Griceus buskeyi, a new genus and species of calanoid copepod (Crustacea) from benthopelagic waters off Hawaii

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Abstract.—The new genus and species of deep-sea, benthopelagic calanoid copepod, *Griceus buskeyi*, differs from other calanoid copepods in the following derived character states: dorsal interlocking extensions of abdominal somites; antenna 2, mandible, and maxilla 1 originate posterior to the labrum and paragnaths; coxal endite of the mandible outside of the labral-paragnathal envelope; praecoxal and coxal endites of maxilla 1 unarmed; praecoxal endites of maxilla 2 unarmed; endopod of maxilliped with four articulating segments. Two setae on middle endopodal segment of swimming legs 3 and 4 suggests the new genus and species belongs to the superfamily Augaptiloidea. A mandibular endopod which is reduced in size to a small unarmed lobe and absence of an endopod on maxilla 1 suggests an affinity with the arietellid genus *Paragaptilus* Wolfenden.

Samples from deep-sea, benthopelagic habitats continue to reveal a diverse fauna of calanoid copepods which often express unusual morphologies. Here we describe an unusual species of calanoid which we believe can be placed in the family Arietellidae as it is presently understood (Ohtsuka et al. 1994), but not in any of its known genera.

Methods

This adult female calanoid copepod was collected 6 July 1997 from seawater flowing from a flexible plastic pipe maintained by Natural Energy Laboratory of Hawaii Authority near Kona, Island of Hawaii, $19^{\circ}43'27.01''N$, $156^{\circ}04'35.46''W$. The intake of the pipe (1 m diameter) is located at 675 m, about 30 m from the bottom, and draws in about 132 cubic m/min. Because of its flexibility, the position of the intake may vary vertically \pm 10 m with the movement of the tide. Water from one outflow pipe (10 cm in diameter) drains through a 53 micron mesh net placed in a large, dark tank. The sample was collected after 12 hrs; the animal reported here may have been dead prior to sample fixation with 4% formaldehyde. The specimen was later cleared in steps through 50% lactic acid/50% water to 100% lactic acid, stained by adding a solution of chlorazol black E dissolved in 70% ethanol/30% water, and examined with bright-field and with differential interference optics.

Cephalic appendages are abbreviated A1 = antenna 1; A2 = antenna 2; Mn = mandible; Mx1 = maxilla 1; Mx2 = maxilla 2. Appendages on thoracic somites are Mxp = maxilliped (thoracopod 1); P1–5 = swimming legs (thoracopods 2–6). The caudal ramus is CR. Designations of appendage segments are according to Ferrari (1995) as follows: medial lobe of a segment = li, lateral lobe = le; rami are exopod = Re and endopod = Ri; ramal segments of Mx2 are exopodal; the Mxp has a basopod with a distal medial lobe, and with at most five endopodal segments in calanoids (Ferrari & Dahms 1998). Armament elements of appendages are termed setae regardless of their position or degree of rigidity. Setules are epicuticular extensions of a seta; denticles are epicuticular extensions of an appendage segment; spinules are epicuticular extensions of a somite.

Calanoid superfamily names follow Andronov (1974) with the exception of Clausocalanoidea for Pseudocalanoida (Bowman 1987, International Commission on Zoological Nomenclature 1988). The changes proposed by Andronov (1991) are not followed here because there is no requirement that a family group name be derived from the oldest included genus name, or by coordination here the oldest included family name (International Code of Zoological Nomenclature 1985, articles 62–64). The correct names in question are Augaptiloidea, Centropagoidea and Megacalanoidea.

Griceus, new genus

Diagnosis.—The following derived character states are assumed to be shared by all species of this genus discovered subsequently: dorsal interlocking extensions of abdominal somites; A2, Mn and Mx1 originating posterior to the labrum and paragnaths; coxal endite of Mn outside of the labral-paragnathal envelope; praecoxal and coxal endites of Mx1 unarmed; praecoxal endites of Mx2 unarmed; endopod of Mxp with four articulating segments.

Type species.—Griceus buskeyi, by monotypy.

Etymology.—The name honors Dr. George D. Grice for his contributions to the exploration of the deep-sea benthopelagic fauna, and to the taxonomy of calanoid copepods. Dr. Grice's family name is latinized to form *Griceus*. The gender of the name is masculine.

Griceus buskeyi, new species

Specimens.—Holotype (National Museum of Natural History, Smithsonian Institution USNM 288058) a dissected female, 0.90 mm in length; prosome—0.74 mm and urosome—0.16 mm.

Female.—Pr (Fig. 1C): 6 segments; 1st a complex of 5 cephalic somites plus Th1; Th2–4 simple and articulated; arthrodial membrane between Th5 and 6 incomplete; reduced in width dorsally. Rostral area a simple, bilobe plate (Fig. 1A, C) without spinules or attenuations of cephalon. Location of base of A2, Mn, Mx1, Mx2 and Mxp as in Fig. 1A, B. Base of A2 posterior to labrum; base of Mn outside of labral-paragnathal envelope. Base of Mxp lateral to base of Mx2; base of Mx1 lateral and posterior to base of Mx2. Rostrum, labrum, and paragnaths as in Fig. 2D.

Ur (Fig. 1D): 4 segments; anterior segment a genital complex of Th7 and Ab1; as viewed dorsally, genital complex symmetrical (Fig. 2A). Viewed laterally (Fig. 2B, C), genital complex with a thickened ridge laterally on right side. Right laterally and dorsad, posterior margin of abdominal somites 1–3 asymmetrical, each with attenuate, finger-like process which engages socket-like depression on anterior margin of following somite (Fig. 2E).

A1 (Fig. 3): A large segmental complex proximally (Fig. 4A) of 19 setae separated by incomplete ventral (anterior) arthrodial membranes into 8 groups of 3, 2, 2+1, 3, 2, 3, 1, 2 setae+aesthetascs with setae of same group laterally displaced relative to each other; aesthetasc of the 3rd group short, triangular with distal sensilla. Distal to the complex an incompletely articulating segment with 2 setae and short, triangular aesthetasc with distal sensilla followed by 13 completely articulating segments with 2+1, 2, 2, 2, 2, 2+1, 2, 2, 2, 2+1, 2, 6+1 setae+aesthetascs.

A2 (Fig. 4B, C): coxa and basis without setae. Re 8 articulating segments with 0, 1,

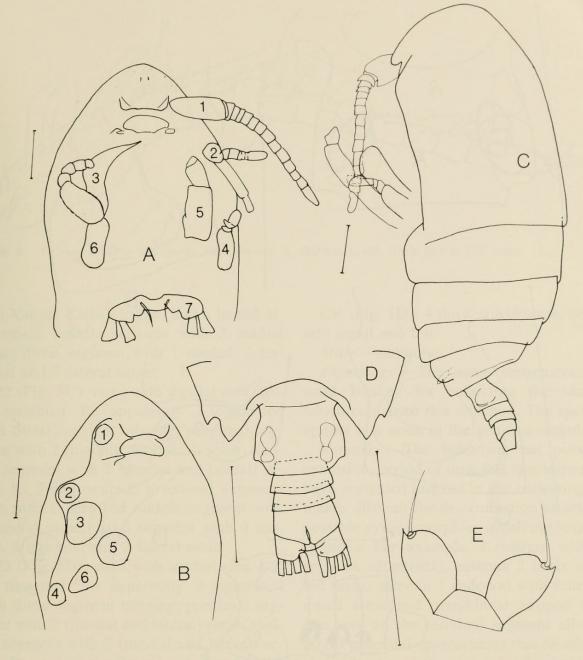


Fig. 1. *Griceus buskeyi* new genus, new species. A, Oral area, ventral, showing location of only one of antenna 1 (1), antenna 2 (2), mandiblar gnathobase (3), maxilla 1 (4), maxilla 2 (5), maxilliped, obscuring mandibular palp (6); both swimming legs 1 (7); B, same, showing location of origin of antenna 1 (1), antenna 2 (2), mandible (3), maxilla 1 (4), maxilla 2 (5), maxilliped (6); C, animal, left lateral; D, Th5–6 and urosome, dorsal; E, leg 5. All scale lines are 0.01 mm.

1, 1, 1, 1, 0, 3 setae. Ri 2-segmented with 1 and 8 (4 terminal, 4 subterminal) setae.

Mn (Fig. 4D): coxa elongate with lobe at mid-length and attenuations medially; basis unarmed. Re 5-segmented with 1, 1, 1, 1, 1 setae. Ri apparently a lobe on the basis medial to the exopod.

Mx1 (Fig. 4E): Praecoxa, coxa and basis with poorly-developed, unarmed lobes. Ri

not distinguished. Re 1-segmented with 1 medial and 3 terminal setae.

Mx2 (Fig. 4F): Proximal and distal praecoxal endites poorly-developed, unarmed; no arthrodial membrane separating praecoxa and coxa. Proximal coxal endite with 2 setae, distal coxal endite with 2 setae. Endites of basis indistinct with 1 and 2 setae. Re unsegmented with 7 setae.

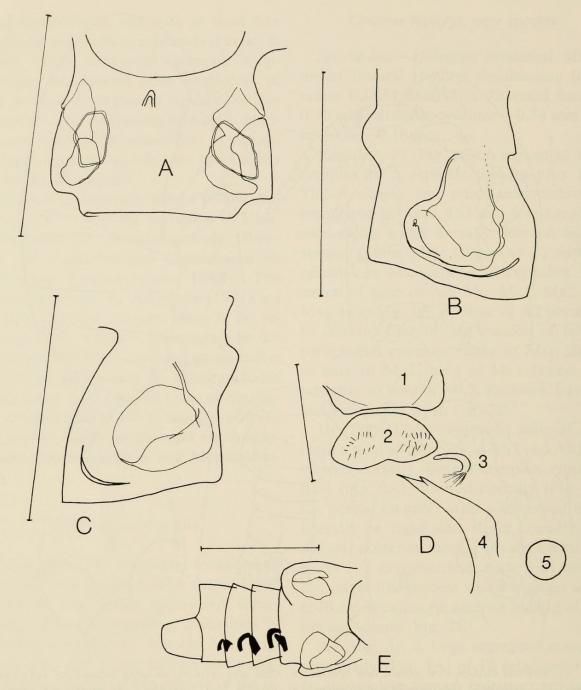


Fig. 2. *Griceus buskeyi* new genus, new species. A, Genital complex, dorsal; B, Genital complex, left lateral, C, Genital complex, right lateral; D, Mouth area, ventral, showing location of rostrum (1), labrum (2), paragnath (3), tip of mandibular gnathobase (4) and origin of antenna 2 (5); E, urosome, dorsal and slightly lateral, with attenuate finger-like processes and socket-like depressions darkened. All scale lines are 0.01 mm.

Mxp (Fig. 5A): syncoxa with 1 seta but without distinct lobes. Basis with 3 setae (2 on a distal medial lobe which is poorly developed and weakly sclerotized) and anterior denticles not organized into a clear pattern. Ri 4-segmented proximal to distal with 1, 2, 3, 4 setae (4, 3, 1, 2 by segmental age).

P1 (Fig. 5B): coxa with medial seta. Basis with medial denticles; medial seta curved only toward its tip with setules along the proximal straight part; lateral seta absent. Re apparently 3-segmented with distal segment missing; proximal segment with 2 (medial and lateral) setae; middle segment with 2 (medial and lateral) setae. Ri 3-segmented; proximal segment with medial seta, a pore on anterio-distal margin (with the inner seta of the basis comprising

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Fig. 3. Griceus buskeyi new genus, new species. A, antenna 1, left. Scale line is 0.01 mm.

Von Vaupel Klein's organ) and a lateral attenuation; middle segment with 2 medial setae; distal segment with 1 medial, 2 terminal and 2 lateral setae.

P2 (Fig. 5C): coxa with medial seta. Basis unarmed. Re apparently 3-segmented with distal segment missing; proximal segment with 2 (medial and lateral) setae; middle segment with 2 (medial and lateral) setae. Ri 3-segmented; proximal segment with medial seta and middle segment with 2 medial setae; distal segment with 3 medial, 2 terminal and 2 lateral setae.

P3 (Fig. 5D): coxa with medial seta. Basis unarmed. Re apparently 3-segmented with distal segment missing; proximal segment with 2 (medial and lateral) setae; middle segment with 2 (medial and lateral) setae. Ri apparently 3-segmented; proximal segment with medial seta and middle segment with 2 medial setae; distal segment missing.

P4 (Fig. 5E): coxa with medial seta. Basis with lateral seta. Re apparently 3-segmented with distal segment missing; proximal segment with 2 (medial and lateral) setae; middle segment with 1 medial seta (lateral seta apparently missing). Ri apparently 3-segmented; proximal segment with a medial seta and middle segment with 2 medial setae; distal segment missing.

Leg 5 (Fig. 1E): coupler uniting limbs which each bear a terminal seta.

CR (Fig. 1D): 4 thick apical setae; dorsal seta small and thin.

Male.—unknown.

Etymology.—The name recognizes Edward Buskey for collecting the sample which contained this copepod. The specific epithet is a noun in the genitive singular.

Remarks.—The unknown, but possibly extensive, period of time this specimen may have remained unfixed in the collecting net makes difficult the determination of several possible synapomorphies involving setae or spinules. For example, a rostrum without spinules (filaments), antenna 2 basis without setae, antenna 2 endopod with four terminal setae and mandibular exopod with one seta on the terminal segment all represent potential apomorphies that should be verified when better preserved specimens are available. For this reason, we have chosen to emphasize the apparently derived nature of the following changes in shape of somites and appendage segments which are presumed apomorphies for species of Griceus: interlocking extensions of abdominal somites dorsally; antenna 2, mandible and maxilla 1 originating posterior to the labrum and paragnaths; coxal endite of the mandible lying outside of the labral paragnathal envelope; praecoxal and coxal endites of maxilla 1 unarmed; praecoxal endites of maxilla 2 unarmed; endopod of maxilliped with four articulating segments.

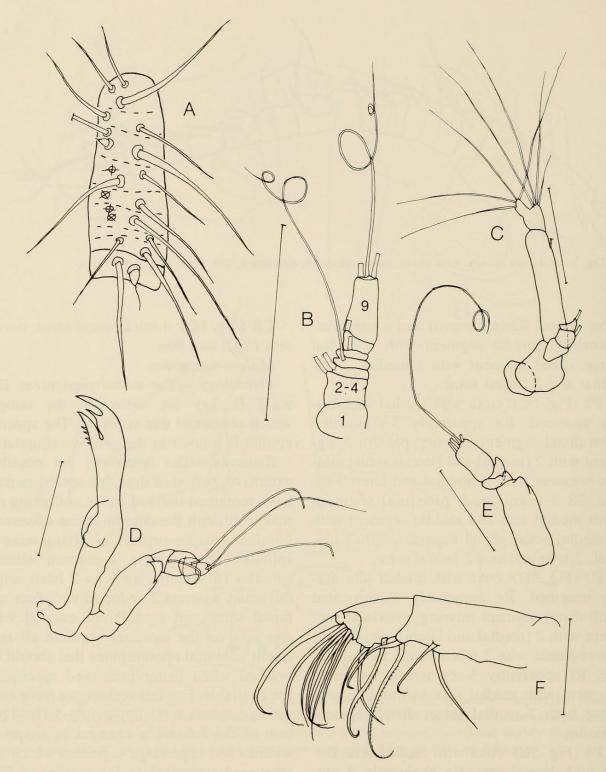


Fig. 4. *Griceus buskeyi* new genus, new species. A, proximal segmental complex plus following incompletely articulating segment of left antenna 1, ventral view, distal is down, wavy line cutoff on broken seta, circle with X is setal scar, broken lines are incomplete arthrodial membranes (scale line as for B); B, exopod of right antenna 2 with, segments 1, 2–4 and 9 indicated; C, left antenna 2, with exopod broken; D, left mandible; E, left maxilla 1; F, left maxilla 2. All scale lines are 0.01 mm.

The effect of the changes in location of the cephalic appendages may be generalized as follows: A2, Mn and Mx1 retain their ancestral positions relative to one another but as a group they have been drawn back posteriorly and laterally from the usual calanoid locations. The penultimate segment of the maxilliped may be a complex

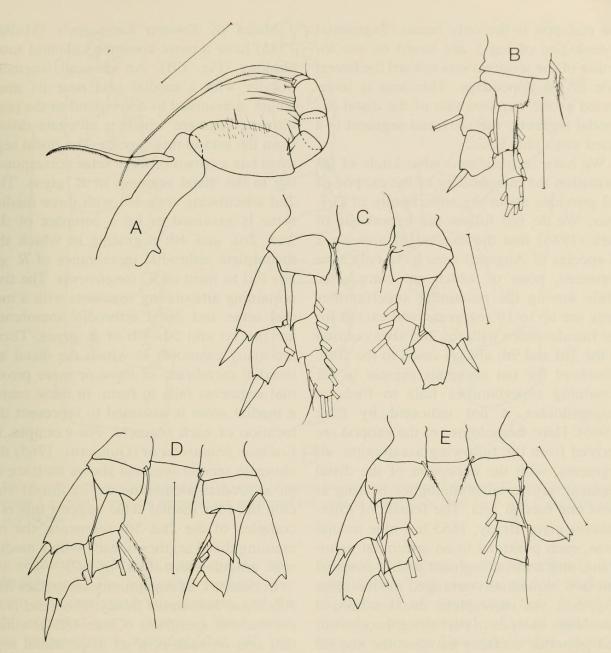


Fig. 5. *Griceus buskeyi* new genus, new species. A, left maxilliped; B, swimming leg 1, anterior; C, swimming leg 2, posterior; D, swimming leg 3, posterior; E, swimming leg 4, posterior. All scale lines are 0.01 mm.

of 2nd and 5th segments with the arthrodial membrane missing because it bears more setae than the two segments proximal to it (see Ferrari 1995, Ferrari & Dahms 1998). The endopod of the maxilliped of derived centropagoideans is poorly sclerotized and without arthrodial membranes; setal additions during development of *Acartia tonsa* Dana, 1849, *Tortanus dextrilobatus* Chen & Zhang, 1965, and *Epilabidocera longipedata* (Sato 1913) suggest these endopods are 4-segmented with one seta on proximal, antepenultimate and penultimate segments, and two setae on the distal segment. The endopod of *G. buskeyi* is well-sclerotized; there is one seta on the proximal, two setae on the antepenultimate, three setae on the penultimate and four setae on the distal segments suggesting that this 4-segmented ramus is not convergent with the centropagoideans. The ramus of maxilla 1 is interpreted as an exopod because its quadrate morphology and terminal crown of setae is similar to the exopod of many heterorhabdids and augaptilids. We know of no calanoid copepod with a maxilla 1 in which the endopod is the only ramus. Segmental homologies of leg 5 are based on the location of the terminal seta toward the lateral side of the appendage. This seta is interpreted as the terminal seta of the distal exopodal segment; the proximal segment is a fused coxa plus basis.

We have reconsidered what kinds of information the morphology of the exopod of A2 provides about the superfamily of Griceus. We do not follow the hypothesis of Park (1986) that the exopod of antenna 2 of species of Augaptiloidea have only nine segments, none of which are complexes, while among the remaining superfamilies there are up to 10 segments, and except for the Eucalanoidea with the 2nd always fused to the 3rd and 9th always fused to the 10th. Which of the ten segments present in the remaining superfamilies fails to form in Augaptiloidea is not indicated by Park (1986). Here, homologies of the exopod are derived from the following assumption: all segments, with the exception of the distal segment, are serial homologues bearing at most one medial seta. The female of Rhincalanus gigas Brady, 1883 has nine medial setae, each proximal to an arthrodial membrane, and a distal segment with a terminal and two sequentially arranged medial setae (Fig. 6A). An incomplete, distal arthrodial membrane extends in part along the anterior and posterior surfaces between the second and third medial setae, while an incomplete, distal arthrodial membrane fails to extend to the lateral surface separating the 3rd and 4th medial setae. Giesbrecht (1892: plate 11, figs. 16, 17) shows the exopod of Eucalanus attenuatus (Dana 1849) and E. crassus Giesbrecht, 1888 which can be interpreted as 11-segmented, a proximal complex of four segments represented by four medial setae, followed by six articulating segments, each with a seta, and a distal segment with a crown of three setae. We have been able to verify only a crown of three setae and nine medial setae each with at least part of a distal arthrodial membrane for these species.

Males of Temora longicornis (Müller, 1785) have a more common calanoid morphology (Fig. 6B). An elongate segment distally with a medial seta near its midlength is assumed to correspond to the penultimate segment which is elongate distad from the seta in this species. The distal segment has a crown of three setae corresponding to the distal segment of R. gigas. The 2nd articulating segment with three medial setae is assumed to be a complex of the 2nd, 3rd, and 4th segments in which the incomplete arthrodial membranes of R. gigas fail to form on T. longicornis. The five remaining articulating segments with a medial setae and distal arthrodial membrane are the 1st and 5th-8th of R. gigas. There are many calanoids in which the distal arthrodial membrane of three or more proximal segments fails to form; in these cases, a medial setae is assumed to represent the location of each segment. For example, in Calanus finmarchicus (Gunnerus, 1765) the elongate second segment shows no trace of an arthrodial membrane on its dorsal surface but four medial setae suggest this is a complex of the 2nd-5th segments; the remaining distal segments, each with a medial seta, articulate distally (Fig. 6C).

In contrast, in augaptiloidean species like Phyllopus bidentatus Brady, 1883 and Heterorhabdus spinifrons (Claus 1863), a medial seta on each of a set of proximal segments fails to form while the distal arthrodial membrane of each of those segments is present (Giesbrecht 1892: plate 18, fig. 29 and plate 20, fig. 9). Ohtsuka et al. (1994) describe arietellids with an elongate, proximal segmental complex in which both the seta and distal arthrodial membrane of a set of segments apparently fail to form. Griceus buskeyi has its 1st segment with a distal arthrodial membrane but no medial seta; the following segmental complex is interpreted as composed of the 2nd and 3rd segments which have neither an arthrodial membrane nor a medial seta, plus the 4th segment with a medial seta and a distal arthrodial membrane. The next four articulat-

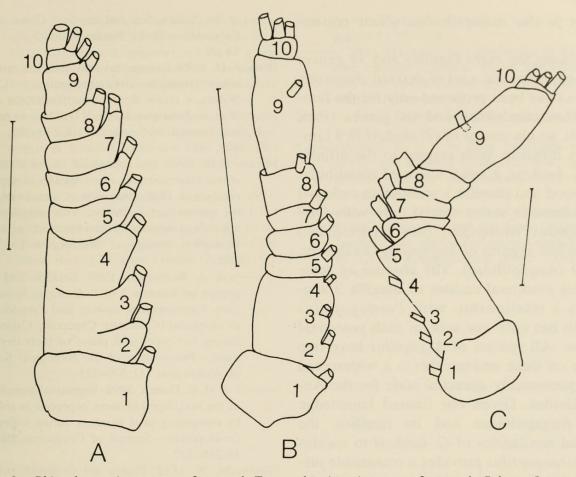


Fig. 6. *Rhincalanus gigas* antenna 2 exopod; *Temora longicornis* antenna 2 exopod; *Calanus finmarchicus* antenna 2 exopod. Presumed segments are numbered proximal to distal; scale lines for A and C are 0.01 mm; B is 0.05 mm.

ing segments each with a seta are the 5th-8th segments. The following elongate segment is an unarmed 9th segment and the 10th segment has a crown of three setae. Our interpretation assumes that all segments homologous to those of R. gigas are present in these calanoids. The alternate hypothesis of Park (1986) that one of the ten segments fails to form, has not been considered because we are unsure of the location on the antennal exopod that new segments are patterned, and whether there is a single location for segment patterning, like the copepod maxilliped (Ferrari & Dahms 1998), or more than one location, like the calanoid antenna 1 (Ferrari & Benforado 1998).

Loss of segments on some of the swimming legs complicates the assignment of this specimen to the correct calanoid family. However, two character states suggest that G. buskeyi belongs to the superfamily Augaptiloidea. Two setae on middle segment of endopod of swimming legs 3 and 4, probably an ancestral calanoid state, are present only on Epacteriscioidea, Pseudocyclopoidea, Augaptiloidea, Centropagoidea, Megacalanoidea, and some Bathypontioidea (Andronov 1974, Suárez-Morales & Iliffe 1996). We note in passing a misprint in Table 1 of Suárez-Morales & Iliffe (1996) in the number of inner setae on the terminal segment of swimming legs 3 and 4 (column E); Pseudocalanoidea (Clausocalanoidea) are unique in having four setae while the Spinocalanoidea with five setae are identical to the remaining superfamilies. The Arietellidae and Heterorhabdidae are the only families among the above six superfamilies with species in which the endopod of maxilla 1 does not develop (Ohtsuka et al. 1994, Park 2000), so an assignment to the Augaptiloidea seems reasonable.

Among the eight families and 39 genera of Augaptiloidea, a set of derived characters states have been proposed only for the family Heterorhabdidae and its genera (Park 2000), so placement of G. buskeyi in a family is difficult. With respect to the affinity of G. buskevi, a small unarmed mandibular endopod and maxilla 1 without an endopod are character states shared only with Paraugaptilus Wolfenden, 1904 (Arietellidae) and a few species of Augaptilus Giesbrecht, 1889 (Augaptilidae). The absence of setae on the praecoxal endites of maxilla 2 suggests a relationship with Paraugaptilus which has only one seta on each praecoxal endite. All species of Augaptilus have two setae on these endites; this is a widespread and presumably ancestral state for the Augaptiloidea. Given our limited knowledge the Augaptiloidea and its families, the shared similarities of G. buskeyi to species of Paraugaptilus provides a reasonable justification for placing this new genus in the Arietellidae.

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