A revision of the Scapholeberinae (Crustacea: Cladocera)

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Abstract

The group of hyponeustonic daphniid cladocera previously known under the generic name *Scapholeberis* is raised to the rank of a subfamily (Scapholeberinae) and contains two genera, *Megafenestra* n.gen. (2 species), and *Scapholeberis* s.s. (7 species and one subspecies). The characters upon which this revision is based are: structure of the rostrum, structure of the first antennae, structure of trunk limbs 1, 2, and 5, presence and nature of headpore(s), structure of the ventral rim of the valves, armature of the distal rim of the valves, structure of the postabdomen and its end-claws. Males were examined in all but two species, and proved to be more primitive than females and much less diagnostic than in the Chydoridae. It also appeared that the shape and armature of the postabdomen are less important taxonomical tools than heretofore supposed. In more than half of the species, it is of generalised shape and hardly usable beyond the species-group level. The same, although less drastically, holds true for the P1 of males. Of greatest diagnostic value at the species level are the shape of the rostrum and the armature of the valve margins.

A phylogeny of the subfamily is proposed, with *Megafenestra* as the more primitive genus, closely allied to *Ceriodaphnia,* and within *Scapholeberis, S. mucronata* as the most apomorphic species.

In biogeographical respect, no species is cosmopolitan, although their ranges may be of continental dimensions. Species and populations appear to concentrate in the temperate and continental climate belts of the northern hemisphere, but more research in the southern hemisphere is needed.

A key for the identification of all species is given.

Introduction: historical background to our knowledge of the Scapholeberinae

O. F. Müller (1776: no 2404) first mentioned *Daphne mucronata* in his Prodromus of the aquatic fauna of Denmark and gave a description with recognisable figures (mucro between 1/2 and 1/3 of the length of the ventral rim of the valves) in his classical 'Entomostraca' in 1785. The genus name *Scapholeberis* was coined by the high-school teacher E. Schoedler (1858) to accommodate three species: Müller's *mucronata, cornuta* n.sp. (the horned form of *mucronata),* and *obtusa,* a synonym of S. Fischer's *Daphnia aurita.*

The discussion on the taxonomical value of a frontal horn on the head is part of the earliest literature on the group. De Geer (1778) categorically argued that not only the presence or absence of such a frontal horn, but even that of a pair of ventral mucrones is due to individual variability. Lievin (1848), Baird (1850), and Leydig (1860), however, correctly observed that horned and unhorned forms never failed to have a ventral mucro, and considered only the frontal horn as a variable character. Schoedler (1858, 1866, 1877) continued to defend the name *cornuta* for the horned form. Like several other workers of his time, he seems to have had a clear knowledge of the fact that horns

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never occur in some populations of mucronata-like animals, but he naturally (and incorrectly) assumed that in populations with horned individuals, this was a constant feature as well. That the latter part of his reasoning is incorrect was illustrated by the experimental work of Grüber (1912, 1913a, b, 1923), with an addition by Werner (1923), which made clear that both frontal horns and mucrones are subject to cyclomorphosis. The mucro tends to become longer as the frontal horn becomes shorter in late summer. In many populations, the frontal horn eventually disappears completely in late reproductive instars. Rammner (1927, 1928a, b, 1929) was originally interested in the same approach, but got struck at an early stage by a population occurring near Leipzig, in which at no time of the year and at no time of the postembryonal development a frontal horn was seen. This eventually led him to look more closely at the morphology of the rostrum (Rammner 1928b), which was triangularly produced in front and not straight (as in typical *mucronata).* He equated the Leipzig populations with G. O. Sars' (1888, 1903) *S. kingi.* In his final paper, Rammner (1929) convincingly sorted out the confusion that had occurred before, and established the presence in Germany of two superficially allied species, *S. mucronata* and *S. 'kingi'.* Dumont (1971) showed that *'kingi'* is widespread in Central Europe, but began to doubt whether the European form was really identical to Sars' species.

Lilljeborg (1900) contributed by providing good descriptions and excellent illustrations of the species *S. mucronata, S. microcephala* (a species originally discovered by him, but formally described by Sars 1890, see also Frey 1978), and *S. aurita,* including data on males, and details of the structure of the trunk limbs. Lilljeborg's figures are so dependable that it is possible to identify one of the animals pictured (plate 22, fig. 15) as the species that was later transferred to *S. kingi* by Rammner, and that will be renamed *S. rammneri* in the present paper.

A further noteworthy event in the history of the group is the simultaneous and independent description by Sars (1903) and von Daday (1903) of a species with spinulated valves from Akmolinsk (= Tselinograd), Central Asia *(S. echinulata Sars),* and from Hungary *(S. erinaceus von Daday)* (see also Hudek in press).

A final advance in our knowledge of the morphology of several *Scapholeberis* species was the paper by Ocioszynska-Bankierowa (1934) who carefully studied the armature of the postabdominal claws, the ventral adhesive plates, and the spinulation along the inner margin of the distal valve rims.

While most of these events deal with European populations and taxa, some species had become known at an early date from South America *(S. spinifera* Nicolet 1849), and from North America *(S. nasuta* Birge 1879, *S. armata* Herrick 1882). The latter two were later sunk into the synonymy of *S. aurita* and of *S. mucronata-kingi,* respectively, but are restored to species-level in the present paper.

We recognize 8 described taxa as valid, two among which (the *aurita*-group) are removed from *Scapholeberis* and accommodated in a new genus. In addition, two new taxa are described, bringing the number of valid taxa in the Scapholeberinae to a total of 10.

The decision to raise this group of Daphnids to the rank of a subfamily is based on the fact that the Scapholeberinae are composed of two genera, separated by a series of characters, but united by the following features: infolded ventral rim of the valves, angular ventro-distal corner of the valves, always more or less produced into a mucro, and presence of a rostral pore connected to an area in or near the brain by a long canal.

Diagnosis of the subfamily Scapholeberinae

1. Medium-sized Daphniid Cladocera with a large head, globular eye and a rhomboidal or elongate ocellus.

2. Rostrum well-developed, but more strongly in females than in males, multiform, protruding over the first antenna. A pore opens near its tip, either on its dorsal or its ventral side. A long canal connects the pore opening to an area near or in the brain ganglion.

3. Valves and head reticulated.

4. Ventral rim of valves infolded, modified into an adhesive sucker-plate on which the animals hang updown at the underside of the surface film of the water.

5. Ventro-posterior corner of valves angular, with at least an indication of a mucro.

6. Five pairs of trunk limbs, of general daphnoid structure.

7. Abdominal process in females short and simple in structure.

8. Postabdomen (Fig. IV) robust, wide, with anus

situated on the floor of a deep and wide perianal cavity, flanked by a number of teeth (not exceeding 10 in number), the distalmost of which are individual spines. The proximal spines may gradually change into a cushion with one larger spine and a series of smaller ones, or into a spinulated, cactus-shaped bud.

9. Dorsum of postabdomen, proximal to the anus, and along its side, with groups of spinules.

10. End-claw of postabdomen with 5–6 pectens (Plate 6).

11. Postabdomen of males usually very similar to that of females. Genital duct and opening inconspicuous, situated dorsal to the intestine.

12. First antenna short, in females with 9 terminal perforated esthetes and one lateral unperforated (no-pore = n.p.) seta. In males, the first antenna is not lengthened or enlarged, but provided with 9 apical esthetes and 2 n.p. setae (exceptions: *S. mucronata).*

13. Second antenna with 4-segmented exopodite and 3-segmented endopodite. Basipodite with two basal sensitive hairs and an apical pore with sensitive rod.

14. Posterior rim of valves partly or entirely set with one or two membranes and/or groups of denticles.

15. Ephippium with a single egg.

Differential diagnosis

The Scapholeberinae differ from all other Daphniidae by points 2, 4, 5, and, in part, 9. *Ceriodaphnia,* the closest ally of the Scapholeberinae, and of *Megafenestra* in particular, has a very similar postabdomen.

Genera: Megafenestra n.gen.; Scapholeberis Schoedler 1858.

Genus Megafenestra n.gen.

Derivatio nominis: Megafenestra or 'large window' refers to the dorsal oval plate that is typical of this genus.

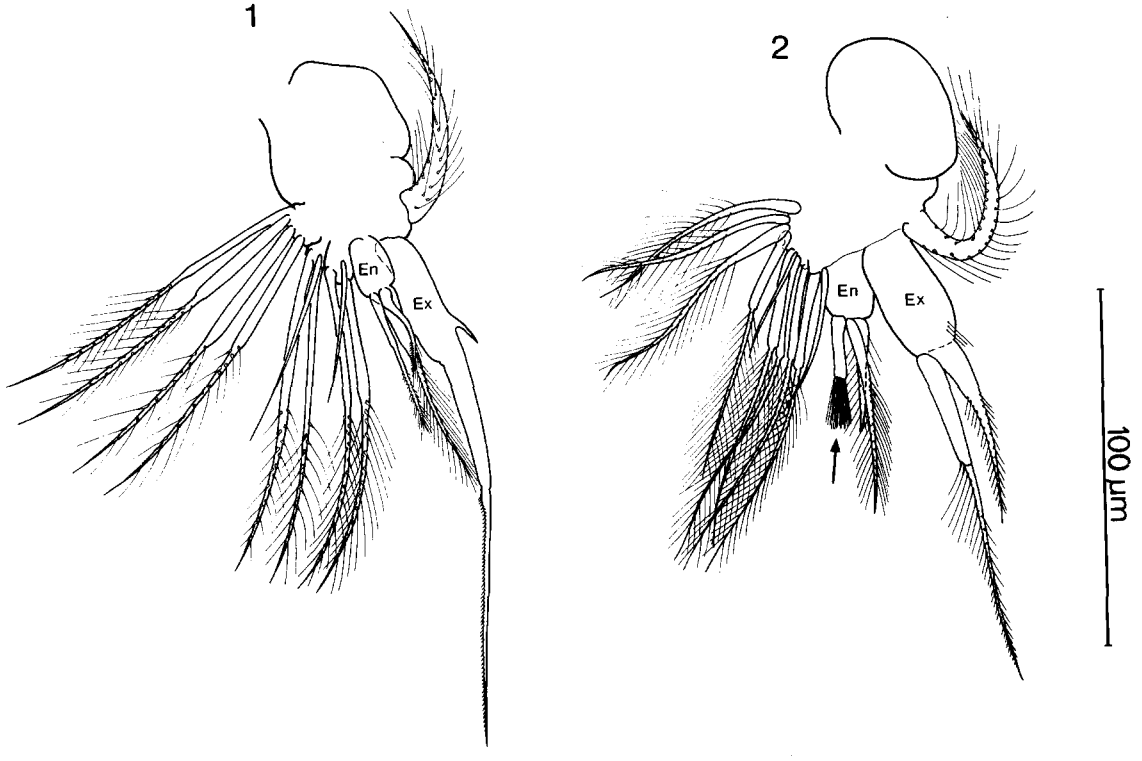

Fig. 1. First trunk limb in females (P1). 1. *Megafenestra aurita* (Lake Donk, B.); 2. *Scapholeberis rammneri* (Lake Donk, B.). En: Endopodite, Ex: exopodite. The arrow in (2) indicates the brush-shaped seta.

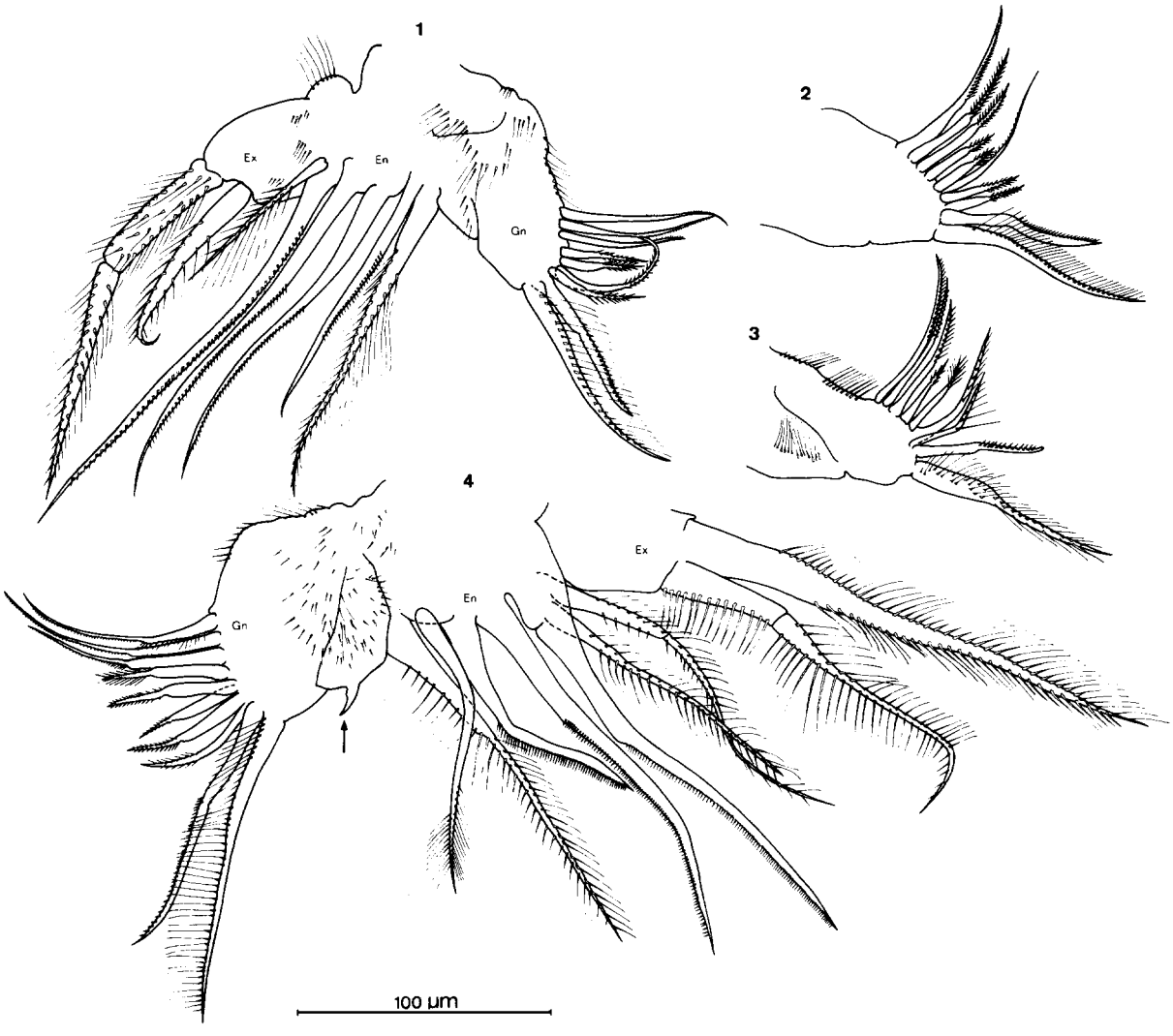

Fig. II. Second trunk limb in females (P2). 1. *S. mucronata* (Teralfene, B.); 2. gnathobase (processus maxillaris) of *S. rammneri* (Lake Donk, B.); 3. idem, *S. kingi* (Aramac creek, Aus.); 4. *M. aurita* (Lake Donk, B.); P2. En: endopodite, Ex: exopodite, Gn: gnathobase.

Type species: Daphnia aurita S. Fischer 1849.

All characters of the Subfamily apply. Additional characters are:

1. Head: female always with more or less pointed rostrum. First antenna: n.p. setae insert halfway the upper rim of the antenna (Plate 2: 2–4).

2. Trunk limb 1: exopodite with one long apical seta (a primitive character shared with most other Daphniids) and one very short, non-articulating setule (Fig. I: 1) in female. In males, the long seta is modified, ends in an anchor-like structure (Fig. III: 1), and extrudes beyond the margins of the valves. Endopodite with three apical setae in the female (Fig. I: 1). In males, the endopodite is modified into an apical claw, which bears four setae at its base (Fig. III: 1).

3. Trunk limb 2: gnathobase with a marginal hook (Fig. II: 4, arrow). Endopodite with 7 setae. The 3 middle setae are serrated, the 2 external setae are ciliated, and of the 2 internal setae the outer one is ciliated, while the inner one is partly naked and asymmetrically set with coarse cilia near its tip (Fig. II: 4).

4. Trunk limbs 3 and 4: of generalized Daphnoid structure and identical with *Scapholeberis* s. str. (Fig. III: 5–7).

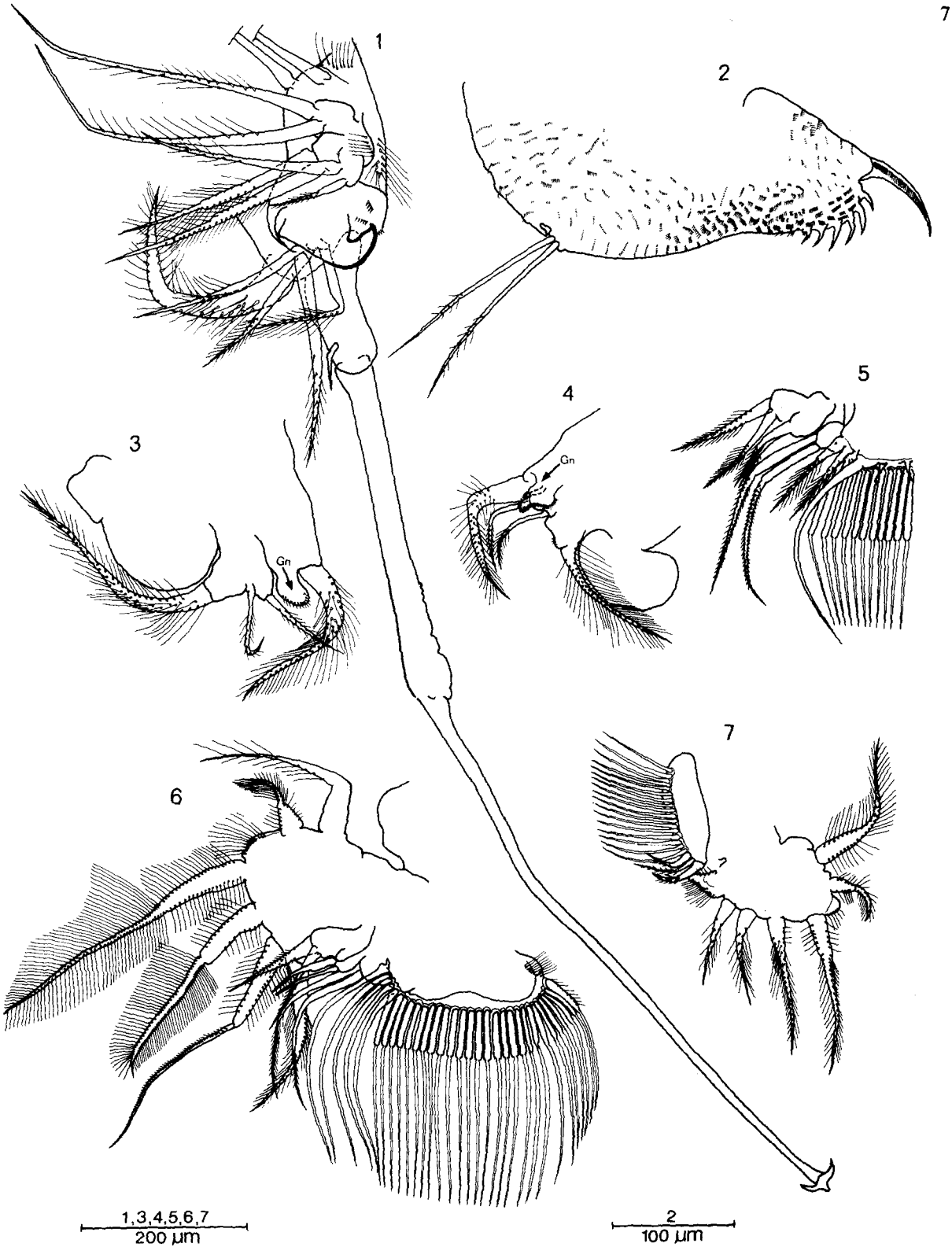

Fig. III. 1. *M. aurita,* male, P1 (Lake Donk, B.); 2. *M. aurita,* male, postabdomen; 3. *M. aurita,* female, P5 (Gn: gnathobase); 4. *M. nasuta,* female, P5 (Elk Island, Can.); 5. idem, P3 (only part of gnathobase figured); 6. *M. aurita,* female, P3 (Zaamslag, Holl.); 7. idem, P4 (Elk Island, Can.).

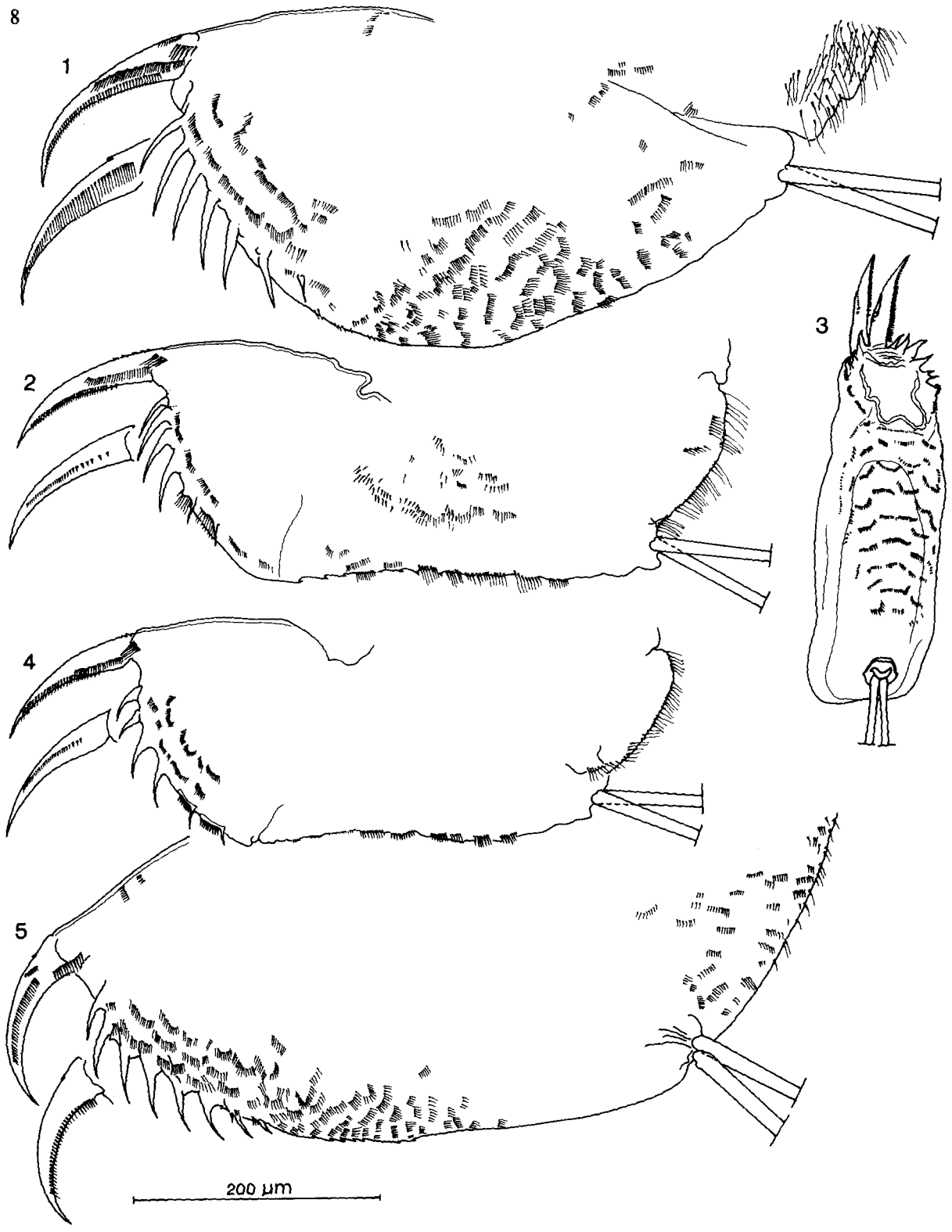

Fig. IV. Postabdomen 1. *S. mucronata* female (Teralfene, B.) 2–3. *S. rammneri,* female (Lake Donk, B.), 2 lateral view, 3. dorsal view. 4. *S. kingi,* female (Aramac creek, Aus.); 5. *M. aurita,* female (lake Donk, B.) (V = ventral side of end-claw, D = dorsal side of end-claw).

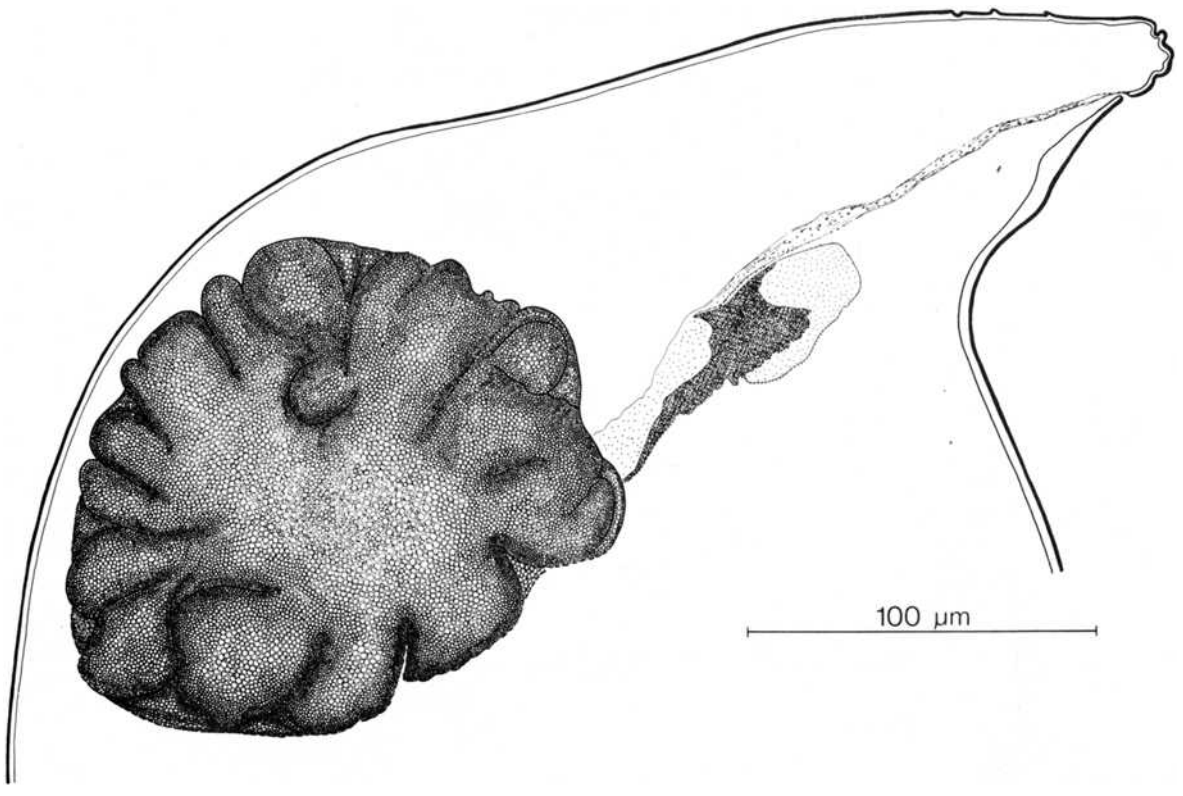

Fig. V. M. aurita, female, head in lateral view (Lake Donk, B.).

5. Trunk limb 5: gnathobase represented by a ciliated hump (Fig. III: 3–4).

6. Ventral sucker-plate comparatively simple, infolded and with thickened margins, fringed with setae at its internal free margin, but without accessory fleeces or membranes (Plate 1: 1–2).

7. Posterior margin of valves partly armed with series of spinules, in which longer spines alternate with short series of minute spinules (Fig. VIII).

8. Mucro short.

9. Dorsum of headshield with a large, median, window-shaped oval plate (Fig. VII; Plate 7: 9, 10), partly or totally delimited by sclerotized ridges but definitely not perforated. Its function is unknown.

10. Rostral pore situated on ventral side of rostrum (Fig. V).

11. Ocellus elongate (Fig. V).

Phylogenetic status

Megafenestra is the more primitive genus of the Scapholeberinae. In many characters, it is related to other genera, including even *Daphnia s.l.* This particularly applies to the structure of the exopodite of P1 in females, and the modification of both the exopodite and endopodite of P1 in the male. The marginal hook on the gnathobase of P2 is another primitive Daphnoid character, while the shape of the male rostrum is reminiscent of a *Ceriodaphnia* rostrum and the male postabdomen (Fig. III: 2), in which the anal spines are grouped on a swelling near the end – claw resembles a *Simocephalus*-postabdomen.

More primitive characters are the persistence of a gnathobase on P5, and the presence of a dorsal oval plate (which is found also in *Ceriodaphnia* and in juvenile specimens of some species of *Daphnia;* the peculiar dorsal pore-set of *Simocephalus* may be thought of as a modified, perforated oval plate).

The genus, as presently understood, accommodates two species:

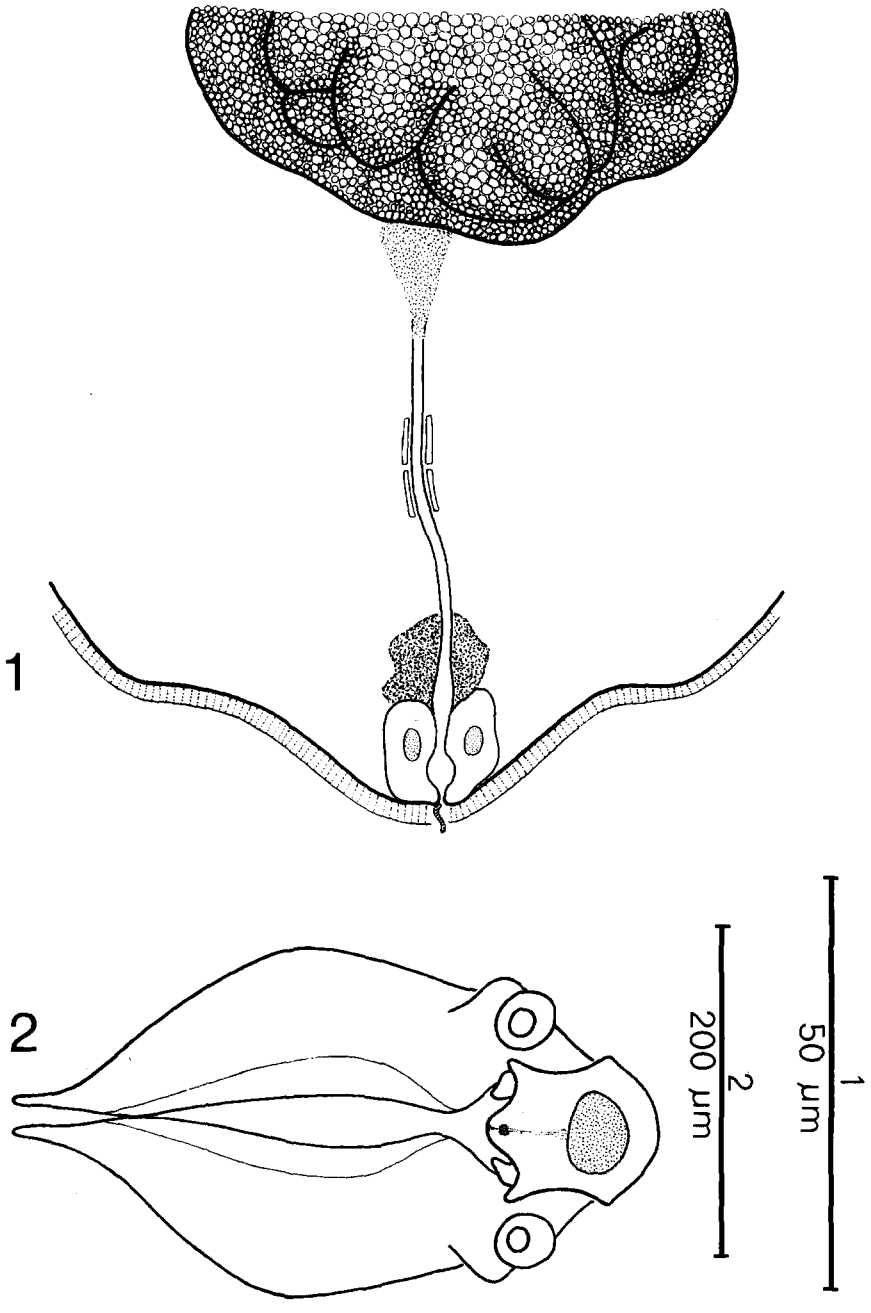

Fig. VI. S. kingi; 1. Female, head, showing the canal between the rostral pore and the brain. 2. Male, habitus, ventral view (note absence of triangular widening of valves in front of sucker-plate).

1. Megafenestra aurita (S. Fischer 1849)

Daphnia aurita S. Fischer 1849: 39.
Scapholeberis obtusa Schoedler 1958: 24.
Scapholeberis obtusa f. curvirostris Werestchagin 1911: 557.
Type locality: Leningrad area (types lost).

Material examined

Belgium: Lake Donk, Flanders, VI.1963, ♀♀ (ephippial), ♂♂. Perebooms Gat Creek, Flanders, 16.VI.1967, ♀♀ De Panne, Polder ditch, 22.VI. 1976, ♀♀.
The Netherlands: Zaamslag (Zeeland, Terneuzen),

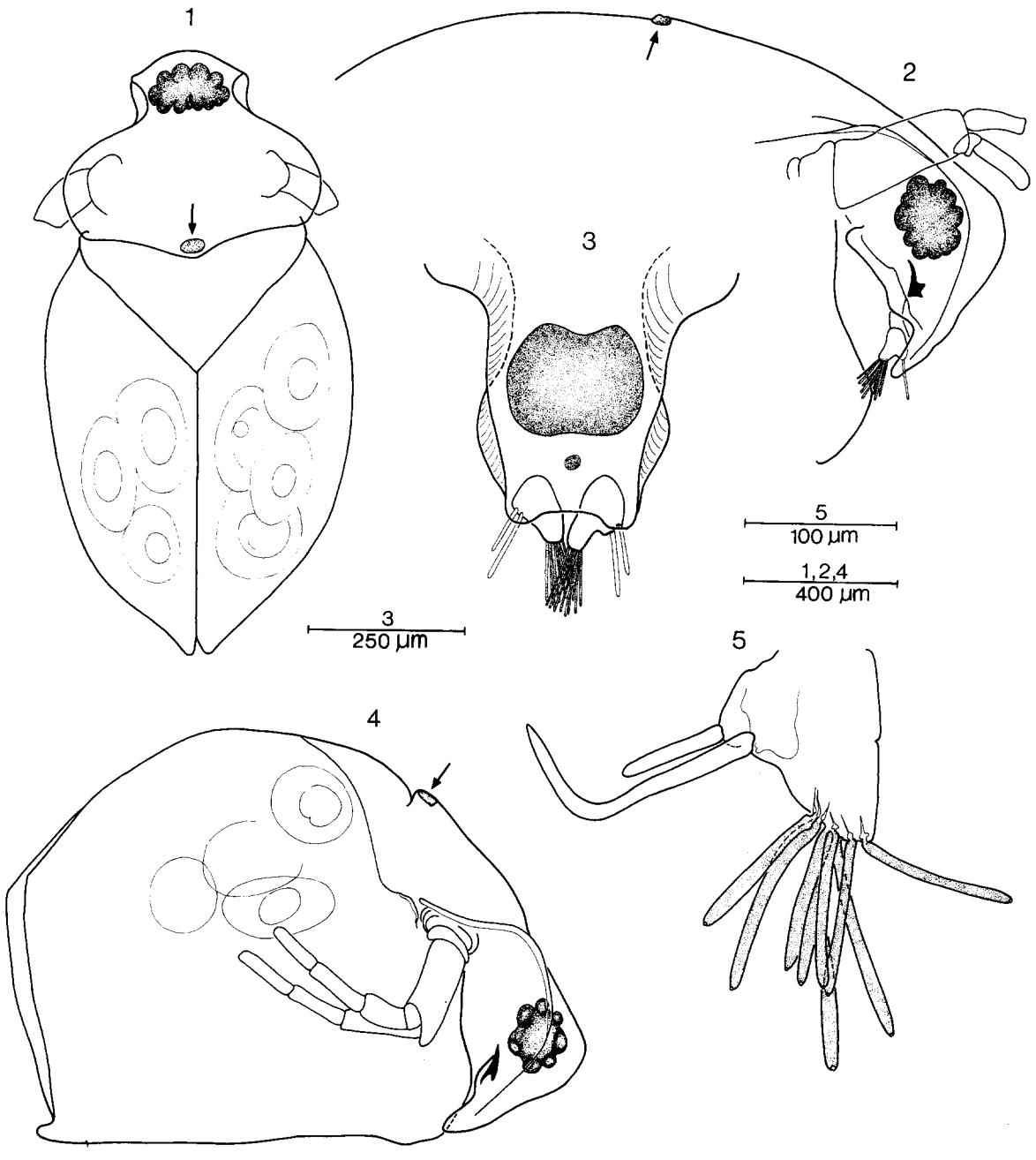

Fig. VII. Megafenestra 1, 4 *M. nasuta,* female (Elk Island, Can.), habitus in dorsal and lateral view, respectively (arrow indicates dorsal plate); 2. *M. aurita,* female, lateral view (Zaamslag, Holl.); 3. *M. aurita,* male (Juist, GFR), head, dorsal view; 5. *M. aurita,* male (Juist, GFR), first antenna.

13.IX.1977, ♀♀; Zevenaar, 4.VII.1977, ♀♀; Eempolder, gemeente Eemnes, 13.VIII.1977 (leg. E. Notenboom-Ram).

Germany: Bodensee, NW-Bank of Insel Mainau, 11.VII.1978 (leg. P. Frenzel), ♀♀. Juist, Hammersee, 30.VII.1978, ♀♀ and Wangerooge, 8.VII. 1979, ♀♀ & ♂♂ (leg. W. Hollwedel).

Austria: Neusiedlersee, Illmitz, 20.VI.1980, ♀♀ (leg. H. Metz, in coll. Hung. nat. Hist. Mus., Budapest).

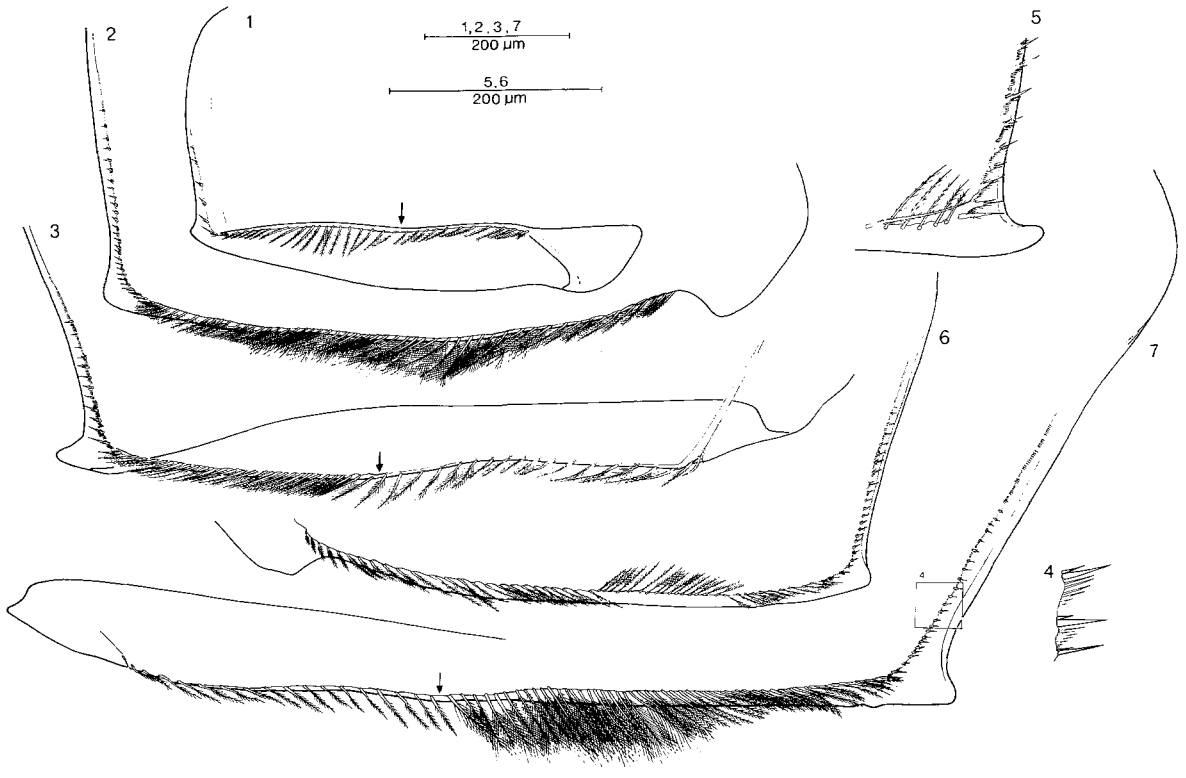

Fig. VIII. Megafenestra, armature of valve margins. 1. *M. nasuta,* juvenile female (Elk Island, Can.) 2. *M. aurita,* male (Juist, GFR); 3. *M. nasuta,* female (Elk Island, Can.); 4. *M. aurita,* female (Zaamslag, Holl.), enlarged section of lower denticulated zone or inner margin of posterior valve rim; 5. *M. nasuta,* female (Asuncion, Paraguay), ventro-posterior corner of valves 6. *M. aurita* male (Lake Donk, B.) 7. *M. aurita* female (Zaamslag, Holl.) (see also, 4). Arrows indicate transition between two types of ciliated zones.

Hugary: Ujszentmargita Cserepes-to, 5.IV.1979, ♀♀ (leg. L. Forro, in coll. Hung. nat. Hist. Mus. Budapest).

Turkey: Mermere, 24.III.1966 (leg. U. Demirhindi, in coll. British Museum, London).

Israel: Lake Hula, XI.1979–VIII.1980, ♀♀ (leg. H. J. Schnurr).

South Africa: Vaal River, 7.IX.1955, ♀♀ (coll. Albany Mus., Grahamstown).

West-Siberia, Kazakhstan, Asian USSR: Akmolinsk (= Tselinograd), no date, ♀♀ (coll. G. O. Sars, in Mus. Oslo).

Measurements: a fairly large species. Female 0.5–1.6 mm; male 0.5–0.6 mm.

Female. Colour light brown. Head with large globular eye and elongated ocellus. Rostrum long, narrowing to its tip, sometimes very acutely pointed and curved ventrad. A pore opens on the ventral side of the rostrum, close to its tip, and is connected, via a canal that runs close to the ocellus, with a part of the brain area (Fig. V). First antenna fairly robust and long, widened in its basal half. A conspicuous oval plate on the dorsum of the headshield (Fig. VII: 2). Mucro short, rarely completely reduced to a rectangular ventro-posterior angle of the valves. Ventral margin of valves: anterior sector triangularly widened around rostrum. Rest of margin infolded, narrowing distally, with thickened rims, and a continuous row of internal, ciliated setae (Fig. VIII). On the anterior 2/5 of the valve margin, 15–20 fairly spaced setae occur. On the posterior 3/5, 45–55 more closely apposed, longer setae are found, the longest of which are more finely ciliated than the neighbouring shorter ones (Fig.-VIII: 7; Plate 1: 9–11). These setae shorten well before the distal angle of the valves, and continue along the inner side of the distal rim as a series of strong spines, alternating with sets of minute spin-

ules (Fig. VIII: 4, 7). Halfway the posterior rim, the long spines disappear and the spinulation becomes uniformly short. It stops completely at about 1/3 of the distance from the dorsal valve junction. Postabdomen with 7–9 anal teeth, numerous groups of lateral and dorsal spinules, and no indication of a concavity on its dorsal margin at the level of the proximal anal spine. Endclaw with three external pectens, a ventral pecten, and a single internal pecten. Each pecten is composed of spinules of uniform length (Fig. IV: 5). Trunk limbs as for genus.

Male. Rostrum truncated, concave in the middle (Fig. VII: 3). Ocellus rhomboidal. First antenna with 9 apical perforated esthetes, and two median n.p.-setae, one of which is blunt-ending and only half as long as the second one (Fig. VII: 5). Trunk limbs as for genus. Postabdomen with a slight but distinct concavity behind the last anal spine (Fig. III: 2). No two types of ciliated hairs on inner margin of ventral plate as in females, but armature of inner margin of posterior valve rim as in females (Fig. VIII: 2, 6).

Distribution

Numerous records are available from European countries, including Scandinavia (Muller 1876; Lilljeborg 1900; Kaiser 1953; a.o.), the British Isles (Gurney 1903), and are summed up in handbooks like Sramek-Husek *et al.* 1962, Manuilova 1964, Herbst 1962, Flossner 1972. Recent German records can be found in Frenzel 1980. The species has also been found in southern Spain (Bigot & Marazanoff 1965), Algeria (Gauthier 1928), in Morocco (Lamoot, pers. commun.), and in Turkey (Demirhindi 1972). Records from the Caucasus Mountains in Georgia are given by Wereschtagin (1911) and Behning (1941), while the species was recently discovered in the northern Jordan Valley as well (H. J. Schnurr, pers. commun.). Specimens from the Vaal River catchment, South Africa, first mentioned by Harding 1961, were reexamined and could not be separated from typical *M. aurita*. This type of disjunct occurrence is not exceptional in the South African fauna, where numerous relicts of Pleistocene faunal connections with the mediterranean, across the East African plateau, still persist today (see Dumont 1979).

2. Megafenestra nasuta (Birge 1879)

Scapholeberis nasuta Birge 1879: 85.

Scapholeberis aurita: Herrick & Turner 1895; Vavra 1900; Von Daday 1903; Brooks 1966; Brandlova *et al.* 1972; Cehngalath 1982.

Scapholeberis angulata Herrick 1893: 176.

Type locality: Wisconsin, U.S.A.; types not indicated and lost (teste D. G. Frey).

Material examined

Canada: Roadside pool on Oster Road, Elk Island National Park, Alberta, 21.VII.1979, ♀♀ (leg. R. Chengalatath, in coll. natn. Mus. Ottawa); Riley Lake, Jasper National Park, Alberta, 5.VIII.1978, ♀ (leg. R. S. Anderson).

Paraguay: Asuncion, Campo Grande, Calle de la Canada, spring fed pond and ditch, ♀♀ (det. E. von Daday, coll. Hung. nat. Hist. Mus. Budapest).

Measurements: Female 1.1–1.3 mm; male unknown.

Female. Very close to the preceding species in colour and morphology of the trunk limbs and the postabdomen, but possibly about 20% smaller. The two species differ in the armature of the inner margin of the sucker plate which bears 15–20 spaced setae on the anterior 3/5 of the rim, and 25–30 closely set setae on the remaining 2/5 of the rim (Fig. VIII: 3). This arrangement also holds true in juveniles (Fig. VIII: 1). The setae are substituted by spines near the mucro, and the length of the last setae and of the first spines is about equal. The spines, set with spinules themselves, shorten gradually in dorsal direction and are separated by series of spinules. They do, however, not reach half the length of the posterior valve rim (Fig. VIII: 1, 3, 5).

Male. Not seen. Birge saw specimens, but gives no measurements, neither in his handwritten Ph. D. thesis (1878), nor in the published description (1879). In the thesis, the postabdomen is figured, showing 5 anal teeth and the seminal duct, which opens dorsal to the intestine. In the 1879 paper, the rostrum is shown obliquely from below. Although not easy to interpret, it shows a blunt, medially concave rostrum as in *M. aurita*.

Distribution

As stated earlier, and as confirmed by D. G. Frey (in litt.), Birge indicates no origin for his type material. However, as the species was described in his doctor's thesis, the types must have come either from Cambridge, Massachussetts, or from Madison, Wisconsin, the latter locality being the most probable one. We do not hesitate to equate our specimens from Canada and Paraguay with Birge's species, since they are all identical inter se and differ from *aurita* in only minor details of structure. It is therefore unlikely that a third Megafenestra-species would occur in North America. The range of *M. nasuta,* which is herewith restored to full specific status, probably encompasses North America and temperate, altitudinal South America. It appears to be a rare species, but it may have been frequently overlooked.

Genus Scapholeberis Schoedler 1858

Type species: Daphne mucronata O.F. Müller 1776.

All characters of the subfamily apply. Additional characters are:

1. Rostrum in females strongly developed, multiform but never acutely pointed, lined by a hyaline membrane, at least in the area between the first antennae. In males, rostrum short but generally of same shape as in female (Fig. XXI).

2. First antenna: short, and shorter in males than in females. No-pore esthete(s) insert in subapical position, not at mid-distance between base and tip (exception: *S. microcephala).*

3. Trunk limb 1: (Fig. I: 2) exopodite with two apical setae. The longest one articulates with the exopodite. The shorter one is less than half as long as the long one, but longer than the exopodite segment itself. It articulates indistinctly with the exopodite. Both setae are ciliated. The endopodite has three apical appendages in the female. Two are ciliated setae, the third one is brush-shaped. In males, the exopodite is structured as in the female, while the endopodite is modified into a prehensile claw with four setae at its base. At least one of these setae is brush-shaped. At the base of the clasper, and elsewhere on the body of the endopodite, rows or groups of spinules may occur.

4. Trunk limb 2: (Fig. II: 1–3) gnathobase without marginal hook. Endopodite with 6 setae. The marginal two setae are set with very long, stiff cilia. The central group of 4 setae is serrated.

5. Trunk limbs 3 and 4 as in *Megafenestra* (Fig. IX: 9).

6. Trunk limb 5: gnathobase completely reduced or reduced to a smallest tubercle (Fig. IX: 2).

7. Females: adhesive ventral rim of valves modified into a sucker-plate, set by a complex pattern of delicate fleeces and membranes, supported by hollow(?), repeatedly ramified skeletal elements. No setae along the inner margin of the sucker, except at its ends. At the anterior extremity, a limited number (2–5) of short setae may occur, set with long and thin cilia. The setae may be so reduced that the cilia seem to insert directly on the margin of the sucker, in which case they appear as a series of long and fine threads. On the distal extremity, 4–5 longer and finely ciliated setae occur (Fig. X: 1, 2; Plate 1: 6–8).

Males: No triangular widening of the valves in front of the sucker plate. Armature of inner rim of sucker as in female on anterior and posterior end, but body of sucker uniformly set with a series of long appendages that seem to have a half-seta, half-membrane structure, and will here be called fleece-setae. No coiled-up set of reinforced anterior membranes (exception: *S. mucronata)* (Fig. X: 3).

8. Posterior rim of valves with an inner, denticulated membrane, which is the continuation of the inner margin of the ventral sucker (both sexes), and mostly with an outer, entire, stiff hyaline membrane, which is the continuation of the outer margin of the sucker, or inserts directly on the base of the mucro.

9. Mucrones always well developed.

10. Dorsum of headshield without oval plate, but simple circular pores without sensillae may occur in the fornix region of the headshield (Plate 4). Like in the Bosminidae, these pores appear to be variable, possibly ephemeral structures, found in some specimens, but not in others.

11. Rostral pore situated on top of the rostrum, slit-shaped or rounded, usually with one or more flagellum-like structures hanging out of the pore opening (Fig. VI: 1; Plate 5).

Phylogenetic status

Scapholeberis displays a set of apomorphic characters as compared with *Megafenestra* and other

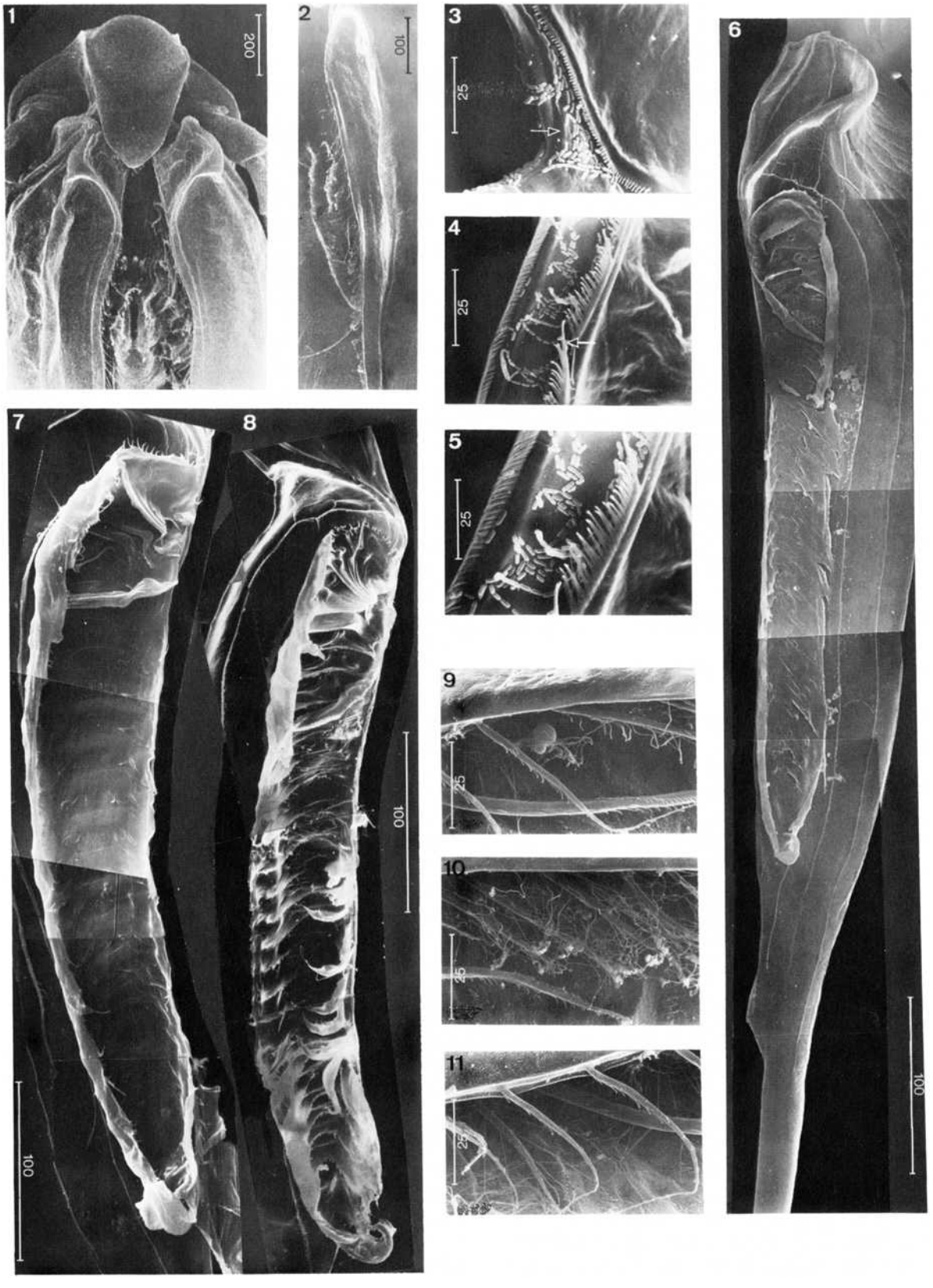

Plate I. 1. *M. aurita,* female, ventral view; 2. idem, sucker plate. 3–5. *S. rammneri,* female. 3. ventro-posterior area of valves. Note base of denticulated membrane and insertion of hyaline membrane on mucro; 4–5. Denticulated membrane at level of first hook; 6. *S. mucronata* female, ventral valve rim, showing anterior embayment, ventral sucker, base of mucro; 7. *S. rammneri,* female. Sucker-plate with lamellae flattened and glued together; 8. *S. kingi* female, sucker-plate with most lamellae in upright position; 9–11. *M. aurita* female, setation along inner margin of sucker-plate; 9. anterior spaced setae; 10. median long and finely ciliated setae; 11. posterior short setae (scales in micrometers).

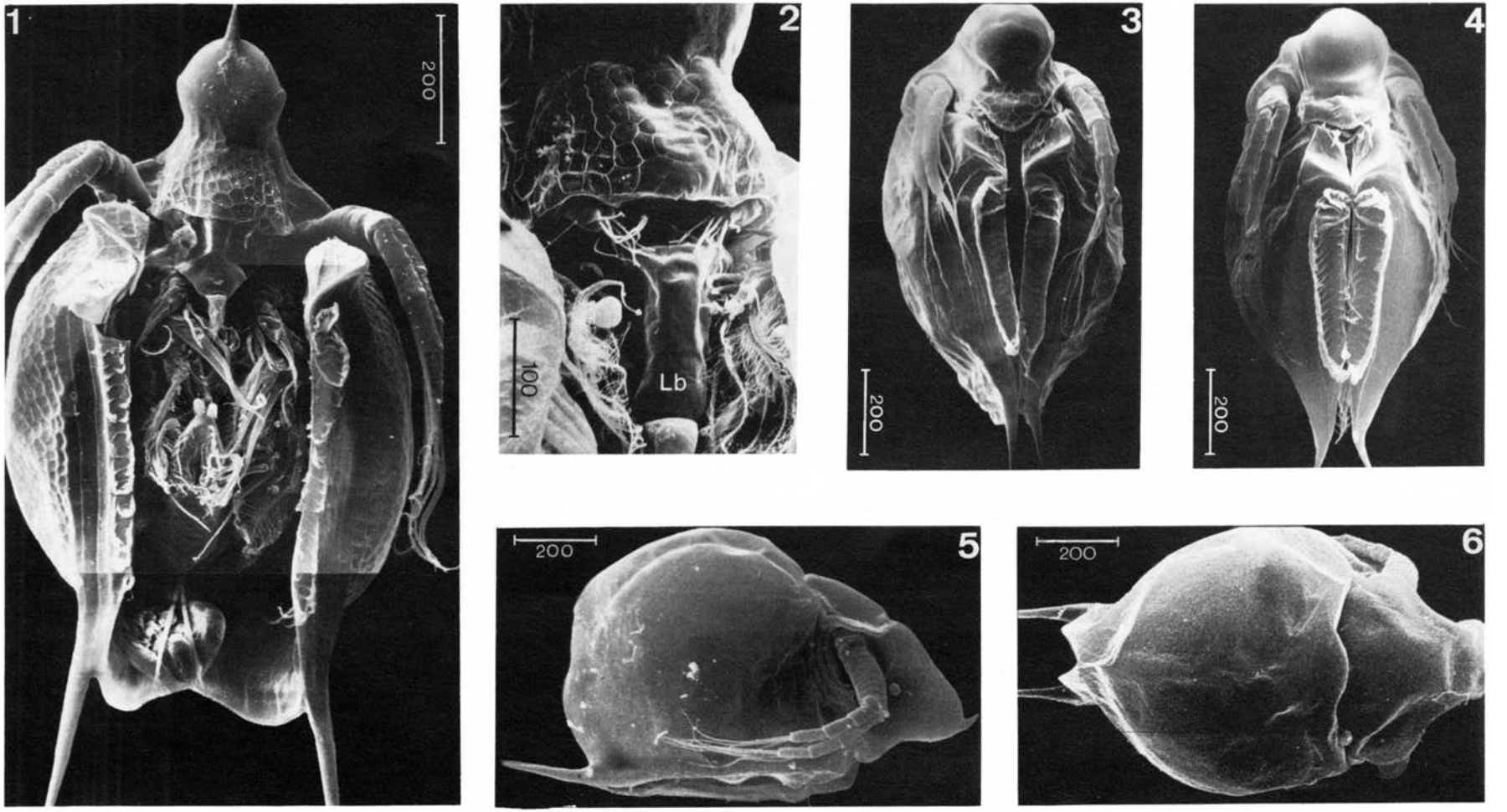

Plate 2. 1. *S. mucronata* female, ventral view; 2. idem, rostrum, first antennae and labrum (Lb); 3. *S. rammneri* female, vental view; 4. *S. kingi* female, ventral view, habitus; 5–6. *S. mucronata* female, lateral and dorsal view (scales in micrometers).

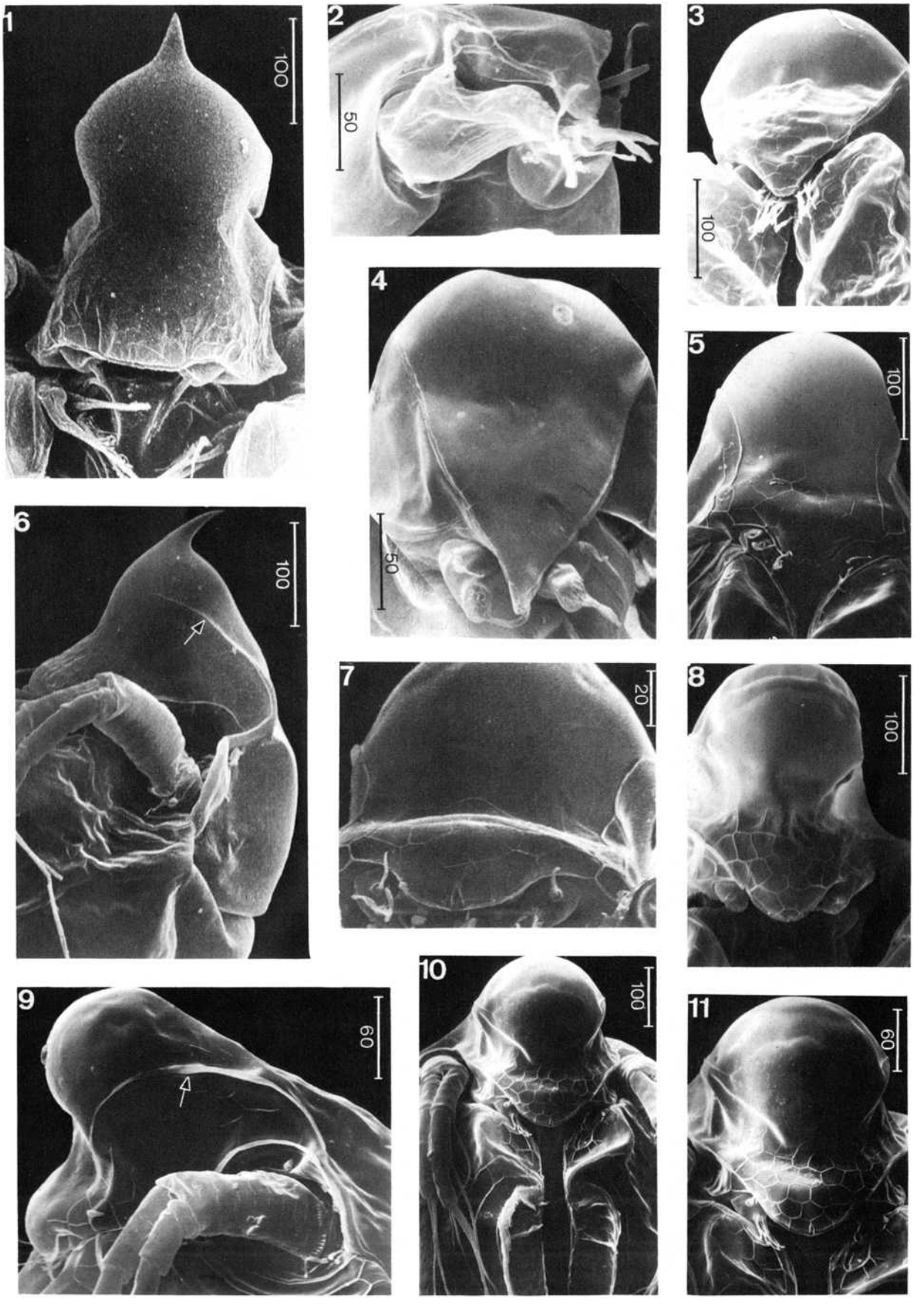

Plate 3. 1. *S. mucronata* female, rostrum; 2-4. *M. aurita.* 2. rostrum, oblique view from below, showing position of antennae; 3-4. frontal view of rostrum; 5. *S. kingi* female (Mali), frontal view; 6. *S. mucronata* female, head, lateral view (note sclerotized ridge on side of head); 7. *S. kingi* female (Australia), rostrum; 8. *S. rammneri,* female (Roumania), head; 9. *S. kingi* female (Australia), head, lateral view (note sclerotized ridges on sides of head); 10-11. *S. rammneri* female (Lake Donk) (note absence of sclerotized ridges on sides of head, as in (8) (all scales in micrometers).

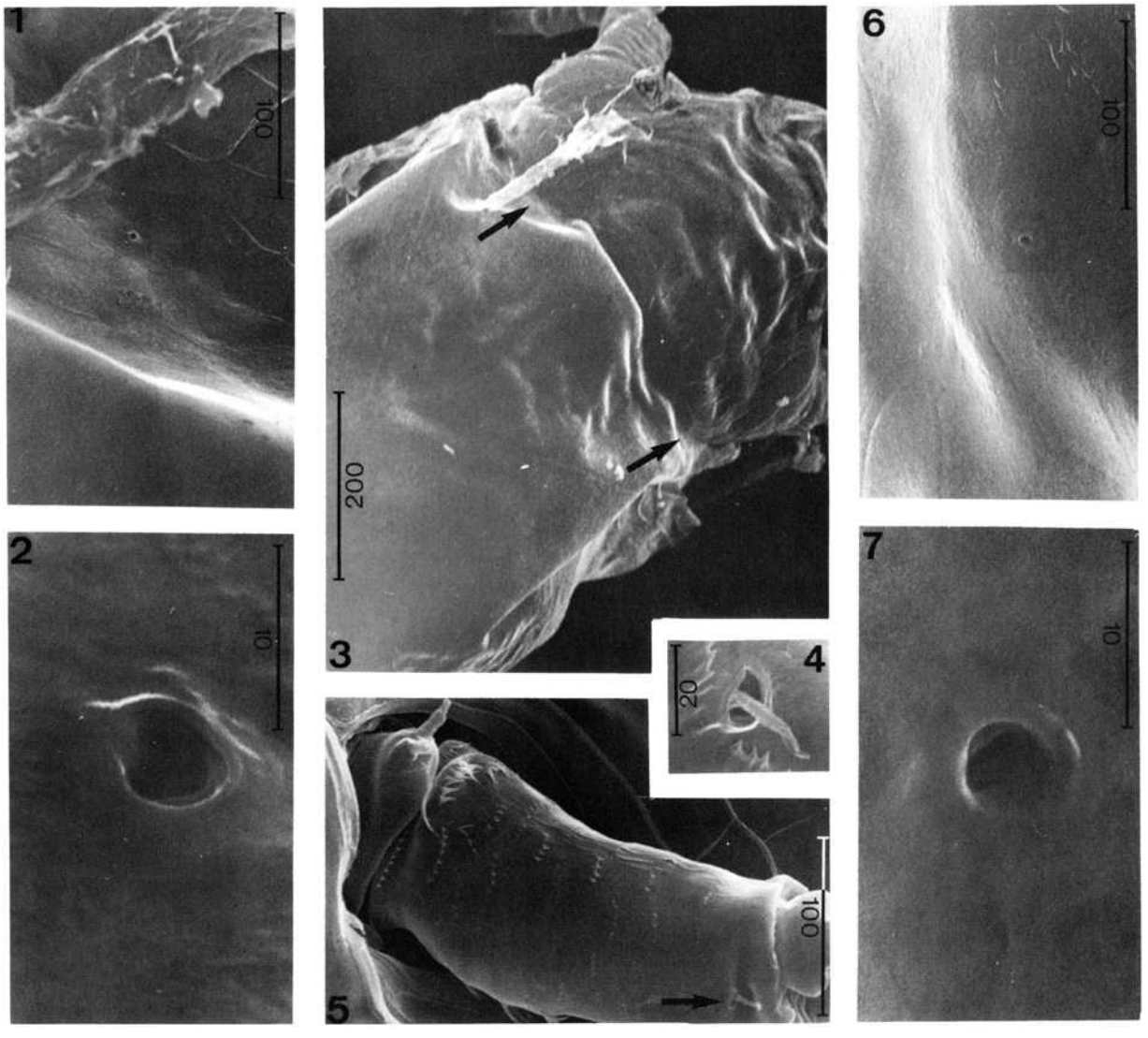

Plate 4. S. kingi female, headpores (1–3, 6–7). 3. Dorsum of headshield; pore areas indicated but pores not visible at this magnification; 1,6 and 2,7. pores progressively enlarged; 4. Pore on top of basipodite of second antenna, enlarged; 5. same pore on top of segment (arrow) (all scales in micrometers).

Daphniids that assign it to a unique status within the family Daphniidae. The specialisation of the sucker-plate and the complete loss of an oval plate are the most obvious ones, but the modification of P1 in the males is also unique. The shift of the rostral pore to the dorsum of the rostrum is another innovation. Although we do not know what the function of the underlying organ(s) is (are), they are likely connected with the hyponeustonic way of life of Scapholeberis-species. It does not seem excluded that the pore leads both to an exocrine gland and holds a receptor function. More research about this structure is definitely needed. Males, in spite of P1, have conserved more primitive features than females. A full discussion of the phylogenetics of the genus will be given at the end of this paper.

3. Scapholeberis mucronata (O.F. Müller 1776)

Daphne mucronata O. F. Müller 1776: no. 2404.
Monoculus bispinosus De Geer 1778: 463.
Daphnia mucronata: O. F. Müller 1785: 94.
Monoculus mucronatus: Jurine 1820: 137.
Scapholeberis mucronata: Schoedler 1858: 23.
Scapholeberis cornuta Schoedler 1858: 24.
Scapholeberis mucronata var fronte-laevi P. E. Müller, 1867: 124.
Scapholeberis mucronata var longicornis Lutz 1878: 43

Type locality: Denmark. Types not indicated and lost.

Material examined

Belgium: Kalmthout, bog, June 1976, ♀♀
Lake Donk, numerous ♀♀ and ♂♂, V-X, 1963–1968.
Teralfene, pond: V.1974,♀♀; IX.1982, ♀♀, ♂♂.
Gent, pond on University campus, VII.1982, ♀♀, ♂♂.
France: Lac de Bourdouze, Central Massif, 29.VI.1981,♀♀.
USSR: Leningrad (Petrodvorets), IX.1979, ♀♀, ♂♂ (leg. L. A. Kutikova).
USA, Alaska: Roadside pond, Mount McKinley natn. Park, 28.VII.1978, ♀♀.

Measurements: female 0.5–1.2 mm; male 0.4–0.7 mm.

Female. Area of sucker dark brown, almost black; rest of body light brown or yellowish-green. Head large with well developed fornices that extend as a sclerotized crest as far as the back of the eye (Plate 3: 6). Rostrum wide, almost rectilinear in front, produced into a couple of lateral, pointed horns (Plate 2: 1, 2; Plate 3: 1; Fig. 21: 1). Median pore slit-shaped, oblique, with a tongue-shaped flagellum extruding from it (Plate 5: 3). Sometimes a cup-shaped structure is seen below the pore (Plate 5: 6–7). First antennae short, largely hidden under the rostrum, and with the usual 9 + 1 arrangement. N.p.-seta in apical position. Head with or without a frontal horn, variable in length. In spite of intensive research, it is still uncertain whether populations exist in which frontal horns never occur, but it is well established that their length varies between biotopes and by cyclomorphosis. Grüber (*loc. cit.*) found that horns decrease in length in the course of postembryonal development, mature animals tending to loose them completely in small ponds but not in larger lakes. Spring populations had a longer horn than summer populations. Green (1963) showed that the latter effect is not due to temperature but, at least in part, to the amount of food available. Also, Rammner (1927) had studied populations in which Gruber's relationship between size of biotope and length of horn did not hold. In part, this was due to a confusion between *S. mucronata* and *S. rammneri*, but it should also be stressed that very little is known about the possible functional or adaptive value of such a horn. Only Herrick & Turner (1895) seem to have speculated that the horn might be of use in clearing away detritus ("rubbish"), but this is clearly too simple an explanation.

Valves dorsally rounded, ventral margin infolded and flat, modified into a sucker-plate. In front of the head, a broad triangular embayment of the anterior corner of the valves (Plate 1: 6) is separated from the sucker by an elevated, arched crest. The sucker itself is widest at its anterior end, where it consists of a series of coiled-up, reinforced lamellae on which foliate membranes insert, that lie partly superimposed and have a spinulated free margin (Fig. X: 1, 2). The body of the sucker is formed by 20–25 more delicately built lamellae, each of which has an internal and an external skeletal element. Both skeletal elements are ramified, and connected to one another by these ramifications, that serve to support a membrane. The inner skeletal element is shortest, and supports a short membrane, while the outer skeletal element supports a long membrane. Both membranes are connected, and the connecting part has a free, spinulated border. The difference in length between the inner and outer membranes decreases caudad. The sucker ends by one or a few large "sails", which have a single, central skeletal element only. The inner margin of the sucker is lined by a stiff ridge, divided into as may sectors as there are lamellae. The free setae on the anterior and posterior end of the sucker, and the internal skeletal elements of the body of the sucker, insert between these sectors. This inner ridge continues on the inner rim of the posterior margin of the valves as a denticulated membrane. The sucker membranes serve to attach the animal to the surface film of the water, a function that had already been attributed to this area of the animal by Scourfield (1896, 1900). It is very probable that the lamellae are mov-

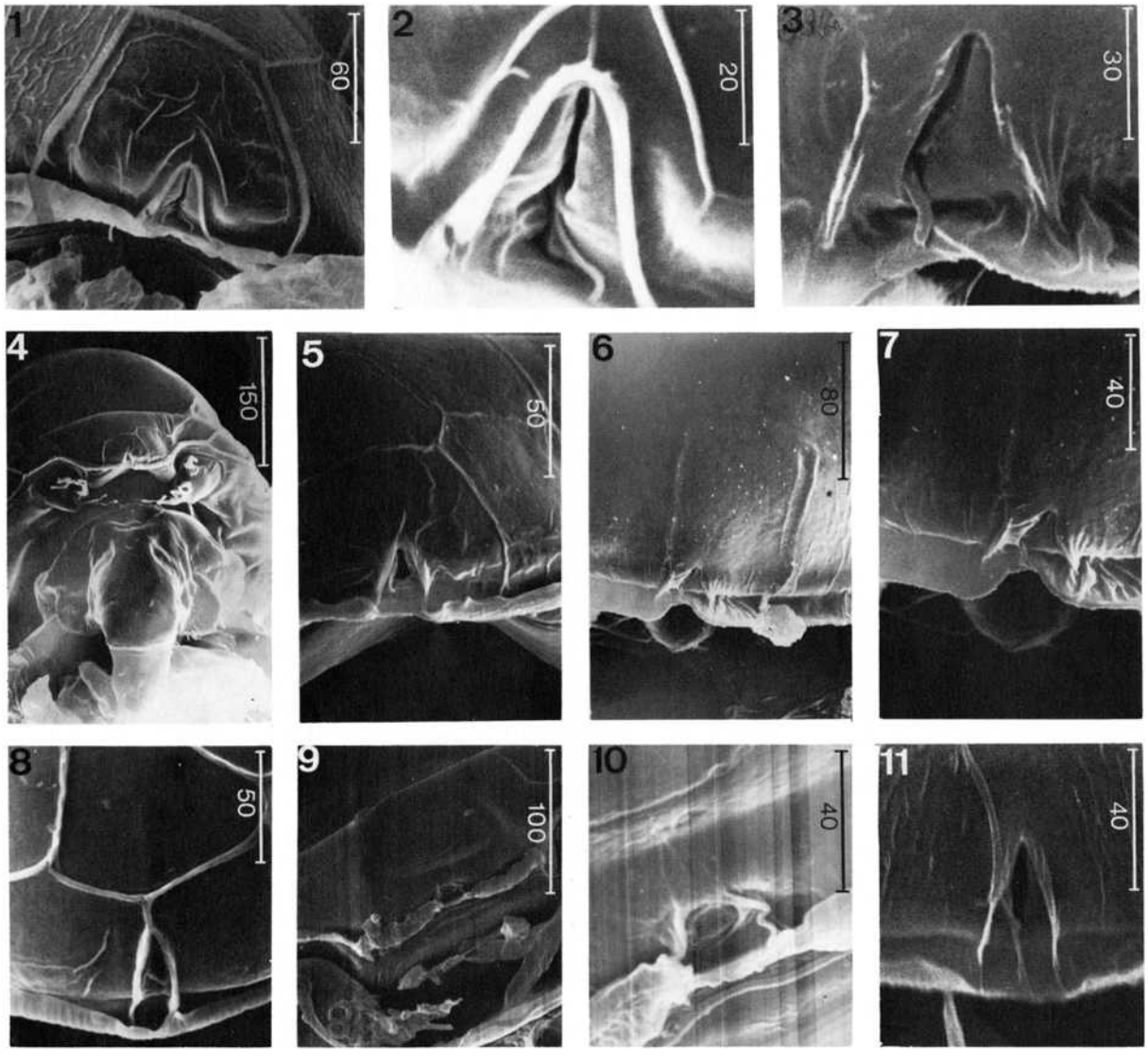

Plate 5. Rostral pores in *Scapholeberis.* 1, 2. *S. kingi;* 3. *S. mucronata;* 4. *S. kingi,* rostrum seen obliquely from below to show pore-opening; 5. same, enlarged; 6-7. *S. mucronata,* pore with underlying cup-shaped structure; 8. *S. rammneri;* 9–10. *S. armata;* 11. *S. rammneri* (all scales in micrometers).

able, and possibly the membranes may be wetted by glands that are situated underneath, because in some critical-point dried animals the fleeces would glue together, but not in others (see Plate 1: 7, 8). In some animals, minute pores were observed near the anterior lamellae. It should be noted that the membranes are so delicate that, even in very carefully dried animals, they would invariably curl up as can be seen on the SEM-micrographs.

The mucro, in spite of cyclomorphotic variation, is always long. Its length varies between 1/2 and 1/3 of the length of the ventral valve rim. Inner surface of posterior margin of valves lined with a denticulated membrane, that curves over the base of the mucro and continues dorsad as far as the valve junction. The basalmost spinules on the membrane are particularly coarse, become much finer after, but long again in the upper third, where 3–4 spines

stand out from the membrane as long, curved hooks subfamily. Postabdomen robust, with numerous rows of dorsal and lateral spinules (Fig. IV: 1). Anal area flanked by 6–10 long spines. Anal corner of postabdomen usually rounded. Endclaw with 3 external pectens, a ventral apical pecten, and two internal pectens (sometimes only weakly differentiated). Each pecten is composed of equally shaped spines. The dorsal external pecten reaches to the very base of the claw.

Male. Rostrum truncated, otherwise shaped as in female (Fig. IX: 5). First antenna short, and with only one n.p.-seta, inserting apically (Fig. IX: 8). Eye larger and darker than in female. No apical triangular embayment on anterior end of sucker-plate, but sucker otherwise organised as in female, i.e. an anterior zone of reinforced membranes, a series of fleeces, and a terminal sail (Fig. IX: 3, 4). The fleeces are, however, distinctly longer than in the female. Claw of P1 robust, lying horizontally over the body of the endopodite, sharply pointed (Fig. IX: 6). A row of spinules at the base of the claw, but no strong spines. Postabdomen with a distinct postanal hump (Fig. IX: 1, 7). Endclaw thickened. Pectens as in female. Middle external pecten with a basal concavity in Belgian examples, straight in examples from Leningrad.

Distribution

Palaearctic and North Holarctic (horned forms were reported from subarctic North America by Bardach 1954, and Reed 1962), but the name *mucronata* has been so often misused for other species

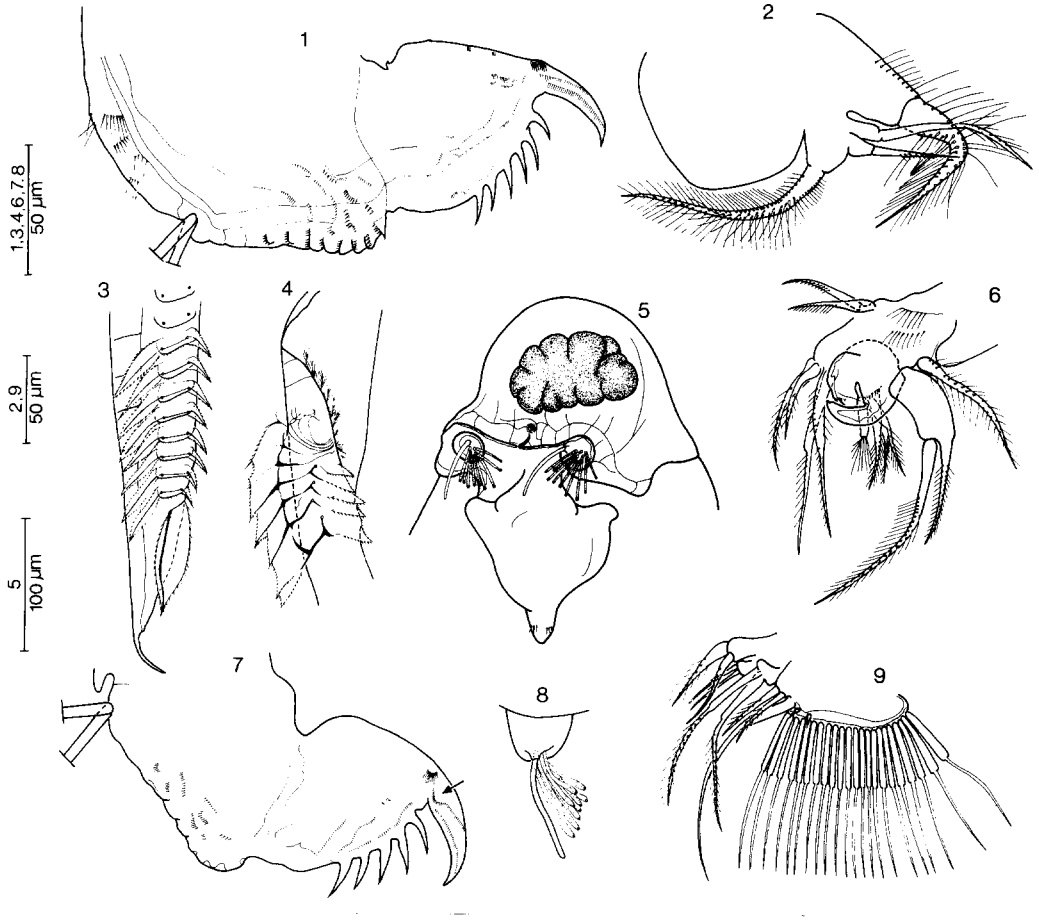

Fig. IX. S. mucronata 1, 7. Postabdomen of male (1. Leningrad, USSR, 7. Teralfene, B.); 2. Female, P5; 3–4. Sucker-plate of male (Leningrad); 5. Frontal view of Head (Teralfene); 6. P1, male (Lake Donk); 8. First antenna, male (Lake Donk); 9. P3, female (Lake Donk).

of *Scapholeberis* that its range needs to be redefined. It occurs with certainty in Central Europe, and extends to Central France and Northern Italy (Parenzan (1932) reports horned forms from Piemonte), while in the north it covers Scandinavia, Greenland (Roen 1977), the European USSR, Western Siberia, and, across the Bering Strait, Arctic and Subarctic North America. Whether it occurs in China or in Japan is uncertain: Ueno (1926, 1932) failed to find horned forms with long mucrones in both countries. But the southern limit of its range in Europe is equally uncertain. *S. mucronata* probably does not cross the Pyrenees (Margalef (1953) cites it from Spain but this is likely a confusion with *S. kingi* and with *S. rammneri*), south of the Po valley, and is not present in the Balkans, but all these assumptions are in need of verification.

4. Scapholeberis microcephala G.O. Sars 1890

Scapholeberis obtusa Hellich 1877: 44, non S. obtusa Schoedler 1858.
Scapholeberis microcephala Sars 1890: 38.
Scapholeberis reticulata Linko 1900: 7.
Type locality: southern Norway.
Type not indicated by Sars, and no preparations present in Oslo Museum.

Material examined

Germany: Langener Meer, Ostfriesland (in Sphagnum), 30.IX.1981, ♀♀,♂♂, leg. W. Hollwedel.
Estonian SSR: acid swamps in Vorstjarv area (leg. A. Maemets), ♀♀.
Measurements: female 0.4–0.8 mm, male 0.35–0.4 mm.

Female. Head small. Rostrum with anterior border almost rectilinear, and sides angular (Fig. XI: 1). First antennae unusually long, protruding beyond margin of rostrum. 9 apical perforated esthetes and one n.p.-seta at mid-length. Frontal horn rarely present and if present, small. No head pores recorded. Rostral pore and bordering membrane distinct. Valves less arched dorsally than in *S. mucronata,* mucro very short (between 1/5 and 1/10 of ventral side of valves). Ventral sucker preceded by triangular invagination, lined externally by 4–5 plumose setae. Lamellar zone as in *S. mucronata,* but terminal sail shorter, not noticeably longer than preceding fleeces. Internal end of ventral rim with 5–6 long, plumose setae (the last of which is shown in Fig. XI: 12). Inner denticulated membrane on posterior margin of valves slightly coarser in its lower 1/3 than in its upper 2/3. Small groups (2–4) of more robust spines occur in 4 or 5 locations, equally spaced along the valve rim. A narrow hyaline membrane is found in marginal position as well. Trunk limbs: P1, P2 as for genus (Fig. XI: 2, 3), P3, P4 as for subfamily. P5 with internal hair of exopodite unusually long, and gnathobase reduced to a smallest tubercle (Fig. XI: 6, arrow). Postabdomen with the usual rows of dorsal and lateral spinules and with 4–7 long, finely pointed paranal spines. Endclaw broadly based, acutely tipped, with three external pectens composed of numerous very fine spinules (Fig. XI: 7). A single, occasionally double internal pecten. Ventral external pecten composed of 25–30 spinules, not of 2–8 longer spines as in most other Scapholeberis-species.

Male. Rostrum much shorter than in female, with rectilinear margin and lateral horns (Fig. XI: 5). First antennae as in female, but with 2 n.p.-setae. Ventral margin of valves without triangular depression in front, and sucker composed of 25–30 long fleece-setae, longest in the middle and gradually shortening backwards. A few very short setae near the anterior end of the sucker (Fig. XI: 9). Trunk limbs: claw on P1 with wavy margins and a series of closely apposed, longish spines at its base. One of the four basal setae distinctly bisinuous (Fig. XI: 4, 10, 11). Postabdomen with 4–6 paranal spines. Endclaw with broad base, acutely tipped, often even constricted near its tip (Fig. XI: 8). Pectens rather indistinct.

Distribution

Restricted to the west of Northern Europe. The southernmost record is an acid, dystrophic bog in the Veluwe area, The Netherlands (Redeke & De Vos, 1932). The species is typically found in acidic water, usually between floating Sphagnum islands. Records are available from the Friesian Islands (Hollwedel leg.), from Germany (review in Flossner 1972), Poland (Ocioszynska-Bankierowa 1934), Czechoslowakia (Sramek-Husek *et al.* 1962), the Estonian SSR (Maemets 1958), Scandinavia (Sars 1890; Lilljeborg 1900). The northernmost record appears to be the White Sea area (Linko 1900).

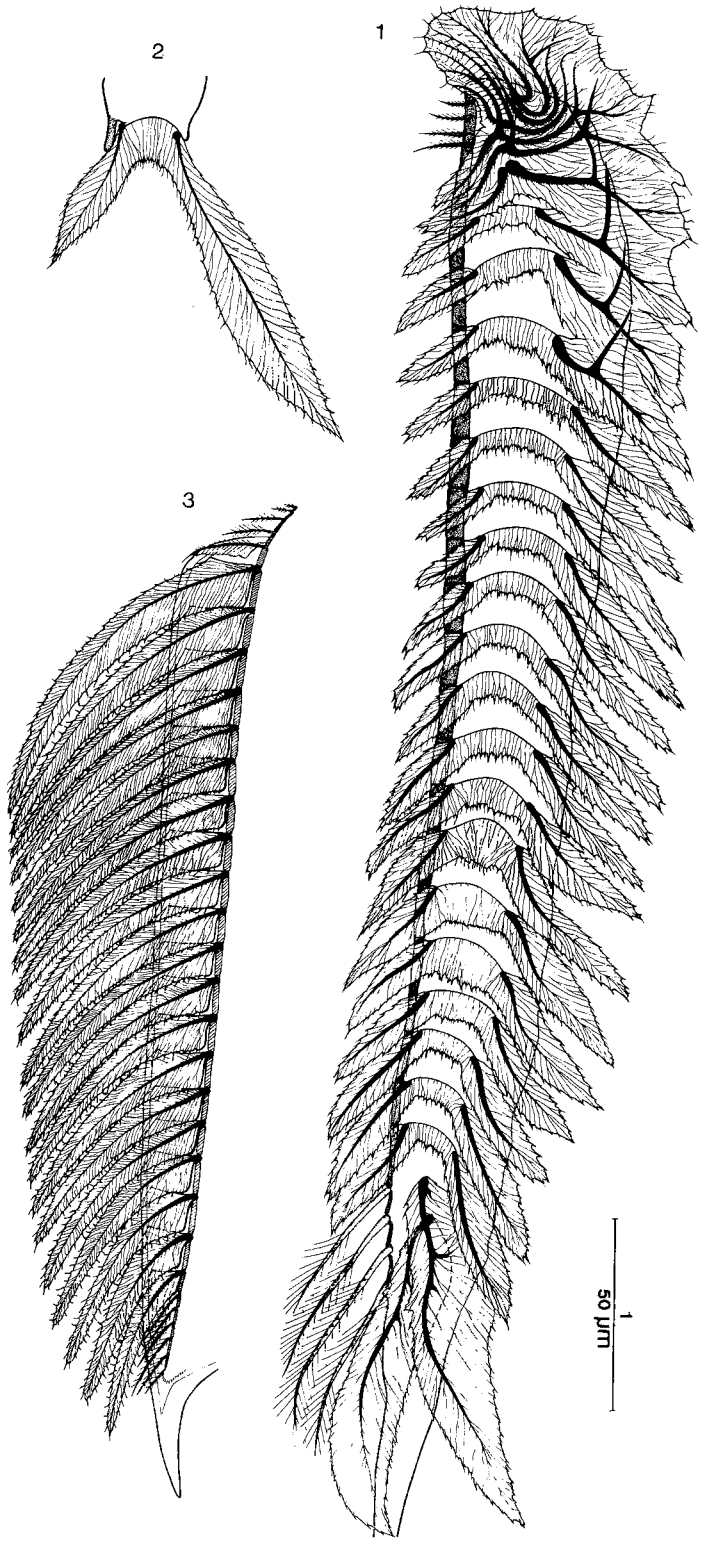

Fig. X. Ventral sucker-plate. 1. *S. mucronata,* female, ventral view. 2. Semi-diagrammatic cross-view of single membrane on a lamella in the central zone of the sucker. 3. Semi-diagrammatic representation of sucker-plate in a male of the *kingi*-group.

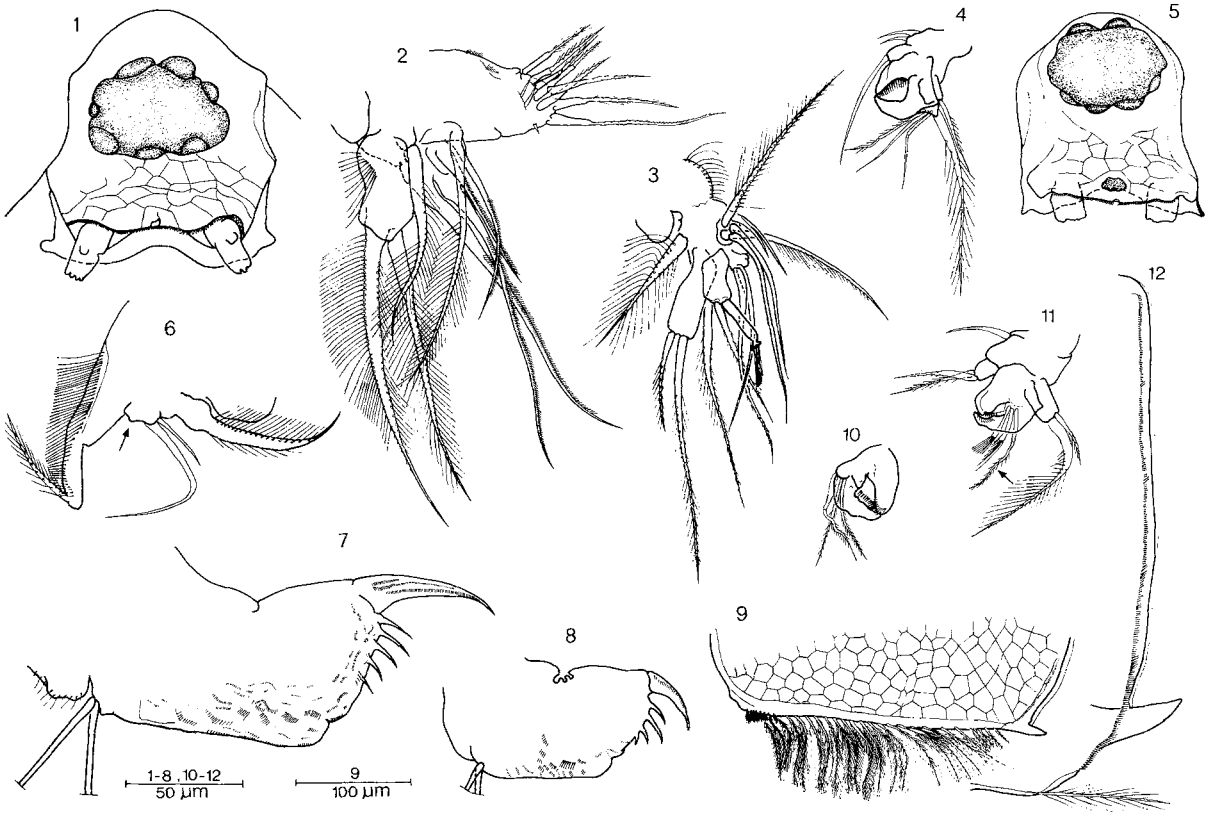

Fig. XI. S. microcephala (Langener Meer, Ostfriesland, GFR); 1. Female, head (frontal view); 2. female, P2; 3. female, P1; 4. male, P1, endopodite; 5. male, frontal view of head; 6. female, P 5; 7. female, postabdomen; 8. male, postabdomen; 9. male; ventral zone of valves; 10-11. male, claw of P1; 12. female, distal rim of valves and mucro.

5. Scapholeberis kingi G.O. Sars 1888

Daphnia mucronata King 1853: 255.

Scapholeberis Kingii Sars 1888: 68.

Scapholeberis kingi Sars 1903: 8.

Scapholeberis kingi: Gurney 1906; Sars 1916; Gauthier 1939, 1951; Brehm 1937; Rahm 1956; Harding 1961; Rey & St Jean 1969; Fernando 1974, 1980; Mamaril & Fernando 1978; Dumont 1971 (partim), in press (review of Australian records); Dumont *et al.* 1977, 1979, 1981.

Scapholeberis mucronata var. intermedia von Daday 1898: 59.

Scapholeberis mucronata: Margalef 1953 (partim); Fryer 1957; De Lepiney 1961.

Scapholeberis spec.: Thomas 1961; Khalaf & Smirnov 1976.

Non: Scapholeberis kingi Rammner 1928; Ocioszynska-Bankierowa 1934; Wagler 1937; Brooks 1959; Herbst 1962; Sramek-Husek *et al.* 1962; Manuilova 1964; Dumont 1971 (partim); Flossner 1972; Notenboom-Ram 1981.

Type locality: South Creek and Paramatta, New South Wales, Australia.

No types were indicated by Sars, and no topotypical material is available in G. O. Sars collection in Oslo Museum. Note that, although Sars fully described this species in 1903 (and emended its name at the same occasion), he first used the name in an appendix to his 1888 paper, stating that the species was distinct from *S. mucronata* by its "much smaller and differently formed head". Since these are pertinent details of structure, the name *Kingii*, 1888 cannot be regarded as a *nomen nudum.*

Material examined

Australia: Aramac Creek, Aramac, Queensland, 17.VII. 1974, ♂, ♀♀.

Lake Beadle, Victoria, 4.XI.1977, ♀♀.

Lake Powalthanga, Charters Towers, Qld, 26.VI.1974, ♀♀.
Nardellos Lagoon, Mareeba, Qld, 11.VII.1974, ♀♀
Teewarina pool, Charters Towers, Qld, 15.VII. 1974, ♀♀.
(all leg. B. V. Timms).

India: Calcutta, Dalhousie; Raphahi, Bengal; Orissa; Chassadharpur, ♀♀ (no further data, all in coll. von Daday, Hung. natn. Mus. Budapest).

Sri Lanka: 5 ♀♀, no dates, no locality, all in coll. von Daday, Hung, natn. Mus. Budapest.

Iraq: Samarrha, Thirtar lake, 11.XI.1974, ♀♀ (leg. A. Khalaf, fide N. N. Smirnov).

Algeria: Lake Oubeira, 24.III.1976, ♀♀.

Senegal: Lakelet at Djourdj; 25.I.1976, ♀♀.

Mali: Goundam, 24.XII.1972, ♀♀ (leg. T. Monod). Swamp at Dyabali, 24.III.1976, ♀♀.

Ivory Coast: Kossou lake, 18.VI.1971, ♀(leg. E. Lamoot).

South Africa: Grahamstown, VII.1979, ♀♀.

Spain: Guadalquivir area, Doñana, Huelva (leg. J. Armengol), ♀♀, III.1978.

Measurements: Female 0.4–1.0 mm; male 0.4–0.5 mm.

Female. Colour deep brown, head rather large. Rostrum trilobate, the middle lobe evenly rounded and with a hyaline membrane in front (Plate 2: 4; Plate 3: 5, 7). An elongate pore (Plate 5: 1, 2, 4, 5) on the rostrum. A couple of simple, circular headpores occasionally present in shoulder-region of headshield (Plate 4). Never a frontal horn. First antenna with the usual 9 + 1 arrangement, short. A sclerotized ridge departs from the insertion of the second antenna and extends to the side of the head (Plate 3: 9). Seen frontally, it may appear as a pair of "auricles" (Plate 3: 7; Fig. XXI: 4). Valves reticulated, these reticulations frequently arranged as vertical lines near the posterior margin of the valves (Plate 7: 5). Sucker preceded by a triangular invagination of the valves; anterior zone of reinforced lamellae followed by 15–20 soft lamellae. Terminal sail long (Plate 2: 4). A broad hyaline membrane extends beyond the posterior valve rim (Plate 7: 5), and a very finely denticulated membrane is found on its internal surface (Plate 7: 4). Two hooks at about 1/3 of the valve junction; dorsad to first hook, the denticles on the membrane much coarser. Mucro 1/4–1/8 of valve length. Trunk limbs as in *S. mucronata*. Postabdomen usually widened and angular at anal corner, flanked by 4–7 paranal teeth. The first of these spines usually solitary. Spine 3–4 and subsequent ones usually implanted on a bud, and flanked by smaller spines, or main spine replaced by a cactus-like bud set with spinules. Numerous dorsal rows of spinules, but few lateral rows (Fig. IX: 4). Endclaws with 6 pectens. Dorsal external pecten reaching from close to tip of claw to just over half its length. Basal 2–4 spinules more robust, and usually a little isolated from the smaller spinules, but not to same degree as in internal pecten where 2–6 large, basal spines stand out of line with the rest of the pecten (Plate 6: 6, 7). Middle external pecten extending from base to just less than half the length of the claw. Upper basal pecten composed of 2–7 long spines. Ventral pecten composed of 20–35 short spinules.

Male. Rostrum short and trilobed, but middle lobe shorter than in female (Fig. XII: 4). First antenna short, 9 + 2. Basal n.p.-seta longest, but top one more than half the length of basal one (Fig. XII: 4). Claw of P1 recurved, and with two strong teeth at its base (Fig. XII: 2, 3) in addition to a single row of spinules on the body of the endopodite. Ventral plate without anterior invagination. Sucker with a few short, finely ciliated setae at its anterior end, followed by up to 30 long fleece-setae. Postabdomen as in female, endclaw longish, not thickened (Fig. XII: 1). Mucro as in female.

Distribution

While it took until the 1920s for the name *kingi* to become established, it was thereafter used incorrectly in a number of cases, resulting in an apparent cosmopolitan range for this species. As will be shown later, the European – Central Asian species that has been confused with it, and the American species are all quite different. The range of true *S. kingi* therefore encompasses Australia, South-East Asia, the Indian Subcontinent, the Middle East, and Africa. Its occurrence on the Balkans is uncertain, but it has been found in Southern Spain, and records from Corsica and Sardinia (Stella *et al.* 1972; Margaritora *et al.* 1975) are also likely correct. The situation on continental Southern Italy is unknown (Margaritora 1979 does not present conclusive data).

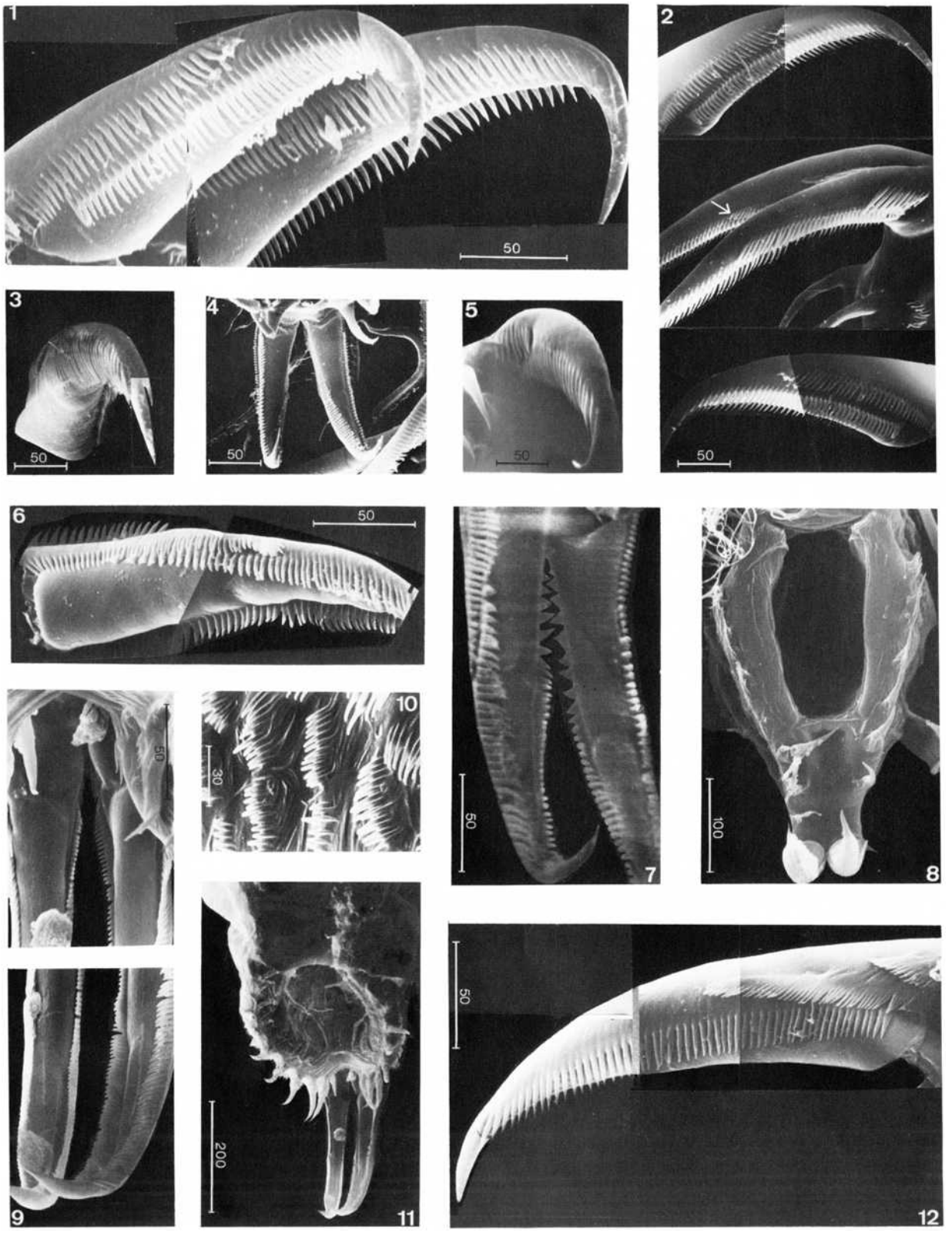

Plate 6. 1–5, 12: end-claw of *S. mucronata,* female, illustrating the variation in the pectens, especially the ventral external pecten (reduced in Fig. 12). In Fig. 1 the internal pecten is single; in the middle photograph of (2) it is double (arrow). 6–7. *S. kingi,* endclaws; 8. *S. kingi,* dorsal view of postabdomen, anal region; 9–11. *M. aurita* female. 9. endclaw; 10. rows of spinules on dorsum of postabdomen, proximal to anus; 11. postabdomen, anal region (all scales in micrometers).

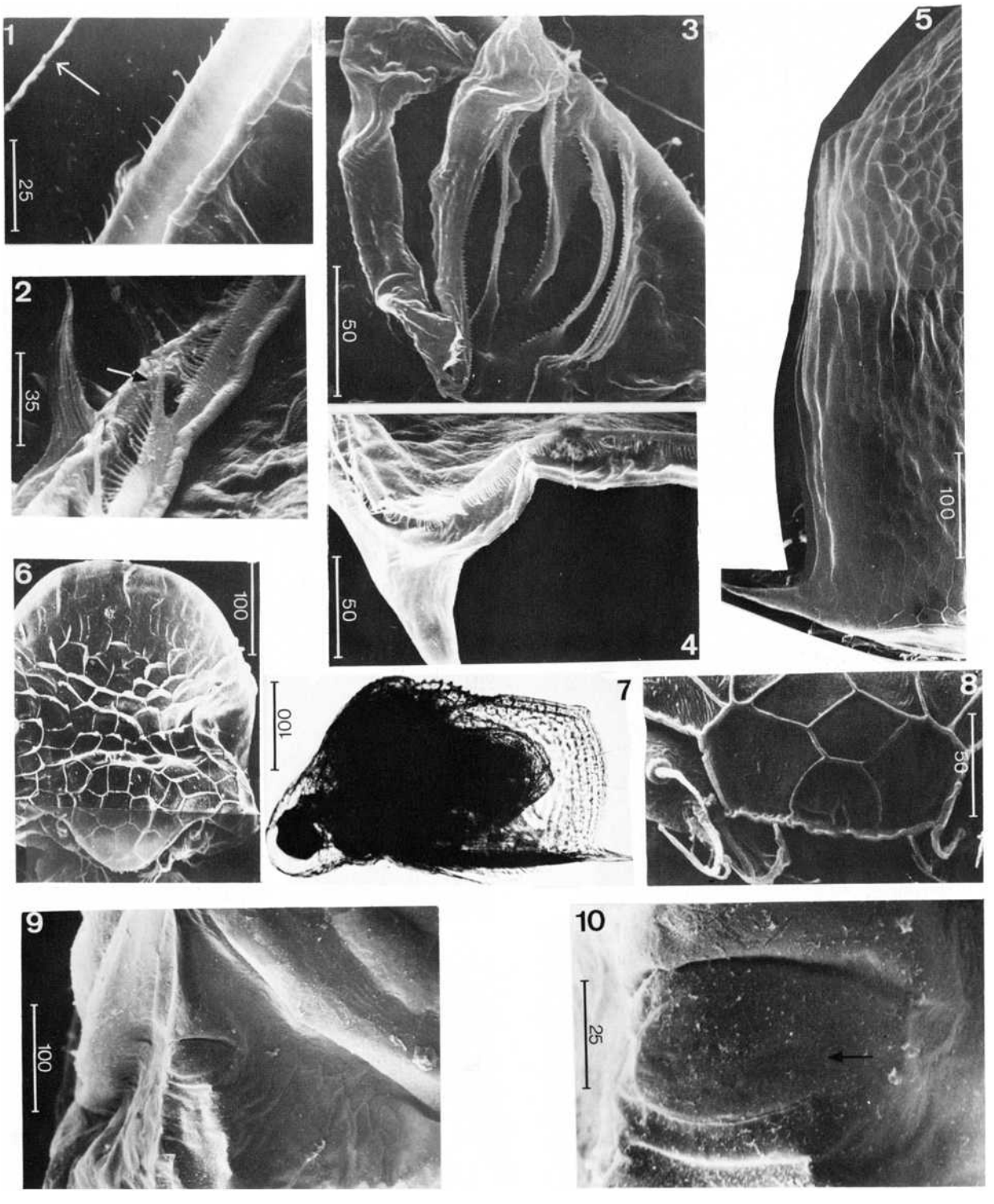

Plate 7. 1. *S. echinulata* female, broad hyaline membrane and finely denticulated internal membrane along posterior valve rim; 2. "hooks" on denticulated membrane of *S. spinifer* (note some large posterior spines on valve rim as well); 3. Lamellar area on tip of sucker in female of *S. rammneri;* 4. Ventral zone of posterior valve rim in *S. mucronata* female, showing grossly denticulated membrane and reduced marginal membrane; 5. posterior valve rim of *S. rammneri:* valve reticulations more or less lined, broad marginal membrane; 6. *S. spinifera* females, head, frontal view; 7. *S. echinulata* male, habitus (Pannonian plain, Hungary 1981; Photo W. Hollwedel); 8. *S. a. armata* female, middle lobe of rostrum; 9–10. *M. aurita* female; 9. dorsum of headshield, showing oval plate; 10. oval plate enlarged. (all scales in micrometers).

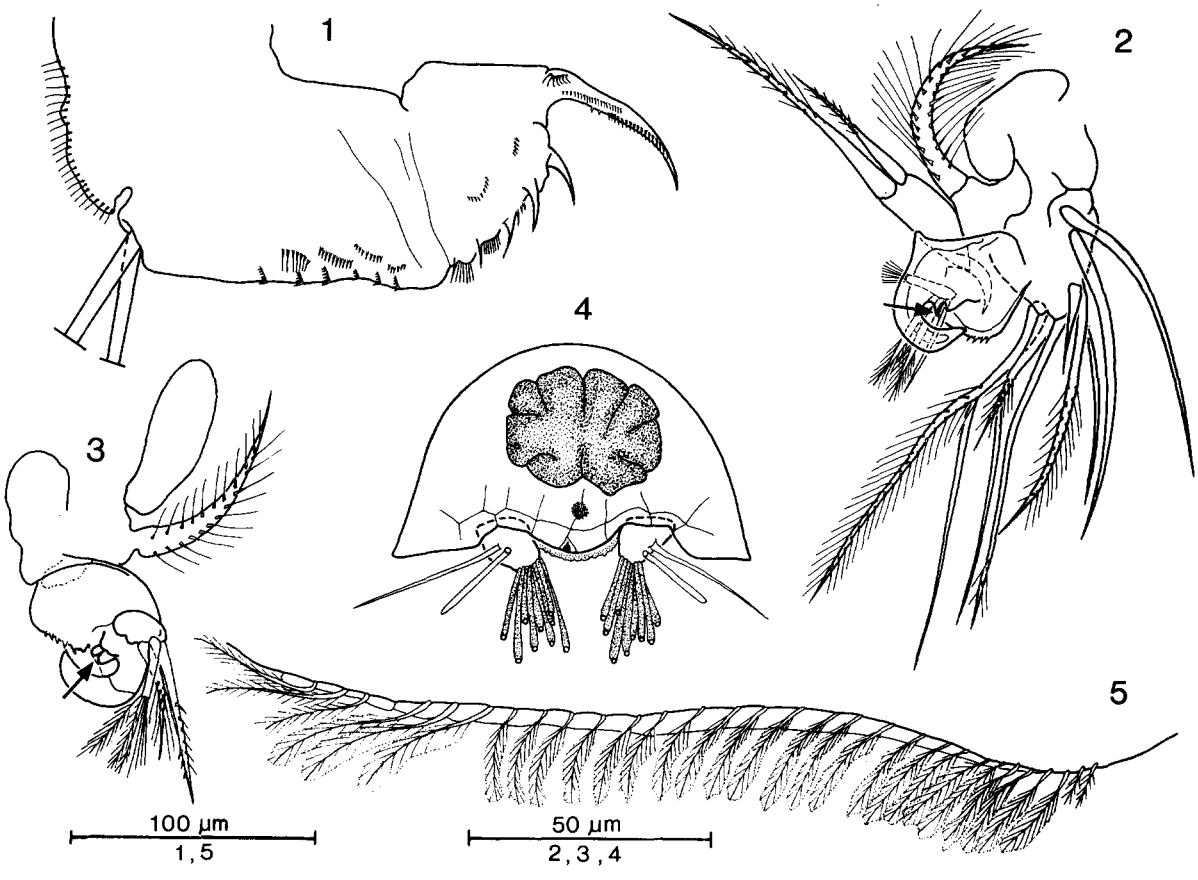

Fig. XII. S. kingi male (Aramac creek, Aus.). 1. Postabdomen; 2. P1; 3. P1, Endopodite; 4. Head, rostral view; 5. Ventral valve rim.

6. Scapholeberis rammneri n.sp.

Scapholeberis kingi: Rammner 1928: 326; Rammner 1929: 280.

Scapholeberis kingi: Osioszynska-Bankierowa 1934; Wagler 1937; Herbst 1962; Sramek-Husek *et al.* 1962; Manuilova 1964; Dumont 1971 (partim); Flossner 1972; Hollwedel 1978; Notenboom-Ram, 1981.

Scapholeberis mucronata: Spandl 1925; Margalef 1953 (partim).

Scapholeberis sp., non S. kingi Sars: Espeel 1982: 77.

Scapholeberis kingi: Anderson 1971, 1974.

Derivatio nominis: the species is named after the German Cladocerologist W. Rammner who first perceived the presence of a Scapholeberis kingi-like animal in Europe.

Holotype: an undissected parthenogenetic female, preserved in a formalin-glycerol mixture, kept at the Zoological Institute, State University of Gent, collected at Lake Donk, Eastern marshy shores, 6.X.1971.

Paratypes: 20 parthenogenetic females, preserved in a formalin-glycerol mixture, same repository and collecting data as holotype.

Allotype: a dissected male, mounted in glycerol, same origin and repository as preceding.

Type locality: Lake Donk, Eastern Flanders, Belgium.

Material examined

Belgium: - Type series from lake Donk and from a nearby ditch (Tweegootsloot), 1970 and 1971, ♀♀, ♂♂. - Oostpolderkreek, Eastern Flanders, 12.VI. 1968, 8.XI, 1970, ♀♀, ♂♂. - Creek at Doel, E.Fl., 18.X.1970, ♀♀. - Clay pits at

Stuivekenskerke, W. Fl., IV–IX. – 1978 (leg. M. Espeel), ♀♀, ♂♂.

Germany: – Juist, Hammersee (East Friesian islands), 21.VII.1974, ♀♀, ♂♂ (leg. W. Hollwedel).

Austria: – Illmitz, Neusiedlersee (20.VI.1980) (leg. H. Metz) (coll. Hung. nat. Hist. Mus.), ♀♀.

Hungary: – Fulophaza Szivosszek, 19.VI.1978, 31.VII.1979, (leg. L. Forro), ♀♀. – Fulophaza Kondor-to, 31.VII.1979 (leg. L. Forro), ♀♀.

Roumania: – Bistritza, Danube valley, 16.IX.1969, ♀♀. (leg. S. Negrea).

Turkey, Anatolia: – lake near Ankara, 15.V.1972, ♀♀.

USSR, Caucasus: – Abkhaz Rep. ditch at farm 'Citrusovyi', 25.IX.1974, ♀. (leg. N. N. Smirnov).

Mongolia: – Chentej Aimak, 20 km SW of Sarov Norovlin (900 m) 19.VIII.1965. (Leg. S. Kaszab), ♀♀. (coll. Hung. nat. Hist. Mus.).

Spain: Tordera ponds, Gerona (leg. J. Armengol), ♀♀, VII.1980.

Canada: Riley Lake, Jasper National Park, Alberta, 5.VIII.1978. leg. R. S. Anderson) ♀♀.

The numerous locality records now available support the view that this species is far more common and widespread than heretofore supposed, and not necessarily restricted to brackish environments as suggested by Dumont (1971).

Measurements: Female 0.45–1.35 mm; male 0.4–0.5 mm.

Female. Colour dark brown, head large, rostrum broadly triangular, not trilobate (Plate 3: 8, 10, 11). Eyes bulbously projecting above rostrum, creating a broad but shallow depression along the sides of the head, dorsally not lined by a sclerotized crest as in *S. kingi*. First antenna inserts at the sides of the rostrum, at the top of a secondary shallow depression or canal (Fig. XXI: 3). No frontal horn. Dorsal head pores present or absent. Valve shape, including ventral sucker (Plate 2: 3), as in *S. kingi,* but total size larger. Distal valve margin with a wide terminal hyaline membrane, and an internal, finely denticulated membrane with 3–4 hooks, and coarse spinules dorsad to the upper hook. An ontogenetic series of parthenogenetic females is shown in Fig. XIII. Neonates are 0.4–0.5 mm in length and become primiparous around 0.75 mm. They reach a maximum length of 1.35 mm. Mucro short, 1/4–1/8 of length of ventral rim. Postabdomen, including endclaws, and trunk limbs, as in *S. kingi.*

Male. Rostrum short (Fig. XIV: 4), middle lobe more or less squared (Fig. XIV: 1). Eye large. A1 with 9 + 2 arrangement (Fig. XIV: 6); distalmost n.p.-seta extremely long, 2½–3 times as long as shorter one (Fig. XIV: 5). Ventral valve rim without anterior widening, a few ciliated setae at the anterior and posterior border of the sucker-plate, and a series of asymmetrical (short internally, long externally) sails in between (Fig. XIV: 7, 10; Fig X: 3, for a semi-diagrammatical interpretation of this structure). Armature of posterior valve rim as in female (Fig. XIV: 11). Mucro short (1/5–1/8 of length of ventral rim) (Fig. XIV: 10). Claw on P1 with thickened base, strongly curved (Fig. XIV: 2, 8, 9), without strong spines at its base, but with two rows of spinules. Postabdomen as in *S. kingi,* but endclaw shorter and thicker (Fig. XIV: 3).

Distribution

From the Pyrenees northwards, through Scandinavia and the European USSR to Siberia. To be expected in Alaska, since it is found in the Rocky mountains, Alberta, Canada, but range on the North American subcontinent in need of clarification.

Widespread in central Europe and the Balkans, extending to Anatolia, the Caucasus, and Central Asia, including at least part of continental China (Spandl 1925; Ueno, 1926). Occurrence in Japan to be confirmed. Confusion with *S. mucronata* and *S. kingi* and unreliable published figures prevent a more precise definition of its range at the present stage.

Differential diagnosis

The closest relative of *S. rammneri* is *S. kingi. S. rammneri* is larger, and the shape of its rostrum is highly distinctive in both sexes. Males may be separated by the presence or absence of two strong spines at the base of the clasper on P1. Both species replace each other in space and doubtlessly have a common ancestral gene pool. The wide terminal hyaline membrane and the absence of spines on the valves will differentiate *S. rammneri* from all other Scapholeberis with which it might co-occur.

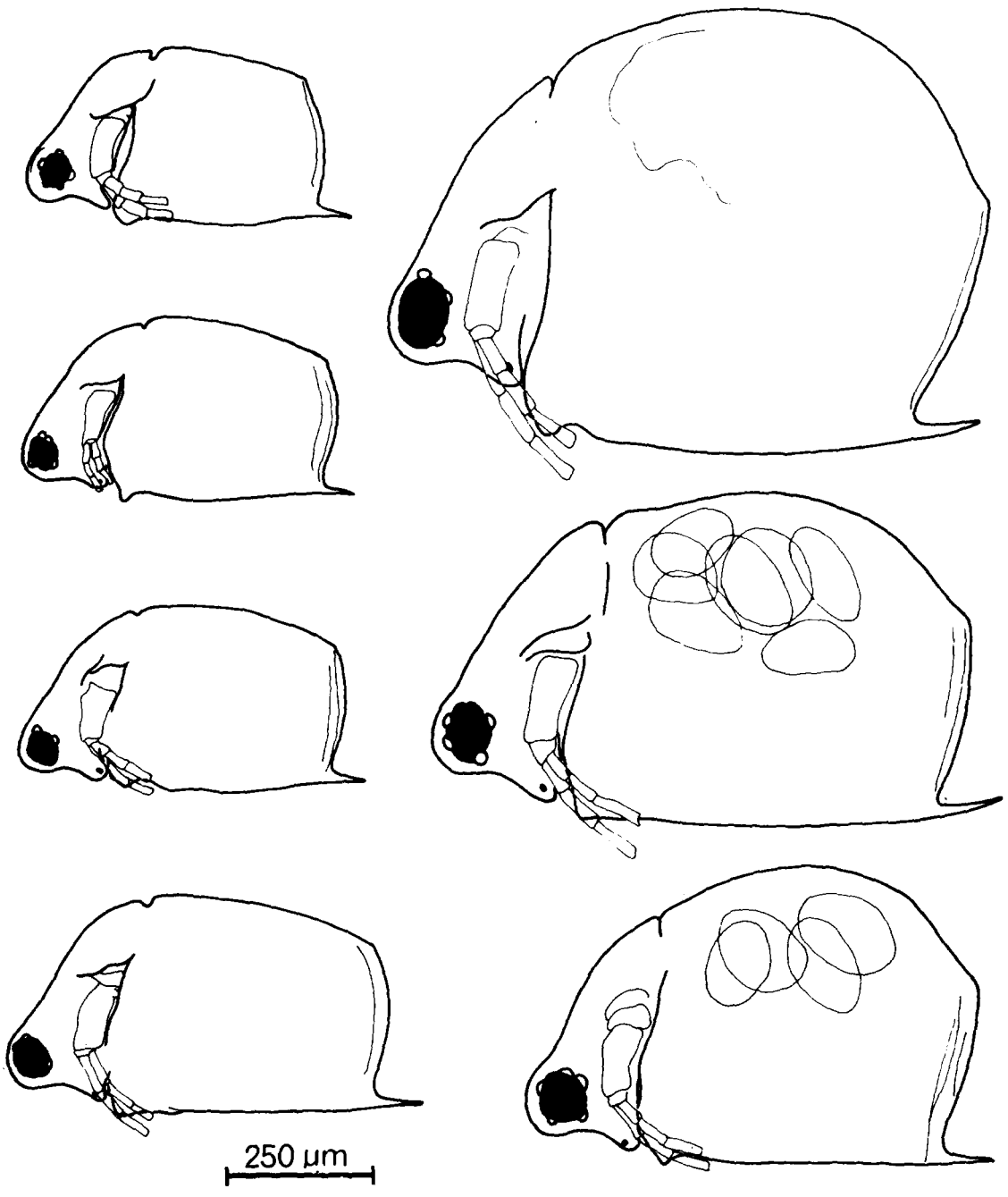

Fig. XIII. S. rammneri, female (Lake Donk, B.). Postembryonal development of females.

7. Scapholeberis echinulata G. O. Sars 1903

S. echinulata Sars 1903 (August): 176.

S. erinaceus Von Daday 1903: 76 (7 August 1903).

S. erinaceus: Brtek 1938; Jermanska 1953, 1956; Vilcek & Hudek 1975.

S. erinaceus var. Kerteszi Ponyi 1955: 312.

S. echinulata: Markovskii 1925; Manuilova, 1964: 178 (male); Hudek 1984.

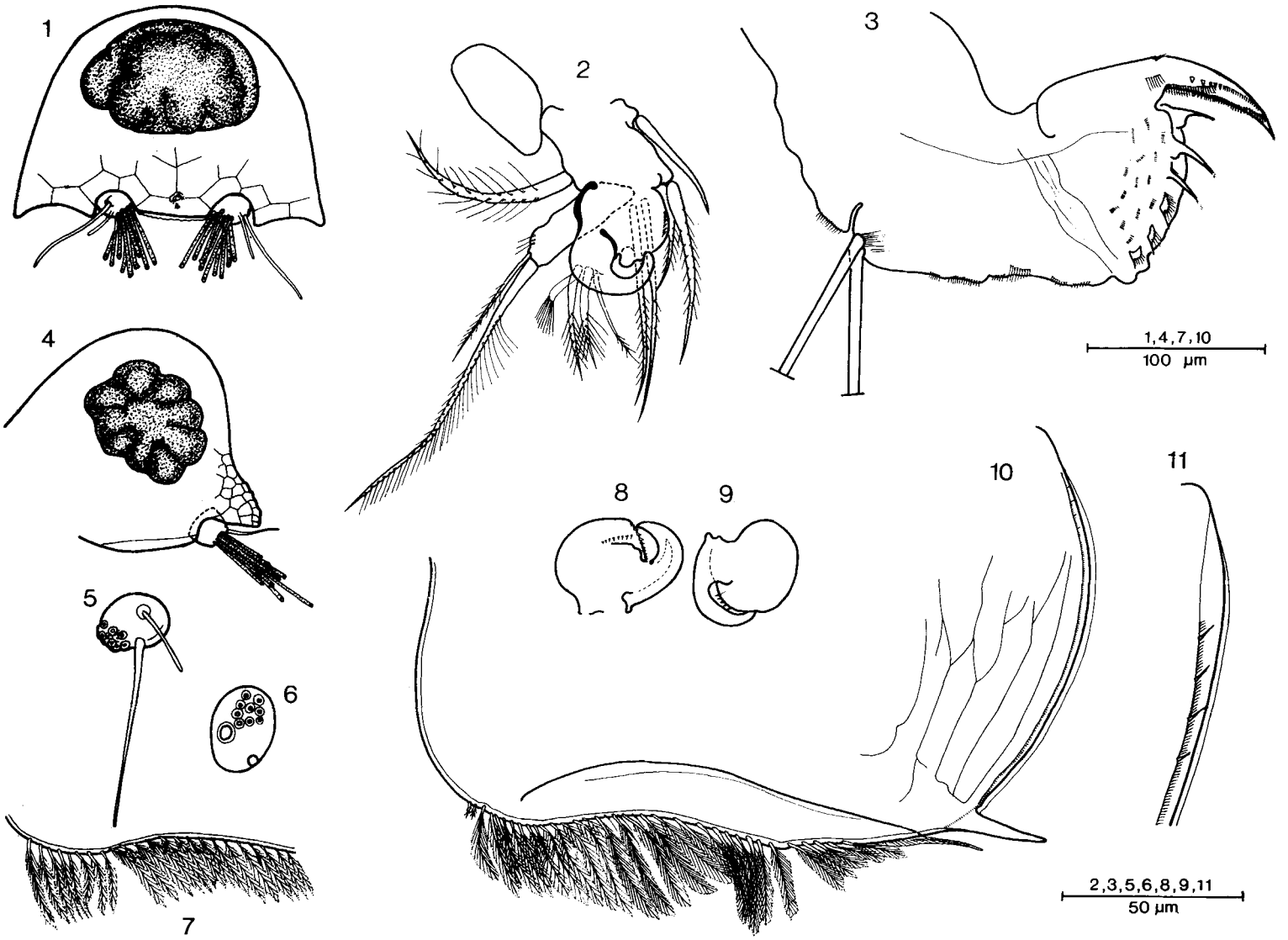

Fig. XIV. S. rammneri, male (Lake Donk, B.). 1, 4. Head. 1, frontal view; 4. lateral view; 2. P1; 3. Postabdomen; 5, 6. First antenna (5: insertion of n.p.-setae; 6 insertion of esthetes and n.p.- setae); 7. anterior zone of ventral rim of valves with internal (short) margin of fleece-hairs; 8–9. claw of P1; 10. ventral rim of valves, focused on external (long) side of fleece-hairs; 11. upper zone of distal valve rim.

Hudek (in press) discusses the improbable but true coincidence of two authors describing independently two rare Cladoceran species, not only in the same year, but in the course of the same month. While the date of G. O. Sars' paper cannot be traced beyond the month of August, his type material is better preserved than Von Daday's. Hence, Hudek proposes to conserve the name *echinulata* Sars, a suggestion which we are prepared to follow.

Type locality: tarn at Noraibek near Akmolinsk (presently Tselinograd), Kazakhstan (USSR).

Type material: lectotype designed by Hudek (in press); paralectotypes 5 parthenogenetic females, on slides F9544 and F9545 in Museum Oslo.

Material examined

Czechoslovakia: Jursky Sur near Bratislava, 12.VI.1976, ♀♀ (leg. I. Hudek).
Kazakh SSR: Sars' type material as indicated.

Dimensions: Female 0.8(?)–1.2 mm (literature data); male 0.5–0.6 mm (Manuilova 1964).

Female. Head large, rostrum triangularly produced with a slight evagination near its tip. Rostrum somewhat reminiscent of that of *S. rammneri,* but antennae in more terminal position (Fig. XV: 2). Central part of rostrum and sides of head covered with outgrowths of the polygonal valve reticulum, sometimes spine-shaped, usually leaf-shaped (Fig. XV: 7). No such outgrowths on eye area. First antenna fairly long with n.p.-seta in subterminal position (Fig. XVI: 5). Valves dorsally and laterally covered with spines or leaflets (Fig. XV: 1, 5, one of Sars' lectotypes). No spines on the very distal margin of the valves, although some may emerge beyond the valves (Fig. XV: 5; Fig. XVI: 3, 4). Sucker as in kingi-group. Distal valve margin with wide hyaline membrane in terminal position and internal finely denticulated membrane (Fig. XVI: 4; Plate 7: 1). Mucro fairly short but rather variable in length (1/4–1/7 of ventral valve length), sometimes with tip upturned (Fig. XV: 5). P1–P5 as for *kingi*-group (Fig. XVI: 2, 6). Postabdomen (Fig. XV: 3; Fig. XVI: 1) rounded, with 4–6 paranal spines, and a fairly limited number of dorsal and lateral rows of spinules. Endclaw with 6 pectens, and structured as in *kingi*-group (Fig. XVI: 1, 7).

Male. Not seen. Manuilova (1964) thinks that a dorsal hump on the valves is distinctive. However, on a photograph of a male collected in Hungary, supplied by W. Hollwedel, this hump, although visible (Plate 7: 7), is not different from that in other species of the genus. Males will thus probably need to be identified by their rostral structure, and by the spinulation of the valves. Although much shorter than in the females, these spines and leaflets should allow an accurate identification to species level.

Distribution

From the Pannonian plain, Poland, and Czechoslovakia eastward into Siberia, where it occurs in the valley of the River Dnjepr (Kiev area) and in the valley of the River Ob (Markovskii 1925; Manuilova 1964).

8. Scapholeberis spinifera (Nicolet 1849)

Daphnia spinifera Nicolet 1848: 290.
Scapholeberis spinifera var. brevispina Richard 1897: 281.
Scapholeberis erinaceus: Von Daday 1903.
Scapholeberis spinifera: Olivier 1962.
Type locality: San Carlos de Chile.
Types not indicated and lost.

Material examined

Argentina: – 5 parthenogenetic females (4 from Argentina, 1 from Brazil) in coll. D. G. Frey (Bloomington), originally in coll. C. Birge. Precise locality not known. – numerous ♀♀ and ♂♂, leg. J. Paggi from a pond near Salado River, Santo Tome (prov. Santa Fe), 5.X.1976; pond near Grande City (Prov. Santa Fe), 16.XII.1975; pool near Arroyo El Espin (Prov. Santa Fe), 9.I.1970.

Measurements: Female 0.6–1.3 mm; male 0.45 mm.

Female. Head large, rostrum trilobate with large, rounded middle lobe. First antennae well separated, projecting from below the side lobes (Fig. XVII: 1). Sides of head without invaginations. Front reticulated, with margins of reticulations raised into sclerotised leaflets (Plate 7: 6). Valves set with rows of long spines (not in the ephippial female). A row of particularly strong, pointed spines lines the distal rim of the valves (Fig. XVII: 6). Ventral sucker as in *mucronata*-group. Mucro fairly long (up to 1/3 of

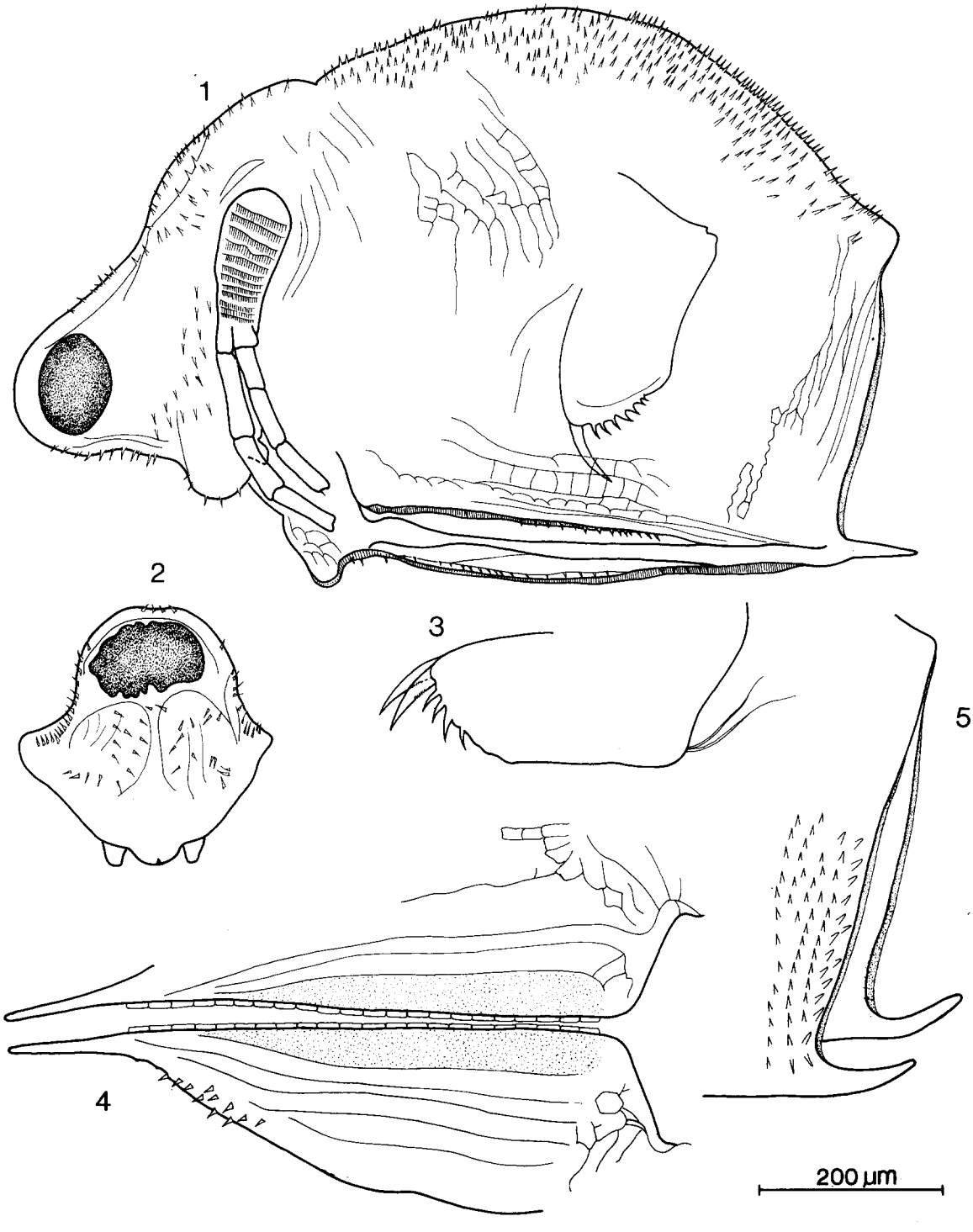

Fig. XV. S. echinulata female, one of Sars' lectotypes; 1. Habitus; 2. Head; rostral view; 3. Postabdomen; general view; 4. ventral view of valve margins; 5. Distal rim of valves.

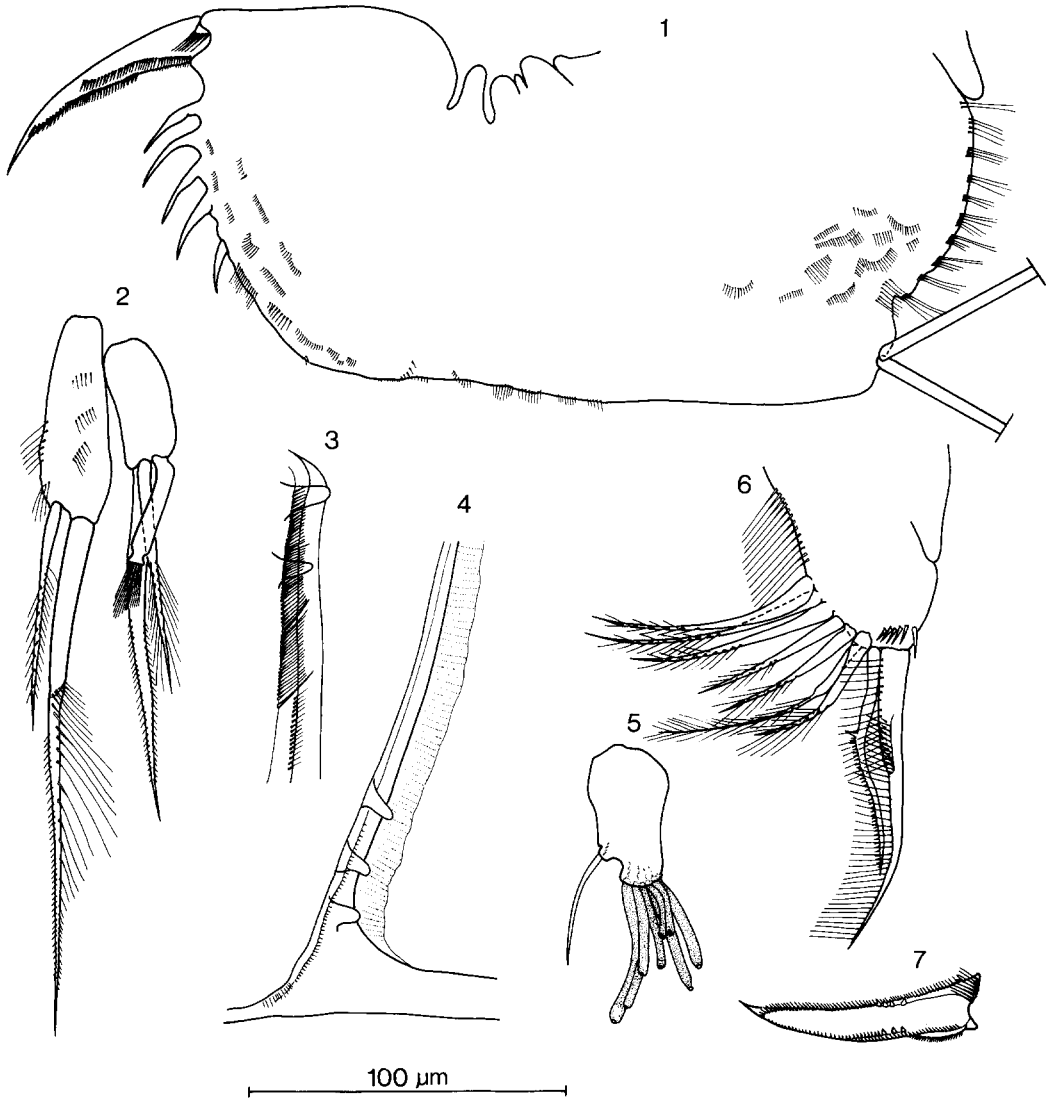

Fig. XVI. S. echinulata female (Bratislava area, Cz.); 1. Postabdomen; 2. Exopodite and endopodite of P1; 3. Upper zone of distal valve rim; 4. Lower zone of distal valve rim; 5. First antenna; 6. P2, gnathobase; 7. Endclaw of postabdomen.

valve length), pointed, slightly upturned. Denticulated membrane in submarginal position, composed of very fine spinules as high as the first hook (Plate 7: 2), thereafter more coarsely denticulated (Fig. XVII: 4, 5). Trunk limbs with the usual structure, but submarginal row of setae on gnathobase of P2 relatively further remote from margin than in *mucronata-kingi* groups. Postabdomen as in *kingi*-group. Endclaw with six pectens. Basal spines of internal pecten reach close to base of endclaw. Ventral internal pecten composed of 25–30 smallest spinules (Fig. XVII: 2).

Male. Rostrum very short, but with pronounced rounded middle lobe. First antenna short, 9 + 2. Short n.p.-seta well over half as long as long n.p.-seta. Valves reticulated, but spines short, sometimes almost completely reduced. Claw of P1 with wavy margins, a strong basal spine, and scattered spinules at its foot (Fig. XVII: 8–11). Postabdomen as in female, but endclaw slightly thickened (Fig. XVII: 6).

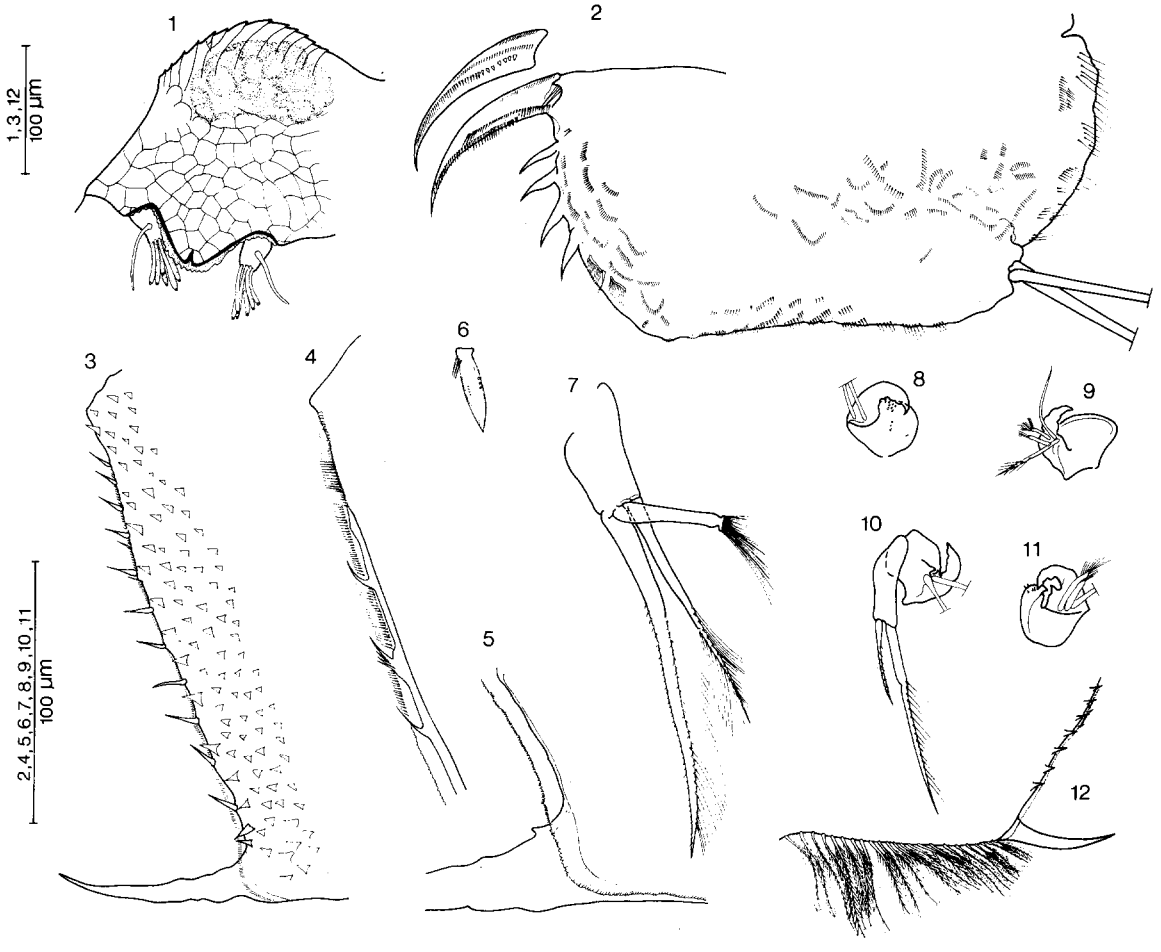

Fig. XVII. S. spinifera (Santo Tome, Chile). 1–5, 7. Female. 1. Head, rostral view; 2. Postabdomen; 3. posterior valve rim; 4. upper zone of (3), enlarged; 5. lower zone of (3), enlarged; 7. endopodite of P1. 6, 8–12. Male. 6. Claw of Postabdomen; 8–11. claw on P1; 12. ventro-posterior zone of valves.

Distribution

Restricted to Latin America: Chile, Argentina, and Brazil (Rio Grande do Sul).

9a. Scapholeberis armata armata (Herrick 1882)

Scapholeberis mucronata var. armata Herrick 1882: 243.

Scapholeberis armata Herrick & Turner 1895: 175.

Scapholeberis mucronata (partim): Birge 1918.

Because of confusion, not only with *S. mucronata* and *S. kingi,* but also with the subspecies to be described in the next section, it is impractical to detail the synonymy much further.

Type locality: Minnesota. Types not indicated, presumably lost.

Material examined

New Hampshire: mud pond near Hanover, 10.VII.1977, ♀♀.

Northern Florida: road drain at Venus, Highlands Co., no. 5147, ♀♀, ♂♂ (horned females) (leg. D. G. Frey), 24.III.1979.

lake Talquin, no 5235, ♀♀, ♂♂ and intermediates with subspecies *freyi*, 29.IV.1979.

Measurements: Female 0.4–1.3 mm; male 0.4–0.5 mm.

Female. Head prominent and very wide. Angle

between eye and rostrum rounded. Rostrum trilobate. Middle lobe produced, rounded, or, more often, angular (Plate 7: 8); side lobes wide, fading out on flattened (no deep concavities!) sides of head. No groove behind the first antennae, which are inserting in deep concavities flanking the middle lobe (Fig. XXI: 2). Valves shaped as in *mucronata,* and mucro about half as long as ventral valve rim, acuteley pointed. Posterior rim with denticulate membrane in marginal position (Fig. XVIII: 7); hyaline membrane reduced. Denticulations on membrane extremely fine on lower half of membrane, coarser at the level of the hooks (2–4). Trunk limbs and postabdomen not different from *kingi*-group (Fig. XVIII: 2, 4, 10). Frontal horn very rare, so far recorded only in a single population in a lake in Northern Florida (no. 5235) (Fig. XVIII: 3).

Male. Ventral rim of valves without triangular widening. A few short setae on anterior zone, a few longer ones on posterior end. A series of fleece-se-

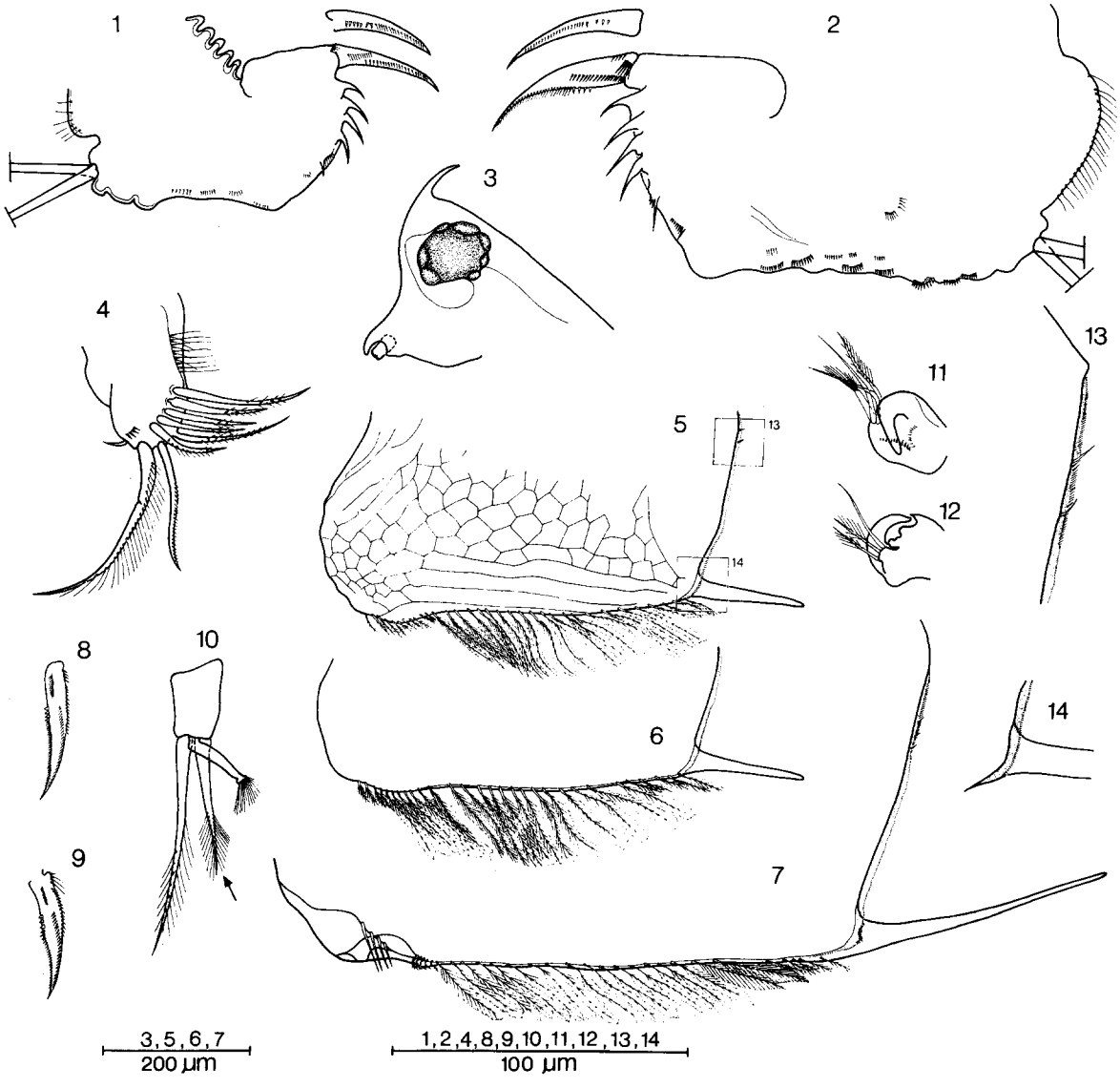

Fig. XVIII. S. a. armata, Florida. 1. Male, Postabdomen; 2. Female, postabdomen; 3, female, horned form, head, 4. female, gnathobase of P2; 5–6. male, valves; 7. female, valves; 8–9. female, end-claw; 10. female, endopodite of P1; 11–12. male, claw on P1; 13–14. upper and lower sectors of inner margin of posterior valve rim.

tae in between. First antenna with 2 n.p.-setae, neither of which is conspicuously long. Mucro about 1/3 of ventral valve length (Fig. XVIII: 5, 6). Claw on P1 sharply recurved (Fig. XVIII: 11, 12). Postabdomen as in female, endclaw not thickened.

Distribution

Eastern USA. To be expected in Quebec as well, and extending as far south as Florida. In the north of the latter state, it meets with ssp. *freyi,* and the population in sample no. 5235 contained forms that showed all lengths of the mucro intermediate between typical *armata* and *freyi.* In the population from sample 5117, however, no such intermediate forms occurred, while some of the females had frontal horns.

9b. Scapholeberis armata freyi n. ssp.

Scapholeberis mucronata var. intermedia: von Daday 1902: 274; Olivier 1962.

Scapholeberis mucronata von Daday 1905: 205 (specimens reexamined).

Scapholeberis kingi: Van de Velde *et al.* 1978.

Like in the preceding case, it is impossible to sort out the confusion which has occurred in many old and unillustrated records.

Type locality: Pond, Northern Florida. Sample 5025 (Alachua Co., jct. Hwy 346 and 325), 4.III. 1979.

Material examined

Northern Florida: pond (leg. D. G. Frey, no. 5025), type population, ♀♀, ♂♂.

California: roadside lake in Yosemite National Park, 13.VII.1978, ♀♀.

Mexico: ponds at San Jose near Tulancingo, 8.X.1974 (leg. I. Van de Velde & P. Grootaert), ♀♀.

Paraguay: von Daday's material, as indicated.

Holotype: a parthenogenetic female, preserved in a mixture of formalin-glycerol, deposited at the Zoological Institute, State University of Gent.

Paratypes: 10 parthenogenetic females, five of which are dissected and mounted in glycerol, while five are preserved undissected in a formalin-glycerol mixture, deposited at the State University of Gent.

Allotype: a dissected male, mounted in glycerol, preserved in the author's collection at the State University of Gent.

Derivatio nominis: the species is named after its collector, the well-known cladocerologist Prof. Dr. D. G. Frey (Bloomington, Indiana).

Measurements: Female 0.4–1.0 mm; male 0.4 mm.

Female. Eye and rostrum make a right angle in side view. Rostrum trilobate, middle lobe very wide, its sides angular (Fig. XX: 3).

Rostral pore rounded (Plate 5: 9–10). Shape of head, otherwise, as in *S. a. armata.* A pair of dorsal headpores present, or obliterated (Fig. XX: 1, 2). Trunk limbs and postabomen, including endclaw, as for *kingi*-group (Fig. XX: 5, 6). Sucker as for genus. Denticulated membrane on posterior valve in marginal position as in type subspecies, but hyaline membrane also well developed and in external marginal position. The origin of the hyaline membrane can often be traced to the external margin of the sucker-plate (Fig. XX: 9, 10). Mucro short, triangular, with sharp tip, about 1/6–1/9 of ventral valve length. An ontogenetic series is shown in fig. XIX. It is taken from the type population and occasionally shows horned forms among its prereproductive stages. Specimens become reproductive at about 0.8 mm. Further growth is mainly by dorsoventral expansion, except in ephippial females.

Male (Fig. XX: 5, 7–8). Not distinguishable from male of *S. a. armata,* except by its very short mucro (1/6–1/8 of length of ventral valve rim).

Distribution and possible variability

The type population is the only one known in which horned specimens occur. Remarkably, this was an allopatric population in a general area where *S. a. armata* also occurs, and the latter tended to have horned individuals in the same area and under allopatric conditions too. Florida appears to be a zone where both taxa meet and briefly overlap, and where, perhaps, some amount of hybridisation occurs. Whether the frontal horn is a factor in reproductive isolation is a question that seems not to have been raised but appears worth exploring. Apart from Herrick (1882), no speculations on the adaptive significance of the presence of

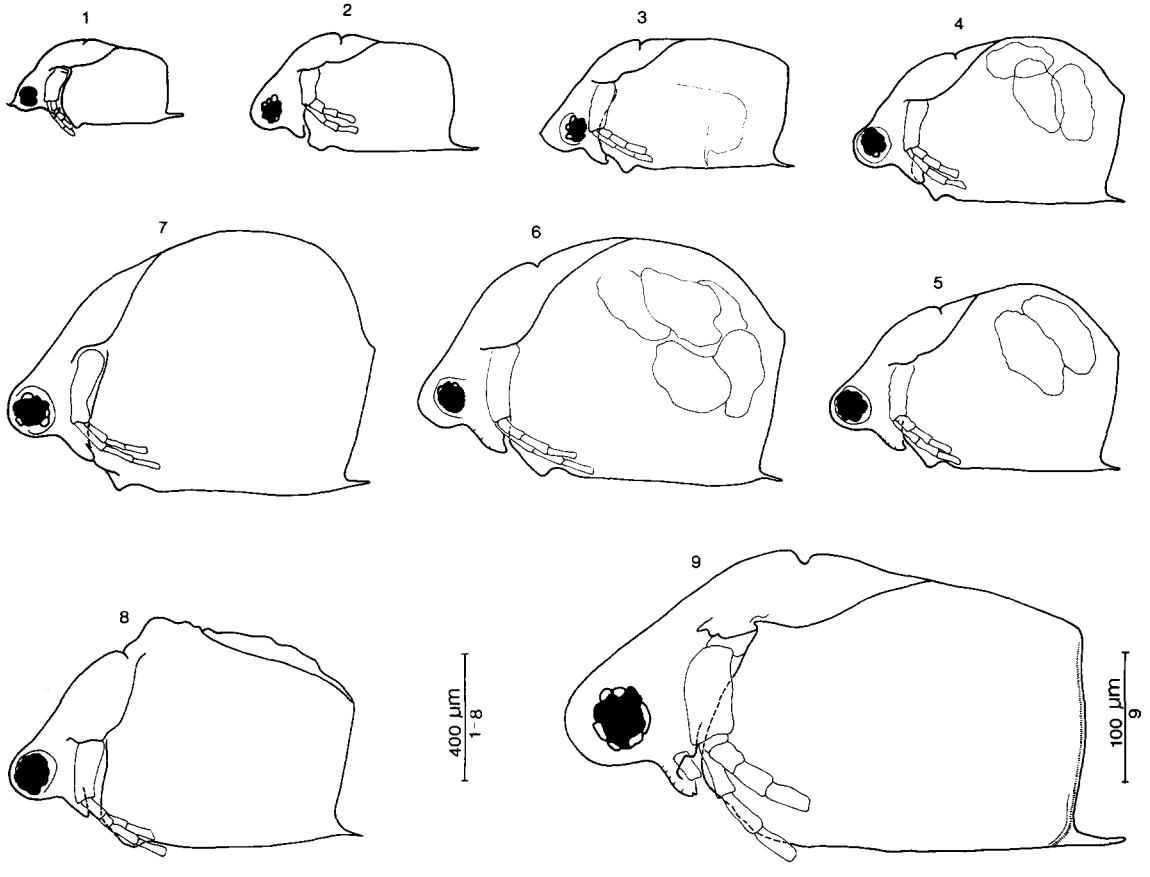

Fig. XIX. S. a. freyi, Florida. Postembryonal development in females (1–7); 8. Ephippial female; 9. Male.

a frontal horn seem to have been offered.

S. a. freyi was also found in samples from California, from Mexico, and from Paraguay. The mucro, especially in Central and South American specimens, tended to be longer and have a more robust base, while the origin of the hyaline membrane (always narrow!) could rarely be traced to the sucker plate, but the shape of the rostrum (as far as could be judged from mounted specimens) was constant. All this is consistent with a geographical subspecies that occupies the southern, and part of the western part of the species' range, but details of ranges remain to be worked out.

Differential diagnosis

S. a. freyi differs from *S. a. armata* by the length of its mucro (both sexes) and by the presence of a posterior hyaline membrane in the former. It differs from all other species by the shape of its rostrum, the absence of spines on the valves, and, in the male, by the shape of the deeply recurved claw on P1.

Discussion

1. Phylogeny of the Scapholeberinae

Primitive Scapholeberinae, as exemplified by the extant species of *Megafenestra*, may be derived from generalised Daphniid stock by a simple infolding of the ventral rim of the valves. The males are more conservative in structure than the females and thus, *Megafenestra* males are extremely close to *Ceriodaphnia* females in habitus and structure. The more specialised genus *Scapholeberis* may be thought of as having evolved through the development of a highly specialised and complex sucker-

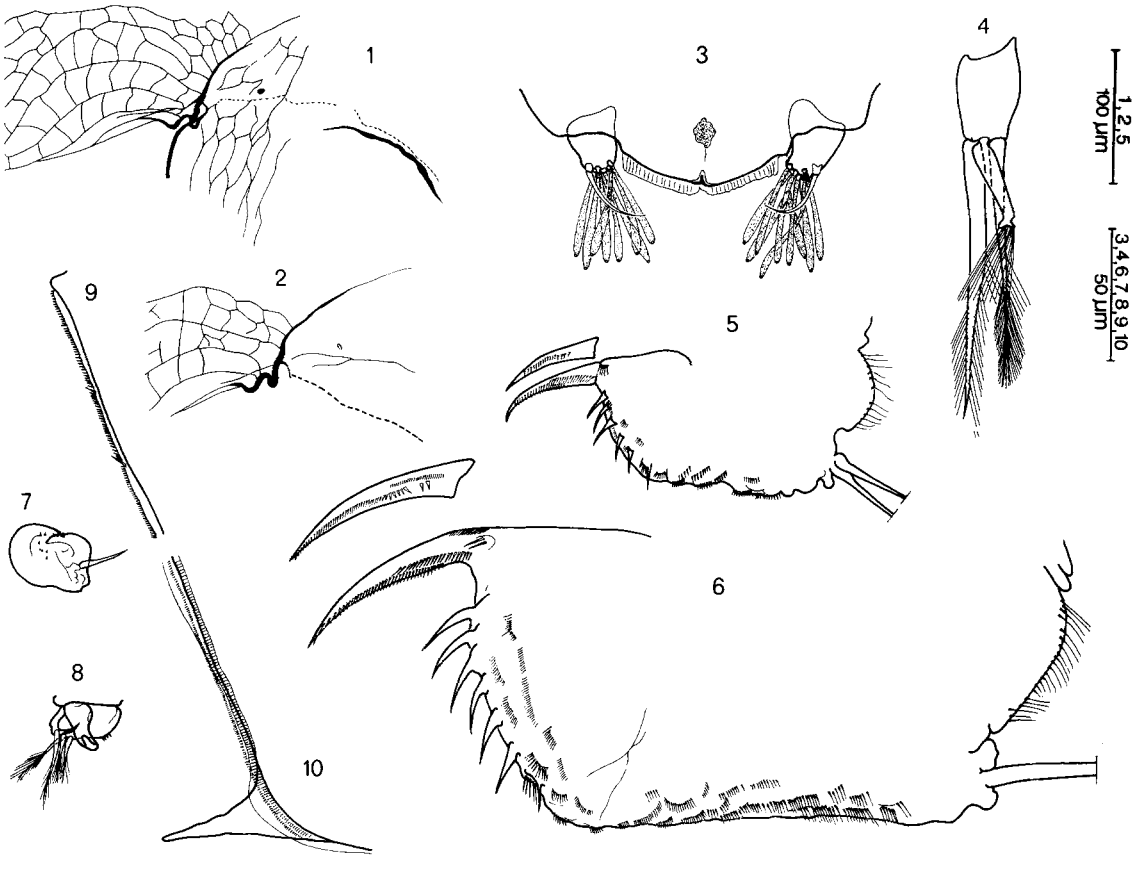

Fig. XX. S. a. freyi, Florida. 1–2. Headpores; 3. middle lobe of rostrum in female; 4. endopodite P1, female; 5. male, postabdomen; 6. female, postabdomen; 7–8. claw on P1, males; 9–10. upper and lower zones of posterior valve rim, females.

plate along the ventral rim of the valves. In males of most species, this structure can be derived from *Megafenestra* females by a transformation of the ciliated setae on the inner margin into long feathers. Females of *Scapholeberis* have again gone one step further: the anterior area of the sucker is modified into an ear-shaped plate, followed by a series of reinforced, coiled-up membranes. *S. mucronata* is the only species known in which the male has started developing a similar structure, and that makes it a likely candidate for the most apomorphic species of the entire group. In parallel to this, certain simplifications in the trunk limbs have occurred: the exopodite of the male has a second long seta, but is no longer modified in the male, the endopodite has a brush, the marginal hook on the gnathobase of P2 has disappeared, a seta from the endopodite of P2 has regressed, and the gnathobase of P5 has almost completely or completely been reduced. *S. mucronata* shares all these characters, while in addition it is one of the few species that has a truly diagnostic postabdomen in both sexes, and only a single n.p.-seta in the male. *S. microcephala* is another distinctive species with a diagnostic postabdomen, but is more primitive in other respects. The first antenna is long, with the n.p.-seta(e) in basal position (a Megafenestra-like character), and the gnathobase on P5 is not completely reduced (a small hump is still clearly visible). Because of the unique serration on the distal valve margin, and the structure of the male claw (P1), *S. microcephala* is probably an early side-branch in Scapholeberis, and not directly related to *S. mucronata.*

The bulk of the genus is made up by the *kingi*-group, all sharing a very similar postabdomen and endclaw, and differing mainly by the structure of the rostrum, almost certainly an expression of food and feeding specialisations. Two groups may be

distinguished: an old-world group in which the head is not widened, and a well developed hyaline lamella fringes the distal valve rim (one species has secondarily entered North America via Siberia), and a new-world group, in which the denticulated membrane has moved into a marginal position along the distal valve rim and the head is widened. It follows that the spinulated species are unrelated,

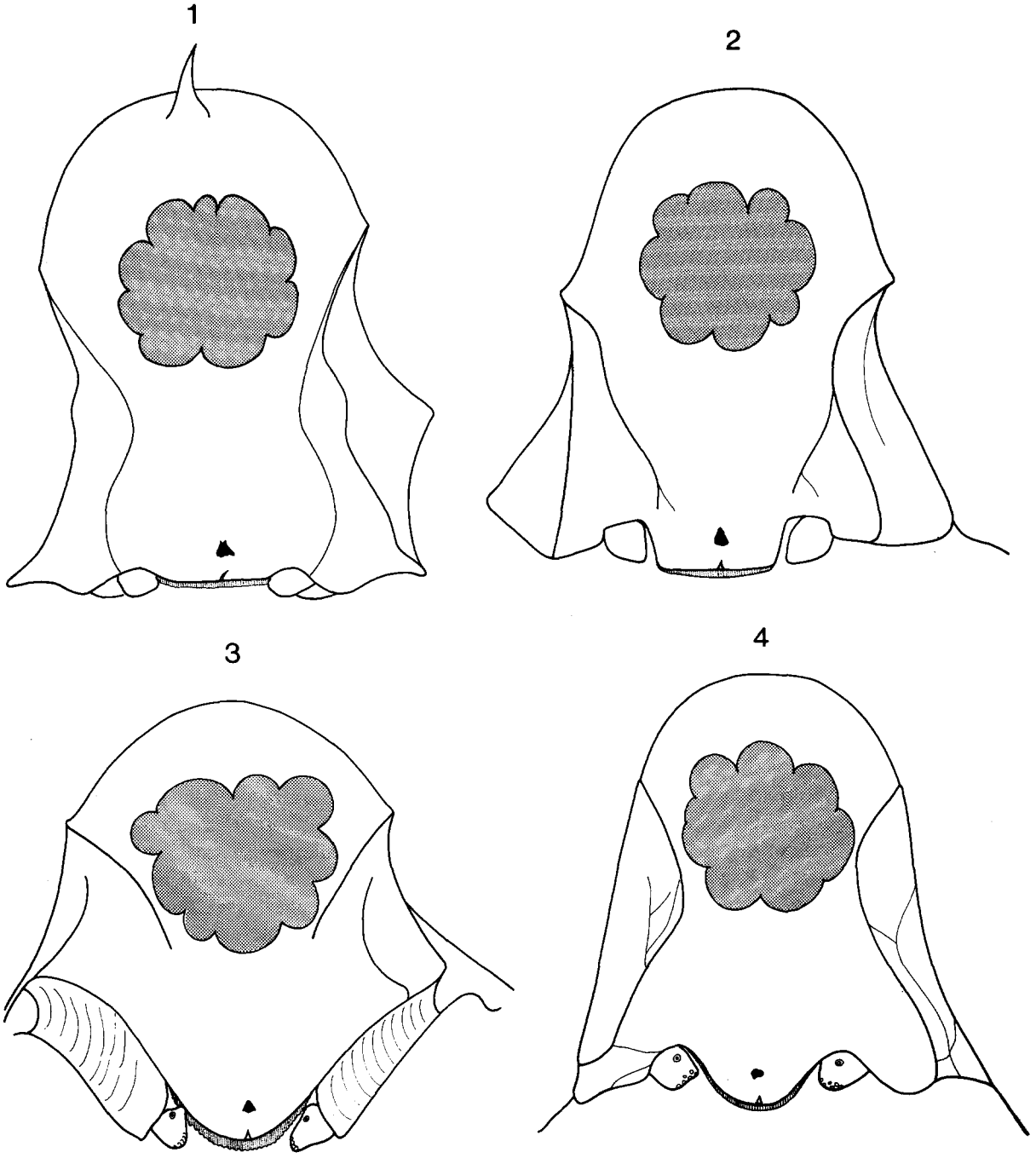

Fig. XXI. Diagrammatic representation (based on SEM-micrographs) of head-shapes in *Scapholeberis:* 1. *S. mucronata;* 2. *S. armata;* 3. *S. rammneri;* 4. *S. kingi.*

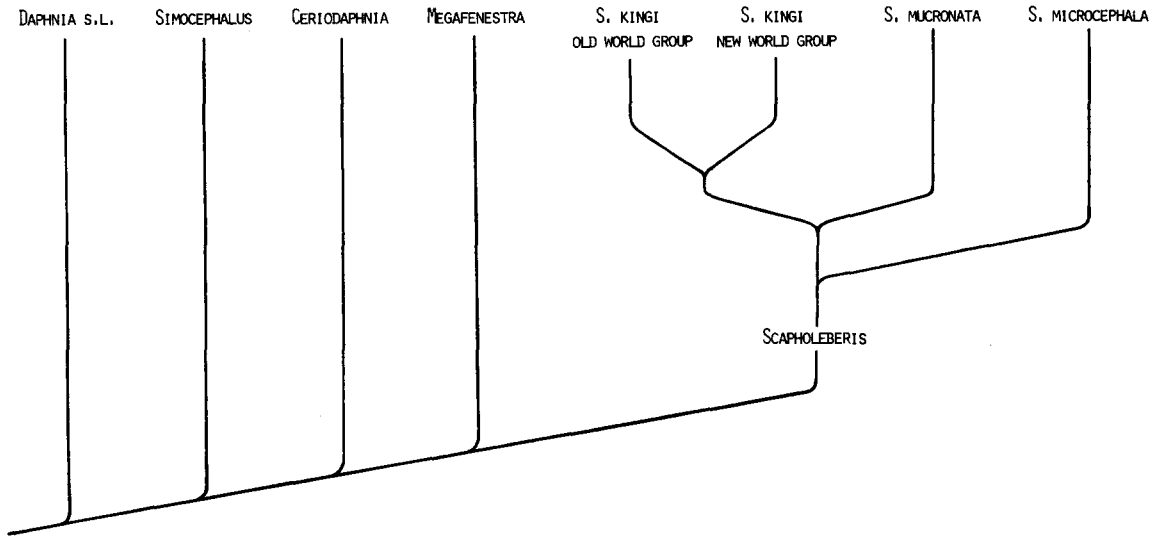

Fig. XXII. Phylogenetic tree of the Scapholeberinae and position within the Daphniidae.

and that spines on the carapace have evolved twice independently.

A phylogenetic tree for the Scapholeberinae is shown in *Fig. XXII.*

2. Chorology of the Scapholeberinae

Although the Scapholeberinae are distributed worldwide, their number of species and frequency of appearance is highest in temperate, continental and boreal climates of the northern hemisphere, where they occur as summer species in the weedy littoral of lakes, slow flowing rivers, ponds and pools.

None of the 10 species and subspecies presently recognized shows a very extensive range and their patterns of distribution are consistent, i.e. no major disjunctions occur. The case of *M. aurita* in South Africa may indeed easily be explained by fairly recent historical events.

S. mucronata and *S. kingi,* still often considered to be cosmopolitan, are definitely not. The former is restricted to Central Asia and Alaska, and extends to Central Europe. The latter is found from Australia, through South-East Asia and the Indian subcontinent, as far as the Middle East and Africa, including the Mediterranean basin.

The paucity or absence of endemics in the temperate and cold climates of the southern hemisphere is intriguing, but may be due to lack of careful research. It is not impossible that undescribed species await their discovery in the south of South America, and in New Zealand.

Key to the Scapholeberinae

Warning. It is strongly recommended to examine whole, undissected specimens, and make a drawing or a photograph of the rostrum before dissection and mounting. On mounted specimens, which are usually distorted, these important structures are usually not recognisable.

1. – Females: rostrum pointed. Exopodite of P1 with 1 long seta and a short hook. Endopodite with 3 ordinary setules. Margin of gnathobase of P2 with a hook. Gnathobase of P5 a ciliated hump. Dorsum of valves with a large oval plate. Ventral rim of valves infolded, inner rim lined with ciliated setae. Inner margin of distal rim with groups of spinules.

Males: exopodite of P1 with a long apical appendix, sticking out of the valves, and ending in an anchor-like structure. Other characters (except rostrum) as in females.

..... MEGAFENESTRA 2

– Females: rostrum never pointed. Exopodite of P1 with two setae. Endopodite with two ordinary and a brush-shaped seta. Margin of gnathobase of P2 smooth. Gnathobase of P5 reduced. No dorsal oval plate. Ventral rim of valves with an elaborate

set of feather- and sail-shaped membranes. Inner margin of distal rim with a finely denticulated membrane and 2-4 hooks (reinforced denticles) along the membrane.

Males: exopodite of P1 as in female. Rostrum short, eye large, ventral rim of valves with a set of long membranes, appearing as long ciliated setae in lateral view....SCAPHOLEBERIS 3

2. – Groups of spinules reaching well over half the length of posterior valve rim. Anterior 1/3 of ventral rim set with spaced setae, posterior 2/3 with closely apposed setae.

..... *M. aurita (Fischer)*

– Groups of spinules reach up to only about 1/3 of length of posterior valve margin. Over half the length of ventral margin set with spaced setules, and remainder with closely apposed setules.

..... *M. nasuta (Birge)*

3. – Front of rostrum rectilinear in both sexes. Pectens on endclaw composed of numerous spinules. Basal spinules not more robust than others.. 4

– Front of rostrum trilobate or triangularly produced. Dorsal internal and external pectens of endclaw with 2–5 more strongly built basal spinules.. 5

4. – Head small, first antenna protruding beyond margin of rostrum. Mucro very short (about 1/10 of ventral valve rim or shorter). Denticulated membrane on distal valve margin with 4 groups of more strongly built spinules evenly spaced along the rim. *Male:* claw of P1 with wavy edges, a single row of spinules at its base. Postabdomen without a dorsal pre-anal hump.

..... *S. microcephala G. O. Sars*

– Head large. First antenna small, not protruding beyond rostrum. Mucro long (1/3–1/2 of ventral valve rim). Denticulated membrane on distal valve rim coarsely denticulated at its base, thereafter finely denticulated and with 2–3 hooks in its dorsal third. *Male:* claw on P1 massive, with smooth edges. Postabdomen with preanal dorsal hump.

..... *S. mucronata (O. F. Müller)*

5. – A conspicuous hyaline membrane along the distal margin of the valves. Denticulated membrane in submarginal position. 6

– A denticulated membrane along the distal margin of the valves. Hyaline membrane absent or inconspicuous 8

6. – Valves and head reticulated and with spines and/or sclerotized leaflets, very long in females, short in males.

..... *S. echinulata G. O. Sars*

– Valves and head reticulated but smooth 7

7. – Female: rostrum triangularly produced in front. A depression between the eyes and the sides of the rostrum. A second groove along the head behind the implant of the first antennae.

Male: endclaw of postabdomen fairly thick. No strong spines at foot of claw of P1. First antenna: longest unperforated seta over twice the length of shorter one ..... *S. rammneri n.sp.*

– Female: rostrum trilobate, middle lobe rounded. No deep grooves along the head.

Male: endclaw of postabdomen slender. Two strong spines at foot of claw of P1. Long unperforated seta of A1 less than twice as long as short one ..... *S. kingi G. O. Sars*

8. – Valves and head with numerous rows of spines, particularly in the female. Rostrum trilobate with narrow, rounded middle lobe.

Male: claw of P1 with wavy margins....*S. spinifera (Nicolet)*

– Valves reticulated but smooth. Rostrum trilobate with wide and angular middle lobe.

Male: claw on P1 with smooth edges..... 9

9. – Female: mucro 1/3–1/2 of length of ventral valve rim. Denticulated membrane in marginal position, wide.

Male: mucro 1/3–1/6 of valve rim.

..... *S. armata armata (Herrick)*

– Female: mucro 1/6–1/9 of valve rim. Denticulated membrane *and* hyaline membrane – if present – in marginal position.

Males: mucro 1/6–1/8 of valve rim...*S. armata freyi n. ssp.* *Note.* Intermediate forms may occur where the ranges of both subspecies meet.

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