A new species of freshwater isopod (Sphaeromatidea: Sphaeromatidae) from an inland karstic stream on Espíritu Santo Island, Vanuatu, southwestern Pacific

DAMIÀ JAUME1 & ERIK QUEINNEC2

1IMEDEA (CSIC-UIB), Instituto Mediterráneo de Estudios Avanzados, c/ Miquel Marquès, 21, 07190 Esportes, Balearic Islands, Spain. E-mail: d.jaume@uib.es

2 Université Pierre et Marie Curie (Paris 6), Équipe Evolution et Développement, UMR 7138 “Systématique, Adaptation, Evolution”, Bat. A, 4ème étage, pièce 405, 7 quai St Bernard, 75005 Paris, France

Abstract

Exosphaeroides quirosi is described from a karstic stream and its associated cave sink located 390 m above sea level and 23.5 km inland from the east coast of Espíritu Santo (Vanuatu, SW Pacific ocean). This is the first purely freshwater sphaeromatid isopod reported from an oceanic island, and is a new example of colonization of an oceanic island freshwater habitat by a typically marine taxon. E. quirosi differs from any other representative of the family in the peculiar condition displayed by the exopod of pleopod 4, which has a falcate outline, is distinctly longer than the corresponding endopod, and has the medial margin of the proximal segment produced into a foliaceous endite. Seemingly, the sexual dimorphism expressed in the presence/absence of a setulose fringe on the pereopods has not been recorded in any other sphaeromatid. Even though the peculiar pleopod 4 and the fusion pattern of pleonites—with complete incorporation of pleonite 1 to rest of pleonites—could suggest a new genus to accommodate the new species, it is included here in the broad Exosphaeroma s. l. cluster, from which most freshwater sphaeromatids seem to derive. This is done with the caveat that it is incertae sedis in Exosphaeroides until such time as a comprehensive revision of Exosphaeroma and related genera has been undertaken. E. quirosi appears to be a Exosphaeroma-derived species with an unusual pleopod 4 and fusion of pleonite 1 to the remainder of the pleon; these features being here regarded as species-level apomorphies within a morphologically diverse genus.

Key words: Crustacea; Isopoda; Exosphaeroides; running waters; Stygofauna; Oceanic islands

Introduction

Epigean freshwater habitats on oceanic islands are prone to being colonised by marine groups that seldom penetrate inland on continental landmasses. Having never been connected to hydrographic networks of any mainland, they offer plenty of vacant niches to marine invaders, which can successfully occupy these habitats without competition from primary freshwater species (Veuille 1979; Bowman 1981). A textbook example of colonization of island freshwaters by a typically marine taxon is Clibanarius fonticola McLaughlin & Murray, 1990, an anomuran crab dwelling in karstic springs and blueholes adjacent to the seashore on the island of Espíritu Santo (Vanuatu, SW Pacific), which is the only freshwater representative of its group known thus far (McLaughlin & Murray 1990). Other notable examples include particular groups of isopod crustaceans, such as some Jaera (Asellota: Janiridae) from the Balearics and the Azores, of which isolated populations are found up to 500 m above sea level in both archipelagos, and up to 16 km inland in the Mallorcan mountains (Veuille 1979; Margalef 1952; Jaume & García 1988).

Here we report a new noteworthy case of colonization of insular epigean freshwaters by a member of a typically marine isopod taxon: the family Sphaeromatidae (ca. 99 genera and 680 species recognized; Schotte et al. 2007). Other than the swarm of taxa restricted to the inland groundwater of the Dinaric karst and neigh-
bouring territories (Sket 1986), sphaeromatids have few purely freshwater taxa (Sket & Bruce 2004; Bruce 2005). Many sphaeromatids are nevertheless known to occur in estuaries or brackish ponds, and may extend their ranges up-river into freshwater, or are found on beaches subject to freshwater flow at low tide (Holdich & Harrison 1983).

*Exosphaeroides quirosi* sp. nov. dwells in a rainforest karstic stream and its associated cave sink located on an uplifted coral reef terrace 390 m above sea level and 23.5 km inland from the east coast of Espíritu Santo Island (Vanuatu; Fig. 1). This is the single purely freshwater sphaeromatid known to occur on an oceanic island, the nearest region with purely freshwater sphaeromatids being New Zealand (Sket & Bruce 2004; Bruce 2005).

**FIGURE 1.** Location of Fapon cave on Santo Island (Vanuatu), type locality of *Exosphaeroides quirosi* sp. nov.

**Material and methods**

Samples were gathered with a hand-held plankton net after stirring up plant debris and overturning boulders in a fast-flowing stream running into a cave sink, and up to 100 m inside the cave. The animals were fixed in
70% ethanol and, once in the laboratory, the internal tissues of several specimens were partially digested with lactic acid to facilitate study. Drawings were prepared using a camera lucida on an Olympus BH-2 microscope equipped with Nomarski differential interference contrast optics. Body measurements were derived from the sum of the maximum dorsal dimensions of individual somites, from tip of rostrum (i.e. excluding epistome) to posterior margin of pleotelson. Appendages preserved in slides were mounted in lactophenol and the coverslips sealed with nail varnish. Material is deposited in the Crustacea collections of both the Muséum National d’Histoire Naturelle, Paris (MNHN), and The Natural History Museum, London (BMNH).

Taxonomy

Order ISOPODA Latreille, 1817
Suborder SPHAEROMATIDEA Wägele, 1989
Superfamily SPHAEROMATOIDEA Latreille, 1825
Family SPHAEROMATIDAE Latreille, 1825
Genus Exosphaeroides Holdich & Harrison, 1983

Exosphaeroides quirosi sp. nov.
(Figs. 2–9)

Material examined. All material: Fapon cave, near Butmas village, Espíritu Santo Island, Vanuatu, 15°20.39’S, 166°57.96’E, 8 Sep 2006, coll. D. Jaume and E. Queinnec. Holotype: ♂ 11.30 mm, partially dissected, part mounted on single slide, remainder preserved in 70% ethanol in single vial [MNHN Is.6235]. Paratypes: 6 ♂♂, adult, 11.42 (partially dissected, with mouthparts mounted apart on single slide), 9.70, 9.35, 8.40, 8.88 and 9.40 mm, partially digested with lactic acid, preserved in 70% ethanol in single vial [MNHN Is.6236]; 3 ♀♀ 8.82 (partially dissected; one pleopod 2 mounted on slide), 8.70 and 8.02 mm, partially digested with lactic acid, preserved in 70 % ethanol in single vial, same data as holotype (MNHN Is.6237); 25 specimens, both sexes, same data as holotype preserved in 70 % ethanol in single vial (MNHN Is.6238); 25 specimens, both sexes, same data as holotype preserved in 70 % ethanol in single vial [(BMNH 2007.841-850).

Diagnosis. Body dorsal integument lacking sculpturing. Pleonite 1 lacking submedian posterior lobes, completely incorporated (i.e. no articulation nor vestige of suture line retained) to pleonites 2–5 comprising single composite somite. Posterior margin of pleotelson evenly arcuate, with no trace of exit channel. Medial margin of merus–propodus of male pereopods with dense setulose fringe; fringe absent in female. Lateral margin of ischium of pereopods lacking cluster of long setae. Exopod of fourth pleopod distinctly longer than endopod, falcate, with medial margin of proximal segment produced into foliaceous endite. Rami of pleopods 4 and 5 lacking ridges or folds. Uropods with both rami extending to end of pleotelson, about equal in length, with tip of exopod rounded, not acute.

Description of adult male. Body (Figs. 2A; 3A) brownish translucent with sparsely set black chromatophores (shown only on lateral surface of right fourth pereonite in Fig. 2A), up to 11.42 mm long, about 2.1 times longer than wide, parallel-sided, strongly vaulted, capable of conglobation.

Head (Fig. 3A; B) anterior margin simple, without incision or transverse ridges, with short, simple rostrum between separate antennule bases. Eyes weakly reniform with black pigmentation, clearly facetted with ommatidia, placed postero-laterally (Figs. 2A; 3A).
**FIGURE 2.** *Exosphaeroides quirosi* sp. nov. A, male habitus, lateral; B, left antennule, dorsal; C, detail of process on distal segment of peduncle of latter, dorsal; D, left antennary peduncle, dorsal; E, detail of spinules covering medial surface of proximal segment of latter; F, antennary flagellum, dorsal.

_Pereonites_ with posterior margin not raised (Fig. 2A). First pereonite longest with anterolateral margin not encompassing head (Fig. 3A). Pereonites 2–4 about equal in length; pereonites 5–7 shorter and subequal. Coxae of pereopods epimera-like, ventrally directed, without distinct suture with corresponding tergite, lack-
ing interlocking ridge-and-groove system (*sensu* Bruce 1994); coxae overlapping anterior over posterior. Coxa 1 distal margin straight, posterolateral angle evenly rounded, anterolateral angle produced into angular rounded lobe. Coxae 2–4 and 7 narrow and rounded, subsimilar, with anterolateral angle wanting. Coxae 5–6 broader than foregoing coxae, but similar in outline.

*Pleon* extending to lateral body margin (Fig. 3A), comprising partially incorporated pleonites 1 to 5 (five pairs of pleopods detach together with the corresponding composite somite in dissections); fusion of somites complete dorsally, partial only laterodorsally, with two well-delimited vestigial articulation lines reaching posterior margin, second line longest (Fig. 2A); sublateral “keys” (*sensu* Bruce 2005) hardly developed, each bilobed. Anterior portion of pleon covered laterally by overlapping coxal plate 7. *Pleotelson* as wide as pleon, cupolate, with scarcely concave even caudal surface (Fig. 3H).

Integument of most limbs ornamented with imbricated, comb-like and frequently setulose cuticular scales (as in Figs. 3I; 4A, F; 5A, B; 8B, D; 9A).

**FIGURE 3.** *Exosphaeroides quirosi* sp. nov. A, male habitus, dorsal; B, frontal view of epistome, with rostrum and insertions of antennules and antennae; C, detail of proximal portion of head with epistome, antennules and antennae, dorsal; D, detail of labrum and lateral lobes of epistome, posterior; E, detail of spinule on distal margin of labrum; F, paragnaths; G, detail of distal spinule on latter; H, pleotelson, ventral; I, detail of right uropod, ventral.
Epistome clearly visible in dorsal view (Fig. 3C) although not covering dorsally insertion of antennules or antennae, roughly triangular (distal margin not produced, truncate), with slightly concave lateral margins; epistome hardly constricted laterally in frontal view (Fig. 3B), deeply excavated distally, with rounded lateral lobes. Labrum globose, truncated distally, with distal margin and posterior surface covered with setules and denticulate spinules (Fig. 3D, E). Paragnaths (Fig. 3F) with densely spinulose outer lobes; distal and lateral spinules denticulated distally (Fig. 3G), medial side of lobes densely setulose; inner lobes wanting.

FIGURE 4. Exosphaeroides quirosi sp. nov., male. A, right mandible, posteromedial; B, detail of distal portion of latter, posterior; C, same, medial; D, left mandible with palp omitted, medial; E, detail of incisor and lacinia of latter; F, left maxilla, anterior.
FIGURE 5. *Exosphaeroides quirosi* sp. nov., male. A, left maxillule, posterior (ornamentation of innermost three papoose distal robust setae of medial lobe omitted); B, right maxilliped, posterior (ornamentation of distal portion of endite and of corresponding robust setae omitted); C, detail of distal portion of endite of latter, with ornamentation of subdistal robust setae omitted; D, same, now showing ornamentation of subdistal robust setae.

*Antennule* (Fig. 2B) with none of peduncle segments flattened or expanded, with up to 10-articulate flagellum. Proximal peduncle segment reflexed, articulating proximoventrally to head (Figs. 2B; 3C), massive, about twice longer than wide with concave posterior margin. Second peduncle segment about one-third length
of preceding segment, with convex anterior margin; third peduncle segment long and slender, narrow, about 4.4 times longer than wide, attaining about two-thirds length and only 27% width of proximal segment of peduncle, with setose process dorsally on distal margin (Fig. 2C). Proximal article of flagellum partially embedded into third peduncle segment, much shorter than contiguous flagellar articles; aesthetasc present on each of distal articles of flagellum except reduced distalmost article.

FIGURE 6. Exosphaeroides quirosi sp. nov., male. A, right pereopod 1; B, detail of distal portion of latter; C, left pereopod 2, anterior; D, right pereopod 3, anterior; E, right pereopod 4, posterior.
FIGURE 7. *Exosphaeroides quirosi* sp. nov., male. A, right pereopod 5, posterior; B, left pereopod 6, anterior; C, detail of distal portion of latter; D, right pereopod 7, posterior.

*Antenna* (Fig. 2D, F) three proximal segments of peduncle subsimilar in length, proximalmost with shortened posterior margin and with strongly convex anterior margin, latter covered with dense setulose fringe (*sensu* Bruce 1994; Sket & Bruce 2004), setules denticulated distally. Fourth peduncle segment 1.5 times longer than third segment. Fifth peduncle segment longest, 1.8 times longer than third segment. Flagellum up to 14-articulate.
**FIGURE 8.** *Exosphaeroides quirosi* sp. nov. A, male penial processes with insertion of first pleopods behind, anterior; B, male left first pleopod 1, anterior; C, detail of seta on distomedial angle of protopod; D, male left second pleopod 2, anterior; E, detail of tip of appendix masculina; F, female left second pleopod 2, posterior.

*Right mandible* (Fig. 4A) with incisor 3-denticulate, denticles evenly rounded. Spine row comprising six heterogeneous elements set on common socle; distal element trifurcate with two of branches multicuspitate terminally (Fig. 4B, C); adjacent two elements stout and blunt, multituberculate/multidenticulate distally; both plus distal element apparently geniculate due to presence of constriction about midway along element (for distal element) or proximally (other two elements). Three proximal elements of spine row long and slender, pap-
pose along one side only with stout spinules. Molar process columnar, cylindrical, with truncate tip; grinding
surface as described below for left counterpart; four serrate molar setae on proximal margin of process.
Smooth sclerotized plate present proximally on medial surface of mandible coxal gnathobase prior to molar
process. Palp 3-segmented, second segment longest, with row of about 14 serrate setae on anterior margin;
distal segment shorter than proximal segment, with row of ca. 16 serrate setae on anterior margin, terminal
seta longest.

![Diagram of Exosphaeroides quirosi](image)

**FIGURE 9.** *Exosphaeroides quirosi* sp. nov., male. A, right pleopod 3, anterior; B, right pleopod 4, anterior; C, right ple-
opod 5, anterior; D, detail of comb-like scales covering spheroidal processes of exopod of latter.

*Left Mandible* (Fig. 4D) as for right mandible but with 4-denticulate incisor and 3-denticulate lacinia, both
with evenly rounded denticles (Fig. 4E); lacinia similar in appearance and orientation to incisor process, with
basis developed as articular condyle associated with incisor, which acts as articular socket. Spine row com-
posed of three pappose elements along one side only, set on common socle. Molar process with broad sclerotised grinding plate smooth except for some striations present laterally about midway; proximodistal margin covered with heterogeneous array of denticles and setules as figured; three serrate molar setae set proximally on molar process.

*Maxillule* (Fig. 5A) medial lobe finger-like with patch of denticulate spinules on posterior margin, and four curved pappose robust setae (ornamentation of just one shown in Fig. 5A) and two reduced smooth robust setae distally; pappose robust setae provided with long denticulate spinules. Lateral lobe with 11 denticulate robust setae and two short, conical smooth robust setae distally; isolated stiff serrate seta plus pore located subdistally on posterior surface of endite.

*Maxilla* (Fig. 4F) medial lobe slender with c. 25 terminal spinulose robust setae disposed following two parallel rows, plus longer unipectinate robust seta on distomedial corner; medial margin of endite covered with long denticulate spinules. Middle and lateral lobes each with 10 distal comb-like robust setae.

*Maxilliped* (Fig. 5B) with unarmed coxa. Basis elongate, about 2.3 times longer than wide, with patch of denticulate spinules proximally on anterolateral margin; endite spatulate with row of eight pappose robust setae distally (Fig. 5C) and row of six spinulose robust setae subdistally (Fig. 5D) on posterior surface; isolated pappose robust seta close to medial margin on anterior surface of endite, and single coupling hook on posterior surface, also close to medial margin; posterodistal and anteromedial surfaces of endite covered with densely set denticulate spinules. Palp segments 2–4 each with densely setose distomedial lobes and with subdistal seta on outer margin; segment 5 about 3.5 times longer than wide and shorter than preceding segment, densely setose distomedially.

*Pereopods* P2 through P7 (Figs. 6C–E, 7) subsimilar, ischium with rounded process distally at each side; distal angle of outer margin of merus produced into lobe crowned with transverse row of short stiff serrulate setae; row of setae present also on outer distal angle of subrectangular carpus; anterior surface of propodus produced distally into rounded plate articulated basally in P3 to P7 (Fig. 7C), fused to propodus in P2 (Fig. 6C; and also in P1; see Fig. 6B); dactylus with short, stout curved unguis and with shorter smooth stout robust seta subdistally on medial margin (“accessory unguis”). *Pereopod 1* (Fig. 6A) lacking distal row of short stiff serrulate setae on anterior margin of carpus, with two short robust setae on distal corner of medial margin of propodus (Fig. 6B). Relative length of pereopods as follows: P3>P4>P6>P5>P2>P7>P1; but P3 and P4 and P5 and P6 about similar in size. *Pereopod 3* differing from rest in presence of additional row of short, stiff serrulate setae on distal corner of medial margin of carpus (Fig. 6D).

*Penes* (Fig. 8A) slender, about 2.8 times longer than basal width and not extending beyond distal margin of protopods of first pleopods, straight and smooth, closely set proximally, converging at rounded tips.

So-called “pleonal sternite” (*sensu* Sket & Bruce 2004; or also “pleonal tergite” provided with “sternal process” *sensu* Bruce 1994), wanting (Fig. 8A). Pleopods biramous, lamellar, 1–3 with medial margin of protopod expanded into wide lobe with setulose margins and with two robust setae on distomedial angle, setae denticulated distally, with several transverse rows of setules proximally (Fig. 8C); pleopods 4 and 5 with lateral margin of protopod inconspicuous and with rami lacking ridges.

*Pleopod 1* (Fig. 8B) protopod lacking outer seta; endopod triangular with rounded angles, distal half of medial and lateral margins fringed with plumose setae, proximal medial margin densely setulose; exopod subrectangular with convex margins, fringed with plumose setae along lateral and distal margins, proximal element of row on lateral margin transformed into robust seta, proximal margin densely setulose.

*Pleopod 2* (Fig. 8D) differing from preceding limb in presence of seta on distal angle of lateral margin of protopod, latter margin setulose; exopod with shorter proximal margin, and with proximal element of armature series along lateral margin as ordinary slender seta instead of robust seta; endopod with slightly concave lateral and medial margins. *Appendix masculina* (Fig. 8E), simple (not acuminated, nor narrowed, nor with apex bent), about 10.5 times longer than maximum width, extending beyond tip of endopod, implanted proximally on medial margin of latter.
**Pleopod 3** (Fig. 9A) resembling second, but with marginal setation of endopod highly reduced, and with exopod apparently 2-segmented due to clear expression of transverse suture.

**Pleopod 4** (Fig. 4B) with tiny seta on distal corner of outer margin. Exopod proximal segment with row of smooth reduced setae along outer margin. Distal segment slightly longer than proximal, with setae along lateral and distal margins only, setae sparsely set, those on distal margin and on distal portion of lateral margin plumose, rest simple and reduced. Endopod foliaceous, smooth, apparently 2-segmented due to expression of transverse suture proximally.

**Pleopod 5** (Fig. 9C) as preceding limb but with setulose distolateral margin of protopod and with foliaceous exopod. Latter also 2-segmented, but transverse intersegmental articulation line not so well defined, looking like strip of distended arthrodial membrane; distal segment smooth except for two pairs of spheroidal processes placed terminally and subdistally on medial margin, respectively; processes densely covered with imbricated crescent comb-like scales (Fig. 9D). Presumed intersegmental suture line on endopod incompletely expressed medially.

**Uropods** (Fig. 3I, H) with both rami lamellar, with naked margins.

**Description of female.** None displaying oostegites or carrying embryos in brood pouches, thus all probably immature. Body smaller than male (up to 8.82 mm long). Morphology as for male except for lack of setulose fringe on pereopods and for morphology of second pleopod (Fig. 8F), lacking appendix masculina and with corresponding medial margin of endopod straight and setulose.

**Etymology.** Species name derived after the explorer Pedro Fernandez de Quirós, the first European to reach Espíritu Santo (1606).

**Remarks.** *Exosphaeroides quirosi* sp. nov. from Vanuatu differs from any other sphaeromatid in the unusual condition shown by the exopod of the fourth pleopod, which has a falcate outline, is distinctly longer than the corresponding endopod, and has the medial margin of the proximal segment produced into a foliaceous endite. Seemingly, the sexual dimorphism expressed in the presence/absence of a setulose fringe on the pereopods had not been recorded previously in other sphaeromatids. Another character state displayed by the new taxon that occurs infrequently in sphaeromatids consists of the complete incorporation of the first pleonite to the rest of pleonites, with no trace of suture line or articulation retained in between.

*E. quirosi* belongs to a group of sphaeromatid genera characterised by a broadly rounded pleotelson which lacks a well-defined posterior exit channel or foramen, uropods with lamellar rami, head and pereonites lacking integumental sculpture, and pleotelson also usually smooth or displaying a weak sculpture at most. These genera include: *Benthosphaera* Bruce, 1994; *Bilistra* Sket & Bruce, 2004; *Exosphaeroides* Holdich & Harrison, 1983; *Exosphaeroma* Stebbing, 1900 (partim); *Lekanesphaera* Verhoeff, 1943; *Neosphaeroma* Baker, 1926; several members of *Sphaeroma* Bosc, 1802; and *Thermosphaeroma* Cole & Bane, 1978 (Sket & Bruce 2004; Bruce 1994; 2005). Apart from the autapomorphic traits listed above, *E. quirosi* is sufficiently different to several of the mentioned genera as to preclude its assignment. Thus, *Neosphaeroma* displays elongated penes and the exopod of uropods is excised and conspicuously shorter than the endopod. *Lekanesphaera* and *Sphaeroma* show a lanceolate, apically acute exopod of uropods and bear stiff setae on the outer margin of ischium of pereopods 1–3. *Benthosphaera* differs in the distally setose endopod of the third pleopod and in the falcate apex of the exopod of uropod. *Thermosphaeroma* has ridges on pleopods 4 and 5 and an acute uropodal endopod. *E. quirosi* differs from *Exosphaeroma s. str.* (as characterised by the type species *E. gigas* (Leach, 1818) and related species; Brandt & Wägele 1989) in lacking flat lobes on pleonite 1 and partial exit groove or channel on the posterior margin of the pleotelson (i.e. it is arcuate, simple), whereas the lateral margin of ischium of pereopods 1–3 bears long setae.

The remaining two genera are rather similar to *E. quirosi*. Thus, *Bilistra* lives in a similar habitat, is similar in size, displays a simple arcuate pleotelson posterior margin, and also a dense setulose fringe on most pereopods; but it shows a short uropodal exopod (Sket & Bruce 2004). *Exosphaeroides* is again very similar, with a similar pleonal morphology, but the inferior posterior margin of the pleotelson is rather wider, ventrally with a partial exit channel (Holdich & Harrison 1983).
Differences considered as of generic significance among these genera mainly involve the morphology of uropods, maxillipedal palp, pereopods and pleopods. Such differences could support the eventual erection of a new, monotypic genus for the new taxon, but it is included here in the broad Exosphaeroma s. l. cluster (see Bruce 2003; which would include Exosphaeroides also), from which most freshwater sphaeromatid seem to derive. This is done with the caveat that it is incertae sedis in Exosphaeroides until such time as a comprehensive revision of Exosphaeroma and related genera has been undertaken. It would be a Exosphaeroma-derived species with an unusual pleopod 4 and fusion of pleonite 1 to the remainder of the pleon; these features being here regarded as species-level apomorphies within a morphologically diverse genus.

Exosphaeroides currently comprises two species. E. fluvialis Holdich & Harrison, 1983, the type species, is restricted to brackish-water sites in rivers along the Queensland coast (eastern Australia; Holdich & Harrison 1983). The second species E. quadricosta Kensley, 2003 has been assigned to Exosphaeroides, although Kensley acknowledged that this generic assignment was a problematic issue and a matter of convenience. It is worth mentioning that E. quadricosta, known only from Easter Island in the south Pacific and presented as a purely freshwater sphaeromatid, actually lives in mixohaline wells and pools on the seashore subjected to freshwater flow only at low tide (D. J., pers. obs.).

According to Sket and Bruce (2004) and Bruce (2005), only six genera of Sphaeromatidae contain purely freshwater taxa. Of those, only the northern Pacific genus Gnorimosphaeroma Menzies, 1954, which includes six freshwater species, contains marine members too. The riverine Pseudosphaeroma platense (Giambiagi, 1922) from Argentina cannot, according to Harrison (1984), be retained in the genus Pseudosphaeroma Chilton, 1909 and a new genus should be erected to accommodate it (Harrison, 1984). Europe harbours the stygotbic genera Caecosphaeroma Dollfus, 1896 (three species) and Monolistra Gerstaecker, 1856 (35 taxa), whereas Thermosphaeroma Cole & Bane, 1978 (eight species) is restricted to thermo-mineral springs of California, Texas and Mexico. Other two strictly freshwater genera are known only from New Zealand, viz. Bilistra Sket & Bruce, 2004 (three species, one epigean and two cave-dwelling), and Makarasphera Bruce, 2005 (coastal rivulets, monotypic).

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