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TRUSTEES OF
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CYCLOPOID COPEPODS OF THE GENUS *KELLERIA* (LICHOMOLGIDAE) FROM INTER-TIDAL BURROWS IN MADAGASCAR

By A. G. HUMES & JU-SHEY HO

AMONG the copepods collected by the first author in 1960 and 1963–64 from intertidal burrows in the region of Nosy Bé, in north-western Madagascar, there are (in addition to the seven species of *Hemicyclops* described by Humes, 1965) two species of the genus *Kelleria*, *K. regalis* Gurney, 1927, and *K. pectinata* (A. Scott, 1909). Since the descriptions of both of these species are incomplete, with only the female of *K. pectinata* previously known, the two species are redescribed, including a description of the male of *K. pectinata*.

The copepods were obtained from water pumped from the burrows by means of a small hand-operated bilge pump. *Kelleria* was found only once in burrows whose occupant was known, namely, *K. pectinata* in burrows of the shrimp *Axius* (*Neaxius*) *acanthus* A. Milne Edwards. Although the occupants of other larger burrows (extending down more than a metre) were never seen or collected, it is possible that they were stomatopods.

The field work in 1960 was supported by the Academy of Natural Sciences of Philadelphia, and that in 1963–64 by the U.S. Program in Biology of the International Indian Ocean Expedition. The staff of the Centre ORSTOM de Nosy Bé generously provided certain facilities during the field work.

The study of the material has been aided by a grant (GB-5838) from the National Science Foundation of the United States.

We wish to thank Dr. J. P. Harding for making available to us syntypes of *Kelleria regalis* from the collection of the British Museum (Natural History).

All figures have been drawn with the aid of a camera lucida. The letter after the explanation of each figure refers to the scale at which it was drawn. The measurements have been made from specimens in lactic acid. The length of the body does not include the setae on the caudal rami. The lengths of the segments of the first antenna have been taken along their posterior non-setiferous margins.

Family **LICHOMOLGIDAE** Kossmann, 1877

Genus ***KELLERIA*** Gurney, 1927

Kelleria regalis Gurney, 1927

(Figs. 1–30.)

MATERIAL COLLECTED. 24 ♀♀, 22 ♂♂, and 16 copepodids in water pumped from

20 large burrows (diameter 3·5 cm.) in muddy intertidal sand, Ambanoro, Nosy Bé, Madagascar, February 15, 1964 [these adults deposited in the British Museum (Natural History)] ; 5 ♀♀, 1 ♂, and 1 copepodid from 5 smaller burrows (diameter 1·5 cm.) in the same locality, February 15, 1964 ; 11 ♀♀, 5 ♂♂, and 5 copepodids from large burrows in muddy intertidal sand, Ampassipohe, Nosy Bé, May 11, 1964; and 1 ♂ from 20 large burrows in intertidal sand, Boloboxo, Nosy Faly, east of Nosy Bé, May 13, 1964.

Female. The body (fig. 1) has a moderately slender prosome, a little thickened dorsoventrally, and a slender elongated urosome. The length is 1·32 mm. (1·25–1·37 mm.) and the greatest width 0·44 mm. (0·42–0·45 mm.), based on 10 specimens. The sclerotization of the body wall is weak. The segment of leg 1 is separated from the head by a dorsal transverse furrow. The ratio of the length to the width of the prosome is 1·55 : 1.

The segment of leg 5 (fig. 2) is 65×153 μm. Between this segment and the genital segment there is no ventral intersegmental sclerite. The genital segment is elongated (203 μm long), in dorsal view somewhat expanded in its anterior two-fifths (greatest width here 143 μm) and narrower with nearly parallel sides in its posterior three-fifths (width about 104 μm). The areas of attachment of the egg sacs are located laterally on the anterior expanded portion of the segment. Each area (figs. 3 and 4) bears a small naked seta 9 μm long, a spiniform process 8 μm, and a little posteriorly removed from these and situated on a noticeable expansion a much longer prominent finely barbed seta 52 μm. The three postgenital segments are 88×91 μm, 65×83 μm, and 52×78 μm from anterior to posterior. The anal segment has a row of minute spinules posteriorly along the dorsolateral and ventrolateral margins.

The caudal ramus (fig. 5) is moderately elongated, 77×34 μm in greatest dimensions including the terminal flange, or 2·27 times longer than wide. The outer lateral seta is 70 μm long and naked. The other setae have lateral spinules. The dorsal pedicellate seta is 65 μm, the outermost terminal seta 81 μm, the innermost terminal seta 109 μm, and the two median terminal setae 220 μm (outer) and 330 μm (inner), both inserted dorsally to a small terminal flange bearing a marginal row of minute spinules.

The dorsal surface of the prosome and urosome bears a few small hairs (sensilla) and refractile points; the ventral surface of the urosome almost entirely lacks ornamentation. The ratio of the length of the prosome to that of the urosome is 1·22 : 1.

The egg sacs (fig. 1) are oval and reach as far as the second postgenital segment. Each sac is about 308×165 μm and contains a moderately small number of eggs about 62 μm in diameter.

The rostrum (fig. 6) is well-defined, with a rounded posteroventral margin, and projects slightly in lateral view (fig. 7).

The first antenna (fig. 6) is about 300 μm long. The lengths of the seven segments are : 22 (55 μm along its anterior margin), 73, 18, 44, 40, 44, and 28 μm respectively. The armature is : 4, 13 (5+8), 6, 3, 4+1 aesthete, 2+1 aesthete, and 7+1 aesthete. All the setae are naked.

The second antenna (fig. 8) is slender. The fourth segment is elongated, 86 μm along its outer edge to the seta, 73 μm along its inner edge, and 19 μm wide, and bears terminally two claw-like jointed setae and five slender simple setae. The outer margins of the second and fourth segments bear rows of small spinules.

The labrum (fig. 9) has two broad hyaline posteroventral lobes. Immediately in front of the labrum the ventral surface of the head is slightly protruded as in figure 7.

The mandible (fig. 10) has on its convex edge a cluster of slender spinules followed by a series of large teeth (the second one smaller than the immediately succeeding teeth), and on its concave edge a row of stout spines. The terminal flagellum is moderately long and barbed. The paragnath (fig. 11) bears very slender spinules. The first maxilla (fig. 12) bears three barbed setae and a subterminal weakly articulated seta ornamented with a terminal tuft of minute spinules. The second maxilla (fig. 13) has a large basal segment which bears distally a small sharp spiniform process. The second segment bears a minute ventral spinule, a posterior surficial naked seta, and a large strongly barbed spine ; the short spiniform lash bears three large spines (the middle one shorter than the other two) followed by several smaller spines. (In the right second maxilla of one female an abnormal spination occurred as shown in fig. 14.) The maxilliped (fig. 15) shows a proximally directed acutely pointed fringed process on the inner margin of the first segment. Both of the two setae on the second segment have a strong spinule on their proximal margins in addition to smaller spinules. The small third segment bears four elements.

The area between the maxillipeds and the first pair of legs is slightly protuberant.

Legs 1–4 (figs. 16, 17, 18, and 19) have the following armature (the Roman numerals indicating spines, the Arabic numerals representing setae) :

P_1	coxa	0–1	basis	1–0	exp	I–0	I–1	III,I,4
					enp	0–1	0–1	I,5
P_2	coxa	0–1	basis	1–0	exp	I–0	I–1	III,I,5
					enp	0–1	0–2	I,II,3
P_3	coxa	0–1	basis	1–0	exp	I–0	I–1	III,I,5
					enp	0–1	0–2	I,II,2
P_4	coxa	0–1	basis	1–0	exp	I–0	I–1	II,I,5
					enp	II,1		

The inner seta on the coxa of legs 1–3 is long and plumose, but in leg 4 this seta is shorter (25 μm) and finely barbed. The inner margin of the basis of all four legs bears a row of hairs. The 1-segmented endopod of leg 4 (fig. 19) is 75 μm long, including the distal spiniform processes; the part of the segment proximal to the outer marginal notch is expanded (25 μm wide) with long hairs along its outer margin ; the distal part is narrower (21 μm wide) with very small outer spinules. The inner plumose seta is 47 μm, and the two terminal fringed spines are 40 μm (outer) and 68 μm (inner).

Leg 5 (fig. 20) has a free segment about 120×53 μm in greatest dimensions with a distally directed tooth-like spinous process about 19 μm long on the inner margin. The two terminal spiniform elements are 65 μm (outer) and 67 μm (inner) in length and unilaterally fringed. The seta on the body near the free segment is 60 μm and feathered. An abnormal left free segment is shown in figure 21 (the segment of the right fifth leg in this female having a normal form).

Leg 6 is probably represented by the two setae near the attachment of each egg sac (fig. 4).

The colour in life in transmitted light is slightly amber, with indistinct red lines ventrally around the epimera of the metasomal segments ; a few orange-red globules in the prosome ; the eye dark red ; the egg sacs grey to reddish orange.

Male. The body (fig. 22) resembles in general form that of the female, though the prosome is less pointed anteriorly. The length is 1·05 mm. (1·00–1·09 mm.) and the greatest width 0·32 mm. (0·31–0·34 mm.), based on 10 specimens. The ratio of the length to the width of the prosome is 1·70 : 1.

The segment of leg 5 (fig. 23) is 46×91 µm. The genital segment is 156×130 µm, with only slightly rounded lateral margins in dorsal view. The four postgenital segments are 62×62 µm, 62×58 µm, 43×53 µm, and 46×60 µm from anterior to posterior.

The caudal ramus is similar to that of the female.

The surface of the body bears very few hairs and refractile points. The ratio of the length of the prosome to that of the urosome is 1·26 : 1.

The rostrum is like that of the female.

The first antenna resembles that of the female but three long aesthetes are added, two on segment 2 and one on segment 3. The second antenna, labrum, mandible, paragnath, and first maxilla are similar to those in the female.

The second maxilla (fig. 24) has an arrangement of spines on the spiniform lash different from that in the female, with two short spines between each of the three large spines.

The maxilliped (fig. 25) is slender and 4-segmented, assuming that the proximal part of the claw represents a fourth segment. The second segment bears inwardly two setae, one of them sickle-shaped with a hyaline concave margin, and three rows of spinules. The claw is 234 µm along its axis and carries proximally two very unequal setae.

The area between the maxillipeds and the first pair of legs is only slightly protuberant.

The formula for the armature of legs 1–4 is like that of the female, except for the last segment of the endopod of leg 1 (fig. 26) which is I,I,4. This endopod is strongly geniculate between segments 2 and 3. The lateral spinules on the inner of the two spines on the third segment are peculiarly broad and obtuse. The last segment of the endopod of leg 2 (fig. 27) also shows sexual dimorphism, the outer of the two terminal spines being naked and the anterior surface of the segment near the insertion of this spine having an erect sharply pointed recurved spiniform process. Legs 3 and 4 are like those of the female.

Leg 5 (fig. 28) has a small unornamented free segment 26×12 µm, without an inner spinous process. The two terminal elements comprise an outer naked seta 37 µm long and an inner spiniform barbed spine 31 µm.

Leg 6 (fig. 29) consists of a posteroventral flap on the genital segment bearing two setae, one 50 µm long and feathered, the other 39 µm and naked, and a sharp spiniform process.

The spermatophore (fig. 30), attached to the female in pairs, is elongated, 120×60 µm, not including the neck.

The colour in life resembles that of the female.

Discussion. Gurney's description of *Kelleria regalis* from the Suez Canal shows many similarities with our Madagascan material. For the purpose of a more detailed comparison we have examined by dissection two syntypes of this species, a male and a female, Brit. Mus. (Nat. Hist.) 1928.4.2.21.

Our specimens agree in all major respects with the syntypes. There are, however, four rather minor differences. The body size of the syntypes is a little larger (the female 1·45×0·53 mm., the male 1·32×0·46 mm.). The caudal ramus is relatively a little longer, in the female 99×39 μm with the ratio 2·5 : 1, and in the male 104×34 μm with the ratio 3·0 : 1. On the convex edge of the mandible there are two small teeth immediately following the large tooth, instead of only one small tooth as in the Madagascan specimens. On leg 5 of the female the two terminal setae are more unequal in length, the outer being 60 μm, the inner 92 μm. Since the other features of the syntypes are identical with those in our specimens, we conclude that the Madagascan material represents *K. regalis*, and that such minor differences as those observed in the two syntypes studied represent intraspecific variation.

We are unable to evaluate conclusively the specific merit of *Kelleria rubimaculata* Krishnaswamy, 1952. Like Stock (1967) we have not found in Krishnaswamy's description dependable differences between this Indian species and *K. regalis*, except the shorter body length (the female of *K. rubimaculata* being 0·7 mm. long and the male 0·637 mm.).

Kelleria pectinata (A. Scott, 1909)

(Figs. 31–53.)

Material collected. 8 ♀♀, 1 ♂, and 4 copepodids in water pumped from 20 large burrows (diameter 3·5 cm.) in muddy intertidal sand, Ambanoro, Nosy Bé, Madagascar, February 15, 1964 [of these 6 ♀♀ and 1 ♂ deposited in the British Museum (Natural History)] ; 6 ♀♀, 1 ♂, and 3 copepodids from 5 smaller burrows (diameter 1·5 cm) in the same locality, February 15, 1964; 1 ♀ from large burrows in muddy intertidal sand, Ampassipohe, Nosy Bé, May 11, 1964 ; 1 ♀ from large burrows in clean intertidal sand, Nosy Roty, east of the northern end of Nosy Sakatia, near Nosy Bé, May 12, 1964 ; 8 ♀♀ from 20 large burrows in intertidal sand, Boloboxo, Nosy Faly, east of Nosy Bé, May 13, 1964 ; and 1 ♀ from burrows of the thalassinidean shrimp *Axius* (*Neaxius*) *acanthus* A. Milne Edwards, Andilana, Nosy Bé, Oct. 8, 1960.

Female. The body (fig. 31) resembles in general form that of *K. regalis*, but the prosome is less pointed anteriorly. The length is 1·01 mm. (0·96–1·09 mm.) and the greatest width is 0·37 mm. (0·34–0·39 mm.), based on 8 specimens. The sclerotization of the body wall is weak and the segment of leg 1 is separated from the head as in *K. regalis*. The ratio of the length to the width of the prosome is 1·63 : 1.

The segment of leg 5 (fig. 32) is 60×109 μm. Between this segment and the genital segment there is no ventral intersegmental sclerite. The genital segment, 156 μm long, shows in dorsal view two lateral protrusions anteriorly, where the width is 127 μm. The areas of attachment of the egg sacs are situated laterally in the anterior third of the segment. Each area (fig. 33) bears a small naked seta 6 μm long, a spiniform process 7 μm, and posteriorly and laterally to these a prominent finely barbed seta 45 μm. The surface of the segment dorsal to the insertion of this long seta is delicately corrugated. The three postgenital segments are 56×63 μm, 42×60 μm, and 50×62 μm from anterior to posterior. The posterior margin of the anal segment is smooth.

The caudal ramus (fig. 34) is elongated, 79×26 μm in greatest dimensions including the terminal flaps, or 3·04 times longer than wide. The outer lateral seta is 58 μm and the dorsal pedicellate seta 25 μm, both naked. The four terminal setae have lateral spinules; the outermost is 108 μm, the innermost 117 μm, and the two median setae 187 μm (outer) and 234 μm (inner), both inserted between smooth dorsal and ventral flaps.

The dorsal surface of the prosome and urosome has a few small hairs (sensilla) and refractile points; such ornamentation is almost wholly lacking on the ventral surface of the urosome. The ratio of the length of the prosome to that of the urosome is 1·45 : 1.

The egg sacs (fig. 31) are oval and extend a little beyond the caudal rami. Each sac is about 385×200 μm, and contains a greater number of eggs than in *K. regalis*, with each egg approximately 51 μm in diameter.

The rostrum resembles that of *K. regalis*.

The first antenna is segmented and armed as in *K. regalis*, but the lengths of the segments are slightly different : 21 (50 μm along its anterior margin), 69, 15, 27, 33, 28, and 33 μm respectively. All the setae are naked.

The second antenna (fig. 35) resembles that of *K. regalis*, but the second and fourth segments are relatively shorter. The fourth segment is 64 μm along its outer edge to the seta, 44 μm along its inner edge, and 17 μm wide. Terminally it bears two claw-like jointed setae (both with their concave margins finely barbed) and five slender simple setae.

The labrum is like that of *K. regalis*. The ventral area of the head immediately in front of the labrum is less protruded than in *K. regalis*.

The mandible (fig. 36) is much like that in *K. regalis*, but the spinules on the convex edge are stouter and arranged in a row rather than a cluster, and the second large tooth in the series distal to these spinules is not unusually shortened. The proximal inner margin of the flagellum is slightly swollen, where the series of teeth merges with the flagellar spinules, as indicated in A. Scott's Pl. LXVIII, fig. 24. Paragnaths were not seen in the dissections made, though probably they are present, since they occur in the male (see fig. 47). The first maxilla (fig. 37) has the same number of elements as in *K. regalis*, but the subterminal element is naked and shows no articulation with the appendage. The second maxilla (fig. 38) resembles that of *K. regalis*, but the spines on the short spiniform lash are differently formed. The maxilliped (fig. 39) has the same number of elements as in *K. regalis*, but on the last segment one spine and the two setae are very short, while the other spine is long and claw-like, as A. Scott showed in his Pl. LXVIII, fig. 26.

The area between the maxilliped and the first pair of legs is slightly protuberant.

Legs 1–4 are segmented as in *K. regalis* and have the same spine and setal formula as in that species. The exopods of these legs closely resemble those of *K. regalis*, but the endopods differ in certain details. The last segment of the endopod of leg 1 (fig. 40) and its spine are relatively longer. The same is true for the endopod of leg 2 (fig. 41). The last segment of the endopod of leg 3 (fig. 42) is relatively longer and its inner terminal spine is markedly longer in relation to the other two spines than in *K. regalis*. In leg 4 (fig. 43) the inner seta on the coxa is short (15 μm) and naked. The inner margin of the basis is naked. The endopod is 61 μm long, including the distal spiniform processes; the width proximal to the outer marginal notch is 18 μm, and distal to the notch 14 μm. The inner plumose seta is 36 μm, and the two terminal fringed spines are 33 μm (outer) and 53 μm (inner).

Leg 5 (fig. 44) has a slender elongated unornamented free segment, with a slight inner proximal expansion. The length is 67 μm, the width at the expansion 19 μm, and the width distally 12 μm. The outer terminal element is setiform and naked, 33 μm, the inner is spiniform and fringed, 50 μm. The seta on the body near the free segment is 36 μm and lightly feathered.

Leg 6 is probably represented by the two setae near the attachment of each egg sac (fig. 33).

The colour in life in transmitted light resembles that of *K. regalis*.

Male. The body (fig. 45) is similar in general form to that of *K. regalis*. The length and the greatest width of 2 specimens are 0·78 × 0·25 mm. and 0·80 × 0·24 mm. The ratio of the length to the width of the prosome is 1·80 : 1.

The segment of leg 5 (fig. 46) is 34 × 75 μm. The genital segment is 121 × 120 μm. The four postgenital segments are 43 × 52 μm, 39 × 47 μm, 29 × 43 μm, and 40 × 47 μm from anterior to posterior.

The caudal ramus is like that of the female.

The first antenna is similar to that of the female, but has three aesthetes added as in *K. regalis*. The second antenna, labrum, and mandible are like those in the female. The paragnath (fig. 47) is a small lobe with a few hairs. The first maxilla resembles that of the female. The second maxilla (fig. 48) differs from that of the female in the lengths of the spines on the short lash and in the spinulation of the large inner spine. The maxilliped (fig. 49) has four rows of spinules on the second segment. One of the two setae on this segment is recurved, with a short fringe on its convex margin. There are two small knobs near the smaller of the two setae on the proximal part of the claw. The claw is 146 μm along its axis.

The area between the maxillipeds and the first pair of legs is a little protuberant.

Legs 1–4 have the same spine and setal formula as in the male of *K. regalis*. The exopods of these legs are very similar in details to those of *K. regalis*. The endopod of leg 1 (fig. 50), with the formula I,I,4 on the last segment, is not geniculate, and the inner of the two spines on the last segment is the shorter and is finely barbed. The last segment of the endopod of leg 2 (fig. 51) is much like that of the female, and the erect spiniform process seen in *K. regalis* is absent. The endopods of legs 3 and 4 are like those in the female.

Leg 5 (fig. 52) has a small slender unornamented free segment 22 × 7 μm. Terminally the outer seta is 30 μm long, the inner spine 20 μm, both naked. The seta on the body near the free segment is 28 μm and naked.

Leg 6 (fig. 53) consists of the usual posteroventral flap on the genital segment bearing two naked setae 37 μm and 45 μm in length and near their insertions a small spiniform process.

The spermatophore, attached to the female in pairs, is 84×43 μm, not including the neck, and is similar in form to that of *K. regalis*.

The colour in life resembles that of *K. regalis*.

DISCUSSION. This species was originally described from a single female as *Pseudanthessius pectinatus* by A. Scott (1909). Gurney (1927) transferred it to his new genus *Kelleria*. The male has been unknown until now.

Although it is impossible to learn the exact nature of certain structures from A. Scott's description and figures, the similarities with the Madagascan specimens have led us to conclude that our material from Nosy Bé represents *Kelleria pectinata*. Among the striking similarities in the female are : the form of the second antenna and its terminal elements, the nature of the mandible, and the armature of the maxilliped, especially on the last segment.

The female described by A. Scott was a little longer (1·35 mm.) than the Madagascan specimens. His description and figures of the genital segment, the caudal ramus, and leg 5, though rather cursory, suggest resemblances with our material. His figure Pl. LXVIII, fig. 25, of the second maxilla, shows a somewhat different number and arrangement of the spines on the short lash. Since variation in these spines exists in *Kelleria* (compare our figs. 13 and 14 of *K. regalis*), it is very possible that A. Scott's description of the spines in his single female may represent individual variation.

A. Scott's female was found in surface plankton in the Bali Sea, 8° 0·3′ S, 116° 59·0′ E. Our specimens from Madagascar occurred in intertidal burrows of unknown origin, except for one collection from burrows of the shrimp *Axius acanthus*. Frequently *K. regalis* and *K. pectinata* occurred together in the same burrows. Often these two species of *Kelleria* inhabited burrows in which *Hemicyclops* also lived. In one collection (that at Ampassipohe, May 11, 1964) both species of *Kelleria* were found in company with *Hemicyclops diremptus* Humes, 1965, *H. carinifer* Humes, 1965, and *H. biflagellatus* Humes, 1965. In another collection (that at Nosy Roty, May 12, 1964) *K. pectinata* occurred with *H. carinifer*, *H. diremptus*, and *H. kombensis* Humes, 1965. In still another (that from *Axius* burrows at Andilana, October 8, 1960) *K. pectinata* occurred with *H. axiophilus* Humes, 1965, and *H. amplicaudatus* Humes, 1965.

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PLATE 1

Kelleria regalis Gurney, 1927, female

FIG. 1. Dorsal (A)
FIG. 2. Urosome, dorsal (B)
FIG. 3. Area of attachment of egg sac, dorsal (C)
FIG. 4. Area of attachment of egg sac, lateral (C)
FIG. 5. Caudal ramus, dorsal (D)
FIG. 6. Rostrum and first antenna, anteroventral (E)