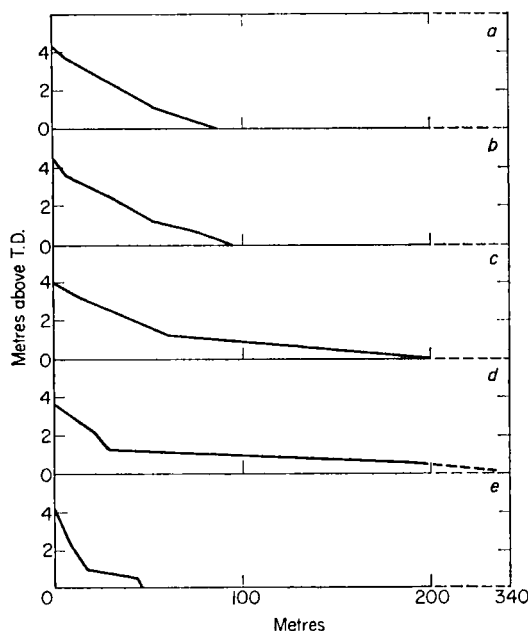


FIG. 10. Beach profiles for transects *a-e* at Watamu (see Fig. 1). T.D., tidal datum from Admiralty Charts for Kilindini.

During the period July–September this area of the beach showed great mobility with large changes in profile, especially in the region of HWN–HWS. On several occasions at spring tides during this period, sand was removed to a depth of up to 1 m on a single tide. It is probable that such changes are not merely produced by spring tides, but also occur through seasonal changes in the force and direction of prevailing winds.

Profile *c* taken in the corner of Turtle Bay shows the effect of the small amount of shelter provided by Kibirijini (Fig. 1). The beach slope above MTL is steepest on account of the constructive action of smaller waves (King, 1966), and below MTL has an extension of the beach area with a md of 0.185 mm placing it in the fine sand category on the Wentworth scale.

Reference to Fig. 1 shows that Blue Lagoon receives complete shelter from the south-east trades, reflected in the short steep slope of the beach above MTL (Fig. 10(d)), giving

way to extensive mud sand flats and marine angiosperm "meadows" (Macnae & Kalk, 1962) below this level. Particle size analysis shows a range from md 0.266 mm at high tide to 0.172 mm below MTL. A negative value for Skewness was obtained (-0.83) together with a high kurtosis value suggesting the presence of a coarse sand fraction washed in from a high energy region elsewhere (King, 1966). The water table lies just below the surface of these flats at MTL and, where pools of standing water occur, *Cymodocea ciliata* Ehrenb. ex Aschers is present. Other common angiosperms growing below LWN are *Cymodocea rotundata* Aschers & Schweinf. and *Thalassia hemprichii* (Ehrenb.) Aschers.

Profile *e* taken across a small sheltered beach among the mangroves (Fig. 1) has a very steep slope down to MLWN with a predominance of medium to fine sand (md 0.210 mm). The upper part of the beach, containing poorly sorted sand, levels out to form a stable muddy flat below this level similar to that found in Blue Lagoon, dropping off sharply, however, in the region of MLWS.

TABLE I

Analysis of sand samples taken at mid-tide and low tide levels from profiles a-e at Watamu

Profile	site	Median particle diameter (mm)	Kurtosis	Skewness
<i>a</i>	MTL	0.396	0.15	+0.03
<i>b</i>	LT	0.290	0.29	-0.02
<i>c</i>	MTL	0.291	0.42	+0.1
	LT	0.185	0.49	-0.22
<i>d</i>	MTL	0.266	0.13	-0.03
	LT	0.172	3.95	-0.83
<i>e</i>	MTL	0.210	3.1	-0.49
	LT	0.480	0.69	-0.02

This profile is not characteristic of typical mangrove areas where there is generally a gentle slope between the tide marks (Macnae, 1963), but perhaps owes its steep profile to its proximity to the main outlet channel to Mida Creek. The steep bank in the region of MLWS marks the edge of a current channel carrying the tidal flow of water into Mida Creek. Particle size analysis in this area gave a md of 0.480 mm (Table I), consistent with a region of strong current flow.

Enhalis acoroides (L.f.) Rich ex Steud. is present at this level on the edge of the channel, but is replaced by *Cymodocea serrulata* (R. Br.) Aschers as the predominant angiosperm at higher levels on the flats extending up to MLWN. The mangroves *Rhizophora mucronata* Lam. and *Brugieria cylindrica* Blum. together with *Avicenna marina* (Forsk.) Vierh. are common above MLWN, the pneumatophores of the latter ramifying through the sand. At higher levels *Brugieria cylindrica* and *Ceriops* sp. are dominant, merging with terrestrial vegetation at HWS level.

The fauna

Although representatives from several animal groups were common in sand samples, only the eurydicid isopods will be considered in the present work. Considerable differences in the distribution of the eight species collected are apparent, both between exposed and sheltered beaches (Table II) and also with regard to vertical zonation on the beach (Fig. 11).

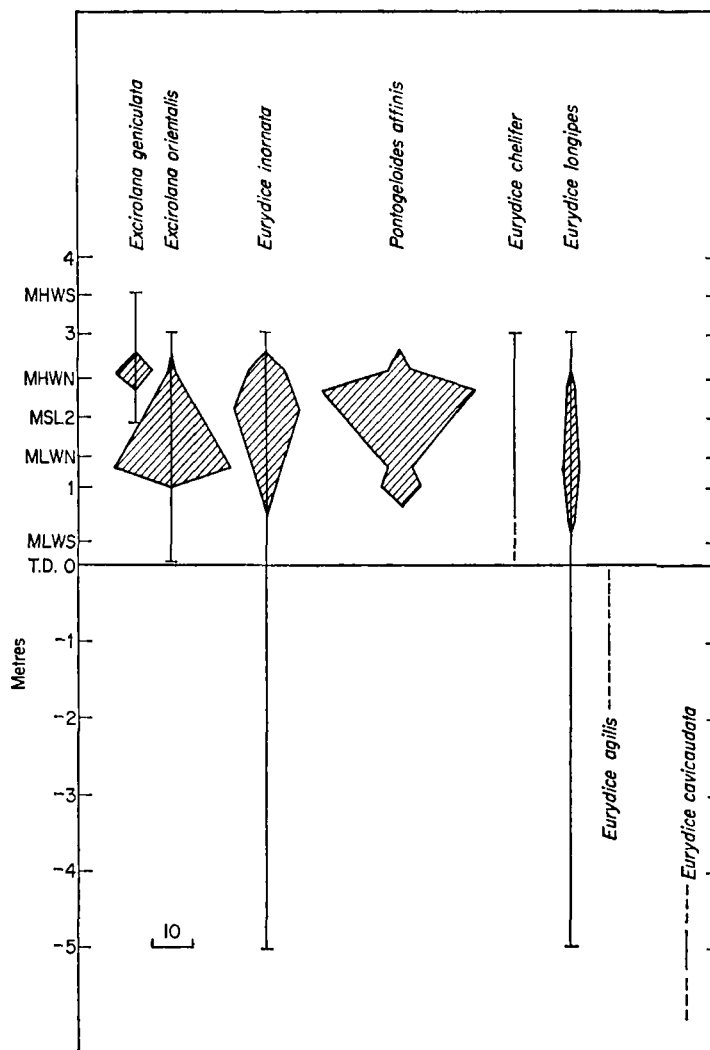


FIG. 11. Vertical zonation of eurydicid isopods at Watumu: vertical range on the beaches (shading); distribution in the plankton (depth over which species were captured) (vertical lines).

From Table II, which shows the total numbers taken on each beach transect, it appears that some species (*Exciorolana geniculata* and *Eurydice inornata*) may prefer the more exposed beaches (transects *a* and *b*, Turtle Bay), whilst others (*Pontogeloides affinis*) are found only on the sheltered beaches of Blue Lagoon and Mida Creek.

Although the numbers are small, it is suggested that *Eurydice longipes* exhibits no such preference as it is found in the sand on all beaches with the exception of Mida Creek. Further collections taken on a sheltered beach bordering a deep coastal inlet at Kilife (30 miles south of Watamu) appear to confirm the preference of *P. affinis* for this type of habitat. Macnae & Kalk (1962) also report the presence of *P. latipes* Brnrd, a closely related species, on sheltered shores of Inhaca Island. This species has also been recorded from areas of fine sand on beaches on the Gold coast (Gauld & Buchanan, 1956).

TABLE II

Total numbers of eurydicid isopods in beach transects taken at Watamu, presence in plankton indicated by*

Species	Transect				
	a	b	c	d	e
<i>Exciorolana geniculata</i>	10*	1*	—	—	—
<i>Eurydice inornata</i>	23*	10*	3*	—*	—*
<i>Eurydice longipes</i>	4*	3*	2*	1*	—*
<i>Eurydice chelifera</i>	—	—	1	—	—*
<i>Exciorolana orientalis</i>	—	—	31*	—*	1*
<i>Pontogeloides affinis</i>	—	—	9	40	14
<i>Eurydice cavicaudata</i>	—	—	—*	—	—
<i>Eurydice agilis</i>	—	—	—	—	—*

Whilst the numbers of individual species collected from quantitative sand samples are too low for statistical analysis in the form shown in Table II, a contingency table to examine the association between beaches and certain species may be constructed if exposed beaches (*a* and *b*) and sheltered beaches (*d* and *e*) are combined, and some combination of species is made (Table III). With these groupings, a χ^2 value of $P < 0.001$ is obtained, indicating that a strong association exists between the species groupings and exposed and sheltered beaches.

The intertidal plankton was sampled at each of the transect sites either using a light at night or by towing a plankton net, and the presence of each species of isopod at a particular site is marked on Table II with an asterisk. The light fishing method proved particularly efficient with catches of over 100 specimens of most species at the various sites indicated. This provides further emphasis for the distribution pattern established from sand samples, with a possible extension for the range of *Eurydice inornata* which occurred in plankton samples from the Blue Lagoon and Mida Creek.

Eurydice agilis was collected only from the plankton in the sheltered region of Mida Creek, perhaps indicating a preference for sheltered waters. Little can be said concerning the distribution of the remaining species, *E. chelifera* known only from two specimens collected intertidally from transect "c," and the single specimen of *E. cavicaudata* taken further offshore in the same area.

The quantitative samples taken at each station on the transects also reveal that the eurydicid isopods collected from Watamu exhibit considerable variation in their vertical distribution on the beach (Fig. 11). Again, using plankton tows and light fishing, it has

been possible to underline these differences for some species and extend the vertical range of others (Fig. 11).

Excirolana geniculata appears to have the narrowest vertical range, extending from HWN to MHW in the sand and from MTL to MHWS in the plankton over exposed beaches. A very similar range has been described for *Excirolana natalensis* (Vanhöffen) (Pichon, 1967). *Pontogeloides affinis* was found most abundantly at a slightly lower level between MHWN-MSL on sheltered beaches, with an overall vertical range extending from MHWN-MLW; this species was absent from the plankton. *Eurydice inornata*, occurring together with *Excirolana geniculata* on the more exposed beaches, has a maximum density at MTL with a vertical range from MHWN to MLW in the sand, thus overlapping to some extent the range of *Excirolana geniculata*, but not competing with *P. affinis*, which occurs in any numbers only on sheltered beaches. *Eurydice inornata* was still present in considerable numbers swimming in to the light over 5 m of water (MT) in the centre of Turtle Bay, suggesting that this species may extend into the sub-littoral.

TABLE III

Contingency table to test association between groups of profiles and species gives $P = <0.001$

	Transects			Totals
	<i>a + b</i>	<i>c</i>	<i>d + e</i>	
<i>Ex. geniculata</i>	44	3	0	47
<i>E. inornata</i>				
<i>E. longipes</i>				
<i>E. chelipes</i>	7	34	2	43
<i>Ex. orientalis</i>				
<i>Pontogeloides affinis</i>	0	9	54	63
Totals	51	46	56	153

Excirolana orientalis, occurring abundantly only on transect *c*, a beach intermediate in exposure, shows a maximum density just below MLWN. This species occurred in intertidal plankton tows, but was not caught below LT level. Pichon (1967) reports a similar vertical zonation for this species on the sheltered beaches of Madagascar.

Eurydice longipes, found at all sites sampled, shows a vertical range in the sand extending from MHWN to MLW, maximum numbers occurring at MLWN. However, this species, in common with *E. inornata*, was taken also from the surface over 5 m depth offshore. A single specimen of *Eurydice chelifera*, the only other species to be taken in intertidal sand, occurred below MLWN at transect *c*.

A number of specimens of *Eurydice agilis* were collected at night at HT over intertidal sand. However, an intensive search of the beach failed to reveal any individuals of this species. It is probable that this species is sublittoral in distribution, migrating inshore only during its planktonic phase.

Although only a single specimen of *Eurydice cavicaudata* was taken it may perhaps be significant that it was captured at the offshore station over 5 m in depth, and was not recorded from intertidal sand. Possibly its distribution may be centred further offshore.

Work on the British populations of *Eurydice* has indicated that breeding is limited by temperature to the summer period (Jones, 1970b), as has been suggested by Salvat (1966) working in south west France. Sampling in the Aegean also revealed a summer breeding pattern for species of this genus (Jones, 1969). The presence of ovigerous females of *Excirolana orientalis*, *Eurydice longipes*, *E. inornata* and *Pontogeloides affinis* amongst the beach samples collected is of interest, as a winter breeding season for these genera at tropical latitudes is indicated. No ovigerous females were caught by light at night, although large numbers of individuals belonging to species known to be breeding at the time were captured. This observation is in agreement with those of other authors (Bacesco, 1948; Fage, 1933; Soika, 1955) on the genus *Eurydice* and may be explained on the basis of changes in photic responses in connection with breeding, the females remaining photonegative for much of this period (Jones & Naylor, 1970).

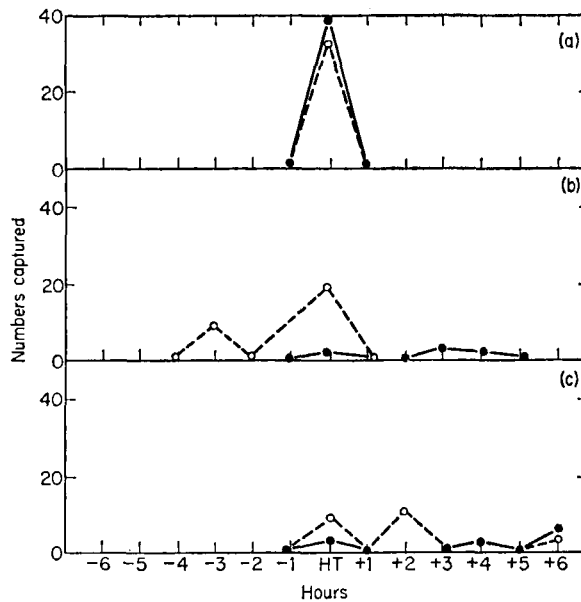


FIG. 12. Numbers of eurydicid isopods retained in standard 50 m surf plankton hauls at transect *b*; samples were taken at hourly intervals as the tide rose and fell throughout the day and night. ○, Night samples; ●, day samples; (a) *Excirolana geniculata*; (b) *Eurydice longipes*; (c) *Eurydice inornata*.

Since British members of the genus *Eurydice* have been shown to exhibit an active swimming phase coinciding with high tide, reinforced by an endogenous tidal rhythm (Jones & Naylor, 1970), experiments were conducted to investigate whether similar activity patterns were displayed by eurydicid isopods at Watamu. The results of 50 m quantitative plankton tows taken at hourly intervals at the edge of the surf, over a full tidal cycle both during the day and night, are given in Fig. 12.

Excirolana geniculata has a relatively short free swimming phase compared with the other species present on this beach (*Eurydice longipes* and *E. inornata* (Fig. 12(b), (c)), which is perhaps not surprising as the area of the beach inhabited by this species (Fig. 11) is only covered by the tide for short periods. *E. longipes* and *E. inornata* have a more

prolonged swimming phase, and both these species, unlike *Excirolana geniculata*, have been taken at the surface over the sublittoral region (Fig. 11). It is also interesting to note that whilst *Excirolana geniculata* was taken in approximately equal numbers both during day and night hauls, the other species, though obtained in small numbers, appeared to be more readily taken during night hauls. British species of *Eurydice* also show similar increases in abundance in the plankton at night (Jones & Naylor, 1970).

Laboratory investigations into the activity were confined to only one species, *Excirolana geniculata*. Observations on *Eurydice pulchra* Leach have shown these isopods, when supplied with sand, burrow and do not reappear (Jones & Naylor, 1970). Thus experiments on *E. geniculata* were designed using two tanks, one containing 5 cm sand together with sea-water, the other seawater alone, ten animals being placed in each tank.

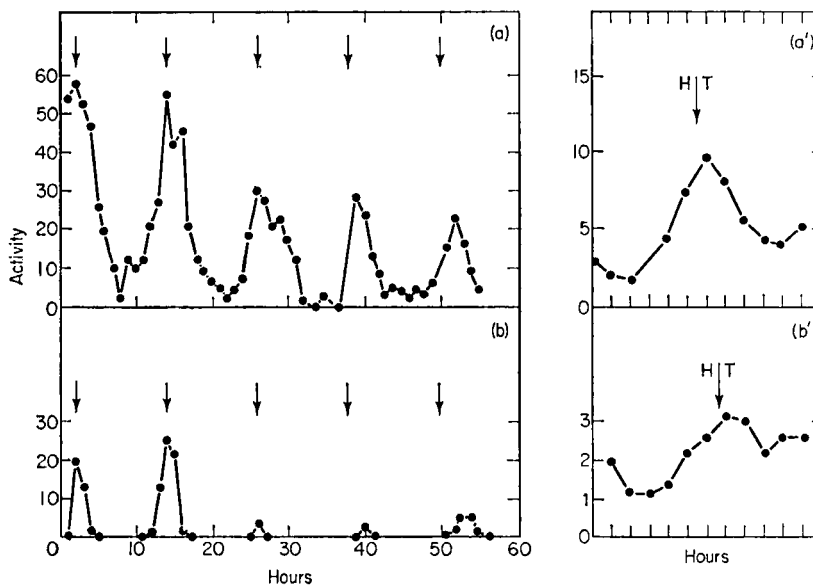


FIG. 13. Hourly activity of freshly collected *Excirolana geniculata* during three days in constant laboratory conditions. (a) Isopods in an aquarium without sand, showing numbers swimming above mid-tank depth during a 30 second observation period every hour. (b) Ten isopods in an aquarium with 5 cm sand subject to a similar observation regime; arrows indicate expected times of HT. (a'), (b') Periodogram analyses of data in (a) and (b).

The results of these experiments (Fig. 13(a), (b)) clearly indicate that *Excirolana geniculata* exhibits an endogenous tidal rhythm of swimming activity which is much more pronounced in the tank without sand (Fig. 13(b)). Maximum activity centred around the time of high water and continued only for a period of three to four hours, especially in the tank containing sand (Fig. 13(a)).

Discussion

From the available literature it appears that the genus *Eurydice* is represented by eight species in the Indian Ocean, three species *E. carangis* (Van Name), *E. latistylis* (Vanhöffen)

and *E. natalensis* (Vanhöffen) having been referred to other genera (Barnard, 1940). All species are found in tropical waters within 20° of the equator, with the exception of *E. longicornis* (Studer) which has been reported only from South Africa (Barnard, 1940; Brown, 1964). Most species have a distribution centred on the western Indian Ocean with the exception of *E. orientalis* Hansen recorded from Celebes, New Guinea, and the Java Sea (Nierstrasz, 1931). *E. chelifera*, *E. inornata*, *E. longicornis* and *E. longipes* are the only species to have been collected intertidally, although *E. agilis* and *E. cavicaudata* have been found close inshore. *E. humilis* Stebbing, known from a single specimen collected at anchor "off Salomon Atoll" (Stebbing, 1909), may have a distribution centred further offshore as does *E. truncata* (Stebbing, 1909; Nierstrasz, 1931; Jones & Naylor, 1967).

With the addition of the new species *Exciorolana geniculata*, there are now three species of this genus in the Indian Ocean, *Exciorolana natalensis* (Vanhöffen) recorded from the coast of South Africa (Vanhöffen, 1914; Barnard, 1940) and from Madagascar (Pichon, 1967), and *E. geniculata* from intertidal sand on the Kenyan coast. *Exciorolana orientalis* has a wide distribution ranging from New Caledonia and north east Australia in the Pacific Ocean, to the Sulu Sea and Nicobar Islands in the east Indian Ocean (Nierstrasz, 1931), and Madagascar in the west Indian Ocean (Pichon, 1967).

The genus *Pontogeloides* contains two species *P. affinis* sp. n. and *P. latipes* Brnrd if one accepts the ruling of Monod (1931) (see also p. 212). The range of the latter species extends from Ghana (as *Exciorolana latipes*) (Gauld & Buchanan, 1956) and St. Antonio and Banana, Congo (Van Name, 1920) on the Atlantic coast of Africa to South Africa (Barnard, 1940), and Inhaca Island, Mozambique (Macnae & Kalk, 1962).

It appears that the intertidal species diversity of eurydicid isopods in the tropical Indian Ocean is greater than in subtropical Mediterranean and Aegean waters, where four species of *Eurydice* occur intertidally (Jones, 1969). On British shores only two species are found (Jones & Naylor, 1967). The intertidal members of the genus *Eurydice* extend as far north as the 64° latitude (Norway) (Vader, 1968), whilst the genera *Pontogeloides* and *Exciorolana* have, as yet, not been found further north on the African coast line than the limit of the Indian Ocean and have not been recorded from the Mediterranean.

In the tropics a range from exposed sand beaches with steep profiles often characterized by a beach step, to sheltered beaches with extensive sand or mud flats, has been recognized by several authors (Macnae & Kalk, 1962; Morton & Challis, 1969; Pichon, 1967). The beaches under consideration in the present survey appear to fit this classification with the profiles *a* and *b* (Turtle Bay) representing the most exposed condition whilst profiles *d* and *e* (Blue Lagoon and Mida) come under the category of sheltered shores. An association between different species of *Eurydice* and beaches of different degrees of exposure has already been described from the Aegean (Jones, 1969), and from British coasts (Jones, 1970a) where the mechanisms involved in selection of habitat have been investigated. Similar associations appear to occur on tropical beaches not only at the species level, but also on a generic level with *Pontogeloides* appearing only on sheltered shores and *Exciorolana* on exposed and semi-exposed shores. The genus *Pontogeloides* appears to be morphologically suited to a fossorial existence, the broad hirsute peraeopods and short antennae together with the absence of a free swimming phase, being reminiscent of haustoriid amphipods. It seems likely that members of this genus feed on or in the sand, unlike most other cirrolanid isopods (Jones, 1968), and thus show a preference for sheltered shores, where the sand is more stable. The larger robust members of the genus *Exciorolana* are by contrast

extremely active and have been reported from exposed beaches in other parts of the world (Enright, 1965; Pichon, 1967; Richardson, 1905; Wade, 1967).

The presence of an endogenous tidal rhythm of swimming activity similar to that found in *E. geniculata* has also been reported for *E. chiltoni* Richardson (Enright, 1965) and *Eurydice pulchra* (Jones & Naylor, 1970). In these two latter species wave action synchronises the rhythm, and Jones & Naylor (1970) have suggested that the rhythm may assist in maintaining the zonation pattern of *E. pulchra*, ensuring that the isopod reburrows at the end of its active period, thereby avoiding being carried out to sea on the ebb tide. A similar function may be served by the rhythm in *Exciorolana geniculata* which also shows a distinct zonation pattern. *Eurydice pulchra* relies on wave action to wash it from the sand at the commencement of its active phase, and thus has a distribution centred on exposed shores (Jones, 1970a). Whilst some activity is shown by *E. geniculata* when placed together with sand, activity is greatly increased in the absence of sand (Fig. 13), suggesting that this species may also rely to some extent on wave action in the field, and thus reach its highest densities on shores exposed to wave action. In view of the role played by the endogenous swimming rhythm in controlling zonation, it would be of great interest to investigate for the presence of endogenous activity in *Eurydice inornata* and *E. longipes*, species which are found not only intertidally, but also some distance offshore in the plankton.

The problem of the establishment of a universal system of classification for zonation on sandy beaches has been considered by several authors in recent years. Most favour a division of the beach into three zones, supra-littoral, middle zone and lower zone (Dahl, 1952; Pichon, 1967; Trevallion *et al.*, 1970); although some authors indicate that further subdivision of zones is necessary (Macnae & Kalk, 1962; Morton & Challis, 1969). Most authors have delimited a zone, usually the middle zone, which is characterized by isopods of the family Eurydicidae (Brown, 1964; Dahl, 1942; Gauld & Buchanan, 1956; Koepke & Koepke, 1953; Trevallion *et al.*, 1970). However, recently these isopods have also been found to be characteristic of the upper supralittoral zone (Pichon, 1967; Wade, 1967).

At Watamu on sheltered shores the middle zone includes the slope of the upper beach, but excludes the water-logged sand-mud flats (Fig. 10), and is thus characterized by *Pontogeloides affinis* (Fig. 11). However, on semi-exposed shores the sand-mud flats are reduced (profile *c*) and they are absent on exposed beaches (profile *a* and *b*), where the lower levels of the beach are composed of clean sand and support populations of eurydicid isopods. Thus *Exciorolana orientalis* and *Eurydice longipes* reach their maximum densities in the sand below MLWN, whilst other species, such as *E. chelifera*, *E. agilis*, and *E. cavi-caudata*, have a vertical range extending into the sublittoral (Fig. 11). Ecological studies on East African shores therefore confirm the conclusions reached from similar studies in the Aegean (Jones, 1969), where it was found that the eurydicid isopods were poor indicators of specific zones of sandy beaches. Several species are often present, each with its own distinct pattern of zonation.

Summary

Eight species, belonging to three genera, of eurydicid isopods were collected during quantitative sampling of sand beaches and inshore plankton at Watamu, Kenya. New species are described and their geographical distribution discussed in relation to other eurydicid isopods in the Indo-pacific region.

Physical measurements of a series of sand beaches in the Watamu area show a range from sheltered to exposed, and sampling reveals that there are both generic and specific differences in the distribution of these isopods in relation to exposure. The genus *Pontogeloides* occurs on sheltered shores, whilst the genus *Exciorolana* is characteristic of exposed beaches.

Further studies indicate that these species have distinct patterns of zonation on beaches, collections from the tidal plankton underlining these differences in zonation.

Investigations into the free swimming phase of the isopods by means of hourly tidal plankton hauls reveals different patterns of activity for individual species, and laboratory experiments conducted with one species, *Exciorolana geniculata*, indicate the presence of an endogenous tidal rhythm for this species.

In view of the apparent differences in zonation and timing of activity periods shown by these isopods, their use by some authors as indicators of specific zones on sand beaches is questioned.

I wish to thank Professor D. J. Crisp for his helpful criticism of the manuscript. This work was carried out during the Bangor/Watamu Expedition and I am grateful to the Royal Society, the Percy Sladen Memorial Trust, the Ministry of Overseas Development, the East African Wildlife Society, and the many other organizations who provided financial support for this expedition. My thanks are also due to the many individuals both in this country and in Kenya who gave their advice and assistance so willingly.

REFERENCES

- Bacesco, M. (1948). Les représentants du genre *Eurydice* (Crustacees Isopodes) dans la Mer Noire. *Notat. biol., Buc.* 6: 108–122.
- Barnard, K. H. (1914). Contributions to the crustacean fauna of South Africa. 3. Additions to the marine Isopoda. *Ann. S. Afr. Mus.* 10: 325a–358a, 359–442.
- Barnard, K. H. (1920). Contributions to the crustacean fauna of South Africa. 6. Further additions to the list of marine isopoda. *Ann. S. Afr. Mus.* 17: 319–438.
- Barnard, K. H. (1925). Contributions to the crustacean fauna of South Africa. 9. Further additions to the list of marine isopoda. *Ann. S. Afr. Mus.* 20: 381–412.
- Barnard, K. H. (1940). Contributions to the crustacean fauna of South Africa. 12. Further additions to the Tanaidacea, Isopoda and Amphipoda, together with keys for the identification of hitherto recorded marine and freshwater species. *Ann. S. Afr. Mus.* 32: 381–515.
- Brown, A. C. (1964). Food relationships on the intertidal sandy beaches of the Cape Peninsular. *S. Afr. J. Sci.* 60: 35–41.
- Dahl, E. (1952). Some aspects of the ecology and zonation of the fauna of sandy beaches. *Oikos* 4: 1–27.
- Dana, J. D. (1853). Crustacea Part 1. *U.S. Explor. Exped. 1838–1842* 13: 696–805.
- Enright, J. T. (1965). Entrainment of a tidal rhythm. *Science, N. Y.* 147: 864–867.
- Fage, L. (1933). Pêches Planctoniques à la lumière effectuées à Banyuls-sur-Mer et à Concarneau. 3. Crustacea. *Archs Zool. exp. gén.* 76: 228–232.
- Gauld, D. T. & Buchanan, J. B. (1956). The fauna of sandy beaches in the Gold Coast. *Oikos* 7: 293–301.
- Hale, H. M. (1925). Review of Australian Isopods of the Cymothoid group. Pt. 1 *Trans. R. Soc. S. Aust.* 49: 128–185.
- Hansen, H. J. (1890). Cirolanidae et Familiae nonnullae propinquae Musei Hauniensis. *K. danske Vidensk. Selsk. Skr.* 5(3): 239–426.
- Hansen, H. J. (1905). Revision of the European marine forms of the Cirolaninae, a sub-family of Crustacea Isopoda. *J. Linn. Soc. (Zool.)*. 29: 337–373.
- Jones, D. A. (1968). The functional morphology of the digestive system in the carnivorous intertidal isopod *Eurydice*. *J. Zool., Lond.* 156: 363–376.
- Jones, D. A. (1969). The genus *Eurydice* (Crustacea: Isopoda) in the Aegean Sea, including *E. longispina* sp. nov. *Cah. Biol. mar.* 10: 15–29.

- Jones, D. A. (1970a). Factors affecting the distribution of the intertidal isopods *Eurydice pulchra* Leach and *E. affinis* Hansen in Britain. *J. Anim. Ecol.* **39**: 455-472.
- Jones, D. A. (1970b). Population densities and breeding in *Eurydice pulchra* and *Eurydice affinis* in Britain. *J. mar. biol. Ass. U.K.* **50**: 635-655.
- Jones, D. A. & Naylor, E. (1967). The distribution of *Eurydice* (Crustacea Isopoda) in British waters, including *E. affinis* new to Britain. *J. mar. biol. Ass. U.K.* **47**: 373-381.
- Jones, D. A. & Naylor, E. (1970). The swimming rhythm of the sand beach isopod *Eurydice pulchra*. *J. exp. mar. Biol. Ecol.* **4**: 188-199.
- King, C. A. M. (1959). *Beaches and coasts*. London: E. Arnold Ltd.
- King, C. A. M. (1966). *Techniques in geomorphology*. London: E. Arnold Ltd.
- Koepck, H. W. & Koepck, M. (1953). Contribucion al conocimiento de la forma de vida de *Ocypode gaudichaudii* M. E. & Lucas. *Publ. Mus. Hist. nat., Lima (A.) Zool.* **13**: 1-46.
- Leach, W. E. (1815). A tabular view of the external characters of four classes of animals which Linné arranged under Insecta. *Trans. Linn. Soc. Lond.* **11**: 306-400.
- Macnae, W. (1963). Mangrove swamps in South Africa. *J. Ecol.* **51**: 1-25.
- Macnae, W. & Kalk, M. (1962). The fauna and flora of sand flats at Inhaca Island, Mozambique. *J. Anim. Ecol.* **31**: 93-128.
- Monod, T. (1924). Isopoda in Parasitologia Mauritanica. *Bull. Com. Étud. hist. scient. Afr. occid. fr.* **9**: 428-445.
- Monod, T. (1930). Contribution à l'étude des "Cirolanidae". *Annls Sci. nat. (Zool.)* (10) **13**: 129-183.
- Monod, T. (1931). Sur quelques Crustacés aquatiques d'Afrique (Cameroon et Congo). *Rev. Zool. Bot. Afr.* **21**: 1-35.
- Monod, T. (1933). Tanaidacea et Isopoda. (Mission Robert Dollfus en Égypte.) *Mém. Inst. égypt.* **21**: 161-264.
- Morton, J. E. & Challis, D. A. (1969). The biomorphology of Solomon Islands shores with a discussion of zoning patterns and ecological terminology. *Phil. Trans. R. Soc.* **255**: 459-516.
- Newell, B. S. (1957). A preliminary survey of the hydrography of the British East African coastal waters. *Fishery Publs colon. Off.* **9**: 1-21.
- Newell, B. S. (1959). The hydrography of the British East African coastal waters. *Fishery Publs colon. Off.* **12**: 1-18.
- Nierstrasz, G. F. (1931). Die isopoden der Siboga-Expedition 111. Isopoda Genuina II Flabellifera. *Siboga Exped.* **32è**: 123-233.
- Pichon, M. (1967). Contribution à l'étude des peuplements de la zone intertidale sur sables fin et sables vaseux non fixes dans la region de Tulear. *Recl Trav. Stn mar. Endoume (Fasc. hors sér.) Suppl.* **7**: 57-100.
- Richardson, H. (1905). A monograph on the isopods of North America. *Bull. U.S. natn. Mus.* **54**: 1-727.
- Richardson, H. (1910). Marine Isopods collected in the Philippines by the U.S. Fisheries Steamer "Albatross" in 1907-8. *Docums Dep. Comm. Lab. Bur. Fish., Wash.* No. 736: 1-44.
- Richardson, H. (1912). Descriptions of a new genus of Isopod Crustaceans, and of two new species from South America. *Proc. U.S. natn. Mus.* **43**: 201-204.
- Salvat, B. (1966). *Eurydice pulchra* (Leach 1815). *Eurydice affinis* (Hansen 1905) Isopodes Cirolanidae, taxonomie, éthologie, écologie, répartition verticale et cycle reproducteur. *Act. Soc. linn. Bordeaux (A.)* **103**: 1-77.
- Shepard, F. P. (1950). Longshore bars and longshore troughs. *Tech. Memo. Beach Eros. Bd U.S.* **20**.
- Soika G. A. (1955). Ethologie écologie, systematique et biogéographie des *Eurydice* s. str. *Vie Milieu* **6**: 38-52.
- Stebbing, T. R. R. (1900). On Crustacea brought by Dr. Willey from the South Seas. In *Zoological results*, pt. 5: 605-690. Willey, A. (Ed.) Cambridge: Univ. Press.
- Stebbing, T. R. R. (1905). Report on the Isopoda collected by Professor Herdman at Ceylon in 1902. *Rep. Ceylon Pearl Oyster Fish.* (Suppl. Rep.) **23**: 1-64.
- Stebbing, T. R. R. (1909). Reports on the marine biology of the Sudanese Red Sea. XIV. On the Crustacea Isopoda and Tanaidacea. *J. Linn. Soc. Lond. (Zool.)* **31**: 215-230.
- Stebbing, T. R. R. (1910). Isopoda from the Indian Ocean and British East Africa. The Percy Sladen Trust. Exp. Indian Ocean 1905, III (6) *Trans. Linn. Soc. Lond. (Zool.)* **14**: 83-122.
- Trask, P. D. & Johnson, C. A. (1955). Sand variations at Point Reyes, California. *Tech. Memo. Beach Eros. Bd U.S.* **65**.
- Trevallion, A., Ansell, A. D. Sivasdas, P. & Narayanan, B. (1970). A preliminary account of two sandy beaches in South West India. *Mar. Biol.* **6**: 268-279.
- Vader, W. (1968). *Eurydice inermis* (Isopoda, Cirolanidae) in Norway. *Sarsia* **33**: 7-12.
- Vanhöffen, E. (1914). Die Isopoden der Deutschen Südpolar-Expedition 1901-1903. *Deutsch Südpol. Exp.* **15** (Zool. vii): 449-598.

- Van Name, W. G. (1920). Isopods collected by the American Museum Congo Expedition. *Bull. Am. Mus. nat. Hist.* **43**(5): 41-108.
- Wade, B. A. (1967). Studies on the biology of the West Indian beach clam *Donax denticulatus* Linné. I. Ecology. *Bull. mar. Sci.* **17**: 149-173.
- Williams, B. G. & Naylor, E. (1967). Spontaneously induced rhythm of tidal periodicity in laboratory-reared *Carcinus*. *J. exp. Biol.* **47**: 229-234.