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RESEARCH ARTICLE

Diversity and distribution of the *Macrothrix paulensis* species group (Crustacea: Cladocera: Macrothricidae) in the tropics: what can we learn from the morphological data?

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Abstract – Over the last 20 years significant progress was achieved in morphological investigations of the genus *Macrothrix* Baird (Cladocera: Macrothricidae). The *Macrothrix paulensis* species group is known from tropical and subtropical regions all around the World. In this paper we redescribe *M. capensis* (Sars, 1916) based on material from the Republic of South Africa, and describe a new species, *M. australiensis* sp. nov. from Australia. A cladistic analysis of 19 morphological characters in 12 taxa (including *M. triserialis* Brady, 1886 as an outgroup) derived from our analysis of original samples and literature data, resulted in 18 equally-parsimonious trees. Within the *M. paulensis* group, we can recognize a basal section with five taxa (*M. atahualpa* Brehm, 1936, *M. smirnovi* Ciros-Pérez and Elías-Gutiérrez, 1997, *M. agsensis* Dumont, Silva Briano and Subhash Babu, 2002, *M. capensis*, *M. australiensis* sp. nov.) which are both biogeographical and phylogenetic relicts. They occur exactly in well-known zones of cladoceran endemism: Australia, South Africa, the Andean highlands and Mexican Plateau with surrounded territories. In contrast, the crown group is widely distributed in tropical lowlands. No truly "Pantropical" taxa were found, all taxa could be classified as: (1) exclusively Neotropical; (2) exclusively Australian; (3) Palaeotropical (Afro-Asian); (4) endemics of Mexican Plateau. Probably a combination of scenarios took place during history of the *M. paulensis* group, but we can conclude that all possible scenarios are old, which confirms antiquity of the *M. paulensis* group. Australia and Tasmania could be a source of additional species from this group.

Keywords: morphology / redescription / new species / pantropical distribution / biogeography / *Macrothrix*

1 Introduction

Taxa of the family Macrothricidae Norman and Brady, 1867 (Crustacea: Branchiopoda: Cladocera) are important members of littoral and phytophylous communities in fresh water bodies around the world. Sometimes, especially in the macrophyte zone of tropical water bodies, they occur in a very high abundance (*e.g.* Thomas, 1961) or, at least, dominate among microscopic animals (Smirnov, 1976; Dumont, 1994). As primary consumers, macrothricids may constitute a significant part of fish diets, including economically important fish species (Baird, 1850; Oliver, 1991; Meschiatti and Arcifa, 2002). However, taxonomy of the Macrothricidae has attracted little attention of cladoceran investigators for a long time. Lack of reliable morphological features for species identification slowed down accumulation of knowledge on the macrothricid diversity and distribution. According to Löffler (1968) macrothricid taxonomy was "hopeless", and Korovchinsky (1996) even concluded that there were no unambigously accepted ("valid" in his understanding) species among the Macrothricidae at the time of his publication. Smirnov (1976, 1992) performed the first global attempts to accumulate all previous taxonomic data on the family and offered original comprehensive identification keys. Of course, in some cases these keys allowed to identify specimens only to the species group level, but his publications attracted attention of the hydrobiologists to certain macrothricid taxa and became a basis for all subsequent taxonomic works.

Afterwards main efforts were concentrated on the revision of the genus *Macrothrix* Baird, 1843, where only few investigations concerned a formal establishment of the taxa new to science (Ciros-Pérez *et al.*, 1996; Ciros-Pérez and Elías-Gutiérrez, 1997; Elías-Gutiérrez and Smirnov, 2000). Some papers were dealing with detailed redescriptions of forgotten taxa (Smirnov and Bayly, 1995; Kotov, 1999;

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Garfias-Espejo *et al.*, 2007; Kotov, 2008) or combined redescriptions of poorly known taxa and descriptions of new species (Silva-Briano *et al.*, 1999; Dumont *et al.*, 2002; Kotov and Hollwedel, 2004; Kotov *et al.*, 2004, 2005; Kotov, 2007b). Moreover, some taxa earlier designated to other genera or subgenera were reinvestigated and transferred to *Macrothrix* (*e.g.* Kotov and Hollwedel, 2004; Kotov *et al.*, 2005). As a result of these efforts, data of macrothricid morphology were significantly supplemented according to current standards accepted in cladoceran taxonomy and new diagnostic features were found, making taxon identification more accurate (Silva-Briano, 1998; Dumont and Silva-Briano, 1998; Kotov, 1999, 2008). As a result, a recent understanding of the genus *Macrothrix* was determined more precisely (Kotov and Hollwedel, 2004; Kotov *et al.*, 2005; Kotov, 2007b, 2008). Although some unresolved problems still remain (especially in discrimination of small-sized taxa), well studied groups within *Macrothrix* have been outlined to date.

The *Macrothrix paulensis* species group is among them (Kotov and Hollwedel, 2004; Kotov *et al.*, 2005). This group was first recognized by Kotov and Hollwedel (2004) and later by Kotov *et al.* (2005), and its relation with dubious genera *Iheringula* Sars and *Echinisca* Liévin was discussed. The members of this group inhabit tropical and subtropical water bodies with a developed macrophyte belt. These taxa have a relatively large size (up to 1.5 mm) and peculiar morphological traits: (1) a large, triangular labrum; (2) a subquadrangular postabdomen; (3) large spines at inner margin of antenna I; (4) robust spinules on the seta located on the proximal segment of antenna II endopod; (5) a single ejector hook on the thoracic limb I (see discussion of these features in Kotov *et al.*, 2005). Well-recognized diagnostic features allow us to consider *M. paulensis* species group as a nice example both for detailed morphological comparison and biogeographical speculations.

According to Kotov and Hollwedel (2004) and Kotov *et al.* (2005), the *M. paulensis* group include three well described species in tropical regions of the New World (*M. paulensis* (Sars, 1900), *M. sioli* (Smirnov, 1982) and *M. brandorffi* Kotov and Hollwedel, 2004) and two species from the Old World (*M. odiosa* Gurney, 1916 and *M. pholpunthini* Kotov, Maiphae and Sanoamuang, 2005). *M. malaysiensis* Idris and Fernando, 1981 from Malaysia (Idris and Fernando, 1981b) is considered as a closest relative of this group, but it still has not been investigated in detail due to its rarity (Kotov *et al.*, 2005). *M. atahualpa* Brehm, 1936 inhabits the Andes and is also considered as a relative of the *M. paulensis* group, but differing from the latter in the morphology of the ventral margin of the head and armature of antenna I (Kotov *et al.*, 2010). Remarkably, material of the *paulensis*-group from Africa and Australia was not studied in detail during previous revisions. Only Smirnov (1992) tried previously to investigate populations of the *paulensis*-like macrothricids from these two continents, yet he did not reveal any valuable peculiarities of African and Australian populations.

This situation reflects the main pattern of recently conducted taxonomic revisions. Tropical regions of the New World are intensively investigated by methods of classical morphological (Cervantes-Martínez *et al.*, 2000; Sinev and Hollwedel, 2002; Sinev *et al.*, 2004; Kotov *et al.*, 2005; Dumont *et al.*, 2013; Elmoor-Loureiro, 2014; Sousa *et al.*, 2015, Sousa *et al.*, 2016a, b and others) and molecular analysis (Elías-Gutiérrez and Valdez-Moreno, 2008; Elías-Gutiérrez *et al.*, 2008). Also, taxonomic papers of high quality were published on the Cladocera of South Asia (*e.g.* Padhye and Dumont, 2014; Neretina and Sinev, 2016) and Southeast Asia (Sinev and Sanoamuang, 2007; Kotov *et al.*, 2013b; Van Damme and Maiphae, 2013; Van Damme *et al.*, 2013a; Sinev *et al.*, 2016 and others). At the same time, detailed taxonomic publications dealing with African cladocerans are not so numerous (Sinev, 2006, 2008; Van Damme and Dumont, 2009; Kotov and Taylor, 2010; Van Damme *et al.*, 2013b; Neretina and Kotov, 2015; Neretina and Sinev, 2016). Also, many Australian taxa are still waiting for a reassessment on the current level of morphological analysis (*e.g.* Smirnov, 1995), although some detailed taxonomic works concerning Australia were published as well (Sinev, 1997, 2004; Van Damme *et al.*, 2007; Sinev and Shiel, 2012).

Keeping in mind obvious problems concerning the cladoceran taxonomy in Africa and Australia, we were not surprised when we found a forgotten species of the *paulensis*-group, *M. capensis* (Sars, 1916), in the Republic of South Africa and discovered populations belonging to a similar form turning put to be a new taxon from Australia. Moreover, our re-consideration of some taxa from Mexican plateau earlier regarded as members of the *M. triserialis* group (Dumont *et al.*, 2002) led to conclusion that they are, in reality, also members of the *M. paulensis* group.

The main aims of our paper are: (1) to redescribe morphology of *M. capensis* in detail; and (2) to describe a new species of the *paulensis*-group from Australia; (3) to discuss the morphology of *M. odiosa* with clarification of some ambiguities in its taxonomy in Africa; (4) to compare the morphology of all currently well-described nowadays members of the *paulensis*-group; (5) to analyze original and literature data on their distribution and to evaluate potential zoogeographic scenarios.

2 Materials and methods

Samples in 4% formaldehyde from Africa (the Republic of South Africa, Namibia and Ethiopia), Southeast Asia (Thailand), Australia and South America (Chile) were preliminarily inspected in small Petri dishes under a stereoscopic binocular microscope LOMO. Specimens were transferred to drops of glycerol–formaldehyde mixture on slides and examined under an Olympus BX41 light microscope. At least two adult parthenogenetic females and two adult males (where they were available) from each sample were dissected *via* tungsten needles, and features important for the taxon identification were checked.

Several specimens were dehydrated in increasing ethanol series (30, 50, 70, and twice in 96%), transferred to 100% acetone (40 min each series), and to hexamethyldisilazane (40 min) (Laforsch and Tollrian, 2000). Then specimens were dried overnight on air, covered with gold *via* S150A Sputter Coater (Edwards, UK) and investigated under scanning electron microscope CamScan MV 2300 (Tescan, Czech Republic), at accelerating voltage 20 kV and working distance 15 mm.

For morphological descriptions we used terminology summarized by Kotov (2013).

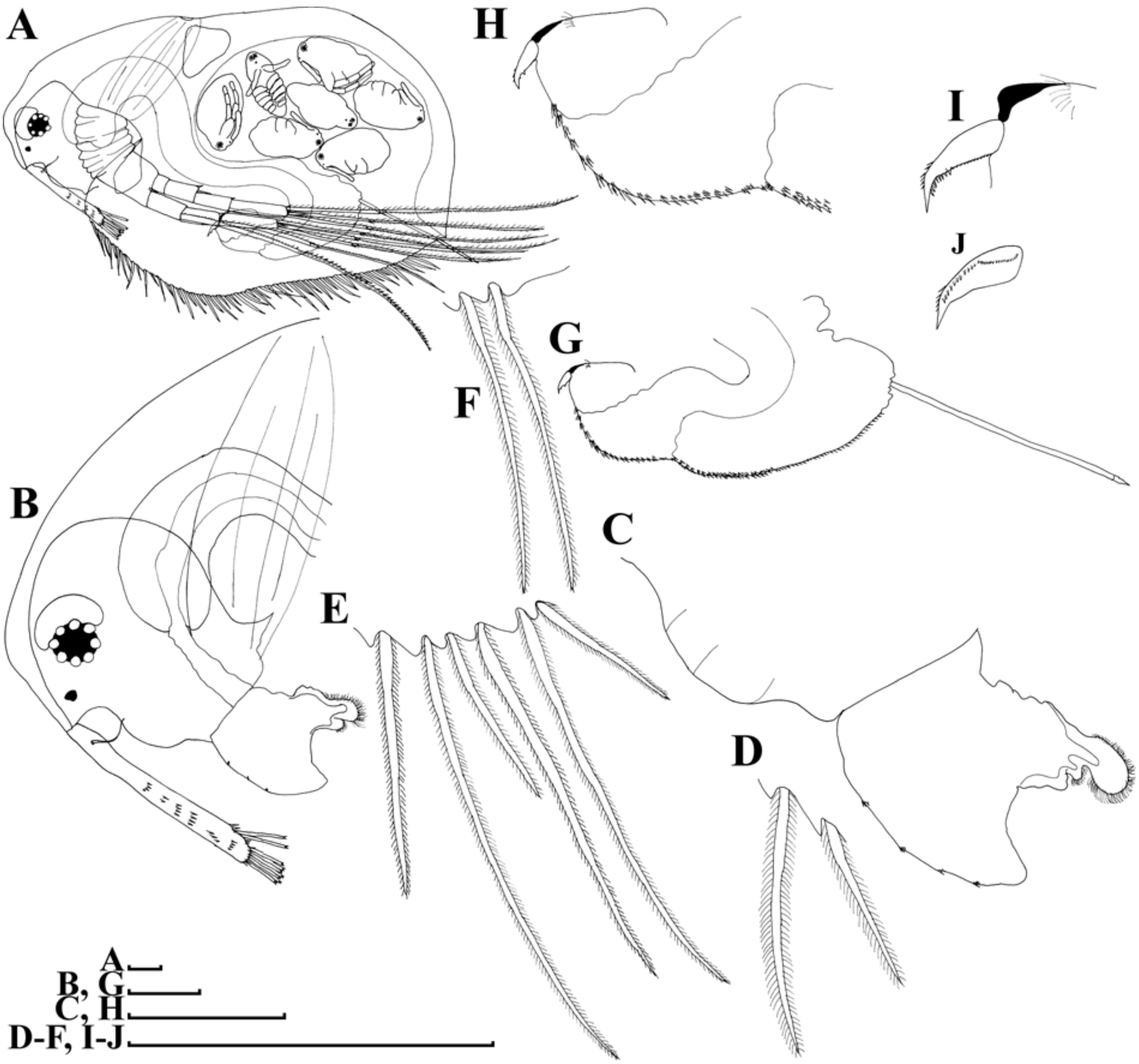

Fig. 1. *Macrothrix capensis* (Sars, 1916), parthenogenetic female from Rocher Pan (S 32.6094°, E 18.3003°), Western Cape, coll. 11.12.2000 by G. Jones, NNS-2002-244. A, Adult parthenogenetic female, general view. B, Head. C, Labrum. D, Armature of anterior margin of valve. E, Armature of ventral margin of valve. F, Armature of posterior margin of valve. G, Postabdomen. H, Distal portion of postabdomen. I, Postabdominal claw, outer view. J, Postabdominal claw, inner view. Scale bars: 0.1 mm.

A cladistic analysis was performed using PAUP program Vers. 4.0a for 32 bit Microsoft Windows (Swofford, 1993), using branch-and-bond search with an aim to elucidate the possible phylogeny of *M. paulensis* group. We considered *M. triserialis* group is an outgroup to the *M. paulensis*-like species. In some cases characters used in this analysis vary within the latter and were encoded as "data missing". A bootstrap simulation of 1000 replications was performed as a test of the robustness of these analyses.

Abbreviations for collections. AAK, Personal collection of A.A. Kotov, A.N. Severtsov Institute of Ecology and Evolution (Moscow, Russia). ANN, Personal collection of A. N. Neretina, A.N. Severtsov Institute of Ecology and Evolution (Moscow, Russia). MGU, Collection of the Zoological Museum of M.V. Lomonosov Moscow State University (Moscow, Russia). NNS, Personal collection of Prof. N.N. Smirnov, A.N. Severtsov Institute of Ecology and Evolution (Moscow, Russia). SAM, South Australian Museum (Adelaide, Australia).

Abbreviations in illustrations and text. I–V = thoracic limbs I–V; e1–e5 = endites 1–5 of thoracic limbs; ejh = ejector hook on limb I; epp = epipodite; ext = exopodite; IDL = inner distal lobe of limb I; ODL = outer distal lobe of limb I; pep = preepipodite; *s* = sensillum.

3 Results

(1) Redescription of *Macrothrix capensis* (Sars, 1916) *versus M. odiosa* Gurney, 1916 and questions on their distribution within Africa

Order Anomopoda Sars, 1865
Family Macrothricidae Norman and Brady, 1867
Genus *Macrothrix* Baird, 1843

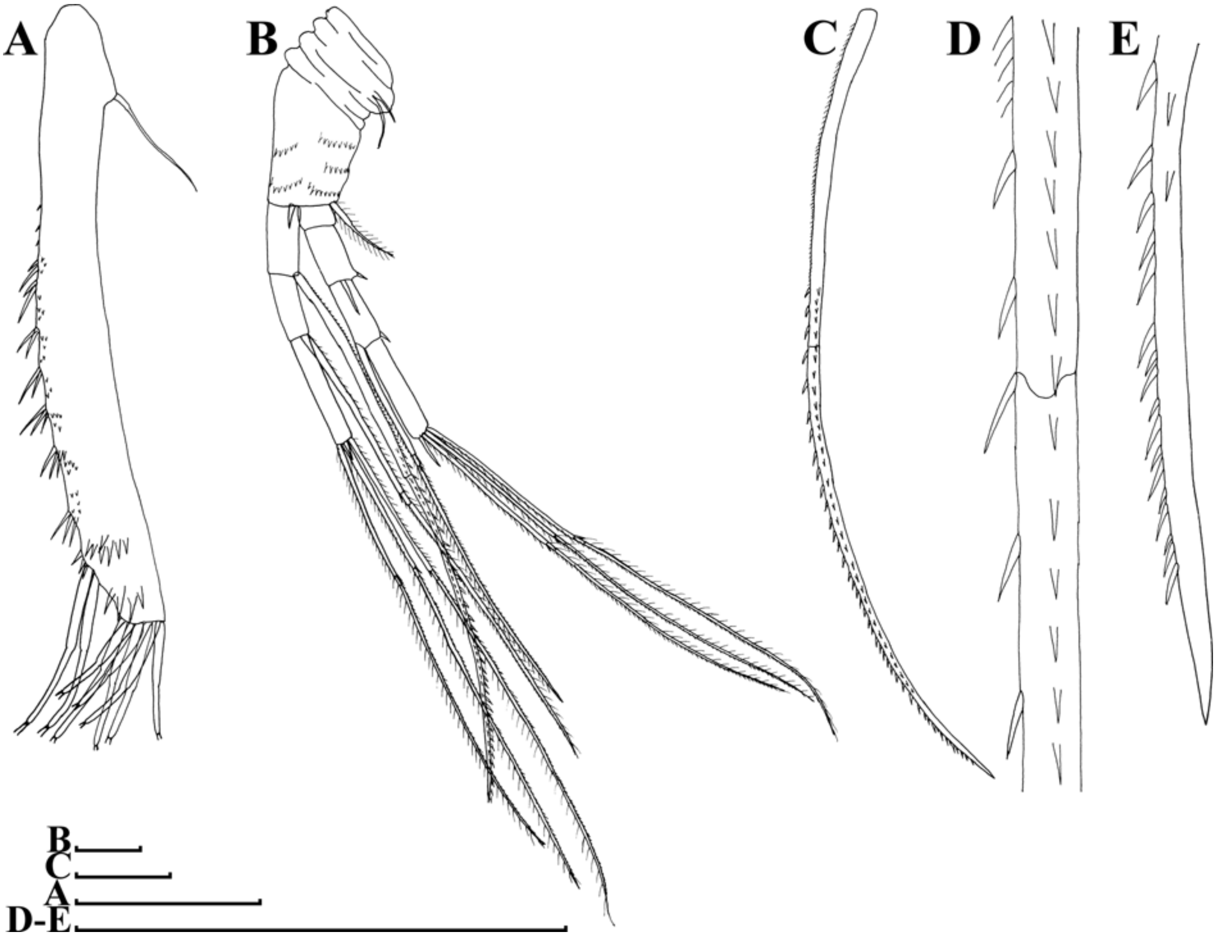

Fig. 2. *Macrothrix capensis* (Sars, 1916), parthenogenetic female from Rocher Pan (S 32.6094°, E 18.3003°), Western Cape, coll. 11.12.2000 by G. Jones, NNS-2002-244. A, Antenna I. B, Antenna II. C, Lateral seta of basal endopod segment of antenna II. D, Its central part. E, Its distal part. Scale bars: 0.1 mm.

***Macrothrix capensis* (Sars, 1916)**
(Figs. 1–5)
Sars (1916): p. 323–324, plate XXXVI, figs. 1a–d.
Smirnov (1992): p. 87–89, figs. 363–374.

Type material. Apparently lost.

Type locality. Port Elizabeth, Eastern Cape, the Republic of South Africa.

Material examined (all samples from the Republic of South Africa). Over 10 parthenogenetic females from Eastern Cape, collection details are unknown, NNS-1997-054; 10 parthenogenetic females from Kruispad (S 32.8700°, E 18.2564°), Western Cape, coll. 10.08.2000 by G. Jones, NNS-2002-205; 10 parthenogenetic females from Springfield (S 34.7375°, E 19.9111°), Western Cape, coll. 24.08.2000 by G. Jones, NNS-2002-215; 10 parthenogenetic females from Wiesdrif (S 34.6750°, E 19.9041°), Western Cape, coll. 23.09.2000 by G. Jones, NNS-2002-219; 10 parthenogenetic females from Lang Pan (S 34.6161°, E 19.8917°), Western Cape, coll. 23.08.2000 by G. Jones, NNS-2002-225; 1 parthenogenetic female from Langvlei (S 33.9914°, E 22.6947°), Western Cape, coll. 11.10.2000 by G. Jones, NNS-2002-236; 10 parthenogenetic females from Langvlei (S 33.9914°, E 22.6947°), Western Cape, coll. 11.10.2000 by G. Jones, NNS-2002-237; 5 parthenogenetic females from Grootrondevlei (S 34.2383°, E 18.3825°), Western Cape, coll. 25.10.2000 by G. Jones, NNS-2002-239; 15 parthenogenetic females from Skulpadvlei (S 34.3275°, E 18.4508°), Western Cape, coll. 06.10.2000 by G. Jones, NNS-2002-240; 10 parthenogenetic females and two ephippial females from Rocher Pan (S 32.6094°, E 18.3003°), Western Cape, coll. 11.12.2000 by G. Jones, NNS-2002-244; 15 parthenogenetic females from Soetendalsvlei wetland (S 34.3672°, E 18.8847°), Western Cape, coll. 31.01.2001 by G. Jones, NNS-2002-246; 3 parthenogenetic females from an unknown locality, coll. in September of 1997 by M. Groodman, NNS-2002-262.

Diagnosis. Species of large size for the genus (length of adult parthenogenetic female up to 1.3 mm). Body of parthenogenetic female as for genus (see Smirnov, 1992). Dorsum not elevated significantly above head. Serration on dorsum not expressed. Posterodorsal angle of valves smooth. Head pore located on the level of head. Ventral head margin with a projection. Labrum of moderate size, rounded. Postabdomen subquadrangular, postabdominal flaps not prominent. Anal margin of postabdomen covered by fine denticles. Antenna I rod-like, with a row of bunches of gracile denticles. Antenna II as for the genus. Armature of

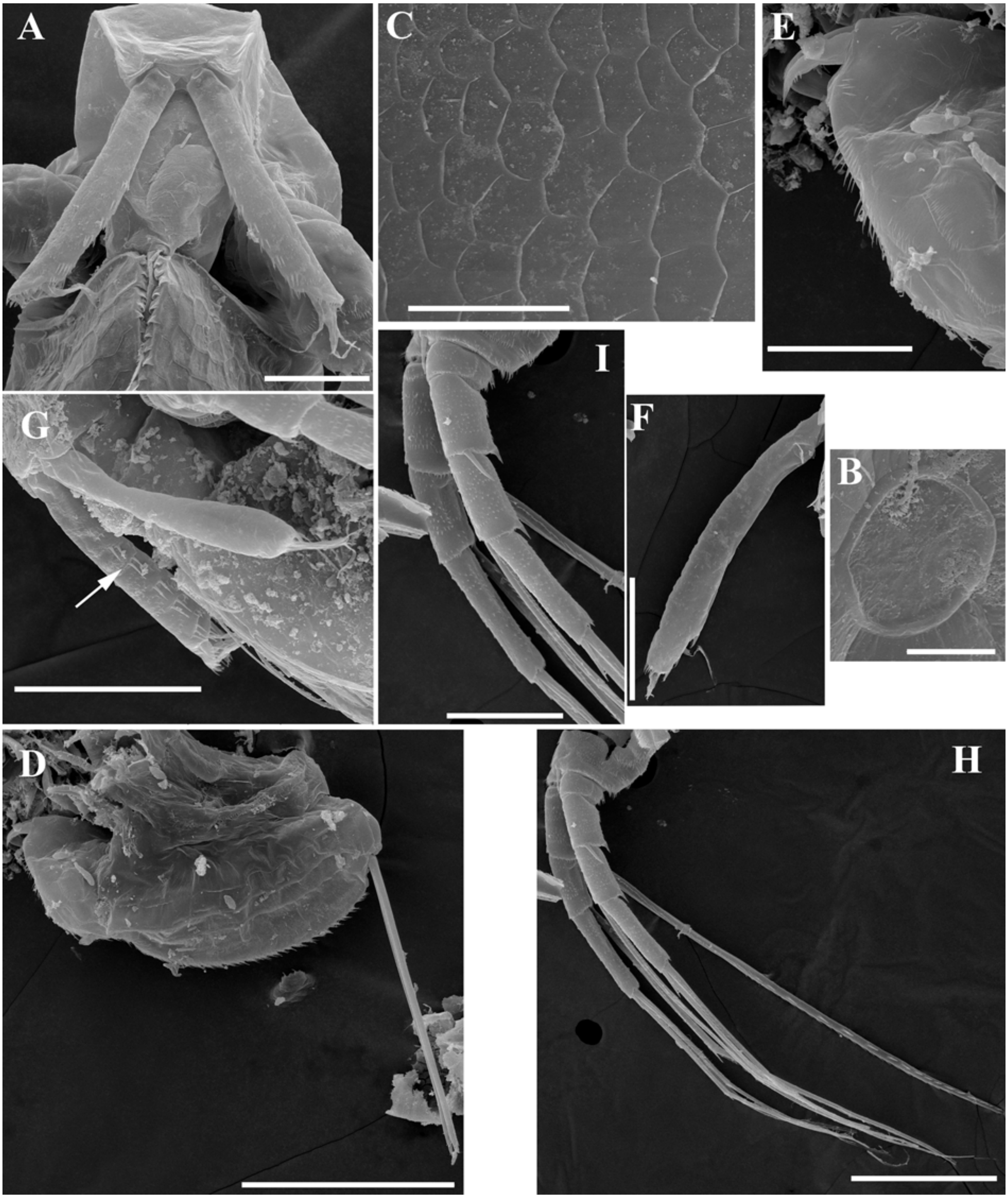

Fig. 3. *Macrothrix capensis* (Sars, 1916), parthenogenetic female from Rocher Pan (S 32.6094°, E 18.3003°), Western Cape, coll. 11.12.2000 by G. Jones, NNS-2002-244. A, Head (ventral view). B, Dorsal pore. C, Central part of valve. D, Postabdomen. E, Distal portion of postabdomen. F–G, Antenna I. H, Antenna II. I, Exopod and endopod branches of antenna II. Scale bars: 0.2 mm for D, H, 0.1 mm for A, F–G, I, 0.05 mm for C, E, 0.01 mm for B.

proximal endopod segment seta of antenna II represented by a row of robust denticles. Spine on the second exopod segment seta of antenna II long, reaches 1/2 length of third exopod segment. Thoracic limb I bears a single ejector hook. Thoracic limb II as for the genus. On exopodite of thoracic limb III seta 3 subequal in length to seta 2. On exopodite of thoracic limb IV seta 2 almost subequal in size to seta 1. Thoracic limb V as for the genus. Ephippial female similar to parthenogenetic female. Ephippium typical for macrothricids, brownish, with elongated inflated hillocks, containing two eggs. Male as for the genus, male seta in the middle of antennular body.

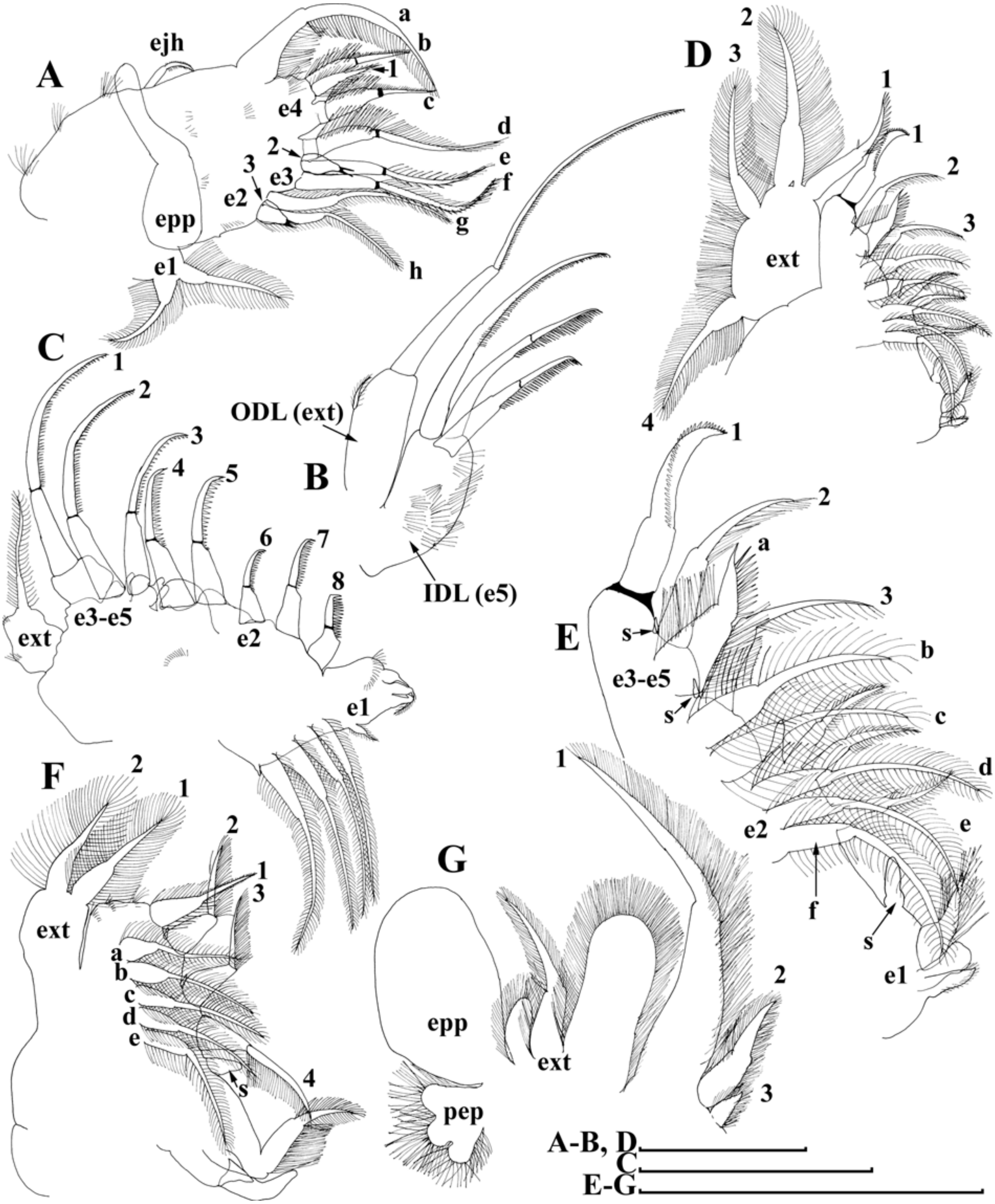

Fig. 4. *Macrothrix capensis* (Sars, 1916), parthenogenetic female from Rocher Pan (S 32.6094°, E 18.3003°), Western Cape, coll. 11.12.2000 by G. Jones, NNS-2002-244. A, Corm of limb I. B, Distal part of limb I. C, Limb II. D, Limb III. E, Fragment of limb III. F, Limb IV. G, Limb V. Scale bars: 0.1 mm.

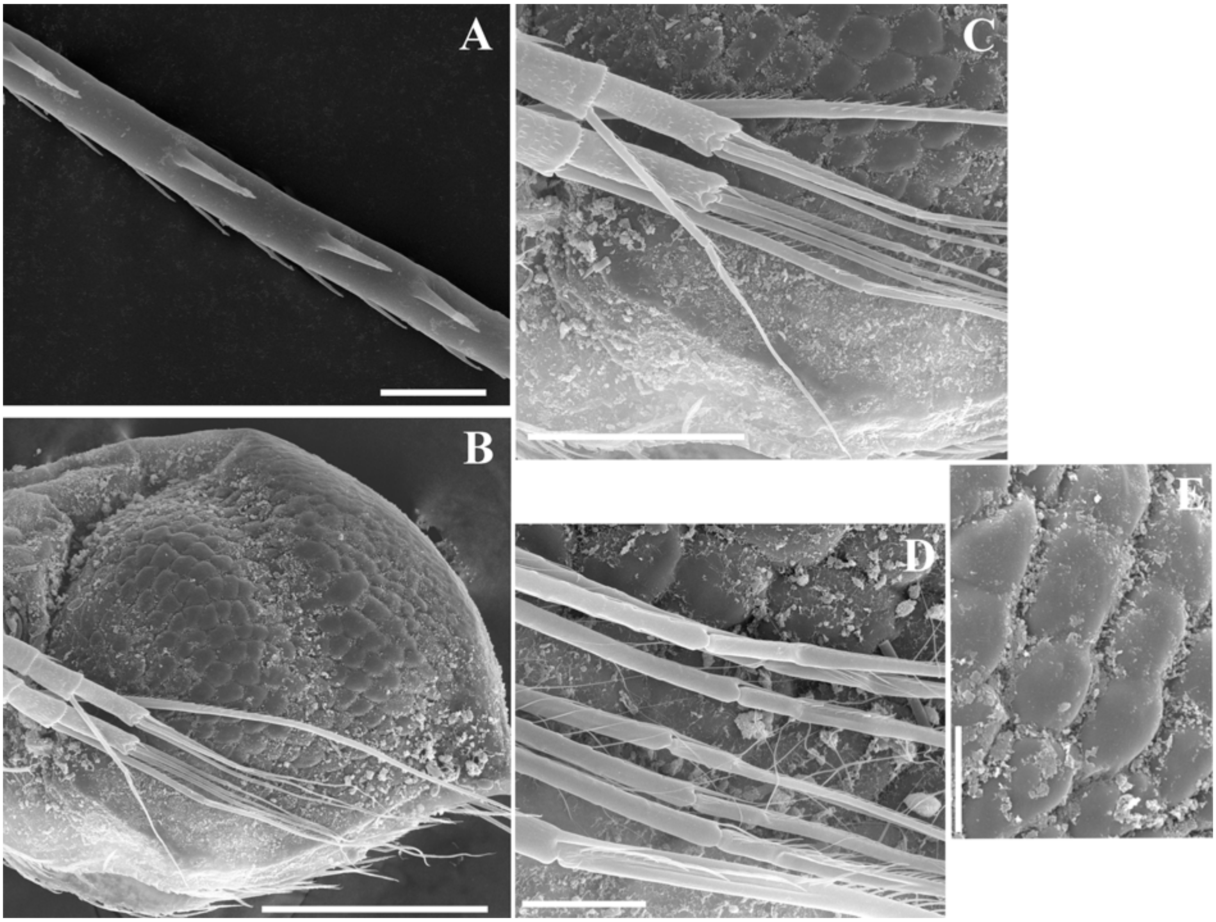

Fig. 5. *Macrothrix capensis* (Sars, 1916), females from Rocher Pan (S 32.6094°, E 18.3003°), Western Cape, coll. 11.12.2000 by G. Jones, NNS-2002-244. A, Parthenogenetic female. B–E, Ephippial female. A, Central part of lateral seta of basal endopod segment of antenna II. B, Ephippium (general view). C, Distal segments of antennal branches. D, Apical swimming setae. E, Fragment of ephippium. Scale bars: 0.2 mm for B, 0.1 mm for C, 0.02 mm for A, D–E.

Redescription

Parthenogenetic female. In lateral view body ovoid (Fig. 1A), maximum height at middle of body (body height/length ratio about 0.65). In dorsal and ventral view body compressed laterally. Dorsal margin arched from tip of rostrum to posterior most point, interrupted by a low dome over compound eye, and small depression posterior to dorsal head pore (Fig. 1A). Dorsal margin of valves not elevated significantly above dorsal margin of head (Fig. 1A). Posterodorsal margin broadly rounded (Fig. 1A). Posterodorsal angle smooth, obtuse (Fig. 1A). Ventral margin convex, covered by setae of different size in different regions of valves (Fig. 1A, D–F). Anteroventral angle rounded (Fig. 1A). Valves with a sculpture represented by polygons (Fig. 3C).

Head large (Fig. 1B), head length from tip of rostrum to border with valves makes up to 0.38 times of body length. In lateral view, dorsal margin of head with a low dome above eye (Fig. 1B). Head ventral margin with a single rounded projection (Figs. 1B, 3A). Compound eye significantly larger than ocellus (Fig. 1B). In anterior view, rostrum compressed laterally, with a small split-like frontal head pore located close to its frontal edge. Dorsal head pore large, rounded, with prominent ring around it, located on posterior part of head shield (Fig. 3B). Labrum of moderate size, with rounded apical portion (Fig. 1C). Ventral margin of labral keel with four transverse rows of setules (Fig. 1C). Distal labral appendage finely setulated (Fig. 1C).

Thorax relatively long (Fig. 1A). Abdomen short (Fig. 1A).

Postabdomen subrectangular in lateral view (Figs. 1G, 3D), slightly narrowing distally; postabdomen length/height ratio about 3.3. Ventral margin straight to slightly convex, with a bunch of fine setules (Figs. 1G, 3D). Preanal margin long, in about 2.6 times longer than anal margin. Postanal margin in three times shorter than anal margin (Figs. 1G–H, 3D–E). Preanal margin bears bunches of stiff setules. Also, transverse rows of stiff setules covered postanal and anal margins, but there are no hair-like setules (Figs. 1H, 3E) (in contrast to *M. paulensis* and *M. brandorffi*, see Kotov and Hollwedel (2004)). Not prominent postabdominal flaps at side of anus (Fig. 1G–H). Postabdominal seta as long as postabdomen (Figs. 1G, 3D), with a short distal segment. Unfortunately, due to failed fixation, setules on postabdominal seta were not kept. Postabdominal claw small (smaller than postanal margin of postabdomen), curved, with a pointed tip and a relatively wide

Q1 **Table 1.** Comparison between *Macrothrix paulensis*-like species (based on original data and Sars, 1916; Harding, 1955; Idris and Fernando, 1981b; Ciros-Pérez and Elías-Gutiérrez, 1997; Dumont *et al.*, 2002; Kotov and Hollwedel, 2004; Kotov *et al.*, 2005, 2010; Garfias-Espejo *et al.*, 2007).

Feature	*Macrothrix paulensis* (Sars, 1900)	*Macrothrix atahualpa* Brehm, 1936	*Macrothrix sioli* (Smirnov, 1982)	*Macrothrix brandorffi* Kotov and Hollwedel, 2004	*Macrothrix odiosa* Gurney, 1916	*Macrothrix capensis* (Sars, 1916)	*Macrothrix pholpunthini* Kotov, Maiphae and Sanoamuang, 2005	*Macrothrix agsensis* Dumont, Silva-Briano and Subash Babu, 2002	*Macrothrix malaysiensis* Idris and Fernando, 1981	*Macrothrix smirnovi* Ciros-Pérez and Elías-Gutiérrez, 1997	*Macrothrix australiensis* sp. nov.
Distribution	The New World (from Argentina to Florida)	The New World (high mountain water bodies of Peru, Bolivia, North Argentina and Chile)	The New World (Brazil, known only from several localities)	The New World (Brazil, known only from type locality)	Tropical regions of the Old World (Africa, South and Southeast Asia)	The Old World (known only from the Republic of South Africa)	The Old World (South and Southeast Asia)	The New World (few localities in Mexican Plateau and close territories)	The Old World (? known only from Malaysia)	The New World (few localities in Mexican Plateau and close territories)	Australia
1. Parthenogenetic female:											
Maximum length	Up to 1.47 mm	Up to 1.15 mm	Up to 1.01 mm	Up to 1.12 mm	Up to 1.03 mm	Up to 1.3 mm	Up to 1.01 mm	Up to 0.8 mm	0.89 mm	0.9 mm	Up to 1.00 mm
Posterodorsal angle of body	Smooth	Smooth	Large triangular spine	Triangular spine	Smooth	Smooth	Large triangular spine	Smooth	Small triangular spine	Smooth	Smooth
Dorsum	Not elevated significantly above head	Not elevated significantly above head	Elevated above head	Not elevated significantly above head	Not elevated significantly above head	Not elevated significantly above head	Elevated above head	Not elevated significantly above head	Not elevated significantly above head	Not elevated significantly above head	Not elevated significantly above head
Serration on dorsum	Not expressed	Not expressed	Present	Not expressed	Not expressed	Not expressed	Present	Not expressed	Not expressed	Not expressed	Not expressed
Head pore	Projected under level of head	On the level of head	On the level of head	Projected under level of head	On the level of head	On the level of head	On the level of head	On the level of head	On the level of head	On the level of head	On the level of head
Ventral head margin	Without projection	Inflated	With projection	Without projection	With projection		With projection		With projection	Inflated	
Labrum	Large triangular	Large triangular	Large triangular	Large triangular	Large triangular	With projection of moderate length, with rounded apical portion	Large triangular	With a slight projection of moderate length, with rounded apical portion	Large triangular	Large triangular	With a slight projection of moderate length, with rounded apical portion
Postabdominal anal flaps	Not prominent	Not prominent	Not prominent	Not prominent	Prominent	Not prominent	Prominent	Not prominent	Not prominent	Not prominent	Not prominent
Armature of anal margin of postabdomen	Long hairs and fine denticles	Fine denticles	Fine denticles	Long hairs and fine denticles	Fine denticles	Fine denticles	Fine denticles	Fine denticles	Fine denticles	Fine denticles	Fine denticles
Distal segment of postabdominal seta	Short	Relatively long	Short	Short	Short	Short	Short	Short	Relatively long	Relatively long	Short

Table 1. (continued).

Feature	*Macrothrix paulensis* (Sars, 1900)	*Macrothrix atahualpa* Brehm, 1936	*Macrothrix sioli* (Smirnov, 1982)	*Macrothrix brandorffi* Kotov and Hollwedel, 2004	*Macrothrix odiosa* Gurney, 1916	*Macrothrix capensis* (Sars, 1916)	*Macrothrix pholpunthini* Kotov, Maiphae and Sanoamuang, 2005	*Macrothrix agsensis* Dumont, Silva-Briano and Subash Babu, 2002	*Macrothrix malaysiensis* Idris and Fernando, 1981	*Macrothrix smirnovi* Ciros-Pérez and Elías-Gutiérrez, 1997	*Macrothrix australiensis* sp. nov.
Armature of inner side of antenna I	With a row of robust large denticles	With a row of bunches of gracile long denticles	With a row of robust large denticles	With a row of small denticles	With a row of robust large denticles	With a row of bunches of gracile long denticles	With a row of robust large denticles	With a row of bunches of gracile long denticles	With a row of robust large denticles	With a row of bunches of gracile long denticles	With a row of bunches of gracile short denticles
Two contiguous denticles near the base of antenna I	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Absent	Present	Absent	Absent
Armature of proximal endopod segment seta of antenna II	A row of robust denticles	A row of robust denticles alternating with stiff setules	A row of robust denticles alternating with stiff setules	A row of robust denticles	A row of robust denticles alternating with stiff setules	A row of robust denticles	A row of robust denticles alternating with stiff setules	Only small setules	A row of robust denticles	A row of robust denticles alternating with stiff setules	A row of robust denticles alternating with stiff setules
Spine on the second exopod segment of antenna II	Shorter than 1/3 length of third exopod segment	1/2 length of third exopod segment	Shorter than 1/3 length of third exopod segment	Shorter than 1/3 length of third exopod segment	Shorter than 1/3 length of third exopod segment	1/2 length of third exopod segment	Shorter than 1/3 length of third exopod segment	About 1/3 length of third exopod segment	Shorter than 1/3 length of third exopod segment	1/2 length of third exopod segment	About 1/3 length of third exopod segment
Number of ejector hooks on thoracic limb I	A single ejector hook	A single ejector hook	A single ejector hook	A single ejector hook	A single ejector hook	A single ejector hook	A single ejector hook	A single ejector hook	Unstudied	A single ejector hook	A single ejector hook
Soft seta between scraper 4 and 5 on thoracic limb II	Absent	Specially large	Absent	Absent	Absent	Absent	Absent	Absent	Unstudied	Specially large	Absent
Ratio between setae 3 and 2 on exopodite of thoracic limb III	Seta 3 about in two times longer than seta 2	Seta 3 and seta 2 subequal in size	Seta 3 about in two times longer than seta 2	Seta 3 about in two times longer than seta 2	Seta 3 about in two times longer than seta 2	Seta 3 and seta 2 subequal in size	Seta 3 about in four times longer than seta 2	Seta 3 and seta 2 subequal in size	Unstudied	Seta 3 and seta 2 subequal in size	Seta 3 and seta 2 subequal in size
Ratio between setae 2 and 1 on exopodite of thoracic limb IV	Seta 2 slightly longer than seta 1	Seta 2 and seta 1 subequal in size	Seta 2 slightly longer than seta 1	Seta 2 significantly (about in seven times) longer than seta 1	Seta 2 in two times longer than seta 1	Seta 2 and seta 1 subequal in size	Seta 2 in three times longer than seta 1	Seta 2 and seta 1 subequal in size	Unstudied	Seta 2 and seta 1 subequal in size	Seta 2 and seta 1 subequal in size

Table 1. (continued).

Feature	*Macrothrix paulensis* (Sars, 1900)	*Macrothrix atahualpa* Brehm, 1936	*Macrothrix sioli* (Smirnov, 1982)	*Macrothrix brandorffi* Kotov and Hollwedel, 2004	*Macrothrix odiosa* Gurney, 1916	*Macrothrix capensis* (Sars, 1916)	*Macrothrix pholpunthini* Kotov, Maiphae and Sanoamuang, 2005	*Macrothrix agsensis* Dumont, Silva-Briano and Subash Babu, 2002	*Macrothrix malaysiensis* Idris and Fernando, 1981	*Macrothrix smirnovi* Ciros-Pérez and Elías-Gutiérrez, 1997	*Macrothrix australiensis* sp. nov.
Number of soft setae on posterior face of limb IV inner distal portion	Five	Five	Five	Five	Five	Five	Five	Five	Unstudied	Five	Five
2. Male:											
Position of male seta on antenna I	Male seta located at distance 1/4 of antenna I length from the apex	Male seta located in middle of antennular body	Unstudied	Male seta located at distance 1/4 of antenna I length from the apex	Male seta and sensory seta located on the same level (at distance 1/4 of antenna I length from its base)	Male seta is located in the middle of antennular body	Male seta and sensory seta located on the same level (at distance 1/4 of antenna I length from its base)	Male seta located in middle of antennular body	Unstudied	Male seta located in middle of antennular body	Male seta located in middle of antennular body

base in lateral view (Figs. 1H–J, 3E). There are several denticles on its dorsal side and more fine denticles on ventral side (Figs. 1I, 3E). Inner part of claw covered by undulated row of small denticles (Fig. 1J).

Antenna I "rod-like" in terminology of Smirnov (1992), long and almost straight, not dilating to apex (Figs. 2A, 3A, F–G). Bunches of 2–3 long slender denticles at inner margin of antenna I (Figs. 2A, 3G). Whole surface of antenna I covered by transverse rows of spinules. Distal edge bears long slender denticles (Figs. 2A, 3G). Antennular sensory seta slender, arising from outer side of proximal part (Fig. 2A). Nine aesthetascs, two of them longer and thicker than the rest (Fig. 2A). Each thicker aesthetasc bears two minute "claws" at the apex (Fig. 2A).

Antenna II large (Figs. 1A, 2B, 3H), coxal region folded, with two small sensory setae unequal in size. Antennal formula: setae 0-0-1-3/1-1-3, spines 0-1-0-1/0-0-1. Basal segment robust, covered by transverse rows of fine spinules (Figs. 1A, 2B, 3H). Small spine located on outer surface of basal segment, a bisegmented short sensory seta on inner surface, it almost reaches third exopod segment. Exopod and endopod subequal in size (Figs. 1A, 2B, 3H–I). All their segments cylindrical, elongated, covered by transverse rows of fine spinules (Fig. 3H–I). Apical swimming setae long, subequal in length, bearing fine spinules and long setules (Figs. 1A, 2B, 5D). Lateral seta of basal endopod segment (Fig. 2B–C) larger than other setae and armed with two rows of spinules: spinules on the edge of this seta thin and densely located (distance between two neighboring spinules is almost equal to width of seta), spinules on the outer surface of this seta more robust and sparsely located (distance between two neighboring spinules significantly – commonly in 3.5 times – larger than width of seta) (Figs. 2D–E, 5A). Seta on middle endopod segment reaches tips of apical setae, covered by long setules and fine spinules (Fig. 2B). Lateral seta of third exopod segment has the same armature (Figs. 2B, 5C). True spine on second exopod segment thin, reaches 1/2 length of third exopod segment (Figs. 2B, 3H–I). Second and third exopod segment bear short additional spines (we do not represent them in the antennal formula) (Figs. 2B, 3H–I). Normally, these additional spines almost subequal in size and three times shorter than true spine on second exopod segment. Spines of both apical exopod and endopod segments thin, exopod apical spine in two times longer than endopod spine (Figs. 2B, 3H–I, 5C).

Thoracic limbs: five pairs (Fig. 4A–G).

Limb I large (Fig. 4A–B). Epipodite ovoid, with a long finger-like projection (Fig. 4A). Accessory seta small (Fig. 4B). ODL conical and large, bearing a single long bisegmented seta, its distal segment feathered unilaterally (Fig. 4B). IDL massive, covered by rows of stiff setules, with three bisegmented setae of different size, each unilaterally setulated in distal part (Fig. 4B). Limb corm almost rectangular in lateral view (Fig. 4A). Endite 4 with three posterior soft setae (among them seta a the longest, with long fine setules on its distal segment, setae b and c shorter, subequal in length, covered by fine setules in proximal part and stiff short setules in distal part) and a single stiff anterior seta 1 (Fig. 4A). Endite 3 with three soft posterior setae unequal in size (among them seta d the longest, bearing fine setules both in proximal and distal segments, seta e and f armed unilaterally by rough setules in

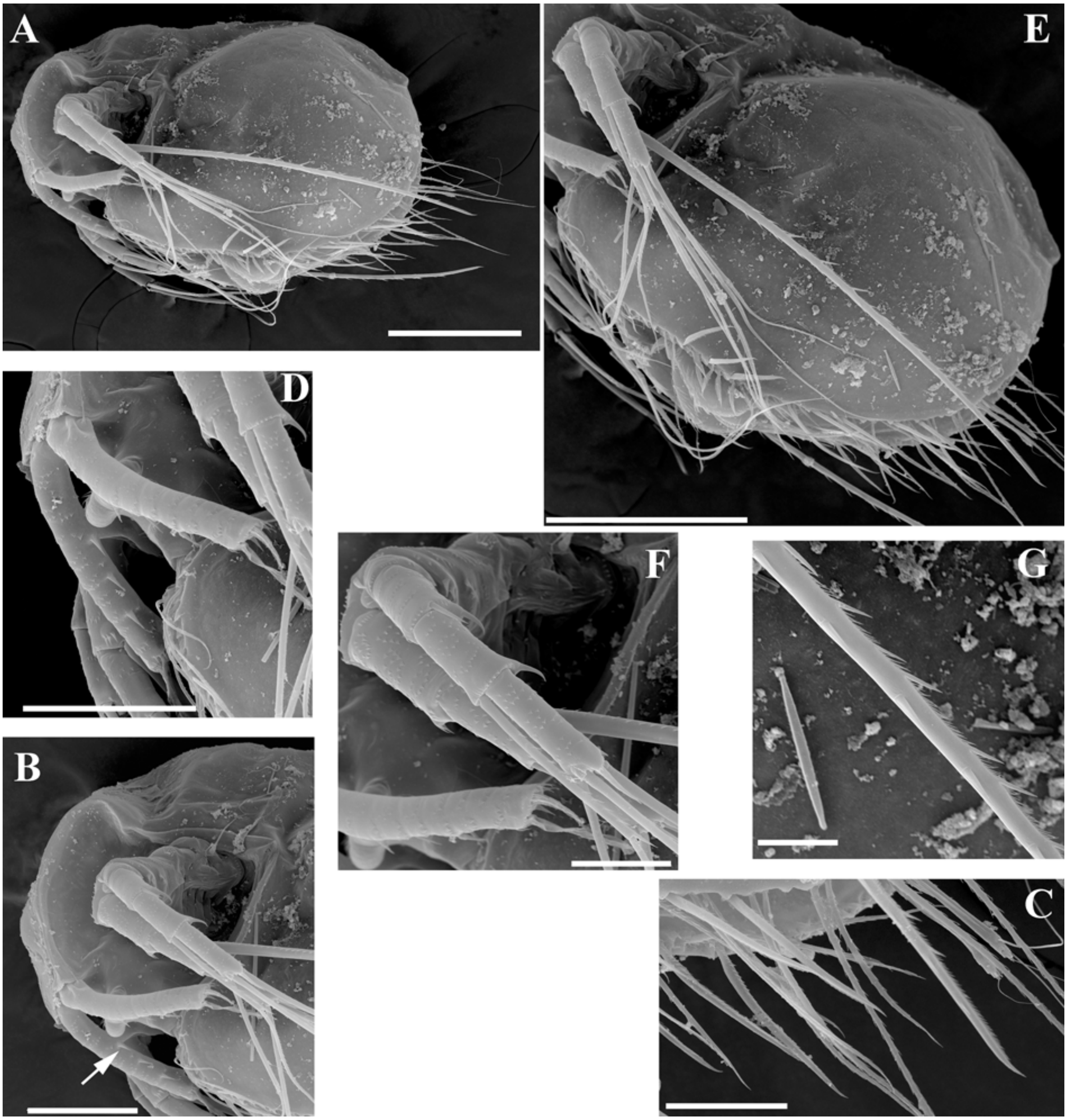

Fig. 6. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from Lake Kud-Thing in floodplain of Mekong River, Nong Khai Province, Thailand, coll. 28.11.1998 by C. Saeng-aroon, AAK-2003-033. A, General view. B, Head. C, Armature of ventral margin of valve. D, Antenna I. E, Antenna II. F, Exopod and endopod branches of antenna II. G, Central part of lateral seta of basal endopod segment of antenna II. Scale bars: 0.2 mm for A, E, 0.1 mm for B, D, 0.05 mm for C, F, 0.2 mm for G.

their distal portions) and a single fork-like anterior seta 2 (Fig. 4A). Endite 2 with two posterior bisegmented setae subequal in size, covered by fine short setules, and a single anterior fork (Fig. 4A). Endite 1 with two bisegmented soft setae. A single ejector hook with setulated distal segment (Fig. 4A).

Limb II triangular-rounded (Fig. 4C). Exopodite ovoid, covered by rows of fine setules, and bearing a single long soft seta. Inner portion of limb II with eight scrapers, among them setae 1 and 2 the longest, setae 3–5 somewhat shorter, and setae 6–8 short (Fig. 4C). Setae 1 and 2 unilaterally covered by stiff fine denticles in their distal portion. Seta 3 bears fine spinules; setae 4-8 feathered by more robust denticles. A deep incision between endite 2 and endite 1. Portion of gnathobase (= endite 1) bordering endite 2 somewhat inflated and bears a row of fine setules. Distal armature of gnathobase with four elements. Filter plate with four bisegmented setae, subequal in length (Fig. 4C).

Limb III (Fig. 4D–E) with subrectangular exopodite (Fig. 4D), bearing a single lateral seta and three distal setae (among them, the middle seta somewhat longer than others). Distal endite in terms of Kotov (2013) with three anterior setae (seta 1 covered by small denticles, setae 2 and 3 bear fine setules on

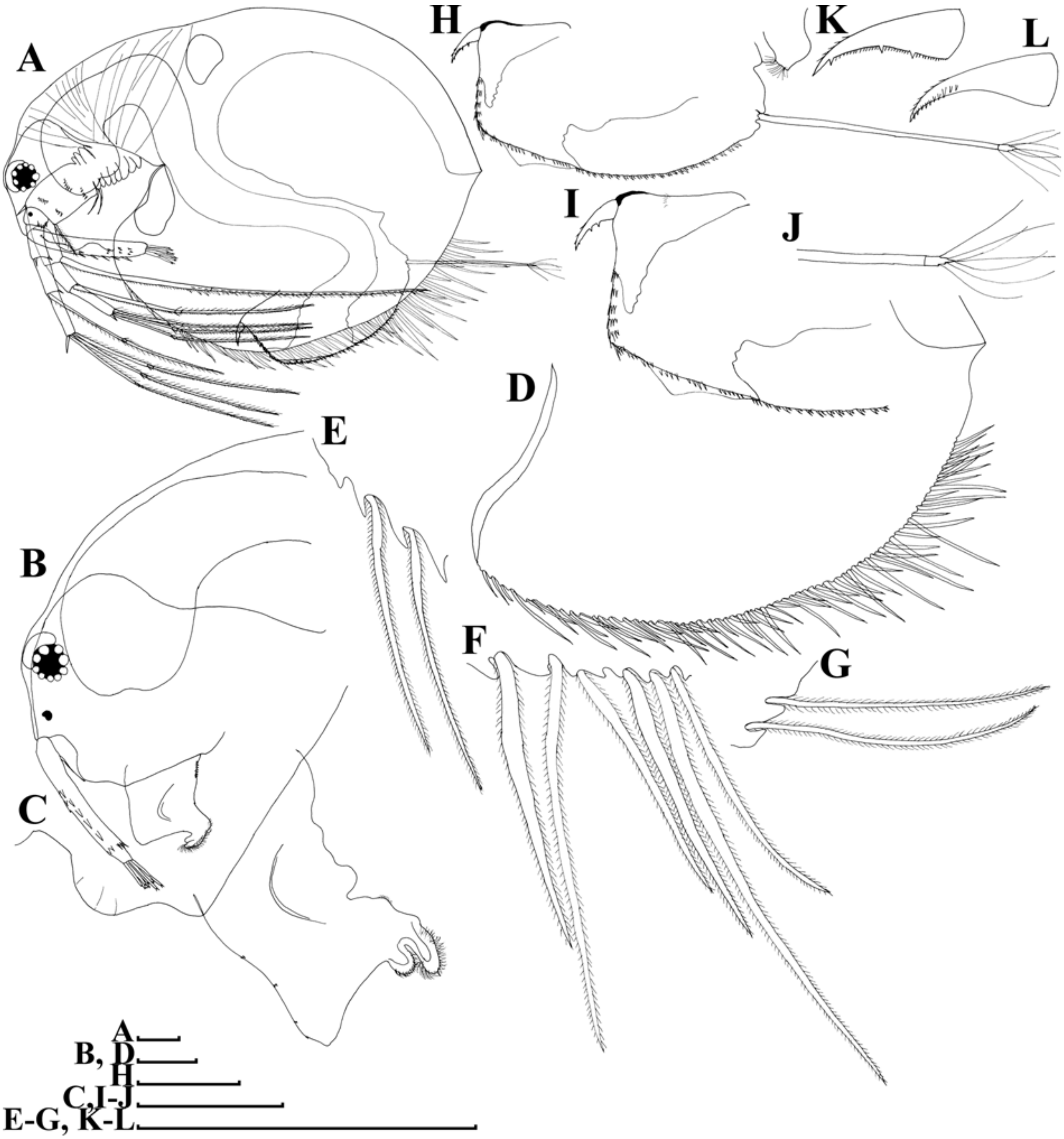

Fig. 7. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from a pool "Yizeb" before Hamusit (N 11.7333°, E 37.5166°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-001. A, General view. B, Head. C, Labrum. D, Valve. E, Armature of anterior margin of valve. F, Armature of ventral margin of valve. G, Armature of posterior margin of valve. H, Postabdomen. I, Distal portion of postabdomen. J, Postabdominal seta. K, Postabdominal claw, outer view. L, Postabdominal claw, inner view. Scale bars: 0.1 mm.

their distal portions), small sensillae near seta 2 and seta 3 (Fig. 4D–E). Proximal endite with a small elongated sensillum and three setae (compare with *M. elegans* Sars, 1901, which has a small bottle-shaped sensillum and four setae on proximal endite (Kotov *et al.*, 2004)) (Fig. 4E). Six setae on posterior face of limb (a–f) (among them seta a short and thick, with stiff setules on its distal portion and long setules on proximal portion; other setae increasing in size proximally). Distal armature of gnathobase with four elements, one of them a bottle-shaped sensillum (Fig. 4E). Filter plate absent (Fig. 4D).

Limb IV (Fig. 4F) with relatively small rounded exopodite, bearing distally two soft setae, subequal in size. Inner distal portion with four anterior setae (1–4) (among them seta 1 covered by short stiff setules, setae 2–4 bearing more long setules) and small sensillum near each seta 2 and seta 3 (Fig. 4F). Posterior face with five soft setae (a–e) increasing in size proximally (Fig. 4F). Distal armature of gnathobase consists of four elements: a small bottle-shaped sensillum, bisegmented seta and two elongated projections. Filter plate absent (Fig. 4F).

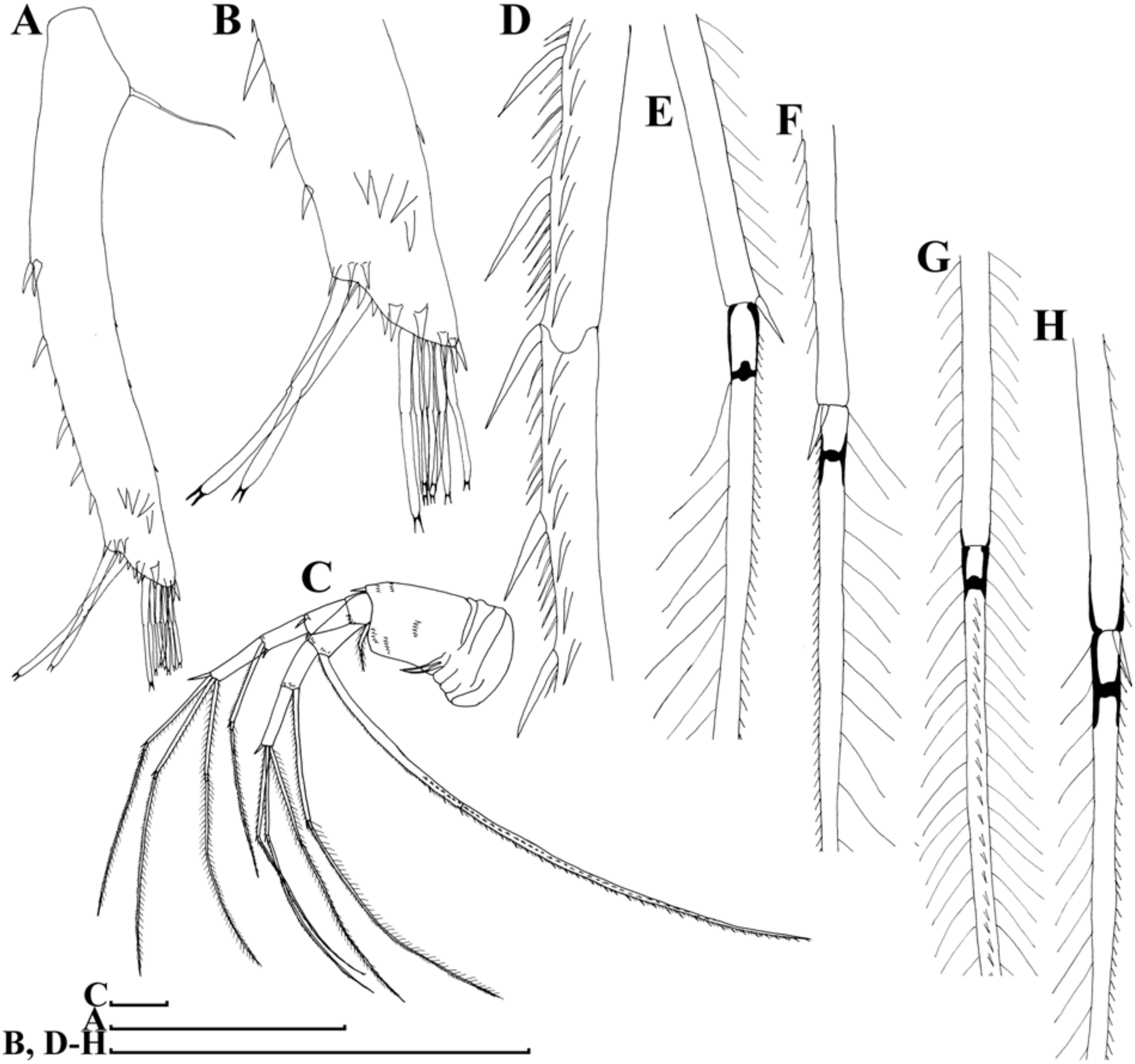

Fig. 8. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from a pool "Yizeb" before Hamusit (N 11.7333°, E 37.5166°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-001. A, Antenna I. B, Distal portion of antenna I. C, Antenna II. D, Central part of lateral seta of basal endopod segment of antenna II. E, Central part of lateral seta of middle endopod segment of antenna II. F, Central part of lateral exopod segment seta. G–H, Apical swimming setae in different position. Scale bars: 0.1 mm.

Limb V (Fig. 4G) with a three-lobed preepipodite covered by fine setules. Epipodite relatively large, ovoid (Fig. 4G). Exopodite with a single seta. Inner distal portion as small flap, covered by setules; three setae on its inner margin (the distalmost seta significantly longer than others) (Fig. 4G). Filter plate absent (Fig. 4G).

Ephippial female. In lateral view, body proportions as in parthenogenetic female. A chitinized plate along dorsal margin on body (Fig. 5B). Almost all valves area is included to the constitution of the ephippium. Surface of ephippium brownish, with elongated inflated hillocks, boundaries between exuviated and unexuviated parts are not delineated (Fig. 5B, E). Two eggs in ephippium.

Males. Not found in our material, but Sars (1916) published a detailed description and a realistic illustration for male of *M. capensis* (Sars, 1916: p. 324, plate 36: figs. 1d). According to his description, male body subrectangular, dorsum almost straight, posterodorsal angle rounded. Sensory seta and male seta on antenna I located quite far from each other.

Size. Maximum length of adult parthenogenetic females 1.3 mm, height 0.84 mm. Maximum length of ephippial females 0.75 mm, height 0.51 mm. Male size unknown, Sars (1916: p. 324) only stated that the male is scarcely half as large as female.

Variability. No significant variability between investigated individuals from all South African localities was found.

Distribution. According to Smirnov (2008) *M. capensis* is a common taxon in the Republic of South Africa. Based on our original data, *M. capensis* is known only from South Africa. Most populations are found in Western Cape, although originally this species was described from Eastern Cape

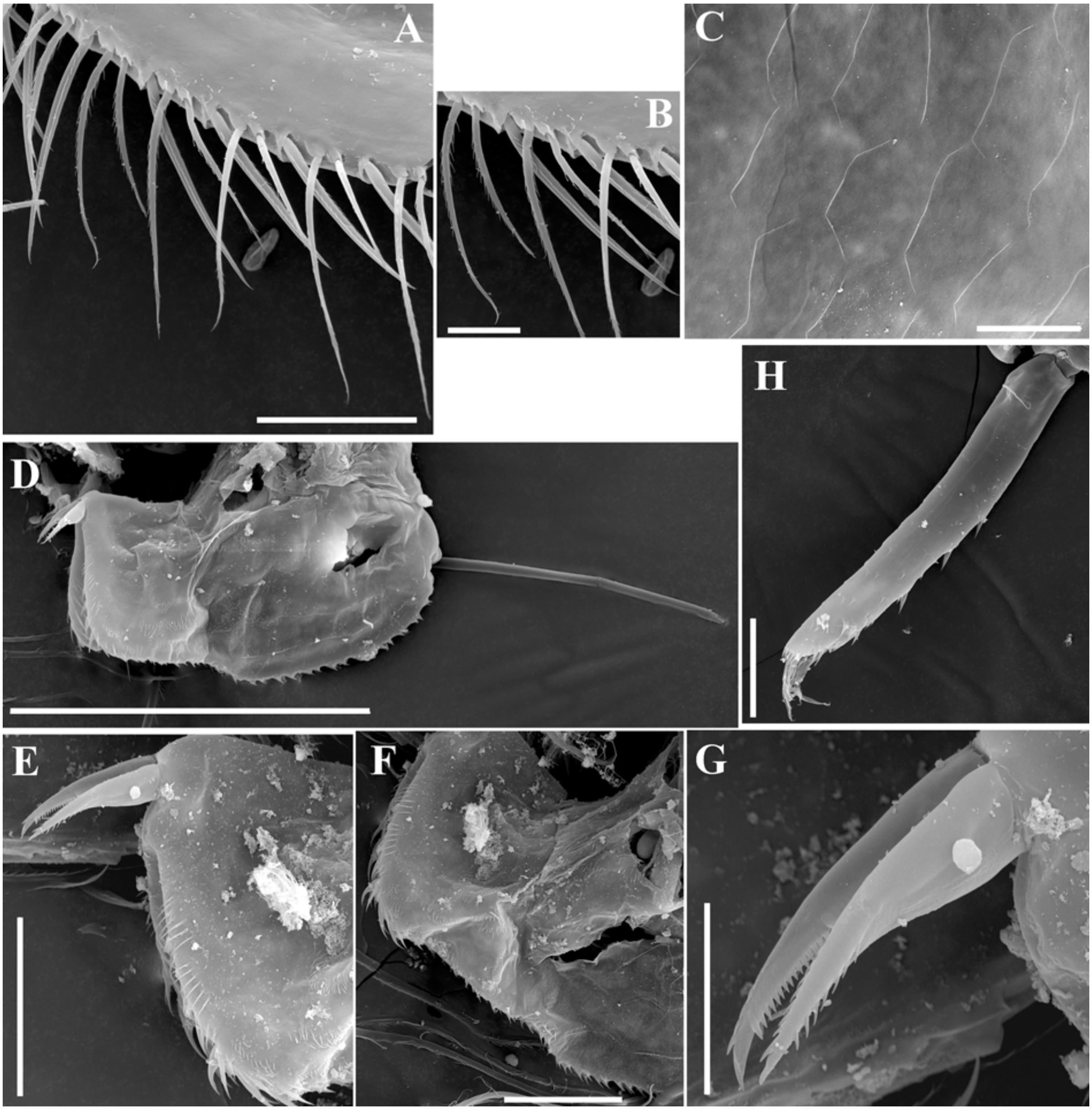

Fig. 9. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from a pool "Yizeb" before Hamusit (N 11.7333°, E 37.5166°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-001. A–B, Armature of ventral margin of valve. C, Central part of valve. D, Postabdomen. E–F, Distal portion of postabdomen. G, Postabdominal claws. H, Antenna I. Scale bars: 0.2 mm for D, 0.05 mm for A, E–F, H, 0.02 mm for B–C, G.

(Sars, 1916), but some populations are present in other parts of the southern half of the Republic of South Africa, *e.g.* in Drakensberg mountains.

Differential diagnosis. There are only two taxa from the *paulensis*-group in Africa, *M. capensis* and *M. odiosa*, which are different in fine morphological traits of both females and males (Tab. 1). The main difference between *M. capensis* and *M. atahualpa* concerns some fine details: proportions of distal segment of postabdominal seta (this segment is short in *M. capensis* and relatively long in *M. atahualpa*), structure of thoracic limb II (additional soft seta between scraper 4 and scraper 5 is absent in *M. capensis* and present in *M. atahualpa*). See differential diagnosis of *M. australiensis* sp. nov. for differences from the latter.

***Macrothrix odiosa* Gurney, 1916**

(Figs. 6–19)

Macrothrix tenuicornis Gurney, 1907: p. 25, plate 1: figs. 1–2, plate 2: fig. 22 – junior homonym of *M. tenuicornis* Kurz, 1875: p. 32–34, pl. 3: fig. 1.

Macrothrix odiosa Gurney, 1916: p. 335; Behning (1938: p. 294, fig. 2; 1941: 225–227, fig. 97); Brehm (1952: p. 41–42, figs. 4–5); Manujlova (1964: p. 185–186, fig. 80); Mukhamediev (1986: p. 69–73, fig. 17); Smirnov (1992: 89–93, figs. 375–393); Saeng-aroon (2001: p. 36: fig. 19); Saeng-aroon and Sanoamuang (2002: p. 16, fig. 8).

Macrothrix capensis var. *monodi* Gauthier, 1930: p. 95–98, figs. 2a–c.

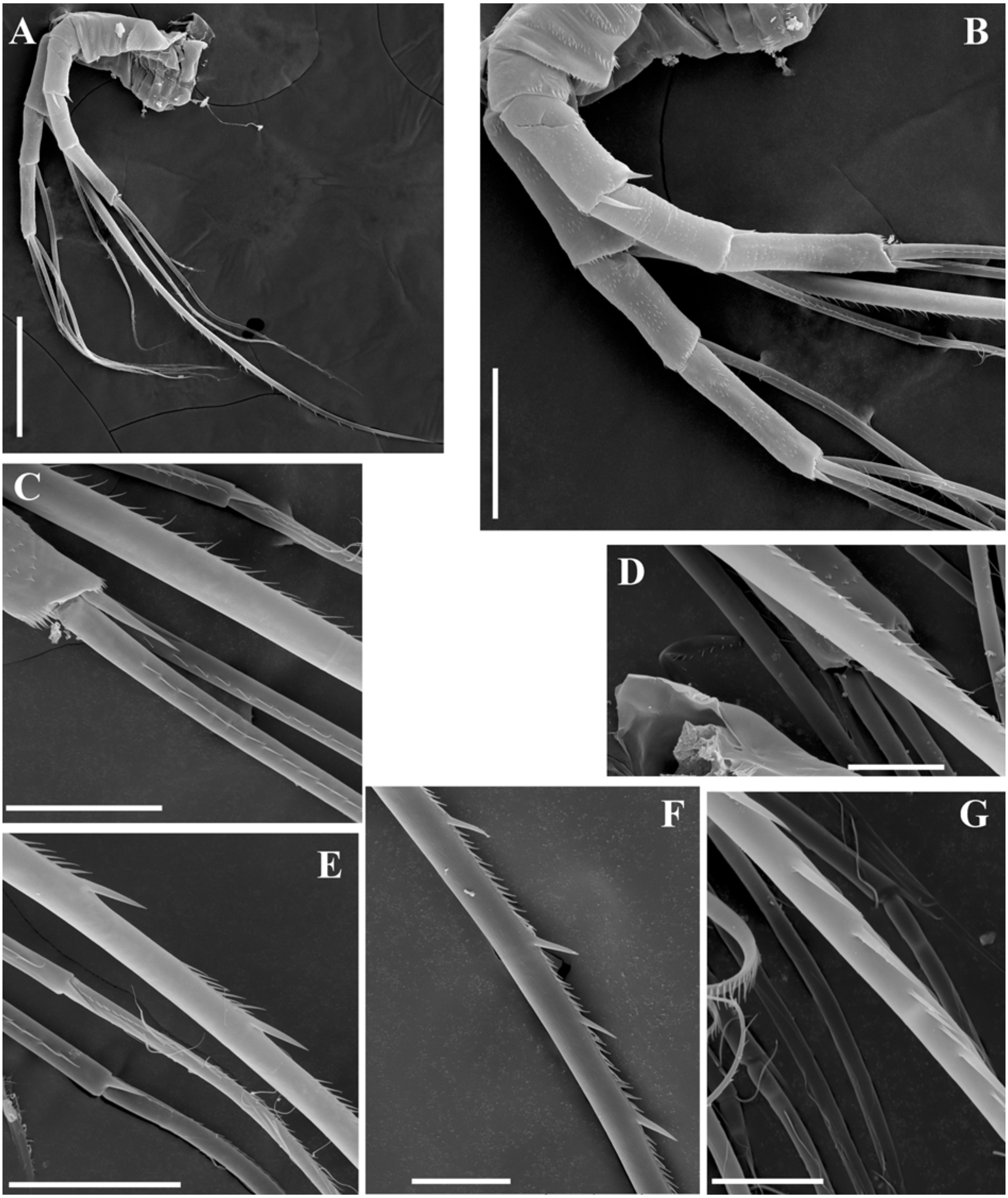

Fig. 10. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from a pool "Yizeb" before Hamusit (N 11.7333°, E 37.5166°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-001. A, Antenna II. B, Exopod and endopod branches of antenna II. C–D, Proximal portion of lateral seta of basal endopod segment of antenna II. E–G, Central part of lateral seta of basal endopod segment of antenna II. Scale bars: 0.2 mm for A, 0.1 mm for B, 0.05 mm for E, 0.02 mm for C–D, F–G.

Macrothrix capensis monodi Gauthier, 1930 in Idris and Fernando (1981a: p. 238–239, figs. 11–15); Idris (1983: p. 47, fig. 22).

Macrothrix madagascariensis (Brehm, 1930) in Brehm (1933: p. 691) and Brehm (1952: p. 41).

Macrothrix monodi Gauthier, 1930 in Dumont and Van de Velde (1977: p. 85–87, figs. 5a–f).

Macrothrix orbicularis Brehm, 1930 in Brehm (1930: p. 681–686, figs. 4–6).

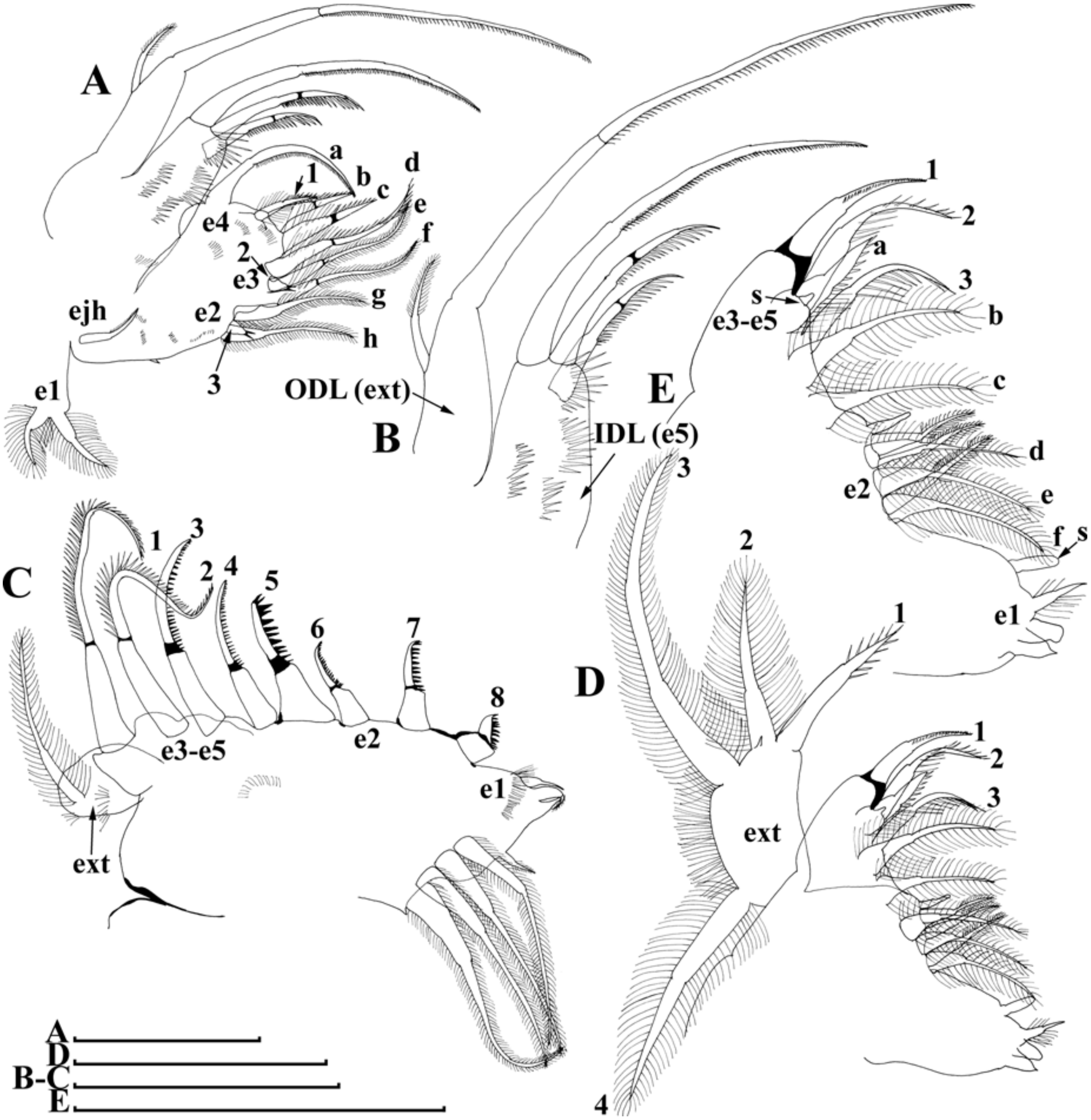

Fig. 11. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from a pool "Yizeb" before Hamusit (N 11.7333°, E 37.5166°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-001. A, Corm of limb I. B, Distal part of limb I. C, Limb II. D, Limb III. E, Fragment of limb III. Scale bars: 0.1 mm.

Macrothrix cf. *paulensis* (Sars, 1900) in Sanoamuang, 1998: p. 48, figs. 15–20.

Echinisca odiosa (Gurney, 1916) in Smirnov (1976: p. 118–119, figs. 94–95); Fernando (1980: tab. 1); Ibrasheva and Smirnova (1983: 66–67: fig. 16); Fernando and Kanduru (1984: p. 72: tab. 1); Michael and Sharma (1988: p. 111–113, figs. 35a–c).

Echinisca capensis monodi (Gauthier, 1930) in Smirnov (1976: p. 122, 124).

Echinisca madagascariensis (Brehm, 1930) in Smirnov (1976: p. 130).

Echinisca orbicularis (Brehm, 1930) in Smirnov (1976: p. 130).

(?) *Echinisca sumatrensis* (Brehm, 1933) in Smirnov (1976: p. 130).

Gurneyella madagascariensis Brehm, 1930 in Brehm (1930: p. 681–686, figs. 4–6).

Gurneyella monodi (Gauthier, 1930) in Brehm (1934: p. 59–61, figs. 4–6); Rey and Saint-Jean (1969: p. 29–31, figs. 8a–d).

Gurneyella odiosa (Gurney, 1916) in Biswas (1971: p. 127, figs. 7g–i).

(?) *Gurneyella sumatrensis* Brehm, 1933 in Brehm (1933: p. 692–693, figs. 17–20); Rammner (1937: p. 44–45, figs. 6–9).

Material examined here from Southeast Asia (Fig. 6): 2 parthenogenetic females from Lake Kud-Thing in floodplain of Mekong River, Nong Khai Province, Thailand, coll. 28.11.1998 by C. Saeng-aroon, AAK-2003-033; 2 parthenogenetic females from Lake Kud-Thing in floodplain of Mekong River, Nong Khai Province, Thailand, AAK-

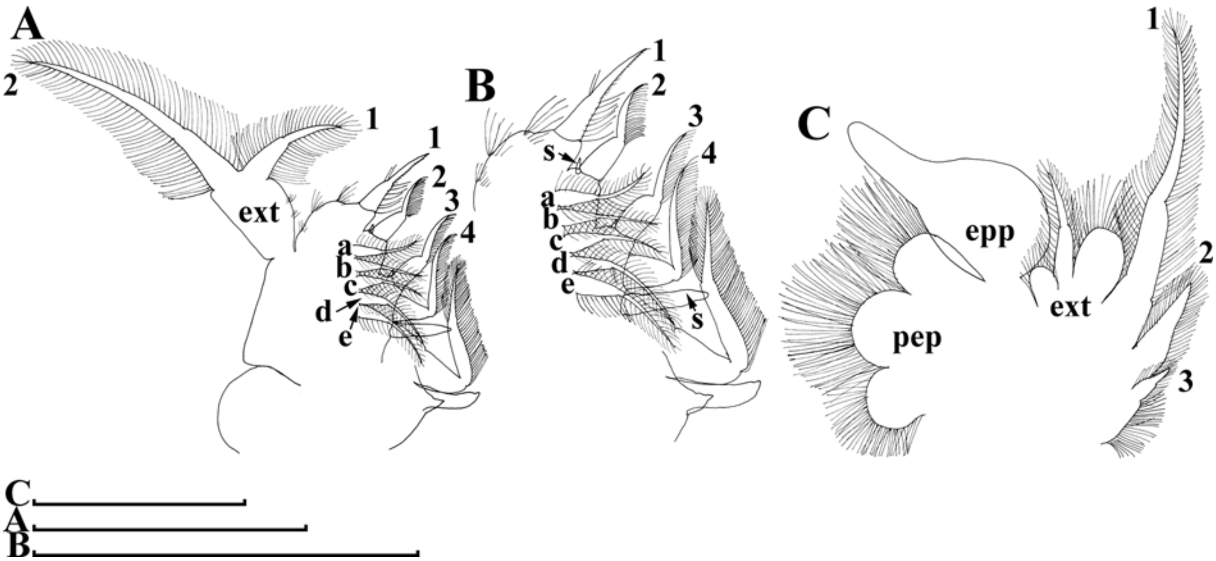

Fig. 12. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from a pool "Yizeb" before Hamusit (N 11.7333°, E 37.5166°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-001. A, Limb IV. B, Fragment of limb IV. C, Limb V. Scale bars: 0.1 mm.

2004-049; 1 parthenogenetic female from Vientiane Province, Laos, coll. by S. Sibioualipha, AAK-2012-043.

Material examined here from Africa (Figs. 7–19): 10 parthenogenetic females from a pool "Yizeb" before Hamusit (N 11.7333°, E 37.5166°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-001; 5 parthenogenetic females from a pool, "Zara" between Hamusit and Worota (N 11.8166°, E 37.6000°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-002; 5 parthenogenetic females from a pool, "Gosho" near to junction of D'tabor and Adiss Zemen road (N 11.9500°, E 37.7000°), Ethiopia, coll. 24.09.2015 by W. Zelalem, ANN-2016-003; 3 parthenogenetic females from Lake Liambezi (S 17.9166°, E 24.3333°), Zambezi floodplain, E. Caprivi, the Republic of Namibia, coll. 10.12.1982, AAK-1998-083; 2 parthenogenetic females from Crane Pan 5, Cobham (S 29.6658°, E 29.3717°), KwaZulu-Natal, the Republic of South Africa, coll. 15.02.1998 by K. Martens and Hamer, NNS-2002-009; 10 parthenogenetic females from Crane Tarn 3, Cobham (S 29.7122°, E 29.3219°), KwaZulu-Natal, the Republic of South Africa, coll. 16.02.1998 by K. Martens and Hamer, NNS-2002-010; 3 parthenogenetic females from Loteni (S 29.3772°, E 29.5425°), KwaZulu-Natal, the Republic of South Africa, coll. 18.03.1996 by K. Martens and Hamer, NNS-2002-020; 2 parthenogenetic females from rock pool 1 (S 29.6739°, E 29.3303°), Cobham, KwaZulu-Natal, the Republic of South Africa, coll. 11.11.1996 by K. Martens and Hamer, NNS-2002-044; 3 parthenogenetic females from Crane Tarn 1 (S 29.7133°, E 29.3238°), Mzimkhulwana, KwaZulu-Natal, the Republic of South Africa, coll. 21.03.1995 by K. Martens and Hamer, NNS-2002-058; 3 parthenogenetic females from Crane Tarn 2 (S 29.7125°, E 29.3219°), Mzimkhulwana, KwaZulu-Natal, the Republic of South Africa, coll. 21.03.1995 by K. Martens and Hamer, NNS-2002-059; 5 parthenogenetic females from Sentinels Plateau Pool 4, Cobham (S 29.6333°, E 29.3939°), KwaZulu-Natal, the Republic of South Africa, coll. 22.03.1995 by K. Martens and Hamer, NNS-2002-066; 4 parthenogenetic females from Siphongweni tarn 2 (S 29.6833°, E 29.3553°), Cobham, KwaZulu-Natal, the Republic of South Africa, coll. 25.03.1995 by K. Martens and Hamer, NNS-2002-077; 5 parthenogenetic females from Sugarloaf Tarn (S 29.2433°, E 29.5106°), Giant Castle, KwaZulu-Natal, the Republic of South Africa, coll. 27.03.1995 by K. Martens and Hamer, NNS-2002-084; 1 parthenogenetic female from Mbaneni rain pool (S 27.6242°, E 32.2575°), Mkuzi Game Reserve, KwaZulu-Natal, the Republic of South Africa, coll. 28.10.1994 by K. Martens, Hamer and Coke, NNS-2002-109; 2 parthenogenetic females from Pan/Dam on Pot River tributary (S 30.9908°, E 28.2647°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-126; 1 parthenogenetic female from Rush Valley Pan (S 30.8506°, E 28.2156°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03. 1993 by K. Martens, de Moor and Barber, NNS-2002-127; 6 parthenogenetic females from Glen Avis pool 2 (S 30.8061°, E 28.2117°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-129; 15 parthenogenetic females from Glen Avis pool 3 (S 30.8072°, E 28.2161°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-130; 8 parthenogenetic females, 1 male and 2 ephippial females from Glen Avis rock pool 4 (S 30.8053°, E 28.2214°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-131; 1 parthenogenetic female from Pan 1 Rd Middelburg-Hofmeyer (S 31.6917°, E 25.4931°), Karoo, Eastern Cape, the Republic of South Africa, coll. 07.04.1993 by K. Martens, NNS-2002-148.

Comments on parthenogenetic female. Morphology of parthenogenetic and ephippial females was identical in all studied African and Asian populations (see complete morphological description for Asian populations of *M. odiosa* in Kotov *et al.* (2005) and our Figs. 6–17, 18A–C). There is just one small-scale feature, which we would like to clarify: the projection on the ventral head margin is not double (see also fig. 24 in Kotov *et al.*, 2005) and looks like as an ellipsoid in the ventral view (Fig. 13C).

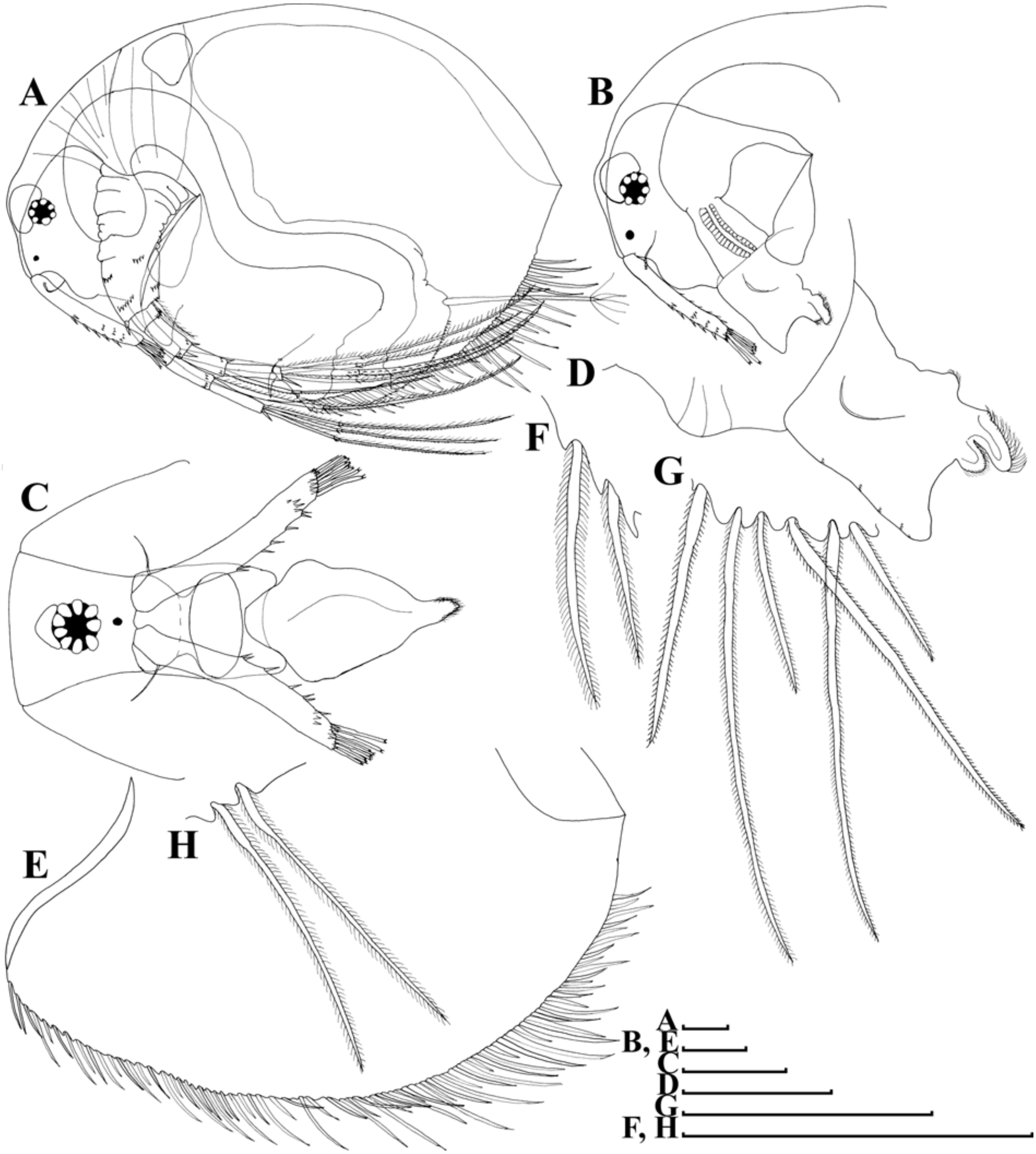

Fig. 13. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from Glen Avis rock pool 4 (S 30.8053°, E 28.2214°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-131. A, General view. B, Head (lateral view). C, Head (ventral view). D, Labrum. E, Valve. F, Armature of anterior margin of valve. G, Armature of ventral margin of valve. H, Armature of posterior margin of valve. Scale bars: 0.1 mm.

Adult male (Figs. 18D–E, 19). Body ovoid, dorsal margin interrupted by a shallow depression between head and valves (Figs. 18D, 19A). Dorsal margin of valves almost straight and not elevated above head (Fig. 19A). Posterodorsal angle distinct, without spine (Fig. 19A). Posteroventral region of valve margin widely rounded; ventral margin significantly convex (Fig. 19A). Head large, with prominent supraocular dome (Figs. 18E, 19B). Ventral margin of head convex, but without prominent projection, typical for parthenogenetic female (Fig. 19B).

Postabdomen subquadrangular (Fig. 19C) (in contrast to adult male of *M. capensis* having a distal part of postabdomen sub-conical (Sars, 1916: plate 36, fig. 1d)), similar in general shape and armature with that in female. Postabdominal flaps prominent (Fig. 19C). Gonopores open on ventral sides of postabdomen near claw base (Fig. 19C).

Antenna I (Fig. 19D) almost subequal in length to head length, rod-like, its inner margin bears robust long denticles and small spinules. Male seta located on the field with fine long

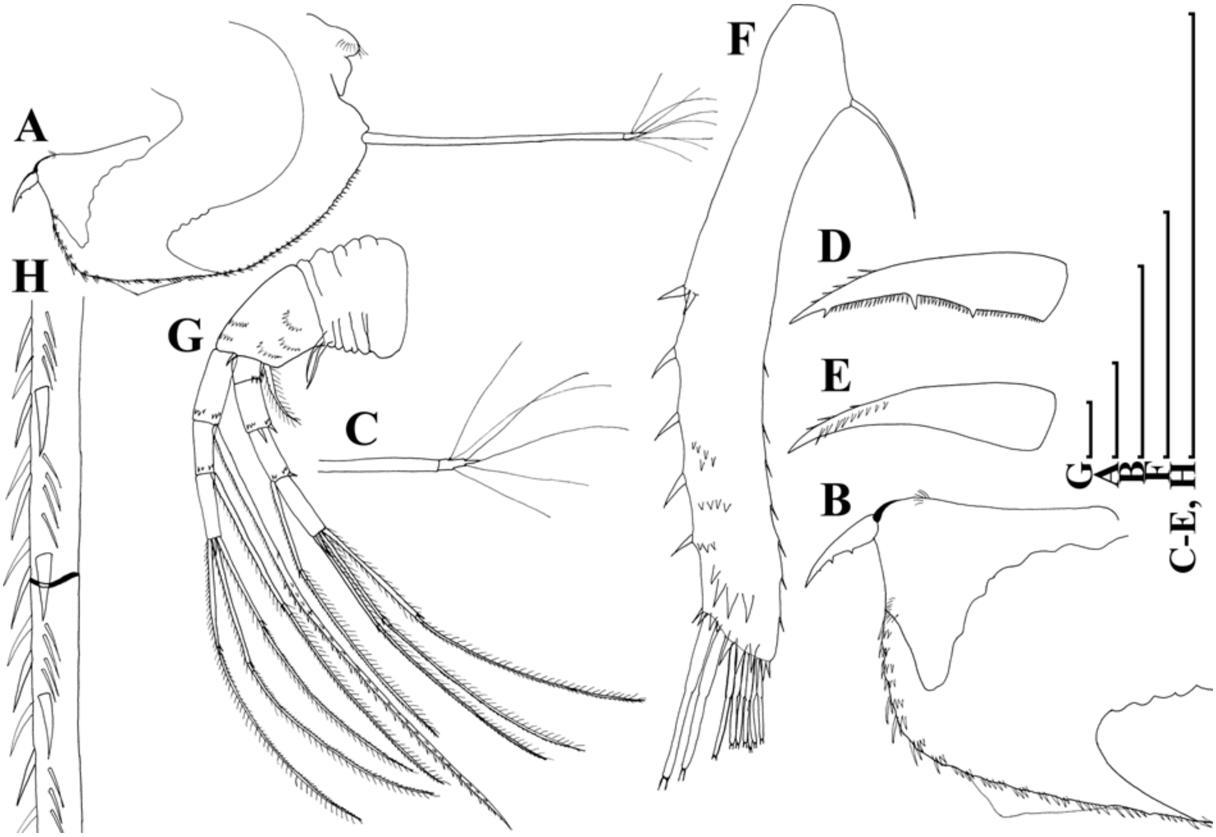

Fig. 14. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from Glen Avis rock pool 4 (S 30.8053°, E 28.2214°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-131. A, Postabdomen. B, Distal portion of postabdomen. C, Distal segment of postabdominal seta. D, Postabdominal claw, outer view. E, Postabdominal claw, inner view. F, Antenna I. G, Antenna II. H, Middle potion of lateral seta of basal endopod segment of antenna II. Scale bars: 0.1 mm.

setules, and subequal in size to sensory seta. Male and sensory setae located on same level (almost near antenna base), but on opposite sides of antenna I body (Fig. 19D). Nine terminal aesthetascs, two of them significantly longer than others (Fig. 19D). Proximal endopod segment seta of antenna II with a row of robust denticles alternating with stiff setules and similar with that in female (Fig. 19A).

Thoracic limb I (Fig. 19E–F) with ODL and IDL as in female (male seta not found) (Fig. 19E), copulatory hook slightly curved, its distal portion covered by fine spinules (Fig. 19F).

Size. A single investigated male 0.41 mm in length and 0.24 mm in height.

Variability. A single male was found in a single sample from the Republic of South Africa, just its complete description is represented here.

Distribution around the world. Widely distributed in tropical-subtropical regions of the Old World, see Kotov *et al.* (2005).

Taxonomic comments. Above we reproduced a list of synonyms, proposed by Kotov *et al.* (2005), and subsequently added with: (1) *M. capensis* var. *monodi* (from Gauthier, 1930), (2) *G. monodi* (from Brehm, 1934 and Rey and Saint-Jean, 1969), (3) *M. madagascariensis* (from Brehm, 1930, 1933, 1952) (= *G. madagascariensis*), (4) *M. orbicularis* (from Brehm, 1930) and (5) *M. monodi* (from Dumont and Van de Velde, 1977). Also, we listed the synonyms associated with the generic name *Echinisca* for African specimens from Smirnov (1976).

Gauthier (1930: p. 92) described *M. capensis* var. *monodi* from Silet (Algeria, North Africa). He apparently dealt with a member of the *M. paulensis* group. Some diagnostic features were illustrated in his figures: a rounded projection on ventral head margin (fig. 2b) and a subquadrangular postabdomen (fig. 2c). At the same time, armature of antenna I was not described in detail, and, obviously, armature of the large seta located on proximal endopod segment is represented inadequately (fig. 2a). We have no opportunities to reexamine the type material, because Gauthier's collection was nationalized by the Algerian government and there is no information about the place, where the collection is now (Hudec, 1993). Based on our data, the distribution range of *M. capensis* is only restricted exclusively by South Africa. Examined populations from Ethiopia and the Republic of Namibia belong to *M. odiosa*, moreover this taxon penetrates in the eastern part of South Africa, but it was not found by us in Western Cape, one of the most important centres of cladoceran endemism within South Africa (Van Damme *et al.*, 2013b). Therefore *M. odiosa* is a widely distributed species of the *M. paulensis* group in Africa, and we offer to consider *M. capensis* var. *monodi* as a junior synonym of *M. odiosa*. The same idea was proposed by Kořínek (1984).

African specimens investigated by Brehm (1934), Rey and Saint-Jean (1969), Dumont and Van de Velde (1977) apparently belong to *M. odiosa* due to their subquadrangular

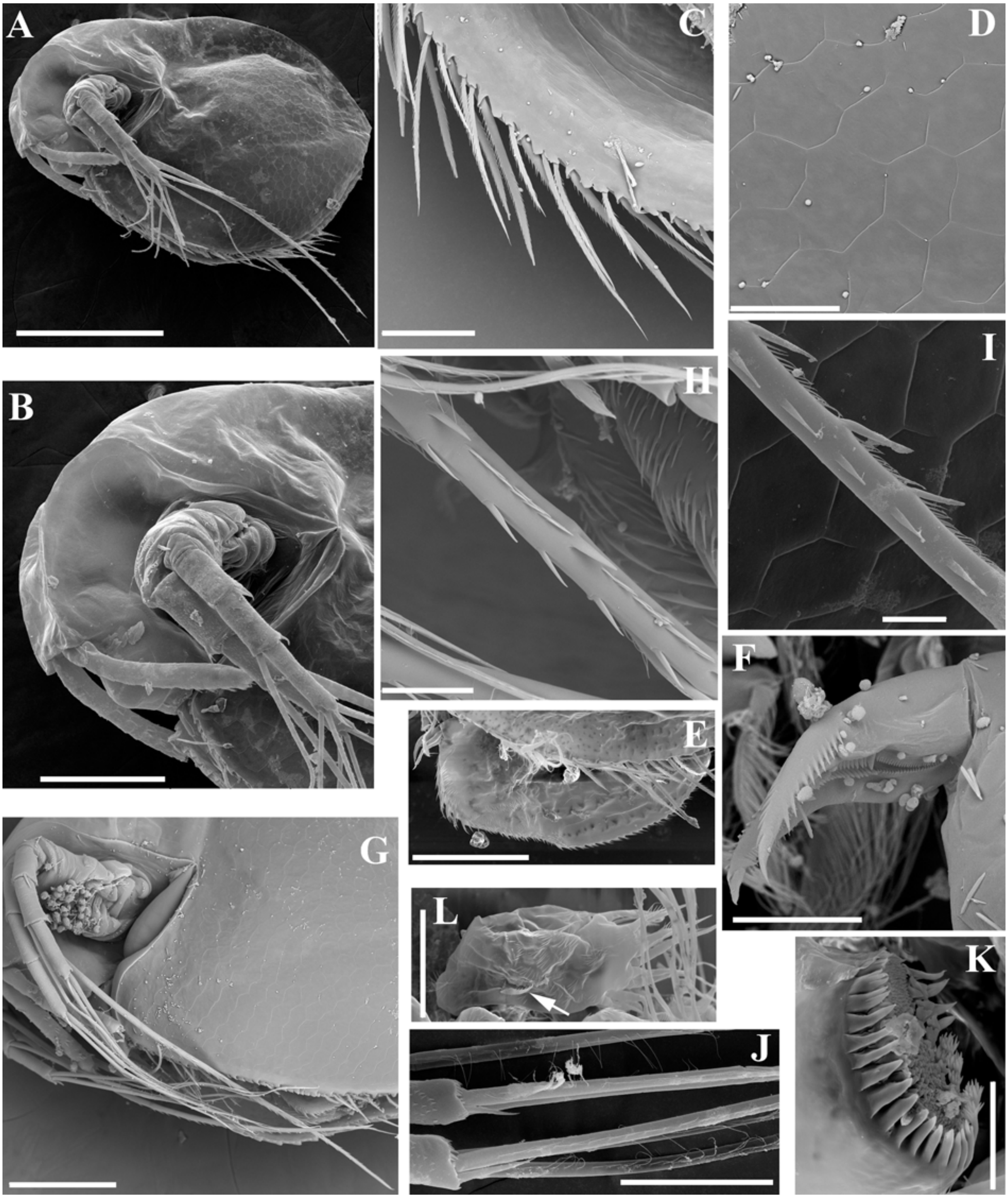

Fig. 15. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from Glen Avis rock pool 4 (S 30.8053°, E 28.2214°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-131. A, General view. B, Head. C, Armature of ventral margin of valve. D, Central part of valve. E, Postabdomen. F, Postabdominal claw. G, Antenna II. H–I, Central part of lateral seta of basal endopod segment of antenna II. J, Apical swimming setae of antenna II. K, Mandible. L, Limb I. Scale bars: 0.5 mm for A, 0.2 mm for B, G 0.1 mm for E, 0.05 mm for C–D, J, L, 0.02 mm for F, H–I, K.

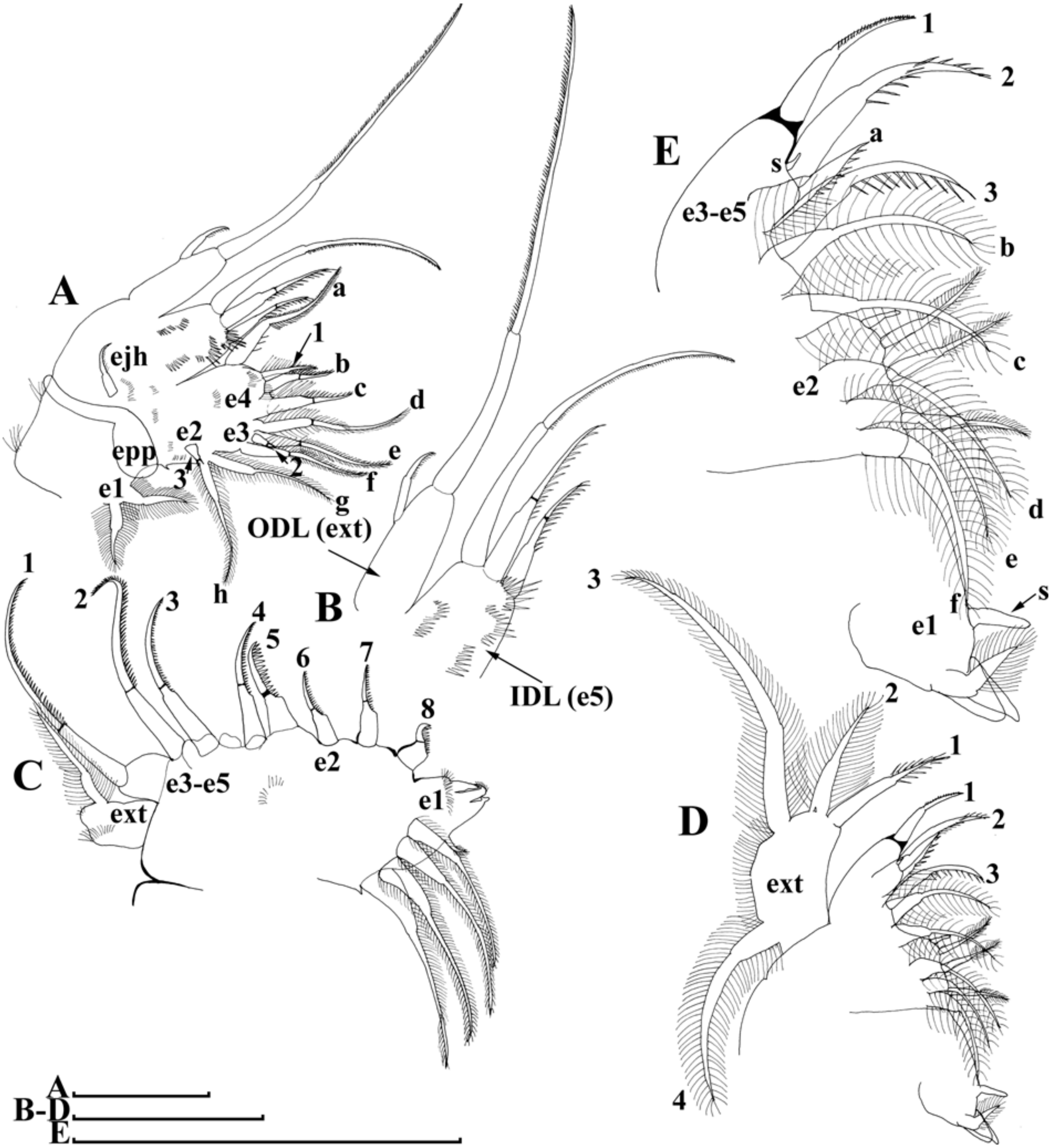

Fig. 16. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from Glen Avis rock pool 4 (S 30.8053°, E 28.2214°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-131. A, Corm of limb I. B, Distal part of limb I. C, Limb II. D, Limb III. E, Fragment of limb III. Scale bars: 0.1 mm.

postabdomen with prominent anal flaps and robust large denticles on the inner side of antenna I (see in Brehm, 1934: figs. 5a–b, 6; Rey and Saint-Jean, 1969: figs. 8b, d; Dumont and Van de Velde, 1977: figs. 5b, f). It enables us to consider *G. monodi* and *M. monodi*, the names used in these publications, as a junior synonyms of *M. odiosa* as well.

A particular difficult task is to clarify the status for two taxa described from Madagascar by Brehm: *M. madagascariensis* (Brehm, 1930) (= *G. madagascariensis*) and *M. orbicularis* Brehm, 1930. Brehm's type material is apparently lost. Descriptions and drawings of *M. orbicularis* do not contain important diagnostic features (Brehm, 1930: p. 681–686, figs. 4–6), and a single helpful trait is a subquadrangular postabdomen in both these taxa (Brehm, 1930: fig. 6). Descriptions for *M. madagascariensis* are dubious and very incomplete (Brehm, 1930: p. 682–683, figs. 3a–b) (see also in Brehm, 1933: p. 691 and Brehm, 1952: p. 41). Brehm himself listed the name *M. odiosa* for populations from Madagascar as well. Unstable generic position (there were at least three generic names for large-bodied African *Macrothrix* species: *Echinisca* Liévin, *Gurneyella* Brehm and *Macrothrix* Baird) had brought additional confusion to the taxonomy of this

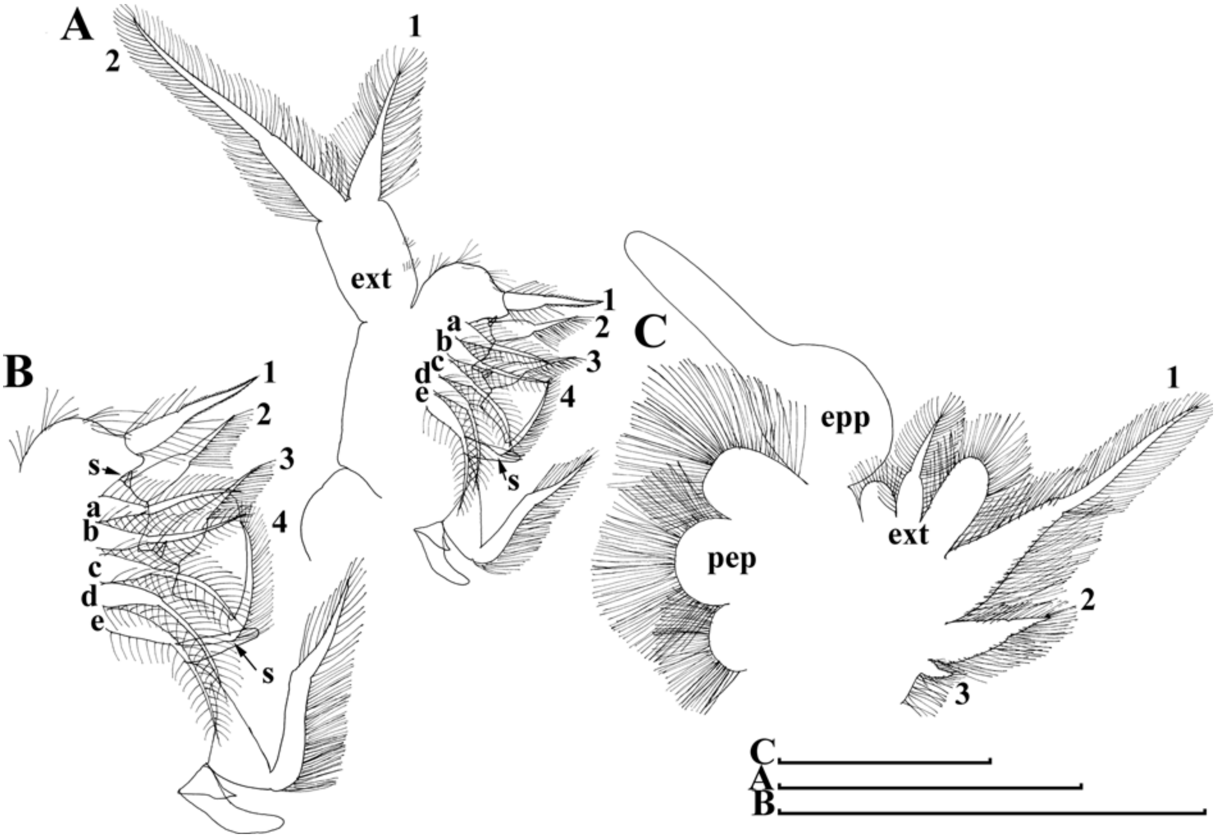

Fig. 17. *Macrothrix odiosa* Gurney, 1916, parthenogenetic female from Glen Avis rock pool 4 (S 30.8053°, E 28.2214°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-131. A, Limb IV. B, Fragment of limb IV. C, Limb V. Scale bars: 0.1 mm.

group. Kořínek (1984) and Smirnov (1992) considered *M. madagascariensis* and *M. orbicularis* as junior synonyms to *M. odiosa*. We also expect that Madagascar is inhabited by *M. odiosa*. This is the most common African species from the *M. paulensis* group. It is known that usually the cladoceran faunas of tropical islands do not contain a large number of endemic taxa (Schabetsberger *et al.*, 2009; Van Damme, 2016). For Madagascar no endemic cladocerans are known to date based on a current level of revision of the cladocerans from this island (see *e.g.* Schabetsberger *et al.*, 2013; Neretina and Sinev, 2016). K. Van Damme (personal communication) revealed few chydorid endemics in the samples from Madagascar, but these data are still unpublished.

Thus, in Africa, *M. odiosa* was found in Ethiopia (our data), Zambia (Kořínek, 1984: p. 51–52, plate 28: figs. 1–9), Chad (Rey and Saint-Jean, 1969); Nigeria (Dumont and Van de Velde, 1977), the Republic of Namibia (our data), Madagascar (Brehm, 1952: p. 41), the Republic of South Africa (our data). It is common in tropical and subtropical Asia (see Kotov *et al.*, 2005). Therefore *M. odiosa* is a widespread taxon from the *M. paulensis* group in tropical regions of the Old World, while the distribution range of *M. capensis* is only restricted to South Africa. These two species clearly differ from each other in morphological features of both females and males (see Tab. 1) and can be hardly confused. The large list of synonyms for *M. odiosa*, from the one hand, reflects the really vast distribution range of *M. odiosa* in the Old World, and, from the other hand, admiration by previous authors of the beauty of this peculiar large macrothricid.

(2) Description of new species of the *M. paulensis*-group from Australia

Macrothrix australiensis sp. nov.

(Figs. 20–25)

(?) *Echinisca capensis capensis* (Sars, 1916) in Smirnov and Timms (1983): p. 76, fig. 89a–d.

(?) *Echinisca capensis capensis* (Sars, 1916) in Smirnov (1976): p. 122, fig. 101.

Etymology. This new species is named after Australia, the continent where it was discovered. This name is intended to reflect a continental endemism, one of the main peculiarities in cladoceran distribution.

Type locality. Lake Fox (37.166°S, 139.777°E), South Australia.

Type material.

Holotype: an adult parthenogenetic female preserved in 96% ethanol and deposited to the collection of South Australian Museum, SAMA C11721. The label of holotype is: "*Macrothrix australiensis* sp. nov., 1 parth. ♀ from Lake Fox, HOLOTYPE".

Allotype: an adult male preserved in 96% ethanol and deposited to the collection of South Australian Museum, SAMA C11722. The label of allotype is: "*Macrothrix australiensis* sp. nov., 1 ♂ from Lake Fox, ALLOTYPE".

Paratypes: 20 undissected parthenogenetic females preserved in 96% ethanol and deposited to the collection of South Australian Museum, SAMA C11723 and SAMA

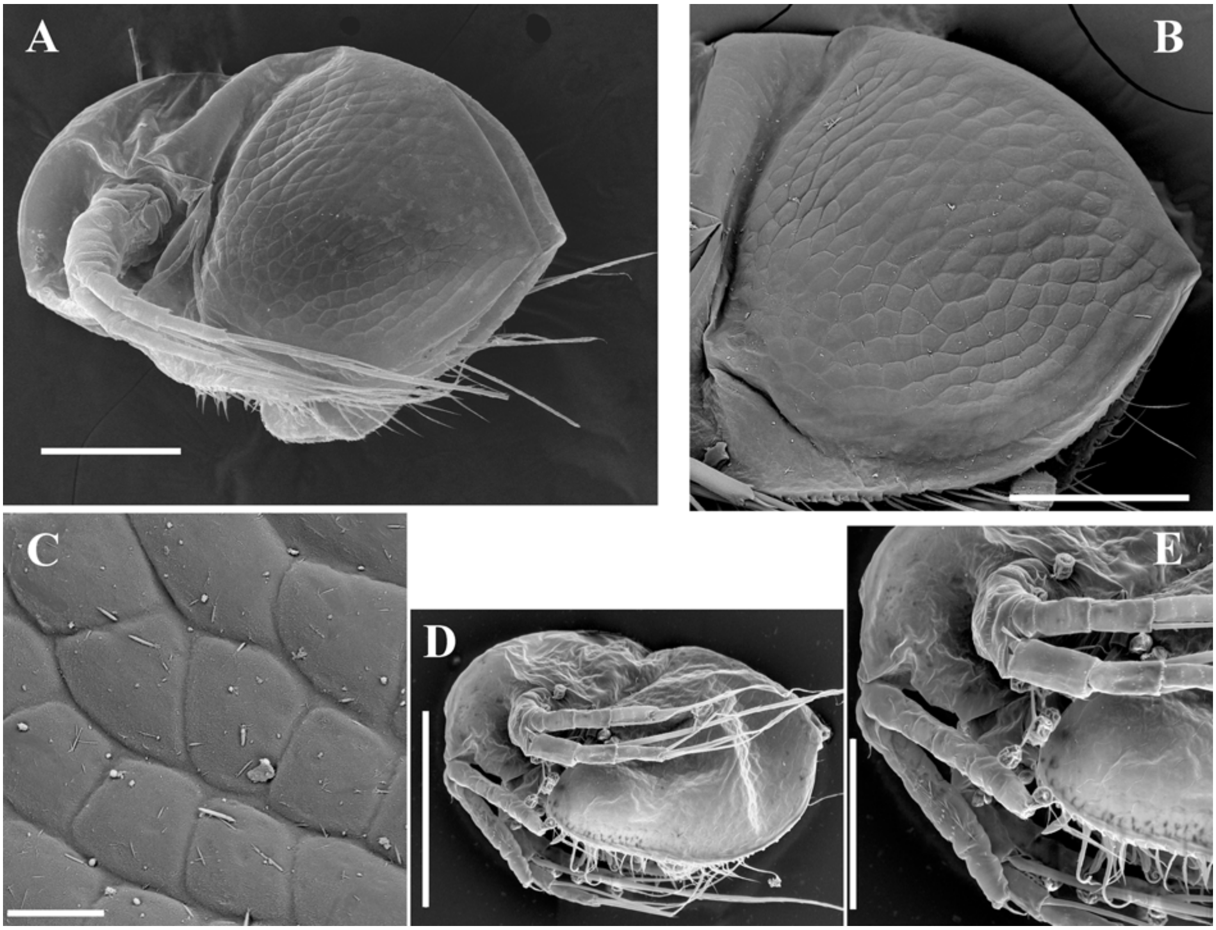

Fig. 18. *Macrothrix odiosa* Gurney, 1916 from Glen Avis rock pool 4 (S 30.8053°, E 28.2214°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-131. A–C, Ephippial female. D–E, Adult male. A, Ephippial female, general view. B, Ephippium, general view. C, Fragment of ephippium. D, Male, general view. E, Male, Head. Scale bars: 0.2 mm for A–B, D, 0.1 mm for E, 0.02 mm for C.

C11724; 10 undissected parthenogenetic females preserved in 96% ethanol and deposited to the collection of the collection of Zoological Museum of M.V. Lomonosov Moscow State University: MGU Ml 160.

Other material studied. 10 parthenogenetic females from Lake Fox (individuals from laboratory culture of A.V. Makrushin), South Australia, collection details unknown, AAK-1998-053; 3 parthenogenetic females from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, AAK-1998-054; 10 parthenogenetic females, 2 ephippial females and 3 males from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, AAK-2005-197; 5 parthenogenetic females from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, NNS-1997-071; 10 parthenogenetic females, 1 ephippial female and 1 male from Lake Ada, region of Kingscote, Kangaroo Island (S 35.9167°; E 137.3667°), South Australia, coll. 09.01.1976 by B.V. Timms, NNS-1997-168.

Diagnosis. Species of large size for the genus (length of adult parthenogenetic female up to 1.00 mm). Dorsum not elevated significantly above head. Serration on dorsum not expressed. Posterodorsal angle of body smooth. Head pore located on the level of head. Ventral head margin with a projection. Labrum of moderate length, with a rounded apical portion. Postabdomen subquadrangular, postabdominal flaps not prominent. Anal margin of postabdomen covered by fine denticles. Antenna I rod-like, with a row of bunches of gracile short denticles. Armature of proximal endopod segment seta of antenna II represented by a row of robust denticles. Spine on the second exopod segment seta of antenna II short, reaches 1/3 length of third exopod segment. Thoracic limb I bears a single ejector hook. On exopodite of thoracic limb III seta 3 subequal in length to seta 2. On exopodite of thoracic limb IV seta 2 almost subequal in size to seta 1. Ephippial female similar with parthenogenetic female. Ephippium typical for macrothricids, brownish, containing two eggs. Male as for the genus, male seta located in the middle of antennular body.

Description

Parthenogenetic female. In lateral view, body ovoid, maximum height at middle of body (body height/length ratio about 0.67) (Fig. 20A). In dorsal and ventral view body compressed laterally. Dorsal margin arched from tip of rostrum to posterior most point, not interrupted over compound eye (Fig. 20A). Dorsal margin of valves almost straight or concave not elevated above dorsal margin of head (Fig. 20A). Posterodorsal margin broadly rounded (Fig. 20A). Posterodorsal angle smooth, obtuse (Fig. 20A). Ventral margin of

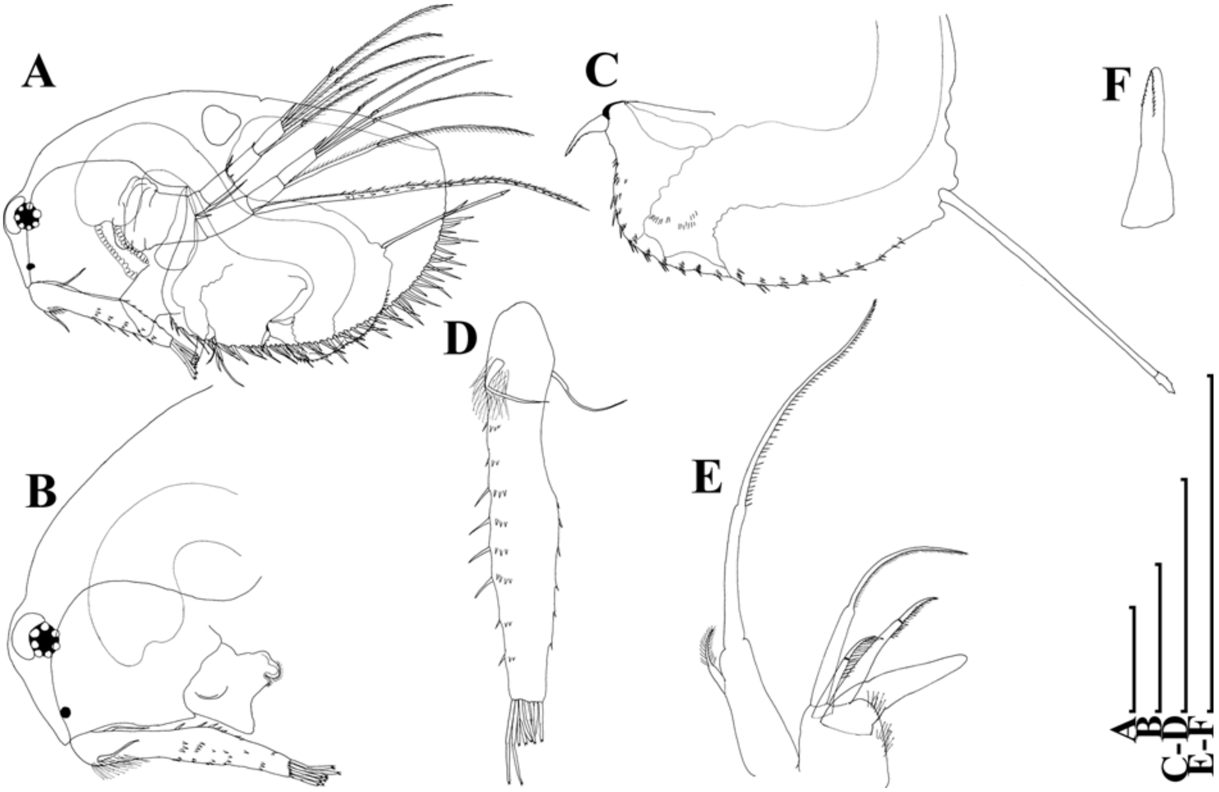

Fig. 19. *Macrothrix odiosa* Gurney, 1916, adult male from Glen Avis rock pool 4 (S 30.8053°, E 28.2214°), McClear, Eastern Cape, the Republic of South Africa, coll. 29.03.1993 by K. Martens, de Moor and Barber, NNS-2002-131. A, General view. B, Head. C, Postabdomen. D, Antenna I. E, Fragment of limb I. F, Male hook. Scale bars: 0.1 mm.

body convex, covered by setae of different size in different regions of valves (Figs. 20E–H, 22C). Anteroventral angle rounded. Valves with prominent sculpture, represented by polygons (Fig. 22D).

Head large (Fig. 20A–B), head length from tip of rostrum to border with valves makes up 0.30 times of body length. In lateral view, dorsal margin of head without dome above compound eye. Head ventral margin with projection or inflated (Fig. 20B). Compound eye significantly larger than ocellus (Fig. 20B). Dorsal head pore large, rounded (Figs. 20C, 22B). Labrum large, triangular in lateral view (Fig. 20D). Distal labral appendage finely setulated (Fig. 20D).

Thorax relatively long (Fig. 20A). Abdomen short (Fig. 20A).

Postabdomen elongated (Figs. 20I, 22E), subrectangular in lateral view; postabdomen length/height ratio about 3. Ventral margin of postabdomen almost straight, with transverse rows of fine setules (Figs. 20I–J, 22E). Preanal margin long, about in 3 times longer than anal margin. Postanal margin significantly shorter than anal margin (Figs. 20I–J, 22E). Preanal and anal margins covered by transverse rows of fine denticles (Figs. 20I–J, 22E). No prominent postabdominal flaps at side of anus (Fig. 20I–J). Postabdominal seta as long as postabdomen, its distal segment short, covered by long setules (Fig. 20I). Postabdominal claw small (almost subequal in length to postanal margin of postabdomen), curved, with pointed tip and broad base in lateral view (Figs. 20K, 22F). Several denticles on its dorsal side and more fine denticles on ventral side.

Antenna I rod-like (Figs. 21A, 24A) long and straight. Its inner margin covered by transverse rows of small denticles, also the whole surface of antennular body bears fine spinules (Figs. 21A, 24A). Antennular sensory seta slender, arising from outer side of proximal part (Fig. 21A). Nine aesthetascs, two of them longer and thicker than the rest. Each aesthetasc bears two minute “claws” at the apex (Fig. 21A).

Antenna II large (Figs. 21B, 22A, G–H), coxal region slightly folded, with two small sensory setae subequal in size (Fig. 21B). Antennal formula: setae 0-0-1-3/1-1-3, spines 0-1-0-1/0-0-1. Basal segment robust, conical, covered by transverse rows of fine spinules (Figs. 21B, 22A, G–H). Small spine (subequal in length to first exopod segment) located on outer surface of basal segment (Figs. 21B, 22G). Bisegmented short seta (subequal in length to first plus second exopod segments) located on inner surface of basal segment (Figs. 21B, 22H). Exopod and endopod branches subequal in size (Figs. 21B, 22A). All their segments cylindrical, elongated, covered by transverse rows of fine spinules (Fig. 22A). Apical swimming setae long subequal in length, bearing fine spinules and long setules (Figs. 21B, 22J–K). Lateral seta of proximal endopod segment (Fig. 21B–C) longer than other setae and armed with two rows of spinules: spinules on the edge of this seta are thin and densely located (distance between two neighboring spinules is almost equal to their length); spinules on the outer surface of this seta are more robust and sparsely located (distance between two neighboring spinules is in two times more than width of seta) (Figs. 21D–E, 22I). Seta on middle exopod segment reaches tips of apical setae, covered by long setules and fine stiff spinules

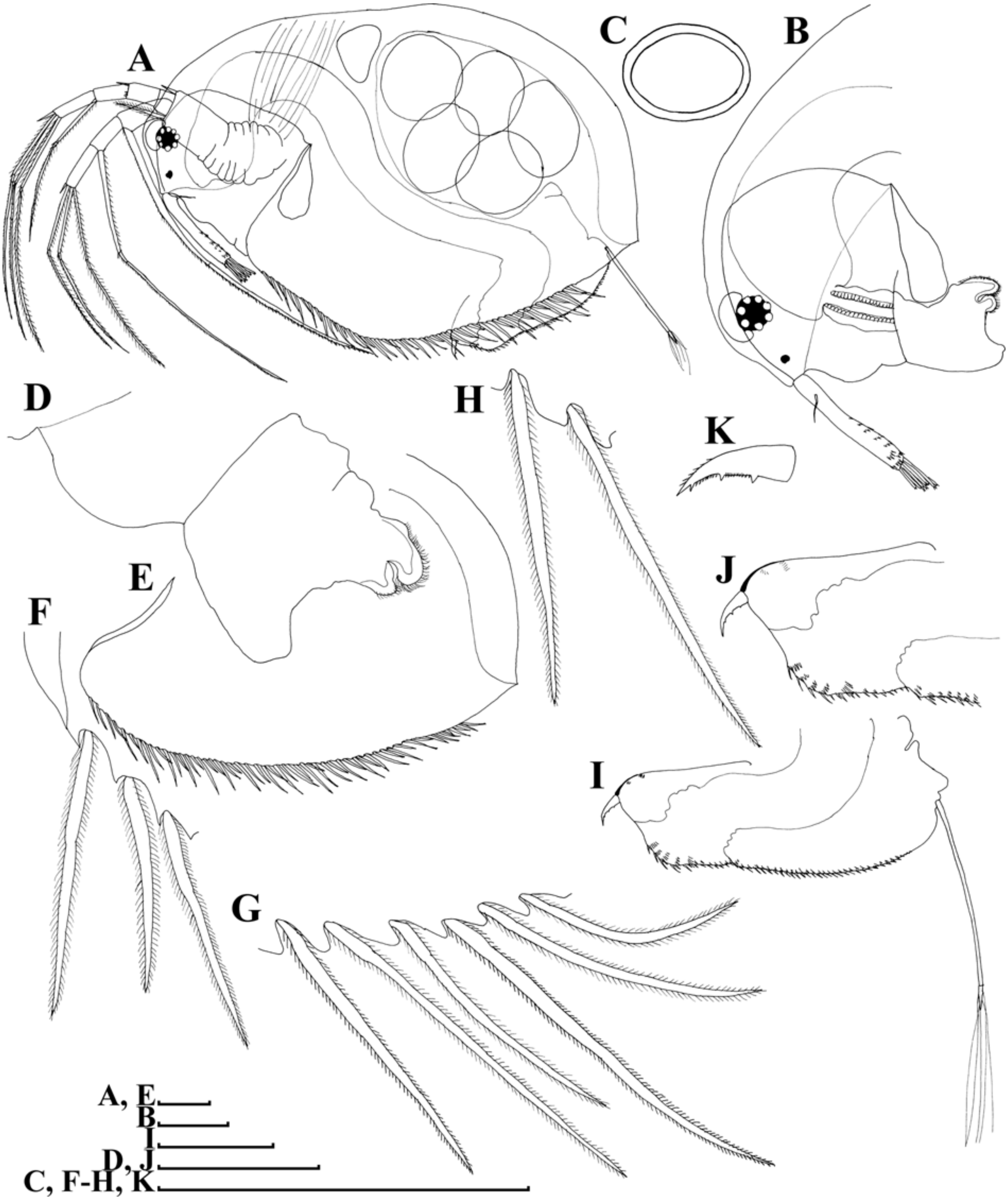

Fig. 20. *Macrothrix australiensis* sp. nov., parthenogenetic female from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, AAK-2005-197. A, General view. B, Head. C, Dorsal pore. D, Labrum. E, Valve. F, Armature of anterior margin of valve. G, Armature of ventral margin of valve. H, Armature of posterior margin of valve. I, Postabdomen. J, Distal portion of postabdomen. K, Postabdominal claw, outer view. Scale bars: 0.1 mm.

(Fig. 21B). Lateral seta of third exopod segment has the same armature (Figs. 21B, 22K). True spine on second exopod segment thin, almost in three times shorter than third exopod segment (Figs. 21B, 22G–H). Second and third exopod segments bear short additional spines, and additional spines on third exopod segment are hardly visible under light microscope (Fig. 21B), but recognizable under scanning electron microscope (Fig. 22H). All investigated individuals had two-three additional spines on the second exopod segment and two significantly smaller additional spines on third exopod segment. Spines of both apical exopod and endopod segments thin, exopod apical spine in two times longer than endopod apical spine (Fig. 22K).

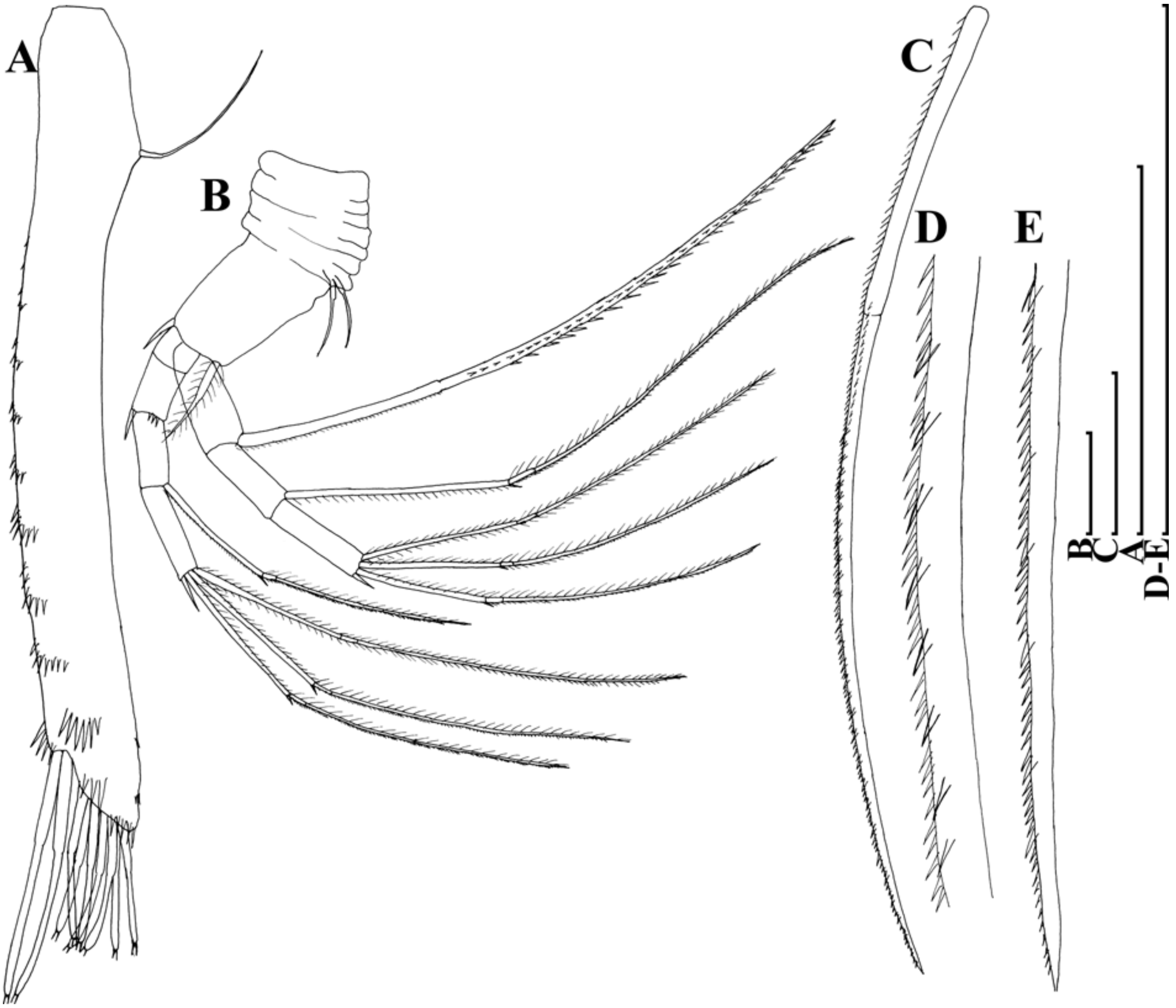

Fig. 21. *Macrothrix australiensis* sp. nov., parthenogenetic female from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, AAK-2005-197. A, Antenna I. B, Antenna II. C, Lateral seta of basal endopod segment of antenna II. D, Its central part. E, Its distal part. Scale bars: 0.1 mm.

Thoracic limbs: five pairs (Fig. 23A–G).

Limb I large (Fig. 23A–B). Accessory seta short (Fig. 23B). ODL conical and large, bearing a single long bisegmented seta, its distal segment feathered unilaterally (Fig. 23B). IDL conical, covered by transverse rows of stiff setules, with three bisegmented setae of different size (Fig. 23B). Distal segment of each IDL seta covered unilaterally by stiff setules (Fig. 23B). Limb corm almost rectangular in lateral view (Fig. 23A). Endite 4 with three posterior soft setae (among them seta a the longest covered by long fine setules, setae b and c significantly shorter, subequal in size, bearing fine long setules in proximal parts and stiff short setules in distal parts) and a single stiff anterior seta 1 (Fig. 23A). Endite 3 with three soft posterior setae unequal in size and a single fork-like anterior seta 2 (Fig. 23A). Endite 2 with two posterior bisegmented setae subequal in length, covered by fine short setules, and a single anterior seta 3 represented by fork (Fig. 23A). Endite 1 with two soft setae. A single ejector hook with setulated distal segment (Fig. 23A).

Limb II triangular-rounded (Fig. 23C). Exopodite ovoid, covered by fine setules, and bearing a single long soft seta (Fig. 23C). Inner portion of limb II with eight scrapers, decreasing in size proximally (Fig. 23C). A deep incision between endite 2 and endite 1. Portion of gnathobase (= endite 1) bordering endite 2 somewhat inflated and bears a row of fine setules (Fig. 23C). Distal armature of gnathobase with four elements (Fig. 23C). Filter plate with four soft setae, subequal in length (Fig. 23C).

Limb III (Fig. 23D–E) with subrectangular exopodite, bearing a single lateral seta and three distal setae (among them, middle seta somewhat longer than others) (Fig. 23D). Distal endite with three anterior setae and small sensillae near seta 2 and seta 3 (Fig. 23E). Proximal endite with a small elongated sensillum and three setae subequal in length (Fig. 23E). Six setae on posterior face of limb (a–f) (among them seta a short and thick, covered by small spinules in its distal part, other five setae with fine long setules) (Fig. 23E). Distal armature of gnathobase with four elements (Fig. 23E). Filter plate absent (Fig. 23D).

Limb IV (Fig. 23F) with small rounded exopodite, bearing distally two soft setae, subequal in size. Inner distal portion with four anterior setae (1–4) and small sensillae near seta 2 and seta 3 (Fig. 23F). Posterior face with five soft setae

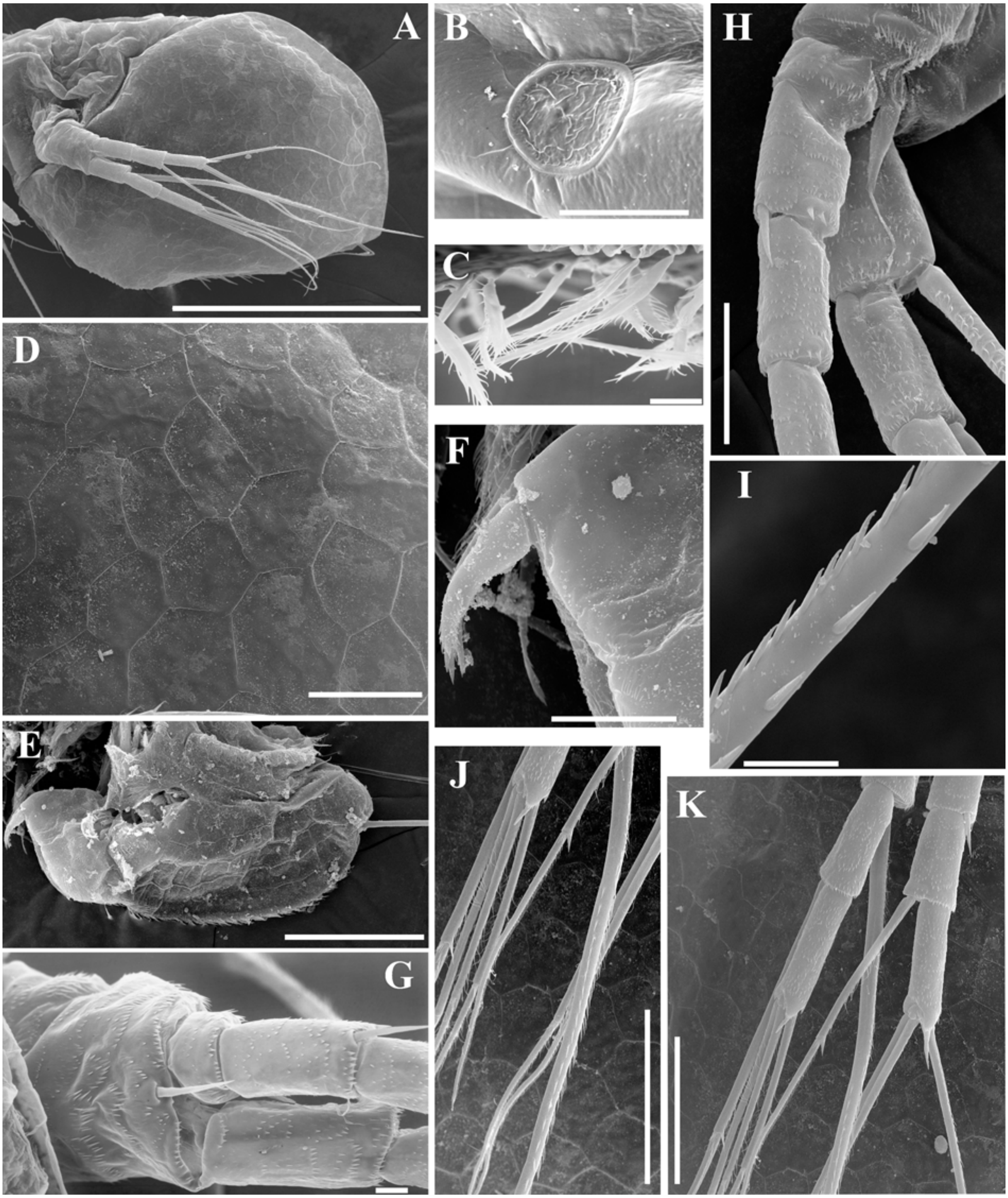

Fig. 22. *Macrothrix australiensis* sp. nov., parthenogenetic female from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, AAK-2005-197. A, Valve. B, Dorsal pore. C, Armature of ventral margin of valve. D, Central part of valve. E, Postabdomen. F, Postabdominal claw. G–H, Exopod and endopod branches of antenna II. I, Central part of lateral seta of basal endopod segment of antenna II. J, Swimming setae of antenna II. K, Apical spines of antenna II. Scale bars: 0.5 mm for A, 0.1 mm for E, J–K, 0.05 mm for D, H, 0.02 mm for F, 0.01 mm for B–C, G, I.

increasing in size proximally (Fig. 23F). Distal armature of gnathobase consists of four elements (a small bottle-shaped sensillum, bisegmented seta and two small projections. Filter plate absent (Fig. 23F).

Limb V (Fig. 23G) with three-lobed densely setulated preepipodite. Epipodite ovoid. Exopodite with a single seta, covered by fine setules (Fig. 23G). Inner distal portion as a small flap, covered by setules; three setae on its inner margin

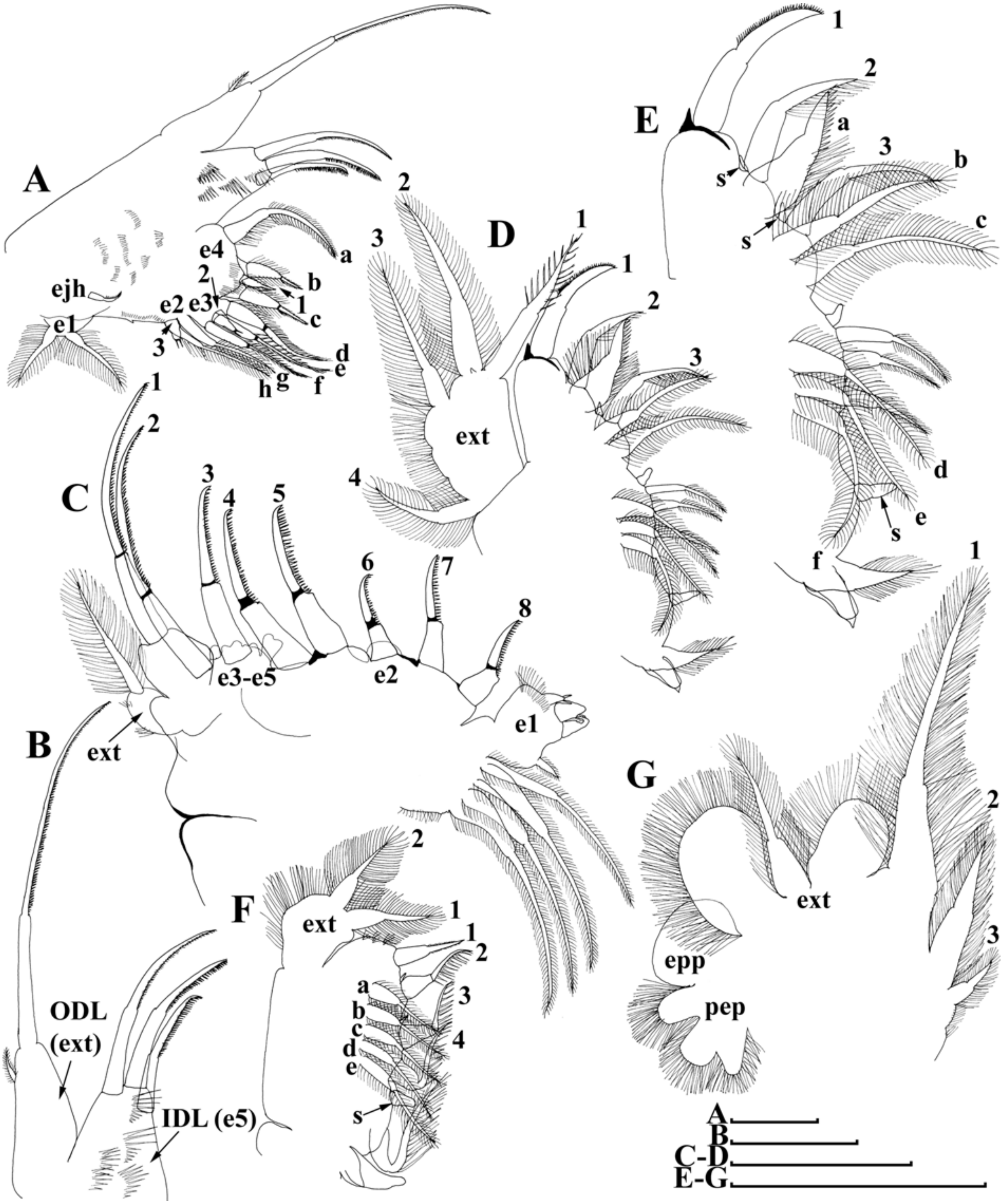

Fig. 23. *Macrothrix australiensis* sp. nov., parthenogenetic female from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, AAK-2005-197. A, Limb I. B, Distal part of limb I. C, Limb II. D, Limb III. E, Fragment of limb III. F, Limb IV. G, Limb V. Scale bars: 0.1 mm.

(the distalmost seta significantly longer and thicker than others) (Fig. 23G). Filter plate absent (Fig. 23G).

Ephippial female. In lateral view, body proportions as in parthenogenetic female. Structure of ephippium typical for the genus (Fig. 24B–C). Almost all valves area incorporated to ephippium. Surface of ephippium with polygonal hillocks (Fig. 24B). Two eggs in ephippium.

Adult male. Body ovoid, dorsal margin interrupted by a shallow depression between head and valves (Fig. 25A). Dorsal margin of valves straight or slightly convex not elevated above head (Fig. 25A). Posterodorsal angle distinct, acute, without spine (Fig. 25A). Posteroventral region of valve rounded; ventral margin convex. Anteroventral angle broadly rounded (Fig. 25A). Head large, with small

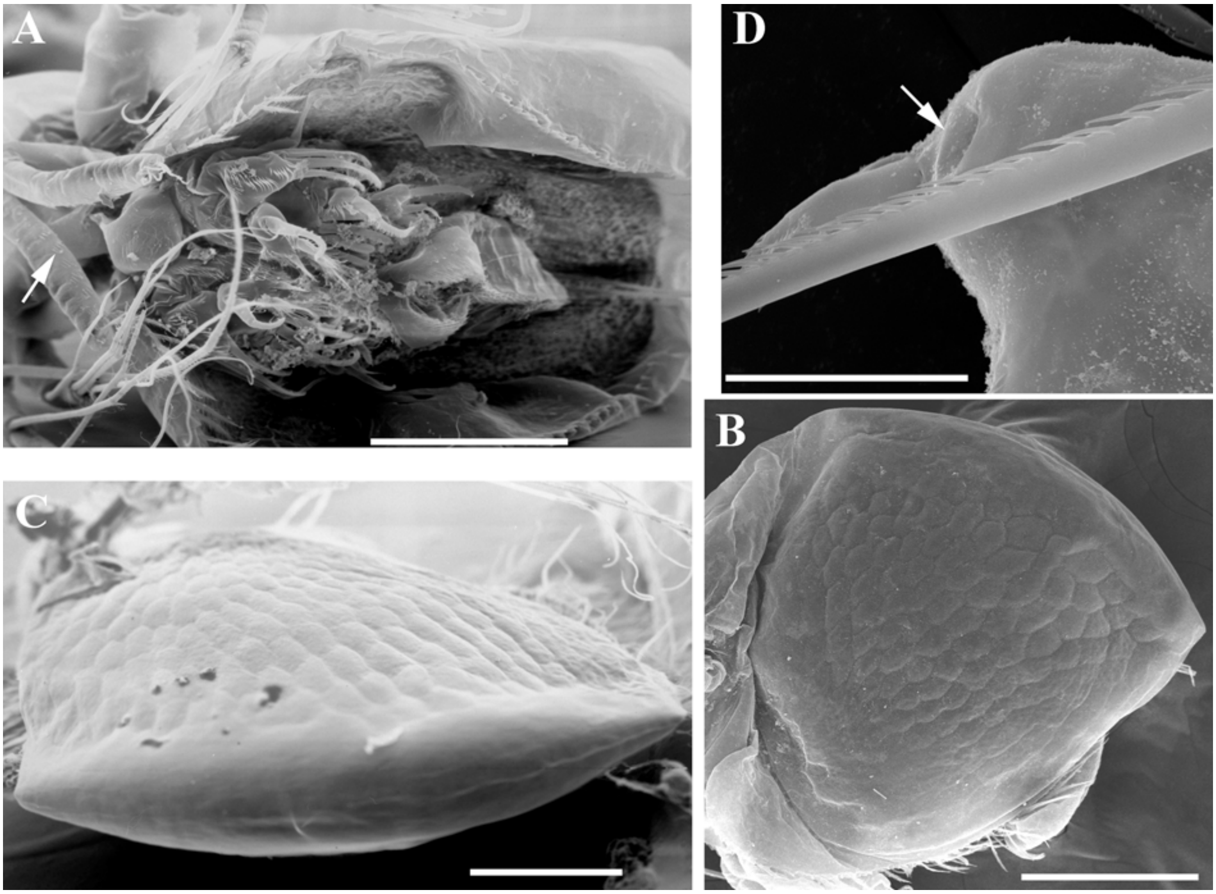

Fig. 24. *Macrothrix australiensis* sp. nov., from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, AAK-2005-197. A, Parthenogenetic female, ventral view (small spines on antenna I are marked *via* arrow). B–C, Ephippial female. D, Postabdomen of adult male (gonopores is marked *via* arrow). Scale bars: 0.1 mm for A, 0.2 mm for B–C, 0.02 for D.

supraocular dome (Fig. 25B). Ventral margin of head slightly inflated (Fig. 25B).

Postabdomen subrectangular (Fig. 25C), with inflated ventral margin. Armature of dorsal margin similar to parthenogenetic female. Gonopores open on ventral sides near claws base (Figs. 24D, 25C).

Antenna I straight (Fig. 25D), rod-like, almost subequal in length to head. Antennular body covered by fine spinules and denticles of different length and thickness. Male seta located in the middle of antennular body on the inner side (Fig. 25D). Sensory seta located on the outer side of antennular body near its base (Fig. 25D). Apex of antenna I bears nine terminal aesthetascs, two of them significantly longer than others (Fig. 25D). Armature of proximal endopod segment seta of antenna II identical to that in parthenogenetic female (Fig. 25A).

Thoracic limb I (Fig. 25E) with ODL and IDL as in female (male seta was not found), copulatory hook elongated, curved, its distal portion with fringe.

Size. Maximum length of adult parthenogenetic females up to 1.00 mm, height 0.64 mm. Maximum length of ephippial females 0.77 mm, height 0.55 mm. Maximum length of adult males 0.46 mm, height 0.26 mm. Holotype is 0.83 mm in length, 0.55 mm in height. Allotype is 0.46 mm in length, 0.26 mm in height.

Variability. No significant variability was found between all investigated individuals.

Distribution. According to Smirnov and Timms (1983), regarding this taxon as *M. capensis*, *M. australiensis* sp. nov. is widely distributed in Australia, but most populations are located in the non-tropical portion of the continent: New South Walles, Victoria, South Australia and Tasmania.

Differential diagnosis. As *M. australiensis* sp. nov. is an endemic of Australia, here we analyze main differences of *M. australiensis* sp. nov. from other well-delineated Australian taxa, possible members of *M. paulensis* group. *M. australiensis* sp. nov. clearly differs from *M. flagellata* (Smirnov and Timms, 1983), *M. schauinslandi* Sars, 1904 and *M. timmsi* (Smirnov, 1976) in antenna II features (length of spine on the second exopod segment, number and length of additional spines, armature of the long seta on endopod proximal segment), as well as structure of postabdomen and postabdominal seta (see Tab. 2). According to some specific characteristic, *M. australiensis* sp. nov. seems to be closer to *M. timmsi*, than to other two species. *M. australiensis* sp. nov. and *M. timmsi* have postabdominal seta with short distal segment covered by long setules, while postabdominal seta of *M. flagellata* and *M. schauinslandi* bears long distal segment (subequal in length to proximal segment or even longer) (see Tab. 2). But *M. australiensis* sp. nov. differs

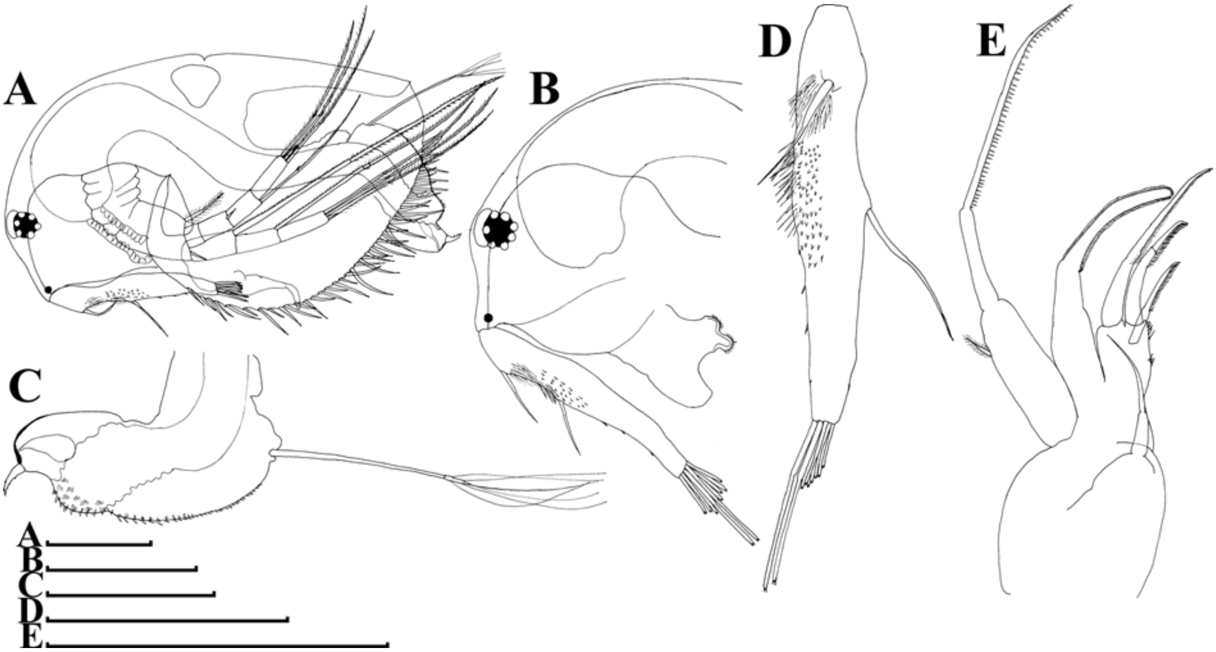

Fig. 25. *Macrothrix australiensis* sp. nov., adult male from Lake Fox (individuals from culture of A.V. Makrushin), South Australia, collection details unknown, AAK-2005-197. A, General view. B, Head. C, Postabdomen. D, Antenna I. E, Limb I. Scale bars: 0.1 mm.

from *M. timmsi* in structure of preanal margin of postabdomen. Preanal margin of *M. timmsi* is covered by very robust bifurcated denticles, while preanal margin of *M. australiensis* sp. nov. is covered by rows of small spinules (see Tab. 2). Main differences of *M. australiensis* sp. nov. from other well-delineated members of *M. paulensis* group are shown in Table 1 concerning mainly fine details (structure of antenna I and antenna II, thoracic limbs), as well as male morphology.

(3) Cladistic analysis

In the present analysis, 19 morphological characters in 12 taxa derived from our analysis of original samples and literature data were incorporated (Tabs. 3 and 4). Characters 6 and 7 were marked as ordered transformation series. Our analysis with *M. triserialis* as outgroup yielded 18 equally-parsimonious trees (TL = 31, CI = 0.807, RI = 0.842), a strict consensus tree is represented in Fig. 26. Bootstrap test resulted in a tree with the same topology.

All examined taxa form a monophyletic *M. paulensis* group with the following synapomorphies: 7, 10, 13, 16, 18. Within the latter, we can recognize: (1) a basal section (*M. capensis*, *M. australiensis* sp. nov., *M. agsensis*, *M. atahualpa*, *M. smirnovi*) with unclear relationships between each other (except *M. atahualpa* and *M. smirnovi* which are closest relatives); (2) a crown group with the following synapomorphies: 11, 15, 17. Within this group, two main clades are differentiated: (A) the Neotropical clade *M. paulensis* plus *M. brandorffi*, supported by the following synapomorphies: 4, 5, 6, 9, 10, and (B) a clade uniting Asian taxa plus Neotropical *M. sioli*, supported by the following synapomorphies: 6, 12, 19.

The homoplastic characters are: 1, 6, 8, 18.

4 Discussion

Diagnosing monophyletic *Macrothrix paulensis* species group

We offer several diagnostic characters of the *M. paulensis* species group among other members of the genus *Macrothrix*. First of all, these characters are important for the differentiation of the former from its possible congeners, the *M. triserialis* group (even some members of former were previously regarded as members of the latter, see Dumont *et al.*, 2002).

Character 7 (see Tabs. 1, 3). A large, usually triangular labrum. Only *M. capensis*, *M. agsensis* and *M. malaysiensis* have a rounded labrum, other taxa of the *M. paulensis* group possess a triangular labrum. Usually all other taxa of *Macrothrix* have a small labrum (Smirnov, 1976, 1992; Kotov, 1999; Silva-Briano *et al.*, 1999; Dumont *et al.*, 2002; Kotov *et al.*, 2004). This size and shape of labrum is widely used in the cladoceran taxonomy, see in Frey (1975, 1980), Smirnov (1996), Bekker *et al.* (2012).

Character 10 (see Tab. 3). Presence of robust denticles on the dorsal (concave) side of the postabdominal claw is a very characteristic of the *M. paulensis* group, moreover, two taxa – *M. paulensis* and *M. brandorffi* – have only robust denticles on the inner face of the postabdominal claw. Appearance of strong denticles on the postabdominal claws instead of fine setules is very characteristic for different daphniids: *Daphnia* O.F. Mueller (Alonso, 1996; Benzie, 2005), *Ceriodaphnia* Dana (Alonso, 1996), *Scapholeberis* Schoedler (Dumont and Pensaert, 1983). Two taxa, *M. smirnovi* and *M. atahualpa*, have a very specific armature of the postabdominal claw: a row of long and robust spines strongly increasing in size distally.

Character 13 (see Tab. 3). A single ejector hook on limb I in the *M. paulensis* group and two ejector hooks in the *M. triserialis* group. The latter character is especially important. All Anomopoda are characterized by two ejector hooks, but there are a few exceptions such as *Ilyocryptus acutifrons* group (Alonso, 1996; Kotov and Elías-Gutiérrez, 2009) and *M. paulensis* group in our new understanding, including *M.*

Table 2. Comparison between Australian members of the genus *Macrothrix* Baird, 1843 (after Smith, 1909; Gurney, 1927; Smirnov and Timms, 1983; Smirnov, 1976 (we kept Russian letters for original illustrations); 1992 and our current data)

Species	Maximum body length, mm	Shape of antenna I	Some main diagnostic features	Remarks
Macrothrix australiensis sp. nov.	1 mm	Rod-like antenna I	Head ventral margin is inflated or with projection. Short spine is located on the second exopod segment (about 1/3 of third exopod segment length) and short additional spines are on the second and third exopod segments. Distal segment of postabdominal seta is short and covered by long setules. Postabdomen with fine spinules on dorsal margin.	Exactly belongs to *M. paulensis* species group because of size, rod-like antennas I and a single ejector hook on the thoracic limb I.
Macrothrix breviseta Smirnov, 1976	0.56 mm for holotype (Smirnov, 1976: p. 95)	Dilating antenna I (Smirnov, 1976: p. 95, fig. 67Г)	Very long spine is located on the second exopod segment (subequal in length to the third exopod segment) (Smirnov, 1976: fig. 67AII). Distal segment of postabdominal seta is short. Postabdomen bears robust spinules on preanal margin (Smirnov, 1976: p. 95, fig. 67П).	Do not belong to *M. paulensis* species group because of dilating antennas I.
Macrothrix burstalis Smith, 1909	0.4 mm (Smith, 1909)	Antenna I are more or less rod-like (see description in Smirnov, 1976)	Morphology is studied inadequately (Smirnov, 1976).	Species inquirenda, not considered as valid taxon (Smirnov, 1992; Kotov *et al.*, 2013a).
Macrothrix carinata (Smirnov, 1976)	0.65 mm for holotype (Smirnov, 1976: p. 124)	Rod-like antenna I (Smirnov, 1976: p. 124, fig. 104AI)	Head ventral margin without projection (Smirnov, 1976: fig. 104Г). Long spine is located on the second exopod segment (3/4 of third exopod segment length) (Smirnov, 1976: fig. 104AII). Distal segment of postabdominal seta is short. Postabdomen bears robust denticles on preanal and postanal margin (Smirnov, 1976: fig. 104П).	Potentially may be a member of *M. paulensis* species group because of rod-like antennas I.
Macrothrix flabelligera Smirnov, 1992	0.6 mm (Smirnov, 1992: p. 82)	Rod-like antenna I (Smirnov, 1992: fig. 343)	Head ventral margin without projection (Smirnov, 1992: fig. 343). Short spine is located on the second exopod segment (1/4 of third exopod segment length) and short additional spines are on the second and third exopod segments (Smirnov, 1992: fig. 346). Distal segment of postabdominal seta is short, with very long setules (Smirnov, 1992: fig. 342). Postabdomen with robust spinules on dorsal margin (Smirnov, 1992: fig. 350).	Potentially may be a member of *M. paulensis* species group because of rod-like antennas I.
Macrothrix flagellata (Smirnov and Timms, 1983)	1.39 mm for holotype (Smirnov and Timms, 1983: p. 80)	Rod-like antenna I (Smirnov and Timms, 1983: fig. 93c).	Head ventral margin slightly inflated (Smirnov and Timms, 1983: fig. 93a). Spine on the second exopod segment is about two times shorter than third exopod segment (Smirnov and Timms, 1983: fig. 93d). Distal segment of postabdominal seta is longer than proximal segment (Smirnov and Timms, 1983: fig. 93b).	Potentially may be a member of *M. paulensis* species group because of size and rod-like antennas I.
Macrothrix hystrix Gurney, 1927	0.72 mm (Smirnov, 1992: p. 70)	Dilating antenna I (Gurney, 1927)	Morphology is studied inadequately (Smirnov, 1992).	Do not belong to *M. paulensis* species group because of dilating antennas I.
Macrothrix indistincta Smirnov, 1992	0.9 mm (Smirnov, 1992: p. 47)	Dilating antenna I (Smirnov, 1992: p. 47, fig. 166)	Spine on the second exopod segment is about two times shorter than third exopod segment (Smirnov, 1992: fig. 167). Distal segment of postabdominal seta is short and covered by long setules (Smirnov, 1992: fig. 168). Postabdomen with robust spinules on postanal margin (Smirnov, 1992: fig. 169).	Do not belong to *M. paulensis* species group because of dilating antennas I.
Macrothrix longiseta Smirnov, 1976	0.73 mm for holotype (Smirnov, 1976: p. 91)	Dilating antenna I (Smirnov, 1976: p. 91, fig. 61AI)	Spine on the second exopod segment is about two times shorter than third exopod segment (Smirnov, 1976: fig. 61AII) Distal segment of postabdominal seta is in 1.5 times longer than proximal segment (Smirnov, 1976: p. 91, fig. 61: general view). Postabdomen with robust spinules on postanal margin (Smirnov, 1976: fig. 61П).	Do not belong to *M. paulensis* species group because of dilating antennas I.
Macrothrix pectinata (Smirnov, 1976)	0.67 mm (Smirnov, 1976: p. 137)	Rod-like antenna I (Smirnov, 1976: fig. 118Г)	Head ventral margin without projection (Smirnov, 1976: fig. 118Г). Long spine is located on the second exopod segment (3/4 of third exopod segment length), and there are groups of long additional spines on the second and third exopod segments (Smirnov, 1976: fig. 118AII). Distal segment of postabdominal seta is short. Postabdomen bears robust spinules on preanal margin (Smirnov, 1976: fig. 118П).	Potentially may be a member of *M. paulensis* species group because of rod-like antennas I.

Table 2. (continued).

Species	Maximum body length, mm	Shape of antenna I	Some main diagnostic features	Remarks
Macrothrix spinosa King, 1853	Not more than 0.5 mm (Smirnov, 1992)	Dilating antenna I (Smirnov, 1992: fig. 69)	Short spine is located on the second exopod segment (less than half of third exopod segment) (Smirnov, 1992: fig. 70). Distal segment of postabdominal seta is short. Postabdomen covered by robust spinules on postanal margin (Smirnov, 1992: fig. 72).	Do not belong to *M. paulensis* species group because of dilating antennas I.
Macrothrix schauinslandi Sars, 1904	1 mm (Smirnov, 1992: p. 60)	Rod-like antenna I (Smirnov, 1992: 246-247)	Head ventral margin is slightly inflated (Smirnov, 1992: fig. 246). Short spine is located on the second exopod segment (less than half of third exopod segment). A short pseudospine is on the third exopod segment (Smirnov, 1992: fig. 250). Seta on proximal endopod segment is covered by robust and long spinules (Smirnov, 1992: fig. 251). Distal segment of postabdominal seta is subequal in length to proximal segment (Smirnov, 1992: fig. 249).	Potentially may be a member of *M. paulensis* species group because of size and rod-like antennas I.
Macrothrix timmsi (Smirnov, 1976)	0.68 mm (Smirnov, 1976: p. 135)	Rod-like antenna I (Smirnov, 1976: fig. 116AI).	Head ventral margin without projection, but slightly inflated (Smirnov, 1976: fig. 116, general view). Spine located on the second exopod segment is about two times shorter than third exopod segment (Smirnov, 1976: fig. 116AII). Distal segment of postabdominal seta is short, with very long setules (Smirnov, 1976: fig. 116Па). Postabdomen is covered by robust denticles on preanal margin (Smirnov, 1976: fig. 116Па–П6).	Exactly belongs to *M. paulensis* species group because of size, rod-like antennas I and a single ejector hook on the thoracic limb I.
Macrothrix williamsi (Smirnov and Timms, 1983)	0.58 mm for holotype (Smirnov and Timms, 1983: p. 80)	Rod-like antenna I (Smirnov and Timms, 1983: fig. 92c).	No information on the head ventral margin. Antenna II possesses very robust additional spines and spinules on all exopod segments (Smirnov and Timms, 1983: fig. 92d). Seta of proximal endopod segments is covered by very long and robust spinules (Smirnov and Timms, 1983: fig. 92e). Distal segment of postabdominal seta is short (Smirnov and Timms, 1983: fig. 92b). Postabdomen bears robust denticles on preanal and postanal margin (Smirnov and Timms, 1983: fig. 92b).	Potentially may be a member of *M. paulensis* species group because of rod-like antennas I.

atahualpa Brehm, 1936 (see a single ejector hook in Kotov *et al.*, 2010: fig. 9d) and two taxa described above. Unfortunately, some previous descriptions of *Macrothrix* taxa (detailed in other traits!) (Ciros-Pérez and Elías-Gutiérrez, 1997; Dumont *et al.*, 2002) are lacking an information on the ejector hook number.

Character 16 (see Tab. 3). Proximal endite of limb III with a small elongated sensillum and three setae in the *M. paulensis* group, but with a small bottle-shaped sensillum and four setae on proximal endite in the *M. triserialis* group. The lack of a seta of full length before three other setae of normal length may be considered as: (1) a complete reduction of the sensillum and partial reduction of seta 4; or (2) a sensillum behind seta 4 is kept, but seta 4 is completely reduced; (3) a sensillum and seta behind it are kept, and one of other setae completely reduced. We could not clarify this phenomenon without investigations of thoracic limbs development, but, interestingly, the same number of sensillae and setae on proximal endite of limb III is characteristic for other members of the *M. paulensis* group (Kotov and Hollwedel, 2004; Kotov *et al.*, 2005).

Character 18 (see Tab. 3). Members of the *M. paulensis* group have no setae at the posterior surface of the thoracic limb IV gnathobase, members of the *M. triserialis* group bear an additional soft seta here. This seta is found in other *Macrothrix* species, having a dilated antenna I (see *e.g.* in Kotov, 2007b). But even basal members of the group, like *M. atahualpa* (Kotov *et al.*, 2010), lacks this seta which makes these taxa similar to taxa of the crown group. Also *M. atahualpa* has five soft setae on inner-distal portion of limb IV (Kotov *et al.*, 2010 noted four setae, but we refuted this opinion based on re-examination of the same samples).

Also, it is necessary to note that usually members of the group are large macrothricids (up to 1 mm). This character was not included to the cladistic analysis as difficult for an adequate analysis due to insufficient knowledge on the maximum size of the taxa under consideration.

Our cladistic analysis based both on original and previously published literature data led us to conclusion that *M. capensis*, *M. atahualpa*, *M. smirnovi*, *M. agsensis* and *M. australiensis* sp. nov. must be included to the *M. paulensis* group in our new understanding (Tab. 1). *M. atahualpa* obviously belongs to the *M. paulensis* species group as well. Take into consideration that the diagnostic features of *M. atahualpa* considered by Kotov *et al.* (2010) are not strong enough to oppose this species to other members of the *M. paulensis* group. We have already shown that the shape of ventral head margin varies within the group (it could be with a projection or without a projection, or somewhat inflated) (see Tabs. 1 and 2), the armature of the inner side of antenna I is also varying among taxa.

Main distinctive features of *M. atahualpa* and *M. smirnovi* as compared with other *paulensis*-like species are: (1) the specific armature of the postabdominal claw (see above) and (2) the presence of soft seta between scraper 4 and scraper 5 on limb II (we checked this feature in particular in some specimens) (see

Table 3. Character descriptions (p, present; a, absent).

1. Body shape: posterodorsal angle as a spine (a = 0, p = 1);
2. Body shape: dorsum elevated significantly above head (a = 0, p = 1);
3. Body: serration on dorsum (a = 0, p = 1);
4. Head: head pore small, projected under level of head (a = 0, p = 1);
5. Head: no gap between head and valves (0), a very deep gap between head and valve (1);
6. Head: ventral head margin without projection (0), somewhat convex (1), strongly convex (2);
7. Labrum: small (0), of moderate length, with a rounded apical portion (1), large and triangular (2);
8. Postabdomen: anal flaps (a = 0, p = 1);
9. Postabdomen: hairs on anal margin (a = 0, p = 1);
10. Postabdominal claw: denticles on outer face only small (0), both small and large (1), rare and robust (2), long and robust spines strongly increasing in size distally (3);
11. Antenna I: large spines along inner margin (a = 0, p = 1);
12. Antenna II: only robust denticles in the middle of largest seta (0), large denticles alternating with fine setules (1), only small setules (2);
13. Limb I: single ejector hook (a = 0, p = 1);
14. Limb II: soft seta near scraper 4 very large (a = 0, p = 1);
15. Limb III: seta 3 on exopodite more than two times longer than seta 2 (a = 0, p = 1);
16. Limb III: proximal endite with a small elongated sensillum and three setae (a = 0, p = 1);
17. Limb IV: setae 2 and 1 on exopodite of unequal in size (a = 0, p = 1);
18. Limb IV: no setae at the posterior surface of gnathobase (a = 0, p = 1);
19. Male: sensory seta and male seta located in antenna I at a short distance (0), far from each other (1), nearby (2).

Table 4. Data matrix of 19-morphological characters in 12 taxa used in cladistic analysis. Data missing, or varying - .

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
paulensis	0	0	0	1	1	0	2	0	1	2	1	0	1	0	1	1	1	1	1
brandorffi	1	0	0	1	1	0	2	0	1	2	1	0	1	0	1	1	1	1	–
sioli	1	1	1	0	0	2	2	0	0	1	1	1	1	0	1	1	1	1	–
pholpunthini	1	1	1	0	0	2	2	1	0	1	1	1	1	0	1	1	1	1	2
odiosa	0	0	0	0	0	2	2	1	0	1	1	1	1	0	1	1	1	1	2
malaysiensis	1	0	0	0	0	2	2	0	0	–	1	0	–	0	–	1	–	1	–
capensis	0	0	0	0	0	2	1	0	0	1	0	0	1	0	0	1	0	1	0
atahualpa	0	0	0	0	0	1	2	0	0	3	0	0	1	1	0	1	0	1	–
australiensis	0	0	0	0	0	1	1	0	0	1	0	2	1	0	0	1	0	1	0
agsensis	0	0	0	0	0	1	1	0	0	1	0	–	1	0	0	–	0	1	2
smirnovi	0	0	0	0	0	1	2	0	0	3	0	0	1	1	0	1	0	1	1
triserialis	–	0	–	0	0	0	0	0	0	0	0	0	0	0	–	0	0	0	–

Tab. 1). In reality, the *atahualpa*-group needs to be revised once more, because *M. smirnovi* could be in fact a junior synonym of *M. atahualpa*. Descriptions of *M. smirnovi* by Ciros-Pérez and Elías-Gutiérrez (1997) and by Dumont *et al.* (2002) contradicts each other is some details, *i.e.* in male characters. Differences between *M. smirnovi* and *M. atahualpa* in our key (based on literature data on these taxa) could be illusory, appeared due to differences in the style of drawings of Harding (1955), Ciros-Pérez and Elías-Gutiérrez (1997) and Dumont *et al.* (2002).

Some characters of *M. malaysiensis* still remains unclear due to its incomplete description (Idris and Fernando, 1981b), but our cladistic search unambiguously attributed it to the *paulensis*-group.

Summarization of all available morphological data led us to the conclusion that morphological diversity of fine details within *M. paulensis*-like taxa is relatively strong, but these features are important for the species discrimination. The same situation, when fine details are critical for accurate and adequate identification, is known from many species groups, among which other large-bodied cladocerans like *Eurycercus* Baird or the *Daphnia similis* group (Bekker *et al.*, 2012; Kotov and Bekker, 2016; Popova *et al.*, 2016). In the future (after careful reexamination of all members of the genus *Macrothrix*) the taxa from the *M. paulensis* group could be attributed to the subgenus *Iheringula* within the genus *Macrothrix* (see also Kotov *et al.*, 2005). However such a designation would depend on a wider revision of the (likely paraphyletic) *Macrothrix*, and not relevant in this study. In any case, investigators of *Macrothrix* species must be ready to dissect specimens for searching of fine details that are critical for accurate identification. Below we are giving a preliminary identification key for all known to date species of *M. paulensis*-group and some close taxa.

Key to known species of *M. paulensis*-group and some close taxa discussed above (modified after Kotov *et al.*, 2005)

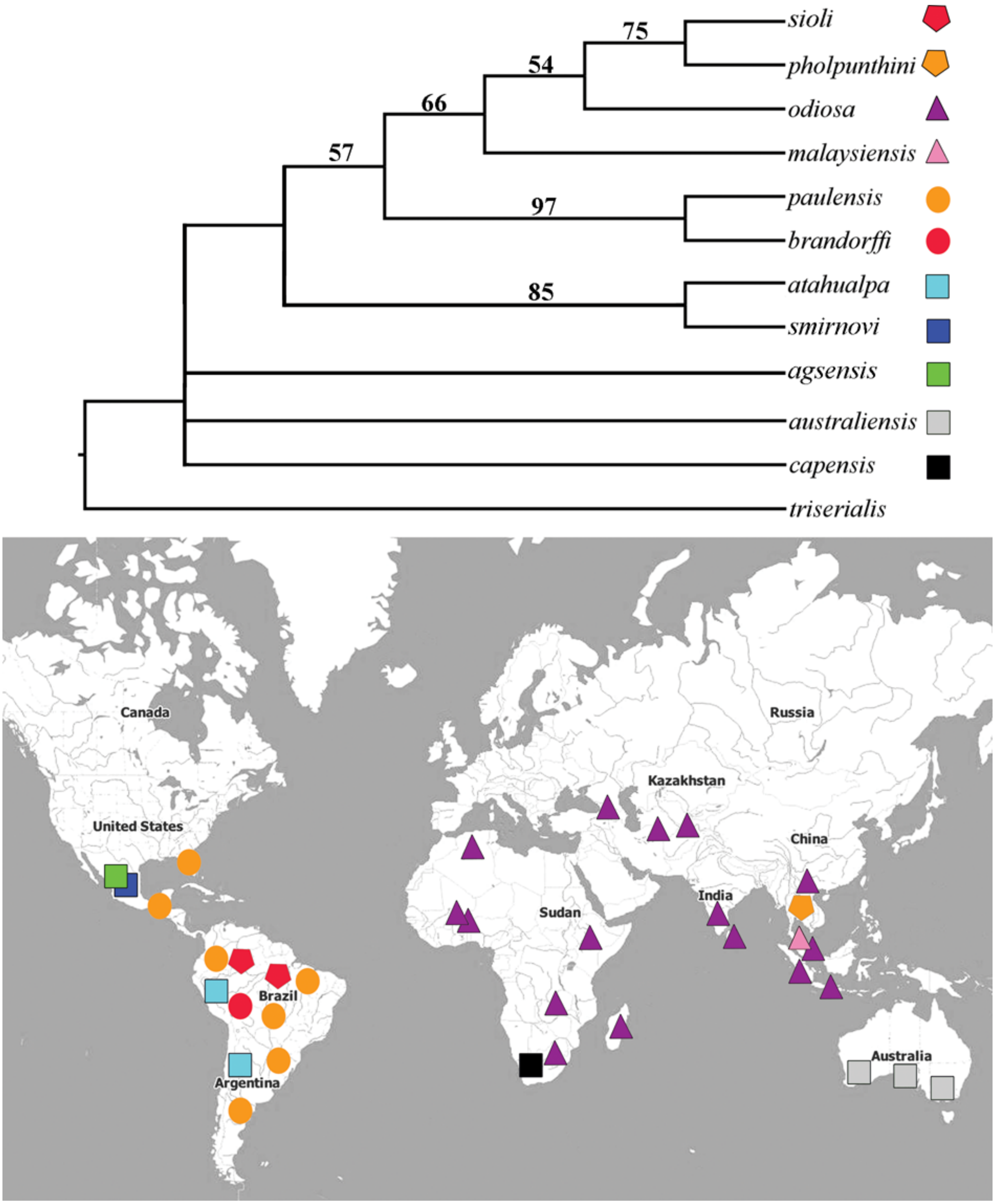

Fig. 26. A strict consensus of 18 equally-parsimonious trees for all investigated members of *Macrothrix paulensis* species group and map of their distribution (TL = 31, CI = 0.807, RI = 0.842). The 50% majority rule bootstrap simulation led a tree of similar topology with the contree. Due to this fact, branch probabilities were assigned to the aforementioned contree.

1 (2) Two contiguous spines near the base of antenna I – ***Macrothrix malaysiensis*** **Idris and Fernando, 1981**

(1) No spines on the base of antenna I – 3

3 (4) Posterodorsal angle of body smooth (or with small triangular spine), serration on the dorsum not expressed – 7

4 (3) Posterodorsal angle of body with a large triangular spine, serration on the dorsum is present – 5

5 (6) Postabdominal anal flaps are prominent, on exopodite of thoracic limb IV seta 2 is in three times longer than seta 1 – ***Macrothrix pholpunthini*** **Kotov, Maiphae and Sanoamuang, 2005**

6 (5) Postabdominal anal flaps absent, on exopodite of thoracic limb IV seta 2 only slightly longer than seta 1 – ***Macrothrix sioli* (Smirnov, 1982)**

7 (8) Antenna I with bunches of more or less fine denticles – 13

8 (7) Antenna I with a row of robust large denticles – 9

9 (10) Anal margin of postabdomen with bunches of fine denticles, without long hairs; the largest seta of antenna II with a row of robust denticles alternating with stiff setules – ***Macrothrix odiosa* Gurney, 1916**

10 (9) Anal margin of postabdomen with bunches of fine denticles and long hairs; the largest seta of antenna II with a row of robust denticles – 11

11 (12) Dorsal keel absent, postero-dorsal angle smooth, distal segment of postabdominal seta relatively long – ***Macrothrix paulensis* (Sars, 1900)**

12 (11) Dorsal keel well-developed, postero-dorsal angle as a spine, distal segment of postabdominal seta very short – ***Macrothrix brandorffi* Kotov and Hollwedel, 2004**

13 (14) Soft seta between scraper 4 and scraper 5 on thoracic limb II absent – 17

14 (13) Soft seta between scraper 4 and scraper 5 on thoracic limb II well-developed – 15

15 (16) Three terminal aesthetascs on male antenna I longer than others, sensory seta very large – ***Macrothrix atahualpa* Brehm, 1936**

16 (15) Two terminal aesthetascs on male antenna I longer than others, sensory seta relatively short – ***Macrothrix smirnovi* Ciros-Pérez and Elías-Gutiérrez, 1997**

17 (18) Middle portion of seta on proximal endopod segment armed by robuster spinules alternating with stiff setules – ***Macrothrix australiensis* sp. nov.**

18 (17) Middle portion of seta on proximal endopod segment armed by uniform spinules or spines – 19

19 (20) Middle portion of seta on proximal endopod segment armed by relatively strong, sparcely located spines – ***Macrothrix capensis* (Sars, 1916)**

20 (19) Middle portion of seta on proximal endopod segment armed by relatively small, dencely located spinules – ***Macrothrix agsensis* Dumont, Silva-Briano and Subash Babu, 2002**

Australia as a possible source of additional taxa of the *M. paulensis* group

Our knowledge on species diversity within the *M. paulensis* species group is probably incomplete. First of all, Australia and Tasmania could be a source of additional species from this group, as the number of *Macrothrix* species described from this region is really large. According to Kotov *et al.* (2013a), and taking in consideration our new data, thirteen species of the genus *Macrothrix* are currently accepted as valid from Australia and Tasmania (listed in chronological order) (also, see Tab. 2):

(1) *M. spinosa* King, 1853;
(2) *M. schauinslandi* Sars, 1904;
(6) *M. hystrix* Gurney, 1927;
(4) *M. breviseta* Smirnov, 1976;
(5) *M. carinata* (Smirnov, 1976);
(6) *M. longiseta* Smirnov, 1976;
(7) *M. pectinata* (Smirnov, 1976);
(8) *M. timmsi* (Smirnov, 1976);
(9) *M. flagellata* (Smirnov et Timms, 1983);
(10) *M. williamsi* (Smirnov et Timms, 1983);
(11) *M. flabelligera* Smirnov, 1992;
(12) *M. indistincta* Smirnov, 1992;
(13) *M. australiensis* sp. nov.

At least one more taxon, *M. burstalis* Smith, 1909, is considered as *species inquirenda*.

Morphology of aforementioned Australian taxa of *Macrothrix* was studied by previous authors (Smirnov and Timms, 1983; Smirnov, 1976, 1992) according to high standards for that time. But now is obvious that these descriptions lack some fine, but very significant details (*i.e.* in structure of antenna I, antenna II and thoracic limbs). Thus a re-examination of Australian *Macrothrix* is an important task for the macrothricid taxonomy. Here we conduct the only formal analysis of available data of other Australian taxa (Smirnov and Timms, 1983; Smirnov, 1976, 1992) in order to clarify a position of *M. australiensis* sp. nov. among them. We have no information on the number of ejector hooks on the thoracic limb I for most Australian species of *Macrothrix.* But most probably *M. timmsi* has a single ejector hook (see in Smirnov, 1976: fig. 117I). Just this feature is maximally important for separation of the *M. paulensis* group from close *M. triserialis* group and all other species with two ejector hooks. We know precisely that (1) normally members of *M. paulensis* group are relatively large cladocerans (up to 1 mm in length, although this character may be confusing: compare size for *M. paulensis* and *M. sioli* in Smirnov (1992) and in Kotov and Hollwedel (2004)) and (2) they have a rod-like (undilated) antenna I. Unfortunately, each of these two features does not allow us to separate any members of *M. paulensis* group from members of *M. triserialis* group, but taxa from the latter reach only 0.7 mm in length (Kotov *et al.*, 2004), however a combination of both aforementioned characters could be helpful for revealing possible members of the *M. paulensis* group among incompletely described forms. We summarized data on Australian *Macrothrix* taxa in Tab. 2, paying special attention to their size and shape of antenna I, as well as to some other diagnostic features. Small-sized *Macrothrix* species with dilated antenna I apparently do not belong to the *M. paulensis* group, and we may exclude them from our comparison.

There are five relatively adequately described Australian species: *M. breviseta*, *M. hystrix*, *M. indistincta*, *M. longiseta* and *M. spinosa. M. burstalis* needs a reexamination, because its morphology is scarcely studied, but Smith's type material is probably lost. Most probably, Smith (1909) dealt with juveniles of another taxon. An individual illustrated in his figure has 0.4 mm in length and no eggs in the brood pouch, but due to a rod-like antenna I it may be considered as a taxon from the *M. paulensis* species group. Kotov and Hollwedel (2004) have already shown that *M. mira* (Smirnov, 1992) is a junior synonym of *M. paulensis*: Smirnov (1992) described juveniles of *M. paulensis* 0.39 mm in length as a separate taxon (see Kotov and Hollwedel, 2004).

Unfortunately, Smirnov (1976, 1992) measured only several individuals or only holotype of each taxon during his revision of the genus *Macrothrix*. It confuses now a species delimitation based on morphometry. Smirnov's style of measurements led to a situation when some species, potentially belonging to *M. paulensis* group, could have length less than

1 mm. But we expect that more taxa from Australia belong to the *M. paulensis* group. Presumably, three following Australian *Macrothrix* species: *M. flagellata*, *M. schauinslandi* and *M. timmsi* also belong to the *M. paulensis* species group, or are at least its closest relatives. Other species with rod-like antennas I needs a careful reexamination.

Therefore, more members of both *M. paulensis* and *M. triserialis* species groups could be hidden among Australian taxa. Probably, Australia is a centre of diversity for both these groups.

5 Short notes on ecology

No detailed investigations on ecology of the *M. paulensis* group were performed to date. Ironically, although members of this group have a very peculiar appearance, they are exclusively rarely recorded in the hydrobiological and ecological studies. Probably, the reason is that applied ecological studies dealt only with few types of water bodies such as lakes, rivers, reservoirs and ponds. However, it seems that at least some members of the *M. paulensis* group are associated with paludal shallow fishless habitats (swamps, rice fields, temporary pools with developed vegetation belt) which are full of life mainly during wet season (Van Damme and Dumont, 2010; Van Damme and Sinev, 2013; our observations), or even with dystrophic water bodies. Van Damme and Dumont (2010) found *M. paulensis* in the water bodies of Lençóis Maranhenses (NE Brazil) under low pH (4.2) and very low oxygen content (0.95–0.99 mg/L O_2). Sometimes members of the *M. paulensis* group may co-occur in the aforementioned types of habitats (*i.e. M. paulensis* and *M. sioli* in our material from Brazil and *M. pholpunthini* and *M. odiosa* in a sole sample from Thailand), and also co-occur with other small-bodied *Macrothrix* species (such as *M. flabelligera*, *M. oviformis*, *M. spinosa*, *M. superaculeata*, *M. triserialis*) as well as with some other littoral cladocerans (*Alona* sp., *Chydorus* sp., *Ilyocryptus* sp., *Moinodaphnia* sp., *Pleuroxus* sp., *Simocephalus* sp.). Paludal habitats may be considered as an ancient water body type for cladocerans (Kotov, 2013) and, undoubtedly, they deserve more attention among cladoceran experts.

6 Biogeography

The cladoceran-based zoogeography periodically (with large time gaps) attracts the attention of the hydrobiologists (*e. g.* Richard, 1892; Brehm, 1933; Frey, 1987; Chiambeng and Dumont, 2005; Korovchinsky, 2006; Van Damme and Sinev, 2013; Van Damme and Kotov, 2016). Development of the cladoceran taxonomy stimulates progress in biogeography and *vice versa*. Recently a new direction of such studies – phylogeography (or genogeography) (Avise, 2000; Hewitt, 2004) – became popular among the cladoceran investigators, but predominantly planktonic cladocerans are used as models for such analysis (*e.g.* Adamowicz *et al.*, 2009; Faustová *et al.*, 2011; Crease *et al.*, 2012; Hamrová *et al.*, 2012), while cladocerans with other mode of life attract insufficient attention (Belyaeva and Taylor, 2009; Kotov *et al.*, 2016). In addition, mostly such studies are limited by the Holarctic region, with few exceptions (Sharma and Kotov, 2013).

It is necessary to take into consideration that the resting eggs/ephippia of the planktonic taxa are well accommodated to the dispersion, *i.e.* by water birds (see Kotov, 2013; Incagnone *et al.*, 2014). Few attempts to explain biogeographical patterns for littoral cladocerans were conducted (*e.g.* Frey, 1987; Korovchinsky, 2006; Van Damme and Sinev, 2013; Kotov *et al.*, 2016; Van Damme, 2016). But it is known that the resting stages of chydorids and macrothricids are not so strongly protected from the unfavorable influence of the environment and dispersed no so actively as the aforementioned resting stages of the planktonic cladocerans. As a result, biogeographical patterns in chydorids and macrothricids could be different from those previously revealed for the daphniids (Kotov, 2013; Van Damme and Sinev, 2013; Kotov *et al.*, 2016).

The *M. paulensis* species group could be regarded as a model for biogeographical speculations based on morphological data due to: (1) a “pantropical” distribution (one of the intriguing distribution pattern in biogeography – see links in Van Damme and Sinev (2013)) and (2) a reasonable (not very small and not very large) number of species with well-recognizable morphological characteristics. Some important conclusions could be made from the analysis of biogeographical patterns in the *M. paulensis*-group:

(1) No truly “Pantropical” taxa were found within this group. Such conclusion was expected keeping in mind “Frey’s non-cosmopolitanism” paradigm of recent cladoceran biogeography (see Frey, 1982, 1987). All the taxa from the *M. paulensis*-group could be classified as: (1) exclusively Neotropical (existence of very rare populations of *M. paulensis* in southernmost portion of North America can be easily explained by an expansion from South America); (2) exclusively Australian; (3) Palaeotropical (Afro-Asian); (4) endemics of Mexican plateau and closest territories (see Tab. 1, Fig. 26). As we told above, more members of the *paulensis*-group could be present in Australia, but their revealing will not change the aforedescribed pattern. Such patterns were found in other cladoceran taxa previously regarded as “cosmopolitan” (Dumont and Silva-Briano, 2000; Sinev *et al.*, 2005; Van Damme *et al.*, 2011; Sharma and Kotov, 2013; Neretina and Sinev, 2016; Neretina and Kotov, 2017).

(2) Five members of the basal section of the tree (*M. australiensis* sp. nov., *M. atahualpa*, *M. smirnovi*, *M. capensis* and *M. agsensis*) are endemics of four well-recognised centres of endemism of the Cladocera: Australian centre (see Smirnov and Timms, 1984; Hebert and Wilson, 1994; Korovchinsky, 2006; Forró *et al.*, 2008), Andean highland centre (Kotov *et al.*, 2010), Mexican plateau centre (Elías-Gutiérrez *et al.*, 2001; Kotov *et al.*, 2003; Korovchinsky, 2006; Garfias-Espejo *et al.*, 2007) and South African centre (see Van Damme *et al.*, 2013b) (Tab. 1, Fig. 26). If the structure of the former two centres of endemism is poorly known, the last centre is relatively well-studied. *M. capensis* belongs to the third group of the South African endemics by Van Damme *et al.* (2013b): taxa widely distributed in the fourth, both in the mountains and in the lowlands. See further comments on this zone of endemism in Van Damme *et al.* (2013b). It is important, that all five aforementioned endemic taxa (*M. australiensis* sp. nov., *M. atahualpa*, *M. smirnovi*, *M. capensis* and *M. agsensis*) are obvious both phylogenetic and biogeographical relicts (Purvis *et al.*, 2005). They could be regarded as “ejected relicts” sensu Korovchinsky (2006) as their

distribution ranges correspond well to this model. These taxa are palaeoendemics sensu Harrison (1965).

(3) The crown group, in contrast, is distributed in the lowlands of South America, Africa and Asia with the range overlapping with members of the basal section only in South Africa (Tab. 1, Fig. 26). The crown group is subdivided into two sub-groups: exclusively Neotropical clade and a predominantly Afro-Asian clade which also includes a single Neotropical taxon. Such pattern is apparently old (see Van Damme *et al.* (2013b)). It could be associated with events like Gondwana break up, or even with older times of Pangaea break up followed by a subsequent extinction in the northern hemisphere.

Korovchinsky (2006) argued that a chance to trace some "Gondwanian" events is too small due to subsequent mid-late Caenozoic extinctions, and we agree with this idea. Indeed, a chance to distinguish between different scenarios is extremely low keeping in mind that some arguments *pro* and *contra* such scenarios could be obtained only from some fossil records. But to date such records are rare, although it could be partly explained by an insufficient attention of carcinologists to fossil collections (Kotov and Korovchinsky, 2006; Kotov, 2007a; Van Damme and Kotov, 2016). The molecular clocks sometimes are regarded as a panacea for dating and discerning between different scenarios, but such approach is strongly vulnerable for a criticism as is needed in a very accurate calibration based on fossil records (Heads, 2005; Pulquerio and Nichols, 2007) keeping in mind very strong differences in the mutation rates of different genes in different groups of organisms and un-regularities (Ho *et al.*, 2005, 2015). Therefore a really accurate molecular clock could be proposed only in cases of future fossil records (Van Damme and Kotov, 2016). Again, an un-proportional extinction on different continents could be regarded as an alternative version to any vicariant scenarios, but it is well-known the latter approach could explain all possible scenarios (see "transatlantic domino" offered by Eskov (1984)).

(4) Within the crown group, there are two main subgroups, and the version on the inter-continental differentiation of each group, correspondingly in South America and in Asia (= inhabited by of a common ancestor for each group on a separate continent), seems to be the most parsimonious (Tab. 1, Fig. 26). The groups, among other territories, occupy two main centres of the cladoceran diversity in tropics: Brazilian tropical lowlands and South-East Asian lowlands. These regions are intensively studied recently, specially for the chydorids (Kotov *et al.*, 2004, 2005; Sinev *et al.*, 2004, 2005; Sinev and Sanoamuang, 2007; Van Damme *et al.*, 2011; Sinev and Kotov, 2012; Van Damme and Maiphae, 2013; Van Damme and Sinev, 2013; Van Damme *et al.*, 2013a; Dumont *et al.*, 2013; Elmoor-Loureiro, 2014; Sinev *et al.*, 2016; Sousa *et al.*, 2015, Sousa *et al.*, 2016a,b). But studies of the biodiversity structure in the Brazilian tropical lowlands and SE Asian lowlands need to be continued. To date we cannot speak about presence/absence of an analogous biodiversity centre in African tropical lowlands due to a clearly insufficient study of this region. Moreover, previous ideas on the lower diversity of the cladocerans in African tropical zone (Dumont, 1994; Chiambeng and Dumont, 2005) could be an artifact of an insufficient level of study of the African cladoceran fauna (Van Damme and Dumont, 2009).

(5) It is necessary to take into consideration that "the existence of antique lineages does not contradict with the possibility of recent speciation and adaptation" (Van Damme *et al.*, 2013b). To date we cannot say, are endemic taxa from the regions marked above (in item 4) relicts, or products of a secondary intensive speciation in these territories? The second version seems to be most likely for us: locally distributed endemics in both sub-groups (*M. sioli*, *M. pholpunthini* and *M. malaysiensis*) are biogeographical, but not phylogenetic relicts (as they are relatively "advanced" taxa in our tree, the members of the crown group) (Tab. 1, Fig. 26).

(6) A close relationship between *M. pholpunthini* and *M. sioli* (Tab. 1, Fig. 26) could be explained by a secondary expansion from Asia to South America through the "boreotropical migration hypothesis", see expanded notes on this subject in Van Damme and Sinev (2013).

Among possible scenarios explaining recent distribution of the taxa of the *paulensis*-group, some Mesozoic scenarios are preferable according to several reasons (see above). Our main conclusion from the analysis of the biogeographical patterns in the *M. paulensis* group is that all these scenarios are very old, they are related to some late Mesozoic – mid Caenozoic tectonic events, as it was also proposed for some other cladocerans (Frey, 1982, 1987; Popova *et al.*, 2016). It means that the genus *Macrothrix* is of at least a Mesozoic origin, similarly to other taxa of the Anomopoda and Ctenopoda (Sacherová and Hebert, 2003; Kotov and Korovchinsky, 2006; Kotov and Taylor, 2011; Van Damme and Kotov, 2016). To our opinion, a combination of different scenarios took place in the evolutionary history of *M. paulensis* group. A single approach as a "mobilistic biogeography" or "ejected relict" version could not give a realistic explanation of all diversity of the biogeographical patterns in the Cladocera.

Remarkably, similar patterns were alreary revealed in some other cladocerans like chydorid *Anthalona* Van Damme, Sinev and Dumont (Van Damme *et al.*, 2011) or ilyocryptid *Ilyocryptus* Sars (Kotov and Elías-Gutiérrez, 2009). Obviously, studies of other cladoceran genera are necessary to confirm a universallity of such pattern among the taxa previously regard as pan-tropical ones.

Macrothrix is the most diverse genus of the Macrothricidae. But the macrothricid-based zoogeographical reconstructions may not be limited only by this genus *Macrothrix*, see Frey (1988), other genera could also be a subject of a biogeographical analysis (Neretina and Kotov, 2017). It is necessary to take into consideration that ideas on the macrothricids as a "primitive" group (Behning, 1941) are quite superficial. They (after separation of Acantholeberidae, Ophryoxidae and Ilyocryptidae) form a specific portion of the crown-group of the suborder Radopoda (Dumont and Silva-Briano, 1998; Kotov, 2013).

Distribution patterns on the genus level could be interesting as well (Korovchinsky, 2004). It is already obvious that some macrothricids and macrothricid-like genera are associated with particular zoogeographical regions. For instance, macrothricid-like anomopods *Acantholeberis* Lilljeborg, *Ophryoxus* Sars, *Parophryoxus* Doolitle and macrothricids *Bunops* Birge, 1893, *Drepanothrix* Sars, are typical for the Holarctic region (Forró *et al.*, 2008). *Neothrix* Gurney is considered to be an endemic of the Australian region; the rare *Cactus* Smirnov is an endemic of Tierra del Fuego. But initial opinion on the continental endemicity of some other macrothricid genera (Smirnov, 1976) was false. *Onchobunops* Fryer and Paggi was considered as an endemic of the Neotropics, but it was subsequently found in SE Asia (Tanaka and Ohtaka, 2010). The genus *Lathonura* Lilljeborg was regarded as Holarctic, but it was subsequently found in South Africa (Hart and Dumont, 2005), although this case could be explained by a human-mediated invasion. Therefore, the investigations of the macrothricids are potentially interesting for analysis of cladoceran distribution patterns, but such studies need be continued using morphological and genetic methods.

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