

THE NORTH AMERICAN *CHYDORUS FAVIFORMIS*
(CLADOCERA, CHYDORIDAE) AND THE
HONEYCOMBED TAXA OF OTHER CONTINENTS

By D. G. FREY

Department of Biology, Indiana University, Bloomington, Indiana 47405, U.S.A.

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The taxon *Chydorus faviformis*, described by Birge from North America in 1893, has been considered to occur also in Asia, Australia, and South America. However, careful study of populations from these regions has revealed that all represent different species, none of which is closely related to *C. faviformis*. The taxa described here are *C. obscurirostris* and *C. opacus* from Australia, *C. obscurirostris tasekberae* from Malaysia, *C. sinensis* from China, *C. angustirostris* from India, and *C. parvireticulatus* from South America. The taxon in Malaysia differs somewhat from the corresponding taxon in Australia, but cannot be characterized more closely until males and ehippial females become available.

The taxa differ among themselves in number of meshes on the shell of parthenogenetic females, surface patterning within the meshes, shape of the rostrum and height of the mesh walls along the edge and near the tip of the rostrum, stoutness and length of the major seta on the inner distal lobe of trunklimb I, shape of the labral plate, and shape and armament of the postabdomen. Ehippial females all have a single resting egg. They differ in the extent of secondary thickenings of the surface network

within the shell meshes and in the amount of pigment deposited in the region of the egg locule. Males are most important for separating the taxa, indicating how necessary they are for working out evolutionary similarities and differences. Unfortunately no males of the taxa from Malaysia, India, and South America have been available. For the others, *C. faviformis* sens. str. is unique in that it is the only taxon in which the male loses its honeycomb (that is, the raised walls of the meshes) on reaching maturity. It also has a sharp pre-anal angle and a marked narrowing of the postabdomen distad from here, which is the pattern typical of species in the *Chydorus sphaericus* complex. None of the other *faviformis*-like species share this characteristic.

Because of the marked differences in morphology and in geographical distribution of the species in North America and in South America, it is certain that even during the glacial ages, when the northern *C. faviformis* would have been displaced farthest southward, there was no exchange of either taxon to the other continent. The taxon from Manáos, Brazil listed as *C. faviformis* in the Birge collection is the *C. parvireticulatus* reported from much farther south in Brazil and Argentina. In Australia and Asia, except for the uncertain distinctness of the taxon in Malaysia, all the other taxa are markedly separate from each other and hence give no evidence for transfer, as by resting eggs, between continents or even from one region to another on the same continent. All the taxa have been stable in their geographical occurrence for very long periods of time.

In addition to the *faviformis*-like taxa present as distinct species in different regions or on different continents, there are many other species groups of chydorids that have different member species on each continent. One possible explanation of this similarity in gross morphology without any long-distance dispersal of resting eggs to accomplish it is that the various protospecies (corresponding to the species groups) had largely evolved before the original land mass broke up into the present continents and subcontinents. As the distances between the continents increased, the salt-water gaps would come to be impassable barriers to dispersal. Evolution of the isolates would then yield new species, all retaining many of the features of the protospecies. Each such group from a single protospecies would form the species groups we are now just beginning to recognize.

1. INTRODUCTION

In his very brief description of *Chydorus faviformis*, Birge (1893) was so struck by the presumed uniqueness of the deep polygonal cells covering the animal that he gave few additional details. He noted a general resemblance to *Chydorus sphaericus* in body form and in the morphology of the appendages and of the postabdomen. The latter he described merely as 'broad, the end rounded, and the anal projection large. There are 9-10 post-anal teeth.' He noted 'nothing peculiar' about the appendages. His two drawings accompanying the description are of the whole animal showing the honeycombs, and of the postabdomen and claw. Details of the postabdomen and claw are not entirely accurate, besides which Birge erroneously shows the anus as opening in the pre-anal portion. This is obviously the reason he considered all the marginal denticles as post-anal, even though roughly half of them are located along the anal groove.

Birge's two figures are the only ones of the North American taxon in the literature, except for small drawings of a whole animal by Bigelow (1922) and of a shell by Deevey (1942). Birge's illustration of the whole animal was used without change in the two additions of *Fresh-water Biology* (Birge 1918; Brooks 1959). Smirnov (1971, 1974) partly redrew this figure, and in addition he included Birge's drawing of the postabdomen, complete with its incorrect location

of the anus. Hann (1975) has good drawings of the trunk-limbs, which unfortunately are not yet published.

So few details are available about this species, aside from its honeycomb pattern, that it would be impossible to judge from the literature alone the likelihood that the honeycombed taxa occurring elsewhere are conspecific with the North American taxon. Taxa resembling *faviformis*, and which are called *faviformis* in the literature, are known from China (Yeh 1956; Chiang & Du 1979), Malaysia (Idris 1979, 1983; Idris & Fernando 1981), Kashmir and Jabalpur in India (Khan *et al.* 1978; C. H. Fernando, personal communication), Australia (not yet in the literature), and Argentina (de Ferrato 1966). The published illustrations of the taxa from China, Malaysia, and Argentina raised doubts for me that these are conspecific with that from North America.

If we take umbrage at the concept of cosmopolitanism, then questions about the identity of these taxa largely disappear: all could well be *faviformis*. But enough instances of claimed cosmopolitanism have been overturned by detailed studies (see Frey (1987) for a partial review of the evidence) that a better strategy in studies of evolution and geographical distribution is not to accept any taxon as being cosmopolitan until it has been demonstrated to be so by appropriate studies. Morphological studies may not provide the ultimate answer, but they constitute a reasonable first step for resolving taxonomic and evolutionary relationships.

Almost none of the species of Cladocera in the world have been described and illustrated sufficiently well that the literature alone can be used for deciding questions of conspecificity. *Chydorus faviformis* is a prime example. Hence, the first task of this study is to describe the North American taxon in detail, then to present correspondingly intensive descriptions of the taxa from elsewhere.

Through the generous cooperation of a number of colleagues elsewhere, I have obtained field samples containing the particular taxa of their countries, which fortunately in three instances contain males and ephippial females. Detailed study of these series has shown that all the taxa are different from one another, and they are here described as new species. The possible exception is the taxon from Malaysia, which, because no gamogenetic specimens are present, cannot be separated unequivocally from the closely related taxon in Australia. Accordingly, it is designated as a geographical subspecies, at least until males and ephippial females can be studied. In general these gamogenetic stages are more highly differentiated than are parthenogenetic females in morphology and ontogenetic development, and are essential to have for any separation of closely related species.

A summary of the populations used in this study is given in table 1. For each sample, except three of these for *C. faviformis*, all specimens of the pertinent taxon were removed during careful examination of the sample and then were equilibrated with glycerol. Each population was sorted into parthenogenetic females, ephippial females, and the three instars of males. All three male instars can be identified positively by ontogenetic changes in morphology (see Michael & Frey 1984). Frequencies of stages and instars within the populations of *C. faviformis*, except that from Catamount Lake, New York, are not representative of their producing populations, because gamogenetic individuals were removed selectively. This was done during the uncertain period of trying to find mature males of the species (Frey 1982*b*). The size frequency distributions of the several reproductive stages and of the three male instars in each population are given in figure 285. These show the considerable range in size between the large *C. faviformis* from North America and the much smaller *C. opacus* from Australia, and the fact, as already

TABLE 1. LIST OF HONEYCOMBED TAXA IN THE GENUS *CHYDORUS* AND THE NUMBER OF INDIVIDUALS IN EACH SEX AND INSTAR CATEGORY IN THE POPULATIONS USED IN THIS PAPER

species	occurrence	partheno- genetic		ephippial		males			total
		no eggs	eggs	no eggs	eggs	I	II	III	
(1) <i>C. faviformis</i> Birge, 1893	glaciated eastern North America								
Olin Lake, Indiana		12	3	24	65	9	29	15	157
Martin-Oliver Channel, Indiana		3	—	—	—	2	15	—	20
Catamont Lake, New York		178	26	—	—	—	—	—	204
Pinehurst Lake, Ontario		85	67	—	62	18	29	52	313
(2) <i>C. obscurirostris</i> n.sp.	Northern Australia	90	1	—	—	—	—	1	92†
(3) <i>C. o. tasekberae</i> n.subsp.	Malaysia	59	5	—	—	—	—	—	64
(4) <i>C. opacus</i> n.sp.‡	Northern Australia	223	115	5	5	—	1	1	350
(5) <i>C. sinensis</i> n.sp.	China	25	5	1	—	2	1	6	40
(6) <i>C. angustirostris</i> n.sp.	India	82	18	—	—	—	—	—	100
(7) <i>C. parvireticulatus</i> n.sp.	Brazil or Argentina	15	4	—	—	—	—	—	19

† Includes the 40 specimens on Deevey's slides, only eight of which yielded reasonable measurements. The rest, including the male, were too distorted.

‡ This is sample N-73 of Timms. Other samples, listed in the species write-up, were not studied in any detail because of the overwhelming dominance of Timms' sample.

noted many times (see, for example, Frey 1980), that chydorids tend to have just two immature instars in parthenogenetic females. Details of the morphology and ontogenetic changes are considered individually for each taxon.

2. TAXONOMIC DESCRIPTIONS

(a) *Chydorus faviformis* Birge, 1893

Synonymy

Chydorus faviformis Birge (1893): pp. 307–308, plate 13, figures 7, 8; Birge (1918): p. 751, figure 1148; Bigelow (1922): p. 121, figure 22; Deevey (1942): p. 252, plate 1, figure 19; Brooks (1959): p. 649, figure 27.106; Smirnov (1971): p. 313, figure 350; Hann (1975): pp. 182–183, 185, figure 49.

Type locality

Lake Kawaguesaga, Oneida County, Wisconsin. Birge (1893) listed several localities in extreme northern Wisconsin and neighbouring Michigan from which he had collected the taxon in August 1892, although he did not specify any one of these as the type locality. However, he noted that the most important collection in terms of species abundance and diversity came from Lake Kawaguesaga at Minocqua. Here he found cast shells first and later living specimens in abundance. Other positive localities were Lake Julia in Oneida County and Twin Lake in Forest County, Wisconsin, and Gogebic Lake in Gogebic County in nearby Michigan. Two slides in the Birge Collection at Bloomington, each with a parthenogenetic female that had been mounted in glycerine jelly, are labelled merely '*Ch. faviformis*. Minocqua. Aug. 1892'. These specimens undoubtedly are from Kawaguesaga.

Type and other specimens

Lectotype. Birge's slide C-58-8, not remounted. Although much of the glycerine jelly has leaked out, the specimen remains in a big enough globule to permit reasonable study of its morphology. The specimen is undistorted and is carrying two early embryos. Maximum length is 0.43 mm, and the length without the mesh walls is 0.41 mm. The slide has been deposited in the U.S. National Museum of Natural History, catalogue number 227014.

Paralectotypes. The parthenogenetic female on Birge's other slide (C-58-18) likewise is relatively undistorted and shows many details of morphology. It measures 0.39 by 0.43 mm. It has been remounted in glycerine jelly and is in the Frey collection in Bloomington.

In addition a tube was found in the Birge Collection labelled 'Ch. faviformis. 1893', which contained 52 specimens of *C. faviformis* in glycerol. All are excessively cleared and show few details even under phase optics. However, they reveal the irregular pattern of reticulation characteristic of this species, with larger meshes in the posterior-dorsal part of the shell. The date 1893 is the date of the published paper, not the year of collection. Considering the circumstances, these specimens must also be treated as paralectotypes, even though they promise little help in resolving any details of morphology. They are in the Frey collection in Bloomington.

Other specimens. Suites of specimens from Pinehurst Lake, Ontario, collected in October 1975 by R. P. Lim, have been placed in several museums, as listed below. The materials deposited consist of: (i) a slide of two parthenogenetic females in glycerine jelly; (ii) a slide of two parthenogenetic females in polyvinyl lactophenol; (iii) a slide of two ehippial females in glycerine jelly; (iv) a slide of two mature males in glycerine jelly; (v) a slide of two instar-II males in glycerine jelly; and (vi) 10 parthenogenetic females in a solution of glycerol and 5% formaldehyde in a 1:1 mixture. The remaining specimens picked out from the Lim samples plus specimens from other samples are in the Frey collection in Bloomington.

museum	catalogue, accession, or registration numbers					
	i	ii	iii	iv	v	vi
Australian Museum	P 35702	P 35703	P 35704	P 35705	P 35706	P 35707
U.S. Natural His- tory Museum	227015	227016	227017	227018	227019	227020
British Museum (Natural History)	1985.177-178	1985.179-180	1985.181-182	1985.183-184	1985.185-186	1985.187-196

General comments

Of the many samples in our collection containing *faviformis* (see distribution records), the two of greatest usefulness were F2549 from Catamount Pond, St Lawrence County, New York, collected 16 August 1969, and F2874 from Olin Lake, Lagrange County, Indiana, collected 11 November 1974. The Catamount Pond population was exclusively parthenogenetic, the Olin Lake population almost as exclusively gamogenetic, although enigmatically it yielded no mature males. A series of samples, from Pinehurst Lake, Ontario, collected in October 1975, yielded a large population with abundant parthenogenetic and gamogenetic individuals. However, this population likewise yielded no males, until quite accidentally a specimen was found that had not moulted completely. It showed in spectacular manner that the *faviformis*

male loses its honeycomb on moulting to maturity (Frey 1982*b*). Non-honeycombed males of *faviiformis* were then recovered in some abundance both from the Pinehurst and Olin samples and from numerous samples collected subsequently. This is the only instance known among all the honeycombed taxa worldwide where the mature male lacks the honeycomb configuration.

Short diagnosis

Covered everywhere, except along narrow edge of rostrum, with deep chitinous meshes, like a honeycomb, that are not organized into any ridges, collars, or spines. Mature male lacks the raised walls of the meshes but retains same pattern of reticulation over most of shell and parts of head. Interior of meshes with elongate lines, sometimes ridge-like, arranged in a variable spiderweb pattern. In ehippial females, meshes in posterior half of shell reduced in height; meshes irregular in outline, often with interior spiderweb ridges enlarged and prominent; anterior part of shell separates from ehippium along predetermined slough line but remains attached ventrally. Antennal formula 0-0-3(1)/0-1-3 in female, 0-0-3(1)/1-1-3(1) in all male instars. Postabdomen of female with subparallel dorsal and ventral margins; long anal groove and short postanal portion, with seven to ten straight, single denticles distributed between these two regions. Postabdomen of mature male strongly narrowed distad from the prominent pre-anal angle; distal end somewhat expanded and bulbous, provided with variable number (generally about four) of very long, slender setae. Postabdomen of instar-II male like that of female, except for strong tendency for denticles to be double.

Parthenogenetic female

Shape and shell. Covered everywhere with deep honeycomb meshes (figures 52–55, 59, plate 4), formed by chitinous extensions of the shell; meshes varying in size and depth but not organized into any ridges, collars, or spines as they are in *C. bicornutus* and *C. bicollaris* (Frey 1982*c*); meshes largest in posterior half of shell; interior of meshes, especially of largest ones, with a spiderweb nexus of long lines, which sometimes extend ridge-like from surface of shell (figure 62). Without the honeycombs, the body shape is similar to that of species in the *Chydorus sphaericus* complex (figures 1 and 2, plate 1). Body very broad, globose, flattened dorsally (figures 55–59). Posterior-dorsal angle of shell (neglecting the honeycomb meshes) rather sharp, sometimes projecting slightly; posterior-ventral angle distinct, rather narrowly rounded (figures 1, 2). Continuous setation along ventral margin of shell (figure 21): anteriorly are about six to nine very long, slender, non-plumose setae, followed by about ten extremely short and delicate setae in region of ventral bulge that are often difficult to see clearly with phase optics; behind the bulge is the typical posterior duplicature of *Chydorus*, of about 30–35 plumose setae, extending about half way around posterior-ventral angle; in continuation with them a submarginal row of extremely fine spinules, extending along posterior margin about half way to posterior-dorsal angle (figure 4); similar delicate spinules occur between bases of posteriormost three or four setae in the duplicature; bases of duplicature setae completely separated from one another, not connected by a line.

Head. Thin marginal border of rostrum transversely striated, completely free of honeycomb meshes and not overhung by such meshes (figures 6, 7); walls of meshes bordering this strip very low (figures 52, 59, plate 5). Meshes distinctly smaller at minor headpores (figure 6) and also with distinctly lower walls (figure 53); major pores located at intersection of three or four

meshes (figure 6), the walls of which dip down almost to head surface at the pores; generally two, sometimes three, very small meshes over compound eye. Rostrum slightly concave on sides of triangular portion beyond expanded fornices (figures 6, 59), evenly tapered to a point that usually has a fine, chitinized emargination (figure 7). P.p. distance always considerably less than i.p. distance.

Antennule (figures 5, 7). Fusiform, somewhat tapered distally; length about twice basal width. Antennular seta arising about midway or slightly less, slender, barely reaching tip of antennule. Nine slender aesthetascs, all terminal, one or two of which are less than half as long as longest; none reach tip of rostrum.

Antenna (figure 3). Formula 0-0-3(1)/0-1-3. One terminal seta on endopodite much shorter than other six swimming setae, which are subequal in length. Terminal spine on exopodite very small; corresponding spine on endopodite not visible.

Labrum (figures 11-16). Anterior margin evenly and shallowly convex, generally slightly concave near ventral tip, which is rather narrowly rounded; margin behind tip usually somewhat concave; angle behind tip usually slightly less than 90°. In mature specimens, tip of labrum extends to or somewhat beyond tip of rostrum (figure 2).

Trunklimb I (figures 8, 9). Two setae on o.d.l., three on i.d.l.; largest i.d.l. seta strongly chitinized, hook-like, provided with conspicuous setules along middle part of distal half. On corm, three setae of ventral group and adjacent seta of middle group short, stout, and subequal in length; middle seta of middle group the longest, followed by dorsal seta of that group; accessory seta of all three groups well developed, conspicuous, that of ventral group being about as long as and as well developed as the setae of that group.

Trunklimb II (figure 10). Scraping spine 3, counting from gnathobase, shortest; spine 4 much longer and stouter than first three and has the stoutest and most conspicuous denticles of all eight spines; scraping spines 7 and 8 show no denticles with 40 × phase objective. Gnathobase with three setae at tip and eight in filtering comb.

Trunklimbs III-V. Examined but not drawn. Counts of 'soft' setae on a number of dissected specimens were seven, seven and four on limbs III, IV and V, respectively; counts of setae in gnathobasic filtering comb were eight, six and four, respectively.

Postabdomen (figures 17, 18). Dorsal and ventral margins subparallel; pre-anal angle large, sharply protruding; postanal angle subdued but still distinct as a break in contour; anal groove longer than pre-anal portion; postabdomen tapers abruptly beyond postanal angle. Dorsal margin provided with seven to ten single, slender marginal denticles, three to four deployed along postanal portion, four to six along distal half of anal groove; proximal half of anal groove bordered at some distance from margin by two rows of very fine setules in series. Lateral surface with a submarginal row of seven to eight crescents of very fine spinules, and a variable development of a second such row farther from margin (figure 18). Pre-anal angle well armed with two or three short rows of stouter and longer setules. Abdominal setae long, almost as long as postabdomen (figures 2, 18).

Postabdominal claw (figures 19, 20). Rather stout toward base; convex margin evenly curved; concave margin somewhat angled near basal spine. Entire concave surface with setules, those of distal two-thirds distinctly longer and stouter than those of proximal third. Subapical seta usually distinct; sometimes with one or even two additional setae near tip. Two basal spines, of which the larger about as long as basal width of claw; shorter spine delicate, only about a third as long.

Size. (Body length in millimetres; figures in parentheses are total length, including the honeycombs.) Catamount Lake: instar I, 0.22–0.26 mm (0.23–0.29) ($n = 73$); instar II, 0.27–0.29 mm (0.29–0.31) ($n = 50$); parthenogenetic females 0.29–0.37 mm (0.31–0.39) ($n = 91$). Pinehurst Lake: instar I, 0.24–0.28 mm ($n = 23$); instar II, 0.29–0.34 mm ($n = 52$); parthenogenetic females, 0.34–0.42 mm ($n = 77$); ephippial females, 0.35–0.40 mm ($n = 62$). Olin Lake: ephippial females, 0.36–0.44 mm ($n = 153$). Birge (1893) gives the length as 0.5–0.6 mm, which is much too large.

Ephippial female

Body somewhat narrowed from side to side (figures 60, 61) and expanded dorsally (figures 56, 57) compared with parthenogenetic female, as generally true of subfamily Chydorinae. Headshield elongated and tapered posteriorly (figure 24, plate 2) to accommodate this change in body geometry. As a result p.p. distance is greater than i.p. distance. Mesh walls of posterior portion of shell lower and much more irregular (figures 56–58): lines of interior spiderweb pattern usually expanded outward conspicuously and irregularly as elevated ridges. Anterior part of shell that separates from ephippium at moulting delimited by a line that angles ventrally and cuts across honeycomb meshes (figures 22, 56, 57); on moulting, this part separates dorsally from ephippium and bends outward, but usually remains attached ventrally (figure 23) in manner illustrated for two other species of *Chydorus* (Fryer & Frey 1981). Ephippium at times has almost no pigmentation, but more commonly has brownish suffusion in part that will cover resting egg. Dorsal margin of shell with conspicuous chitinous thickening (figures 22, 23), characteristic of ephippial females in general. Except for modifications of headshield and shell associated with production of ephippium, ephippial female identical in structure to parthenogenetic female.

Males

C. faviformis has two immature instars and one mature instar, as do other chydorids. Instars I and II are readily distinguishable under low magnification from their female counterparts by the considerably larger antennules (figures 25, 26) and by the structure of the rostrum, which is broadly and convexly tapered to a stubby point (figures 28, 29, 50, plate 3) that at times is weakly emarginate as in the female. In addition, at higher magnification the developmental stages of the copulatory hook can be seen: short and peg-like in instar I (figures 25, 44), much longer and J-shaped in instar II (figures 26, 45). Furthermore, the genital pores are visible on the postabdomen. In instar III the functional copulatory hooks (figures 27, 46–48) are large, U-shaped, and broadly open to accommodate the elaborate edge of the shell of the female, and the postabdomen is highly modified (figures 42, 43). Most striking, however, is the great reduction in height of the mesh edges (figures 63, 64); usually the raised walls are completely lost, although the characteristic pattern of reticulation is still readily apparent from the lines on the shell. This loss of the raised honeycomb in mature males of North American *faviformis* is apparently unique among all honeycombed species of *Chydorus*. The dorsal margin of the shell of males less strongly arched (figure 27) than in females (figure 2), because the brood pouch is non-functional, and as a result the p.p. distance is much shorter than the i.p. distance (figures 30–31) compared with females (figure 6). In all three instars the antennal formula is 0-0-3(1)/1-1-3(1), the males having a short seta arising from the basal segment of the endopodite (figure 32) and also a short spine at the tip of this branch, neither of which is present in the females.

Instar-I male. Postabdomen shorter and broader than in female (figures 25, 39), subrectangular; all marginal denticles single; genital pores small, located ventrally at some distance from base of claw. Tips of antennules reach more than half distance from ocellus to tip of rostrum (figure 25), but none of the nine aesthetascs reach tip. Rostrum broadly and roundly tapered to bluntish point (figure 28), typically is directed forward; occasionally tip indistinctly and finely emarginate. Trunklimb I (figure 44) similar to that of instar-I female, except for peg-like, slightly curved Anlage of copulatory hook.

Instar-II male. Postabdomen resembles that of female in shape and armament, except that marginal denticles exhibit a strong tendency toward doubling (figures 40, 41); genital pores small, located closer toward base of claw than in instar I (figure 40). Postabdominal claw (figure 41) indistinguishable from that of female. Antennule already has size and asymmetrical shape of mature male, but still only nine aesthetascs, all of which longer and stouter than in female but none as long as antennule, even though some project beyond tip of rostrum (figure 26); antennular seta has shifted basally as compared with female; early developmental stage of two-segmented male seta prominent. Trunk limb I with large Anlage of male seta on i.d.l.; copulatory brush seta developing. Rostrum not appreciably different from instar I.

Mature male. Raised honeycomb pattern absent (figures 63, 64). Tip of rostrum broadly truncate, with rounded corners (figures 51, 64); most commonly mildly crenulate, although occasionally provided with stoutish point, as in instars I and II; seen from side, tip appears blunt and is bent backward (figure 27); thin edge of rostrum clear, not transversely striated (figure 51) as in females and immature males. Size and shape of antennule not appreciably different from that of instar II, but now 12 aesthetascs (figure 33), nearly all considerably stouter than in instar II; some longer than the antennule; two of three additional aesthetascs subapical along the convex margin, one very markedly so; in intact specimens aesthetascs spread out fan-like between rostrum and shell and project well beyond tip of rostrum (figure 27); male seta long, heavily chitinized basally but with distal part much thinner and tapered to a fine point, attached medially about one-half distance toward tip (figure 33); antennular seta rather short, delicate, sharply pointed, arising about one-third distance toward tip. Large copulatory hook, very broadly open, free arm slender, irregularly tapered distally, inner margin of tip with two curved transverse ridges (figure 46); the three i.d.l. setae that also occur in female much reduced in size in mature male, leaving the fourth seta that develops only in mature males as largest on this lobe; copulatory brush of relatively few long, slender setae; copulatory brush seta distinct, with an expanded bulbous base and a finely attenuated tip, about same length as setae of copulatory brush. Postabdomen markedly narrowed distad from sharp, protruding, and prominent pre-anal angle (figures 42, 43); distal portion thinly chitinized, slightly expanded and somewhat bulbous, provided with variable number (generally about four singles or four groups) of very long, slender, straight spines, attached mostly at some distance from margin; ventral margin of postabdomen relatively straight; dorsal margin of bulbous tip tapered evenly to base of claw; lateral surface of postabdomen provided with many crescents of long spinules, stoutest distally, tending to be arranged in two rows as in female; pre-anal angle well armed on each side with two rows of long, rather stout setules; genital openings large but indistinct, located far distad near base of claws. Postabdominal claw much as in female, except that larger basal spine usually absent (figure 43) and smaller basal spine reduced in size; subapical seta uncertainly visible with 100 \times phase objective.

Size. (Body length in millimetres; figures in parentheses are total length, including the honeycombs.) Olin Lake: instar I, 0.24–0.26 mm (0.26–0.29) ($n = 19$); instar II,

0.27–0.31 mm (0.29–0.33) ($n = 58$); mature, 0.28–0.32 mm ($n = 14$). Pinehurst Lake: instar I, 0.24–0.26 mm (0.26–0.29) ($n = 18$); instar II, 0.27–0.29 mm (0.29–0.31) ($n = 29$); mature, 0.27–0.30 mm ($n = 52$).

Comments. A number of matters concerning the males of *faviformis* deserve special mention.

(i) In the formalin-preserved samples from Olin and Parkhurst Lakes, a number of mature males had the soft parts of their postabdomen pulled away from the exoskeleton, as if they were about midway in a typical inter-moult development. However, no details could be distinguished at all of a new exoskeleton, leading me to believe that the animals were not actively preparing for a moult to a second mature instar (= instar IV). Such a conclusion is substantiated in part by the complete absence of exuviae of mature males in the collection detritus, whereas those of instar I, and particularly instar II, were commonly found. I had previously suggested (Frey & Hann 1985) that the uncoupling of reproduction from the growth–moult cycle in mature chydorid males may well represent the only such pattern of definite growth in all the Cladocera.

(ii) Males from Olin and Pinehurst lakes had precisely the same smallest size in each instar, but instar-II males and mature males in Olin Lake attained a significantly larger size than in Pinehurst (figure 285). Because the frequency curve for instar-II males from Olin Lake seemed bimodal, suggesting that possibly two instars were involved, I carefully examined all the instar-II males from Olin Lake without finding any evidence for two developmental morphotypes. There were no differences between small and large specimens in (a) the structure of the J-shaped copulatory hook and in the size and shape of the Anlage of i.d.l. spine 4; (b) the shape of the antennule and the number and size of aesthetascs on it; (c) the structure of the postabdomen, which in instar II involves a strong tendency toward doubling of marginal denticles; (d) the structure of the next instar postabdomen, which in all specimens far enough developed to show details was clearly the postabdomen illustrated in this study (figure 41), being compressed distally and having a somewhat bulbous tip and long slender spines.

Data from the Pinehurst Lake population (figure 285) show that instar-I males tend to be slightly smaller than instar-I females, that instar-II males are much smaller than instar-II females, and that mature males are only slightly larger than instar-II males, demonstrating a striking curtailment in growth of these males even before reaching maturity. The greater range in size of instar-II males in Olin Lake and the possibility of bimodality suggests that possibly two kinds of instar-I males are present, having either low or high growth potential on moulting to instar II. As the length range of mature males is no greater than for instar-II males, whatever produced the greater size range and bimodality in instar II was not able to increase the size range still further in instar III.

(iii) The most disturbing aspect of male morphology is that none of the mature males from Olin Lake, which had a greater length range than in Pinehurst Lake, had a basal spine on the postabdominal claw, whereas some of the mature males from Pinehurst Lake distinctly had such a spine (cf. figures 42 and 43). Great care was taken to observe this feature closely. Even though such a range in morphological detail would not be expected in a single species, it is certain that specimens both with and without a spine were *faviformis*. In Olin Lake males of another species of *Chydorus* that had a well developed spine on the claw were present. They were so close in general appearance to the *faviformis* males that they could not be distinguished for certain at $50\times$ stereomagnification. Yet when examined at higher power with a compound microscope, which enabled the two species to be separated readily, none of the *faviformis* males had a spine on the postabdominal claw.

Distribution

C. faviformis is known to occur from easternmost Newfoundland across southern Canada to the Riding Mountain National Park in Manitoba, and southward into northern Indiana and extreme northeastern Pennsylvania (see figure 1 in Frey (1987)). It is restricted to the part of the continent that was glaciated. Specific instances of occurrence are listed in appendix 1.

Chydorus faviformis has now been described more nearly completely than by Birge, which makes possible comparisons with the populations we have of honeycombed *Chydorus* from other continents. The conclusion that has emerged unequivocally is that all the latter, although showing a gross resemblance to one another and to *C. faviformis* in possessing the honeycombs, are markedly different at the species level, with the possible exception already noted, of the taxon from Malaysia. Males are necessary for working out the details of the relationships. For example, the male of *C. faviformis* resembles those of the *Chydorus sphaericus* complex in that its postabdomen is strongly constricted distally and has a marked pre-anal angle, whereas the males of three of the other taxa – the only three for which males are present – are not constricted and have lost the pre-anal angle. Furthermore, among these four species, only the males of *C. faviformis* lose their honeycomb on reaching maturity. There are many other differences (see descriptions) and each population is highly distinctive, with many morphological characters contributing to their distinctness.

(b) *Chydorus obscurirostris* n.sp.

Synonymy

Chydorus faviformis Birge, 1893: Idris (1979): pp. 128–130, figure 36; Idris & Fernando (1981): pp. 243–244, 246, figures 44–46; Idris (1983): pp. 76, 78–79, figure 36.

Johnson (1963) also found a form similar to *C. faviformis* in Malaysia, but according to Idris & Fernando (1981) he considered it to be *Chydorus reticulatus* Daday, 1898. There are no reports in the literature of a honeycombed *Chydorus* from Australia (Smirnov & Timms 1983).

Comments

More than 3000 km, involving a number of major salt-water barriers, separate the populations in Western Australia and in Malaysia. Yet the taxa are very close to one another in morphology, being distinguishable only by minute details, which at the present state of our knowledge scarcely seem to be of the magnitude for defining different species. Accordingly, for the moment, at least, I have considered these two taxa to belong to the same species but to different geographical subspecies. A more satisfactory resolution of this matter cannot be made until males from both populations are available. The description of the primary taxon is based chiefly on the Australian population, but with any consistent differences exhibited by the Malaysian population being pointed out. At the end of this section the differences between the two taxa are tabulated. The illustrations presented are of both taxa, partly intermixed to make comparisons easier.

W. D. Williams some time ago sent me a split of his sample, and he also sent a split to G. B. Deevey. She prepared four slides, containing a total of 39 females (half of which were immature), a mature male, and nine heads or shells. In her remaining liquid material were 21 specimens and some shells. In my subsample were 55 total specimens, consisting of 47 of this species and eight of *C. opacus*. All my specimens are distorted as if from not having been

preserved immediately: various head appendages are displaced from their normal relationships, and much of the body contents has been dissolved, making the specimens quite soft and clear. All animals of immature size from the liquid samples were examined, but no additional males were found. Hence, except for the single mature male, all other specimens were parthenogenetic females.

Etymology

From (L) *obscur* covered, dark, and (L) *rostrum* beak, snout, referring to the free edge of the rostrum being almost obliterated by the high marginal meshes that strongly overhang it.

Localities

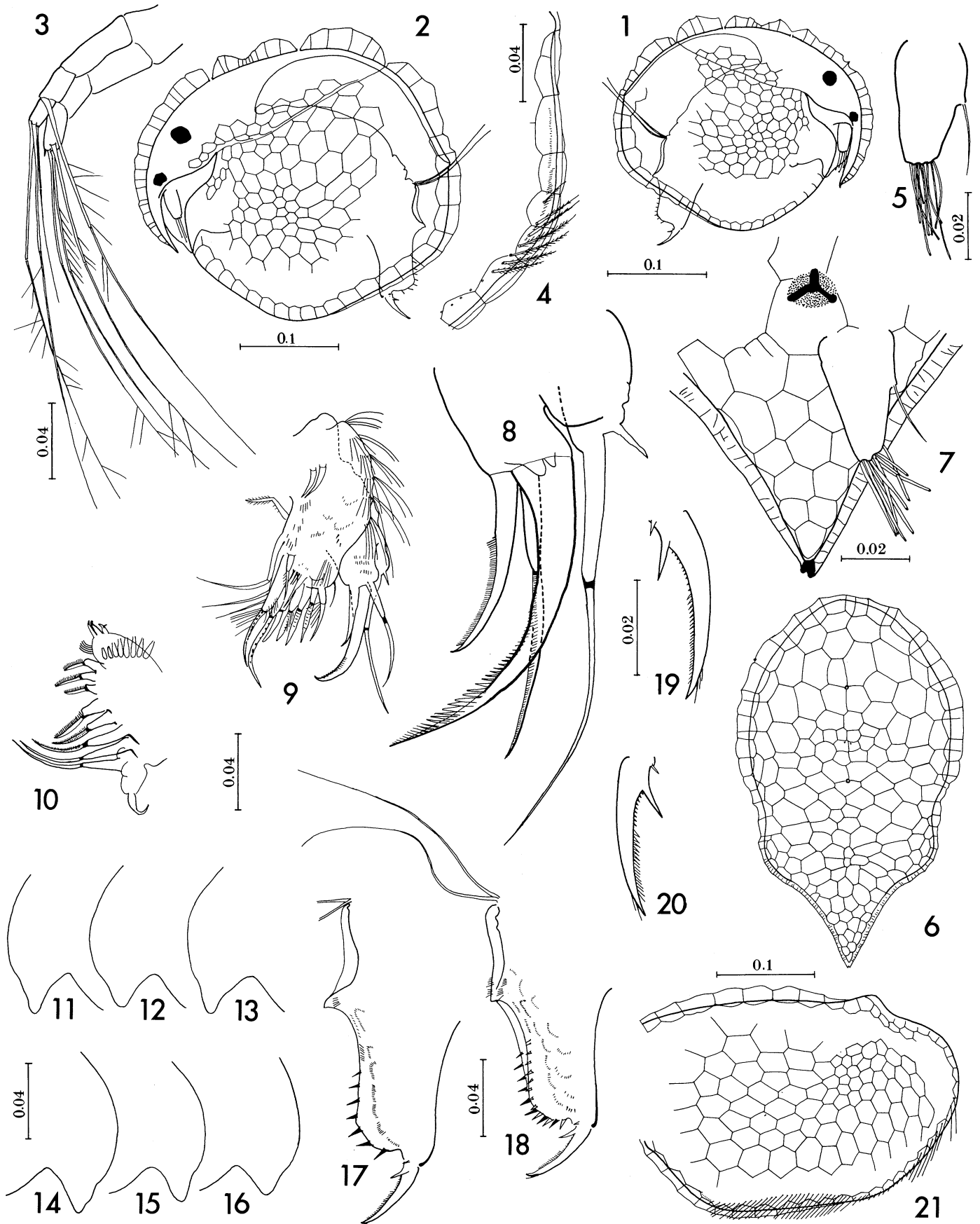
Type locality. Billabong on Crossland River, south of Couchman Range, ten miles north of Drysdale (15° 40' S, 126° 34' E), Kimberly, Western Australia, May 1965. W. D. Williams collection number 596. The split in the Frey collection is accessioned as F2403.

Other localities. Unnamed billabong on Marakai Road, beyond Marakai Crossing, Northern

DESCRIPTION OF PLATES 1–5

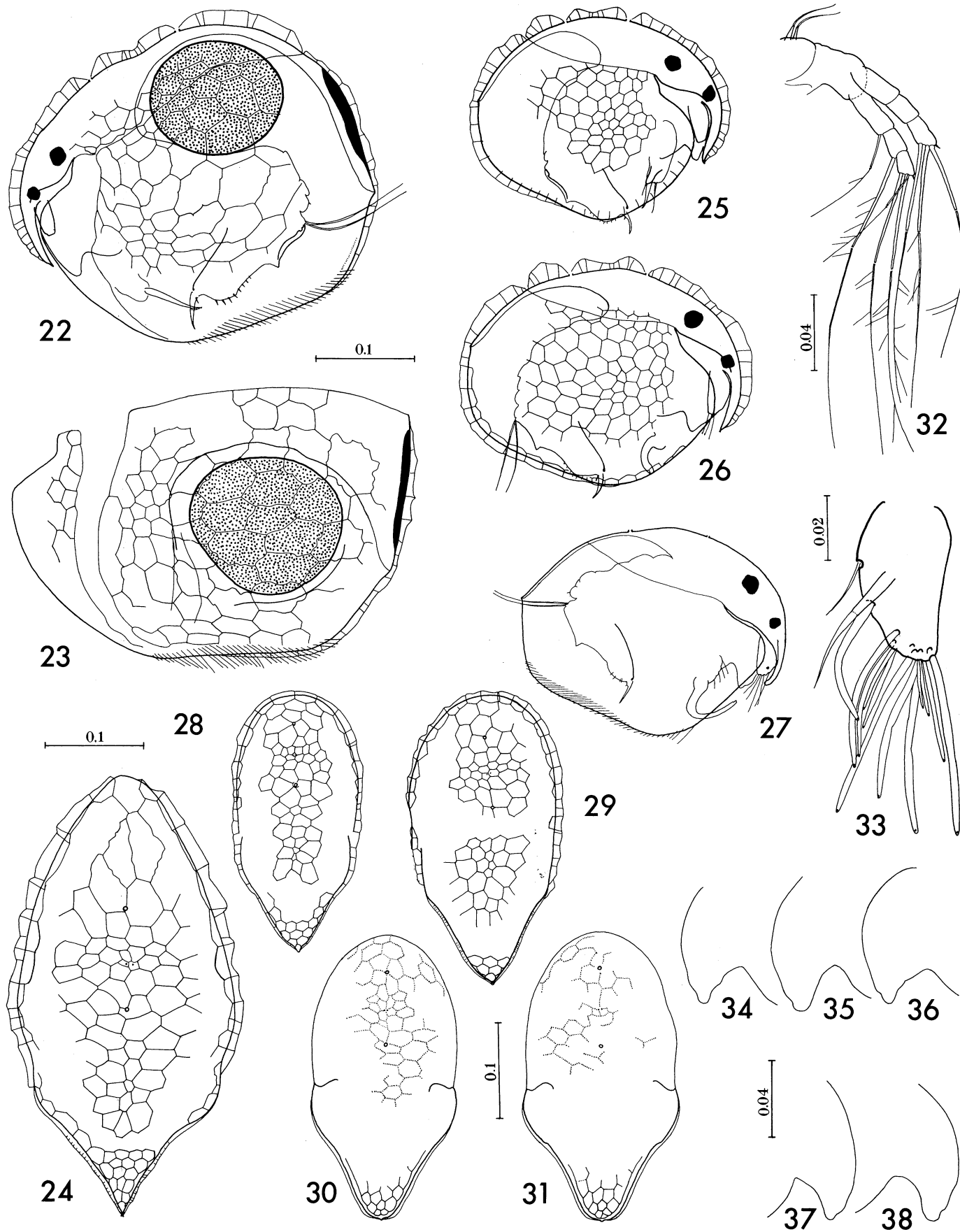
Scales in all plates: millimetres for all line drawings; micrometres for all scanning electron micrographs.

- PLATE 1. *Chydorus faviformis* Birge, 1893. Parthenogenetic females. Figures 1–2, 9, and 11–21 are of specimens from Catamount Pond, New York; 3, 5, and 7 from Pinehurst Lake, Ontario; 4, 8, and 10 from Olin Lake, Indiana; and 6 from Raquette Lake, New York. (1, 2) Side views of instar-I and mature females, respectively; (3) antenna; (4) posterior-ventral angle of shell, showing setae of duplicature unattached to any solid line, and submarginal row of fine setules extending dorsally along posterior margin; (5) antennule; (6) headshield; (7) rostrum showing bifurcated tip, and antennule in place; (8) o.d.l. and i.d.l. of trunklimb I (o.d.l. = outer distal lobe; i.d.l. = inner distal lobe); (9) medial view of trunklimb I; (10) trunk-limb II; (11–15) labrum of mature females; (17–18) postabdomen and postabdominal claw (17 is better for the shape, but 18 is better for the lateral armament); (19–20) postabdominal claw; (21) shell, showing continuation of ventral setae in front of the posterior duplicature.
- PLATE 2. *Chydorus faviformis* Birge, 1893. Ehippial females and males. Figures 22–26 and 28–29 are of specimens from Olin Lake, Indiana; 27 and 30–38 from Pinehurst Lake, Ontario. (22) Ehippial female; (23) cast ehippium, showing anterior portion of shell separating from ehippium along pre-determined slough line (also visible in figure 22); (24) headshield of ehippial female, showing posterior elongation and narrowing; (25, 26, 27) sideviews of instar-I, instar-II, and mature males, respectively, showing progressive development of copulatory hook, enlargement of antennule, and change in postabdomen; (28, 29) headshields of male instars I and II, respectively; (30, 31) headshields of mature males; (32) antenna of mature male, showing seta arising from basal segment of endopodite; (33) antennule of mature male; (34–38) labra of mature males.
- PLATE 3. *Chydorus faviformis* Birge, 1893. Males. Figures 39, 41, and 44–45 are of specimens from Olin Lake, Indiana; 40 from Martin–Oliver Channel, Indiana; and 42–43 and 46–51 from Pinehurst Lake, Ontario. (39, 40) Postabdomens of instars I and II, respectively; (41) postabdomen of instar-II male, with developing exoskeleton of mature male inside; (42, 43) postabdomens of mature males; (44, 45, 46) o.d.l. and i.d.l. of instar-I, instar-II, and mature males, respectively, showing progressive development of copulatory hook and male seta, shortening of i.d.l. setae, and elongation of basal portion of i.d.l. (c.h., copulatory hook; m.s', male seta Anlage; m.s., male seta; c.b.s., copulatory brush seta); (47, 48) copulatory hooks of mature male; (49) shell of mature male; (50, 51) rostra of instar-II and mature males, respectively.
- PLATE 4. *Chydorus faviformis* Birge, 1893. Parthenogenetic and gamogenetic females. (52–55) Lateral, dorsal, ventral, and posterior views, respectively, of parthenogenetic females from Raquette Lake, New York; (56–58) ehippial females from Olin Lake, Indiana, showing prominent slough line anteriorly, reduction in height of mesh walls, and development of elongate and irregular supporting ridges within meshes in posterior-dorsal part of shell.
- PLATE 5. *Chydorus faviformis* Birge, 1893. Figures 59–62 are of specimens from Olin Lake, Indiana, and 63 and 64 from Pinehurst Lake, Ontario. (59) Frontal view of parthenogenetic female; (60, 61) frontal and dorsal views, respectively, of ehippial female, showing narrowing of body dorsally, presence of slough lines (figure 60), and posterior narrowing of headshield (figure 61); (62) elongate ridges within meshes of ehippial female; (63, 64) ventral view and enlarged tip of rostrum, respectively, of mature male.

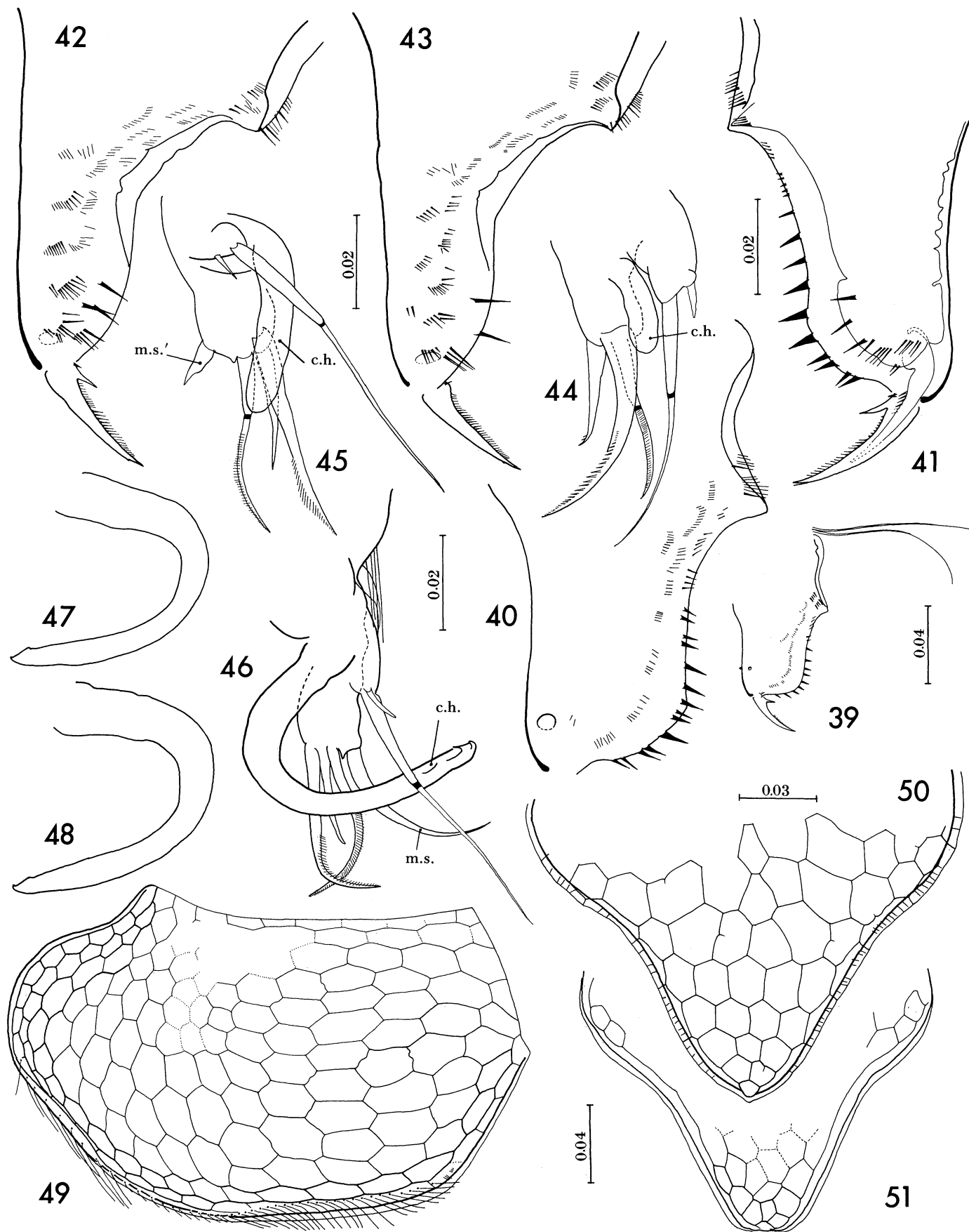


FIGURES 1-21. For description see opposite.

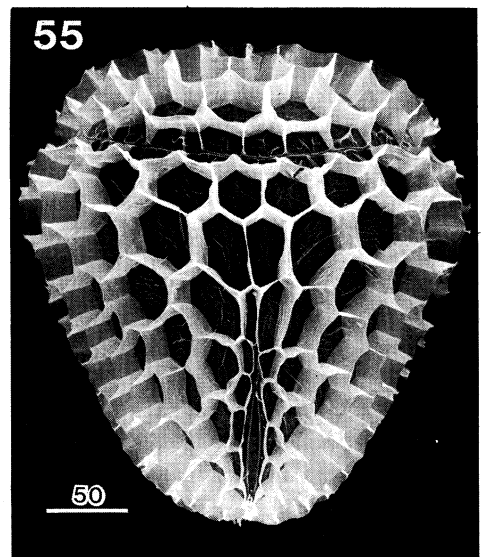
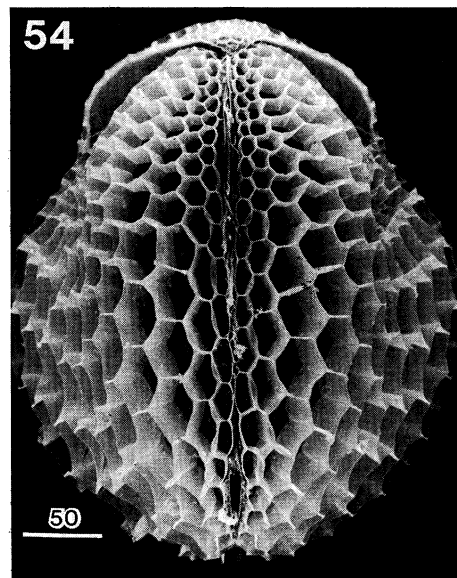
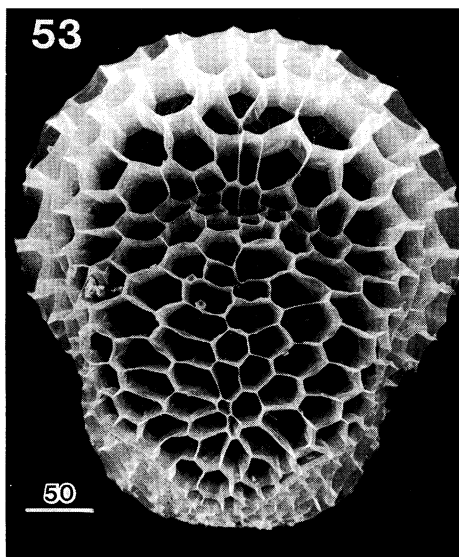
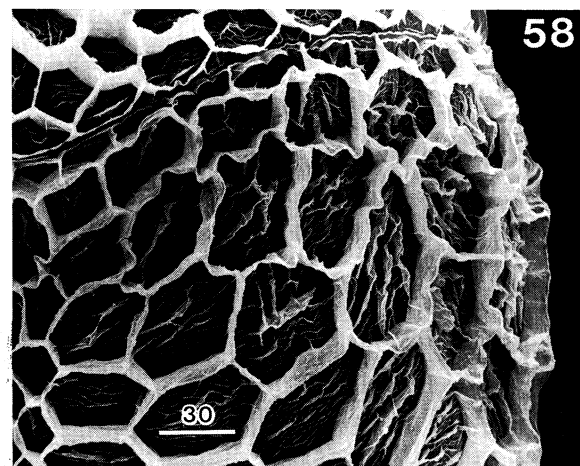
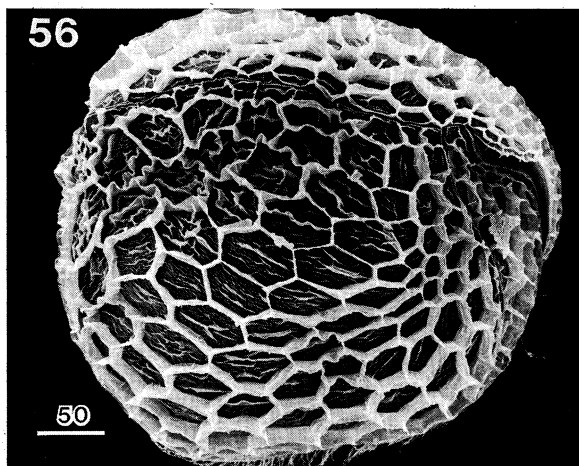
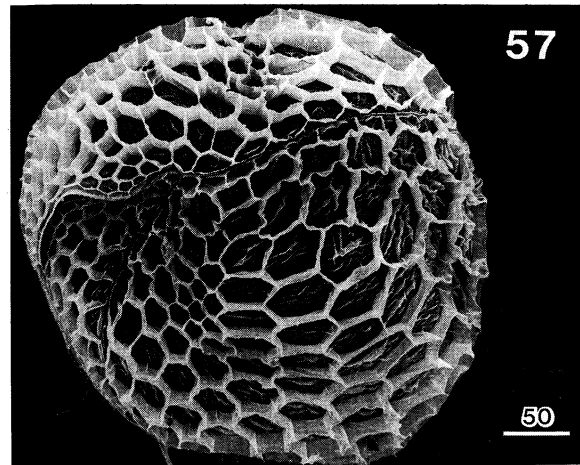
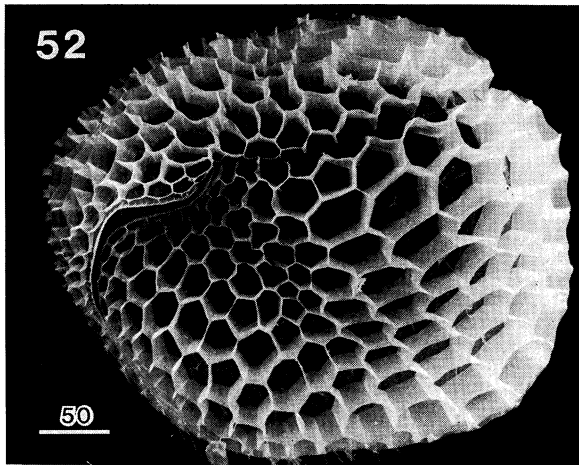
(Facing p. 364)



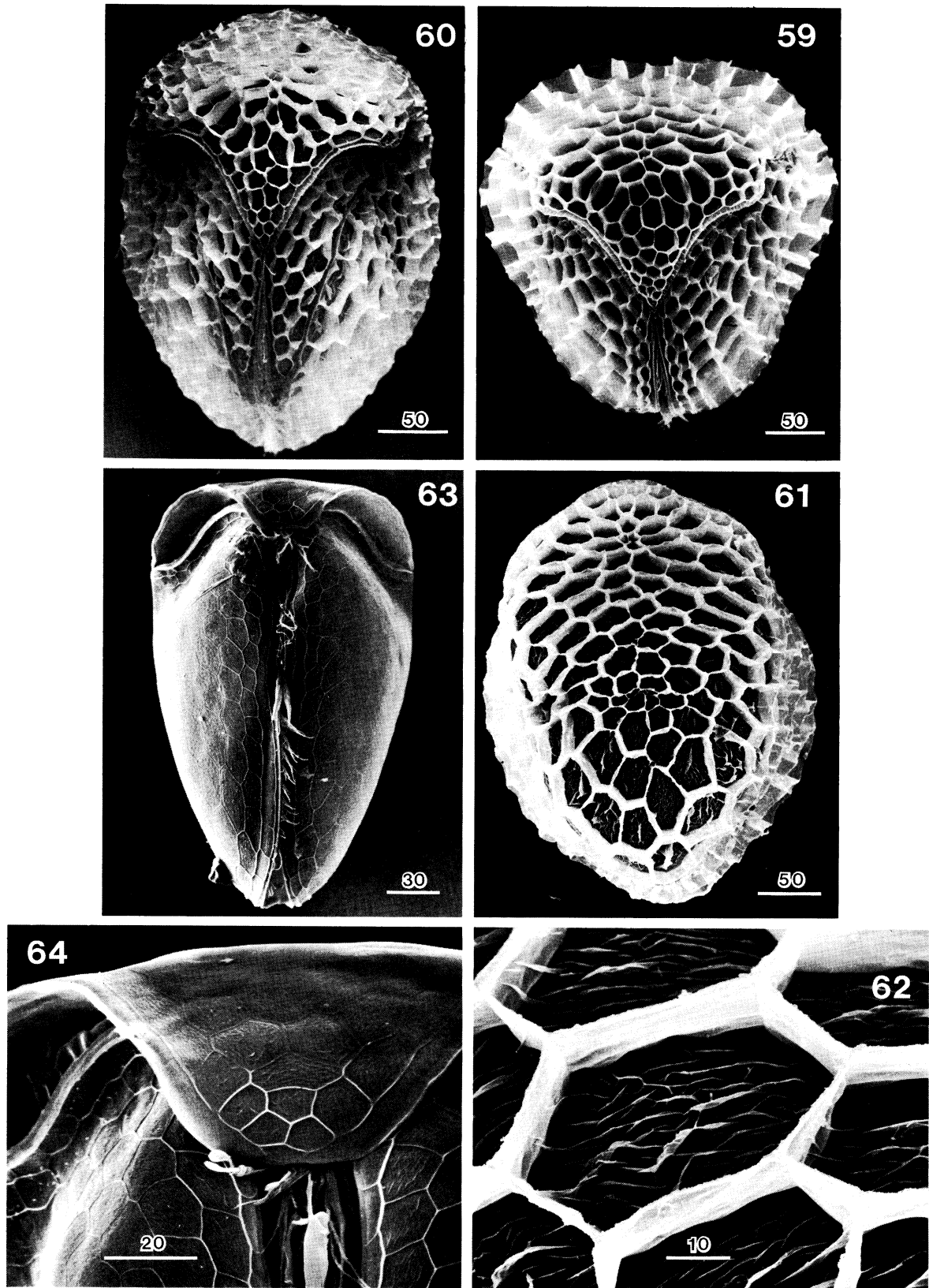
FIGURES 22-38. For description see p. 364.



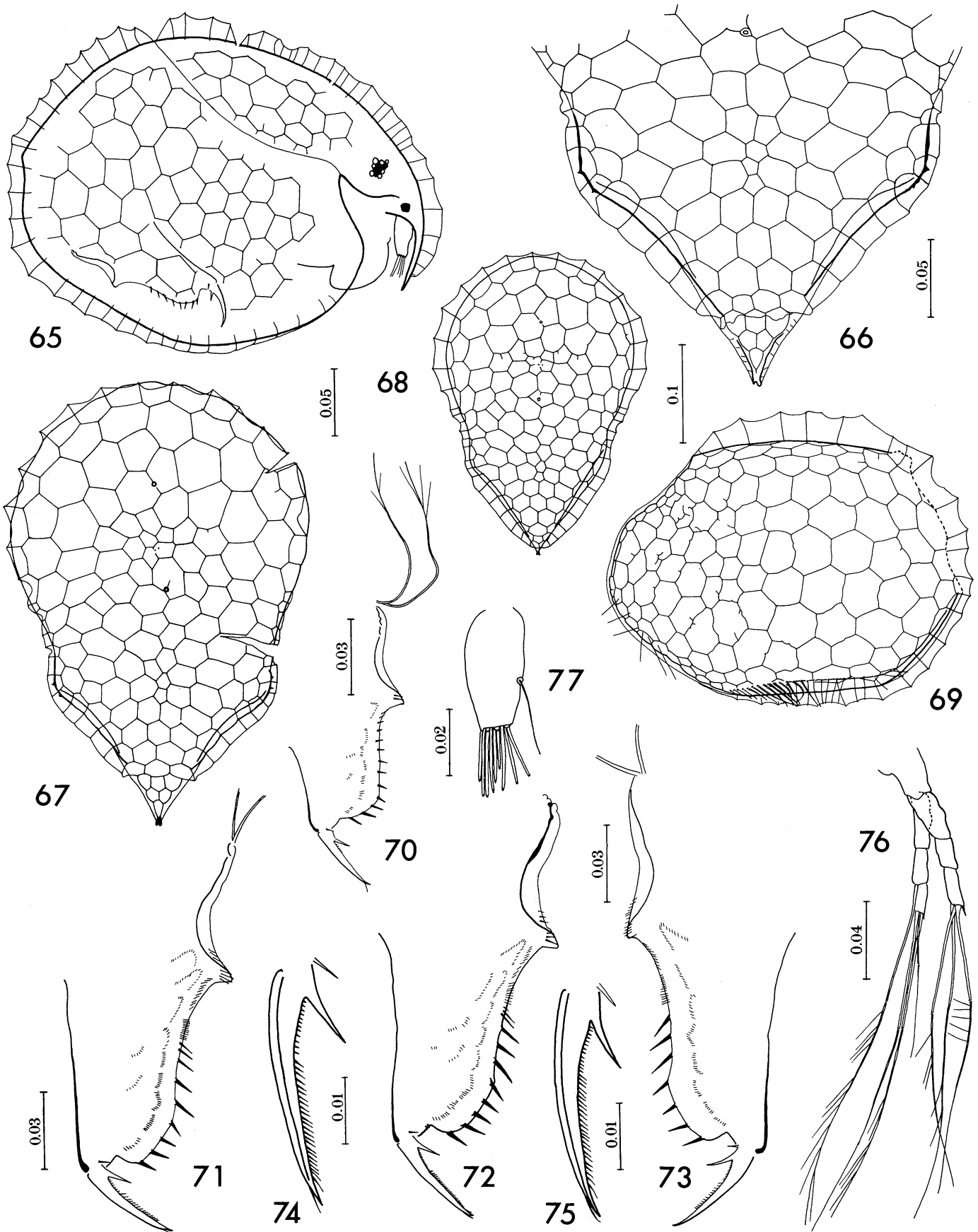
FIGURES 39-51. For description see p. 364.



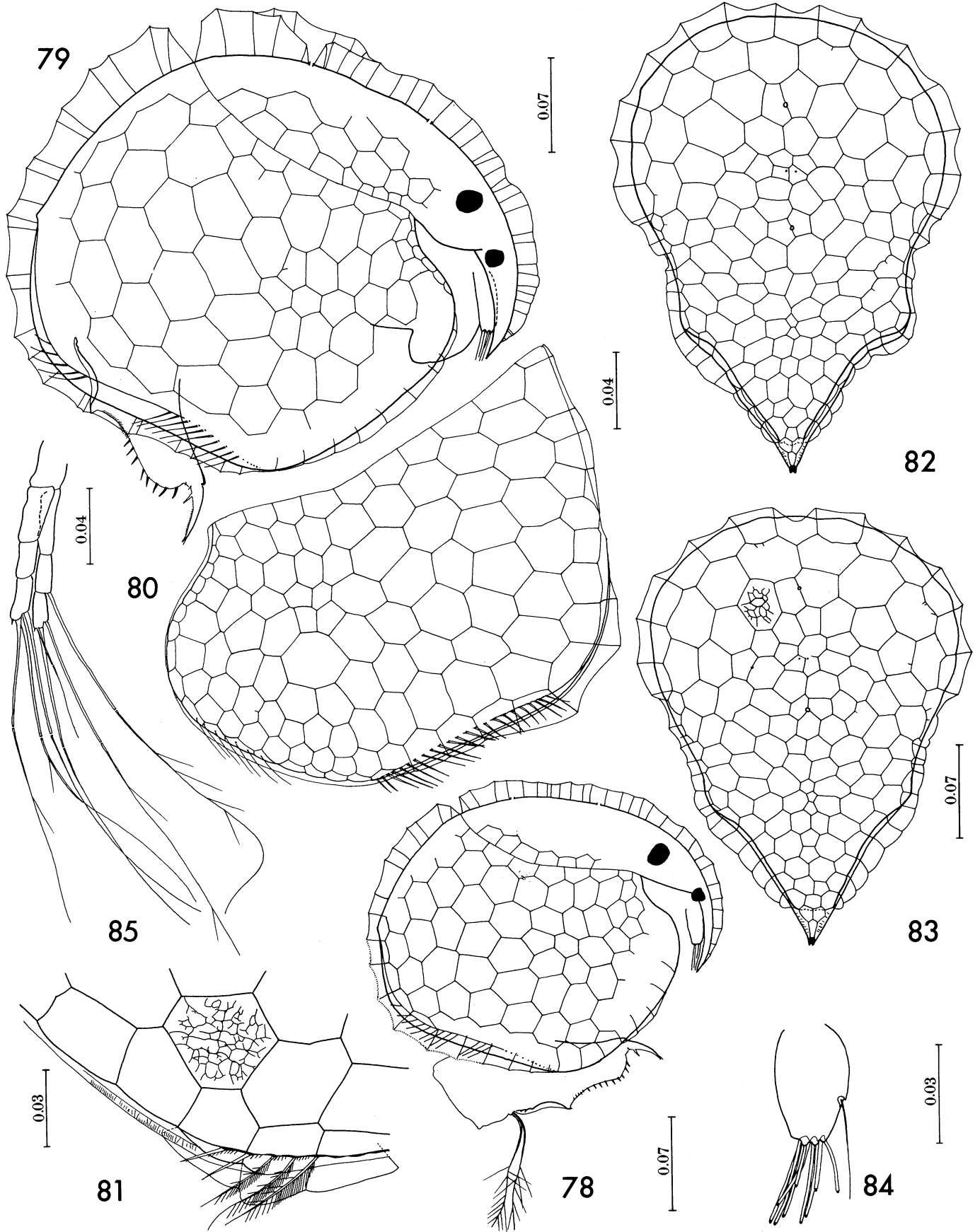
FIGURES 52-58. For description see p. 364.



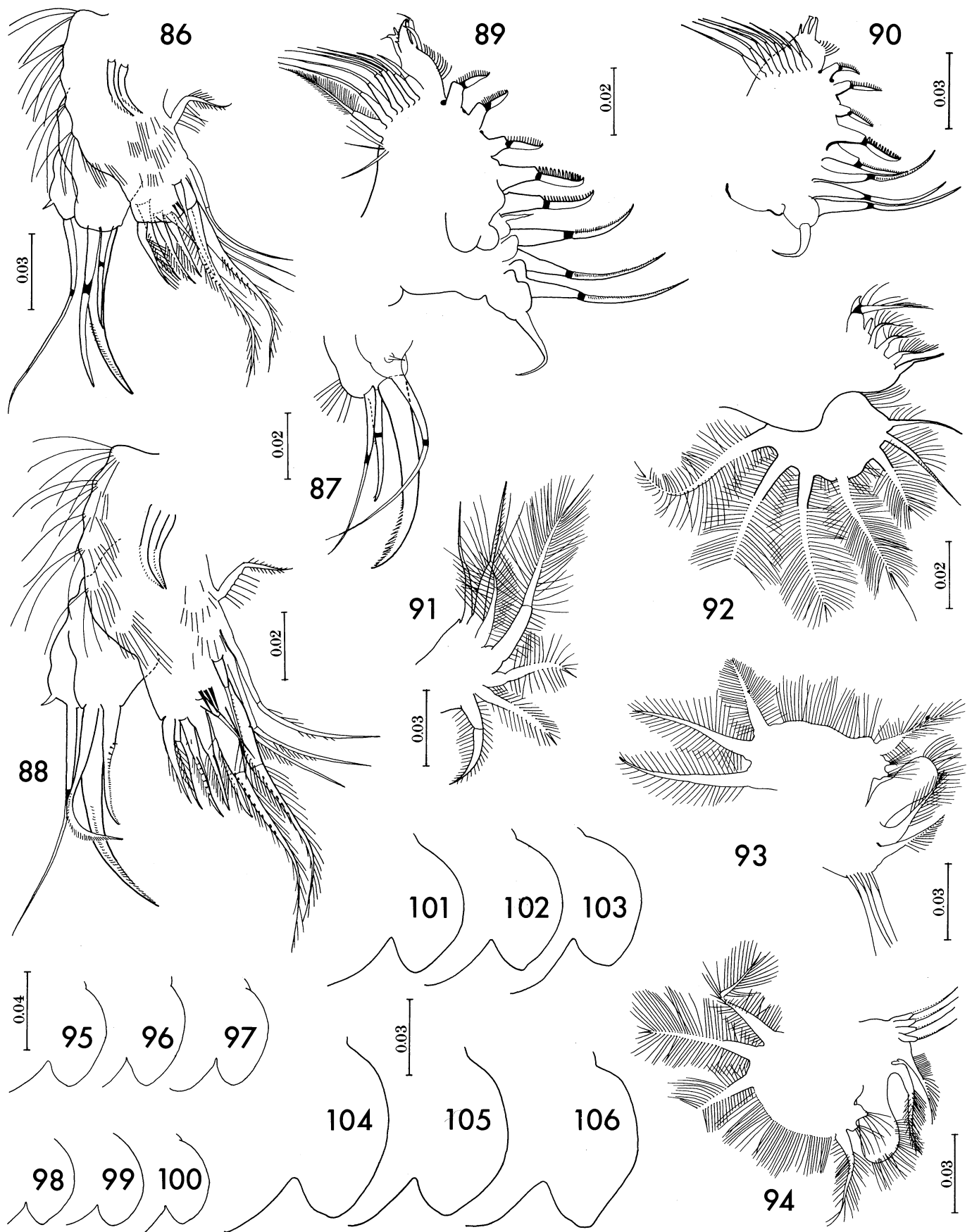
FIGURES 59-64. For description see p. 364.



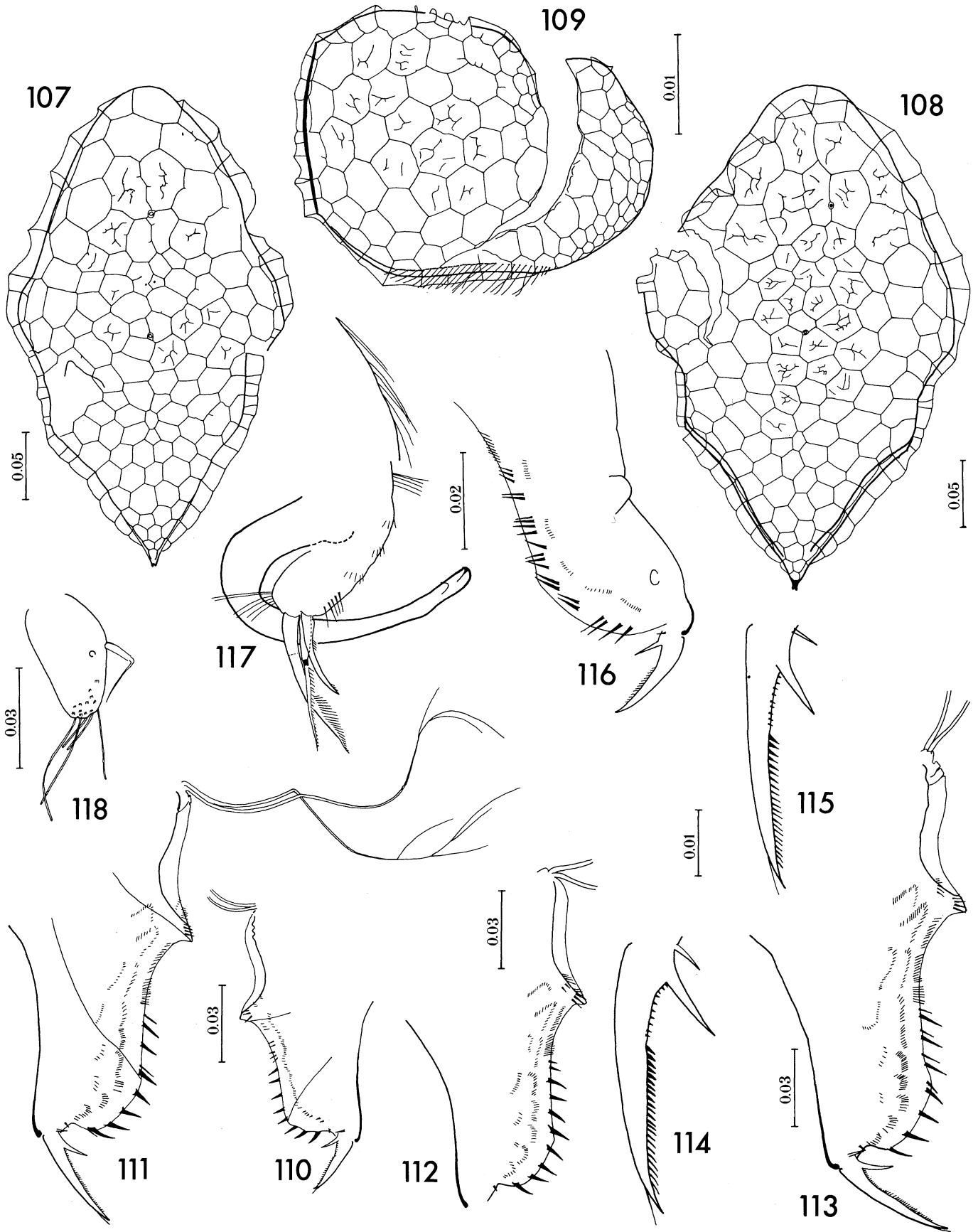
FIGURES 65-77. For description see p. 365.



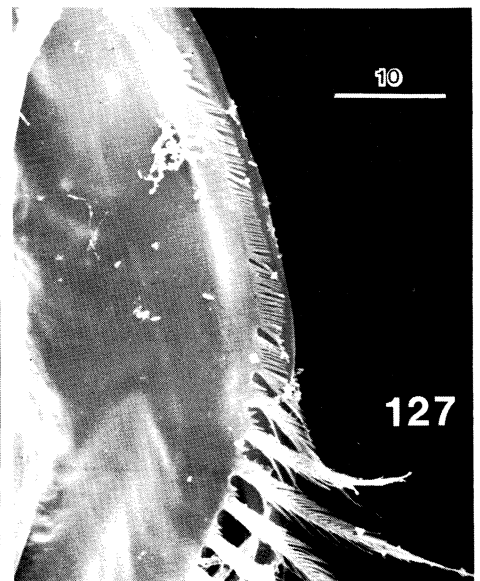
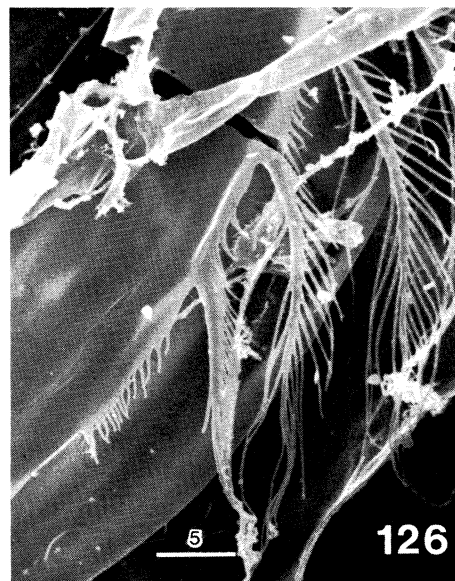
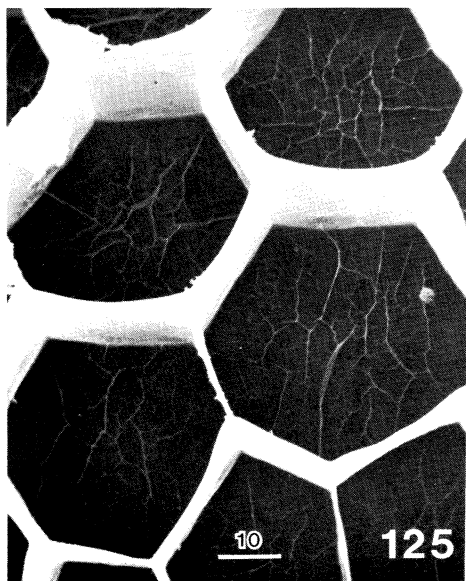
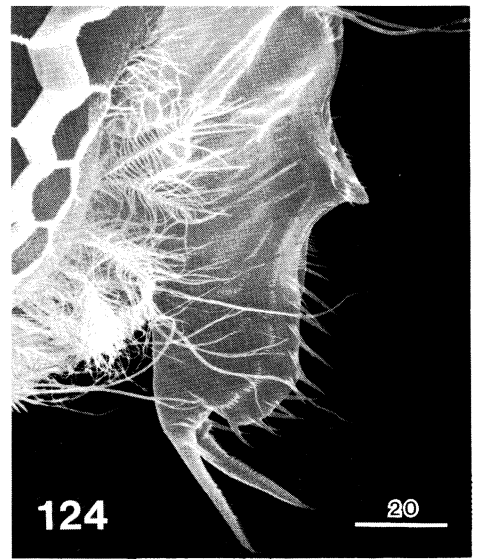
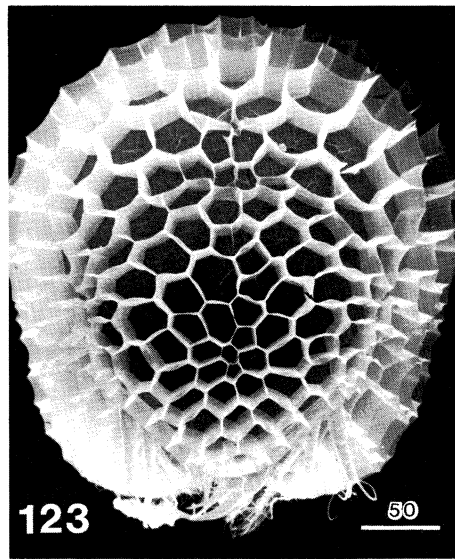
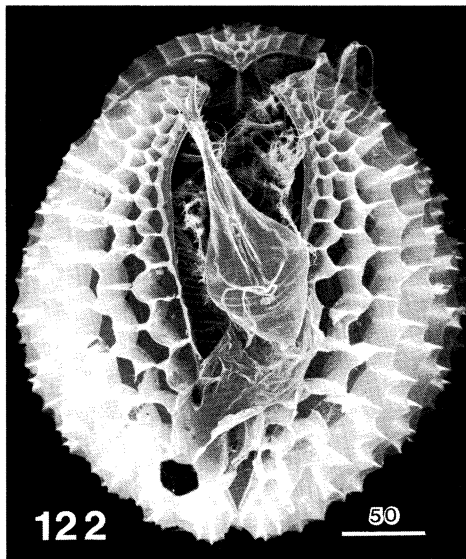
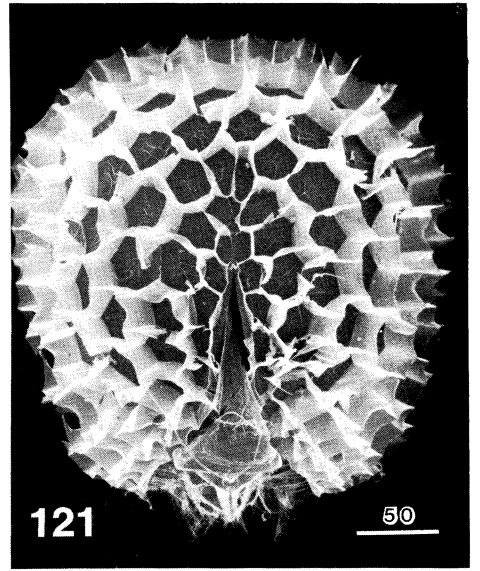
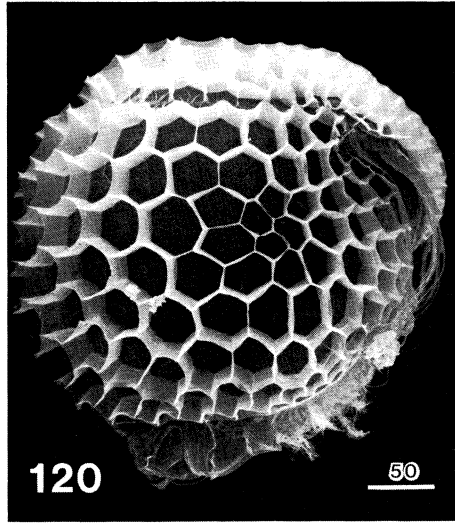
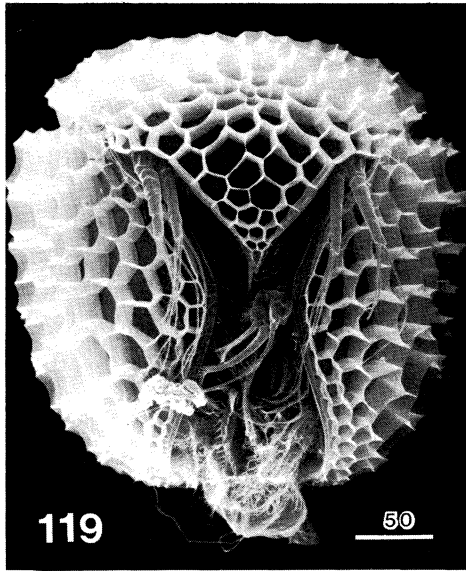
FIGURES 78-85. For description see p. 365.



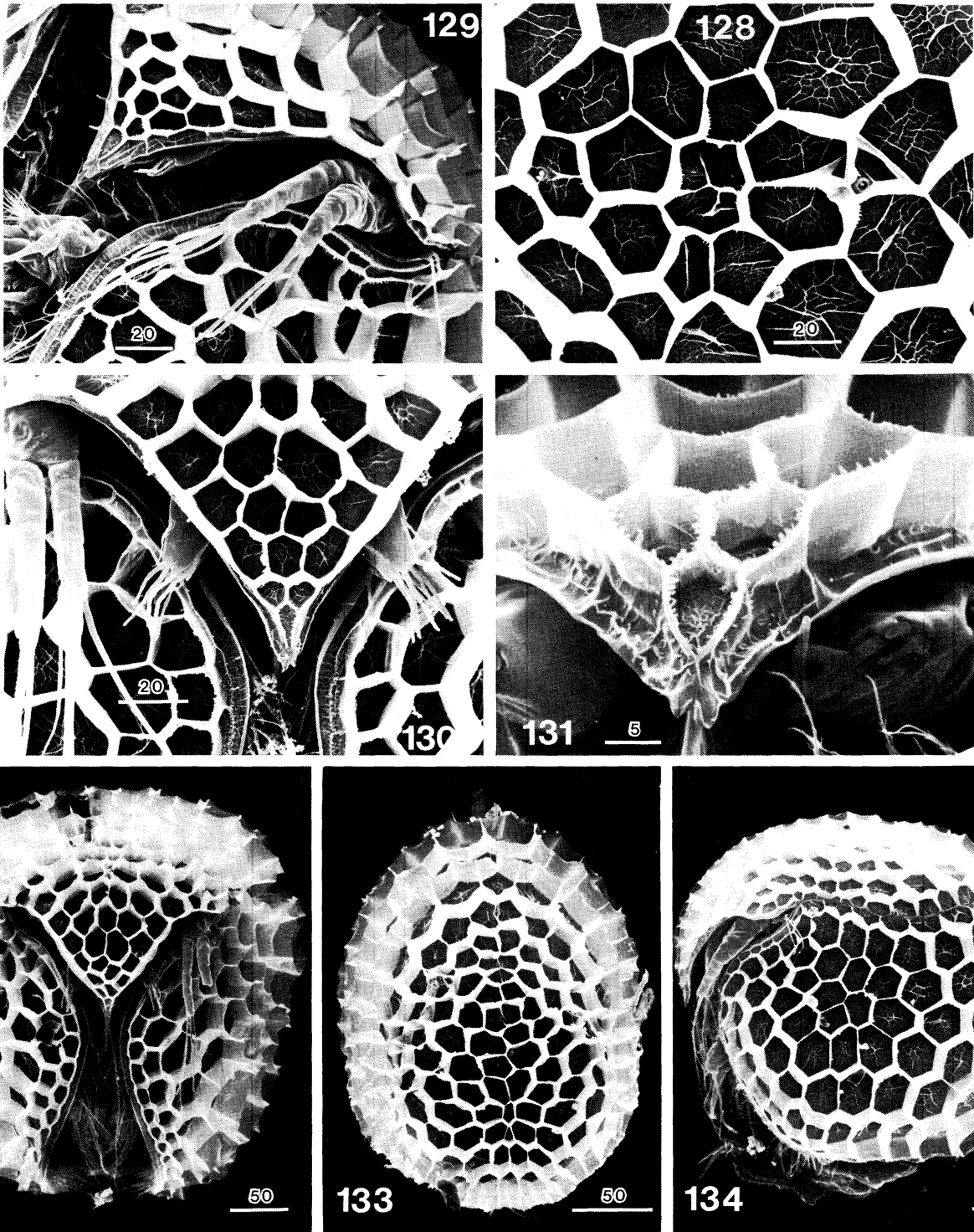
FIGURES 86-106. For description see p. 365.



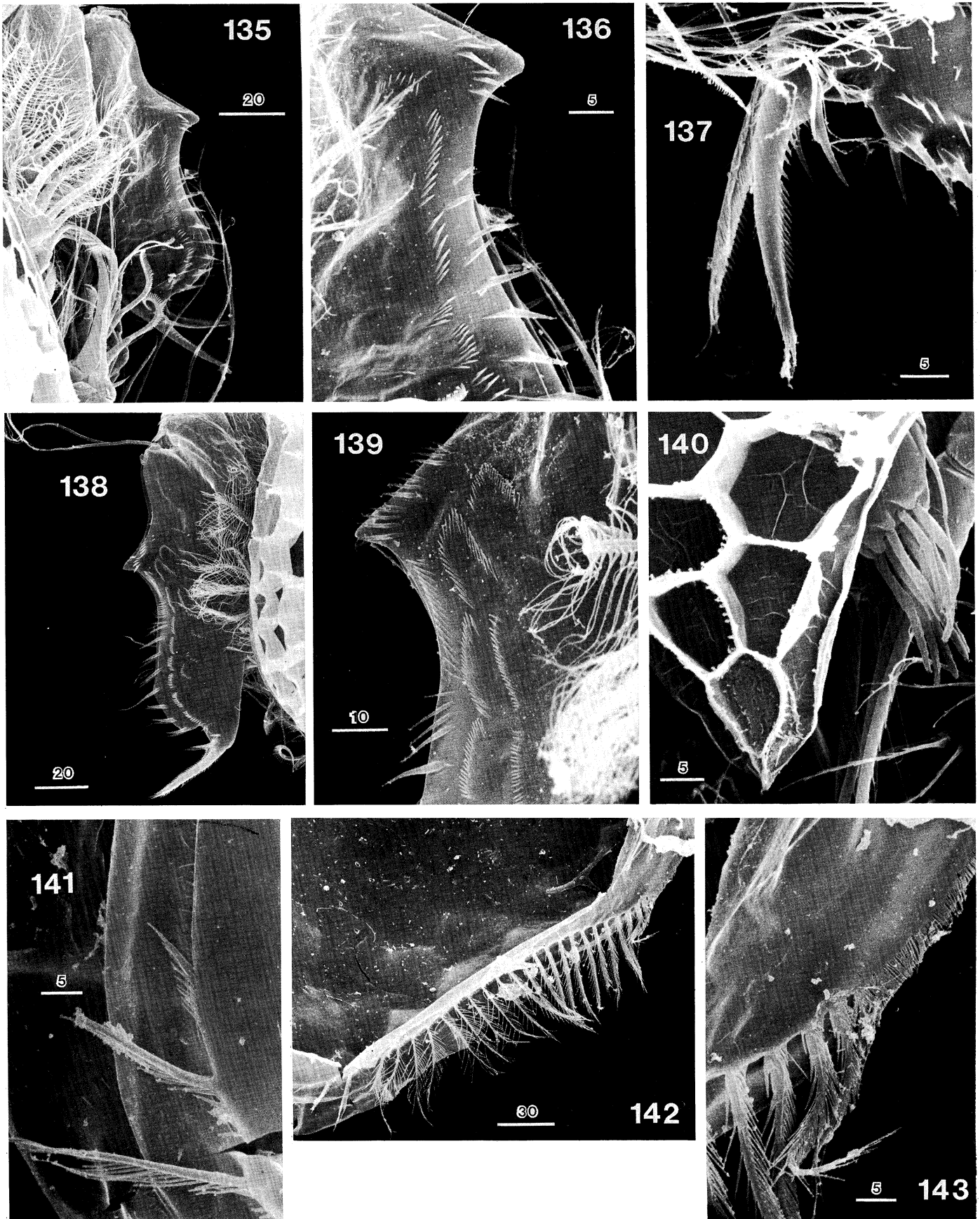
FIGURES 107-118. For description see p. 365.



FIGURES 119-127. For description see p. 365.



FIGURES 128-134. For description see p. 365.



FIGURES 135-143. For description see opposite.

Territory, Australia, 11 September 1982, B. V. Timms sample N-114. This sample contained just a single specimen of *C. obscurirostris*, along with 10 specimens of *C. opacus*.

Types

Type series. All the specimens and exuviae from the type locality, amounting to a total of roughly 100 specimens plus various parts.

DESCRIPTION OF PLATES 6-12

- PLATE 6. *Chydorus obscurirostris* n.sp. All specimens are from the W. D. Williams collection from Western Australia. Figures 65, 70, 74, and 75 are of specimens on the Deevey slides; the rest were obtained from the liquid samples. All are parthenogenetic females. (65) Lateral view; (66, 67) headshield and rostrum of another headshield; (68) headshield of immature specimen; (69) shell of dissected female; (70) postabdomen of immature female; (71-73) postabdomens of mature females; (74, 75) postabdominal claws of mature females; (76) antenna; (77) antennule.
- PLATE 7. *Chydorus obscurirostris tasekberae* n.subsp. All figures are of parthenogenetic females from slides or liquid samples from Tasek Bera, Malaysia, provided by B. A. G. Idris. (78) Lateral view of immature female; (79) mature female; (80) shell of mature female; (81) posterior-ventral margin of shell, showing setae of duplicature attached to an irregular solid line, and no fine setules along this line dorsal from the posteriormost seta; (82, 83) headshields from mature females; (84) antennule; (85) antenna from mature female.
- PLATE 8. *Chydorus o. obscurirostris* n.subsp. All figures are of parthenogenetic females from W. D. Williams' sample from Western Australia. (86) Trunklimb I; (87) i.d.l. and o.d.l. of trunklimb I; (90) trunklimb II; (93) trunklimb V; (95-97) labra of mature females; (98-100) labra of immature females.
Chydorus o. tasekberae n.subsp. All figures are of parthenogenetic females from samples collected by B. A. G. Idris in Tasek Bera, Malaysia. (88) Trunklimb I; (89) trunklimb II; (91) 'soft' setae on trunklimb III; (92) trunklimb IV; (94) trunklimb V; (101-103) labra from instar-I females; (104-106) labra from mature females.
- PLATE 9. *Chydorus o. tasekberae* n.subsp. Specimens from Tasek Bera, Malaysia, collected by B. A. G. Idris. (107, 108) Headshields of ephippial females; (109) shell from exoskeleton of ephippial female, showing the chitinous thickening along the dorsal margin (at left) and strong development of the slough line; (110) postabdomen of instar-I female; (111-113) postabdomens of mature females; (114, 115) postabdominal claws of females.
Chydorus o. obscurirostris n.subsp. Specimen of mature male (= allotype) on slide prepared by G. B. Deevey from sample collected in Western Australia by W. D. Williams. (116) Postabdomen; (117) i.d.l. of trunk limb I; (118) antennule, showing basal articulations of 12 aesthetascs plus antennular seta; two-segmented male seta projecting from right margin.
- PLATE 10. *Chydorus o. obscurirostris* n.subsp. All figures are of mature parthenogenetic females from the W. D. Williams collection from Western Australia. (119-123) Front, side, back, bottom and top views, respectively; (124) postabdomen and postabdominal claw; (125) patterning within meshes on shell; (126) posterior end of ventral duplicature, showing cluster of fine spinules along line continuing toward posterior-dorsal angle; (127) anterior end of ventral duplicature, showing existence of groups of fine submarginal setules that do not project beyond margin.
- PLATE 11. *Chydorus o. obscurirostris* n.subsp. All figures are of parthenogenetic females from the W. D. Williams collection from Western Australia. (128) Part of headshield, showing pores and general type of sculpturing within meshes; (129) anterior end of female, showing the occlusion of the free margin of the headshield by the middle mesh-walls arising at the edge; (131) tip of rostrum, showing roundly and obliquely bifid tip, free edge at either side, and mesh walls fringed with short, hair-like setules.
Chydorus o. tasekberae n.subsp. All figures are of parthenogenetic females from Tasek Bera, Malaysia, collected by B. A. G. Idris (130) Tip of rostrum and antennules; (132) frontal view of mature parthenogenetic female; (133, 134) dorsal and lateral views, respectively, of an instar-I female.
- PLATE 12. *Chydorus o. tasekberae* n.subsp. All figures are of females from Tasek Bera, Malaysia, collected by B. A. G. Idris. (135, 136) Postabdomen of instar-I female, showing its shortness compared with that of mature female and also the lack of fine setules along the proximal part of the anal groove; (137) postabdominal claws of instar-I female; (139) proximal portion of postabdomen of mature female; (140) antennule and tip of rostrum of instar-I female; (141-143) setae along the ventral duplicature; posterior to the posteriormost seta is a small cluster of setules increasing in size dorsad and ending in an almost respectable seta, and anterior to the duplicature there is a row of clusters of fine, closely packed setules all about the same length, which extend barely past the margin of the shell.
Chydorus o. obscurirostris n.subsp. (138) Postabdomen and postabdominal claw of specimen from W. D. Williams' collection from Western Australia.

Holotype. An immature parthenogenetic female 0.27 mm long, mounted on a slide in glycerine jelly, Australian Museum (registration number P 35708).

Allotype. The mature male under the right coverslip of a slide prepared by G. B. Deevey has been transferred to the Australian Museum (registration number P 35709). This is a distorted specimen, but most of the necessary details can be observed with phase contrast optics.

Paratypes.

(i) Australian Museum. Registration numbers: the 13 specimens under the lefthand coverglass of the Deevey slide (registration number P 35709). These consist of five mature females, four immature females, two headshields, and one each of shell and exoskeleton. There is also a specimen of *Dadaya macrops* under this coverglass. In addition a slide of two females in glycerine jelly (P 35710), and a slide of two females in polyvinyl lactophenol (P 35711).

(ii) United States Natural History Museum. Catalogue numbers: slide of two females in glycerine jelly 227021; slide of two females in polyvinyl lactophenol 227022.

(iii) British Museum (Natural History). Accession numbers: slide of two females in glycerine jelly 1985.197–198; slide of two females in polyvinyl lactophenol 1985.199–200.

All the remaining specimens and exuviae, including the other three slides of the Australian taxon mounted by G. B. Deevey, are in the D. G. Frey collection in Bloomington.

Size

Overall length of Australian taxon excluding the honeycomb meshes, 0.22–0.35 mm ($n = 44$); instar-I females, 0.22–0.24 mm ($n = 14$); instar-II females, 0.26–0.28 mm ($n = 10$); mature parthenogenetic females, 0.29–0.35 mm ($n = 20$). Only one female 0.30 mm long contained any eggs, the others obviously having lost theirs in preservation.

Diagnosis

Globose: width great relative to length and height. Meshes variable in size: large in central and posterior parts of shell and in posterior part of head; walls high, top edges seemingly slightly concave between intersection points; edges with fine setules along free portion of shell, ecdysial line, and anterior part of rostrum, sometimes more widely distributed; interior of meshes with coarse spiderweb network more or less radiating out from centre; some members of network enlarged and may intersect mesh walls, producing irregularities in configuration on shell; in lateral view meshes project prominently beyond body except along anterior-ventral portion of shell. Headshield broadly rounded behind; i.p. usually greater than p.p.; minor pores about one major pore diameter apart; rostrum with meshes attached close to free edge along mid part of border, leaving only a very thin and irregular strip free; mesh walls high, obscuring free edge except for about distalmost two or three tiers of meshes, which have much lower walls; marginal strip here transversely or obliquely striated; apex conspicuously bifid, with tips blunt and dark. Antennule stubby and broadly fusiform; nine aesthetascs, longest about three fifths length of antennule, shortest about one third, none reaching tip of rostrum; antennular seta arises beyond middle, very slender, pointed, longer than any aesthetasc. Labrum broadly and uniformly convex anteriorly; tip short, rather broadly rounded, occasionally weakly concave on anterior side, strongly convex behind; posterior indentation narrow, constricted, with angle much less than 90°. Postabdomen with pre-anal part generally somewhat longer than anal groove; postanal part about half as long, markedly tapering; seven to nine long, straight, very

slender marginal denticles, four or five of which arise from postanal portion; proximal half of anal groove with usually two rows of setules, occasionally three, those of distal group long and projecting considerably beyond margin, those of proximal group much shorter, strongly angled anteriorly, and not projecting beyond margin; two, sometimes three, clusters of spinules on pre-anal angle. Postabdominal claw slender, weakly curved; concave margin with marked flexure about one third from spine; thence almost straight distad from here; subapical flagellum delicate but distinct, projecting well beyond tip of claw; larger basal spine slender, sharply pointed, distinctly longer than basal width of claw; smaller basal spine very slender, about half as long.

Mature male

Shell and head completely honeycombed, as in female. Postabdomen elongate, finger-like; pre-anal angle greatly reduced and obscure; lateral surface near dorsal margin armed with groups of two to four very long and slender denticles, four groups along postanal region, total number of groups corresponding to number of single denticles in the female; genital pore associated with a subterminal ventral bulge, located some distance from tip and from ventral margin. Claw similar to that of female but shorter and stubbier, and small basal spine smaller relative to large; subapical flagellum not visible at 50 × oil phase. Copulatory hook large; free limb greatly elongate and very slender, with two curved ridges near tip. I.d.l. setae much reduced in relative size compared with female; male seta on i.d.l. not visible, nor is copulatory brush seta.

Parthenogenetic female

Shape. Broadly robust (figures 119–123); dorsal margin highly arched, curvature greatest at head-shell junction (figure 65); posterior-dorsal angle distinct, bluntly pointed, slightly protruding; posterior margin short, relatively straight; posterior-ventral angle broadly rounded; midventral bulge distinct. Rostrum tucked backward against shell. Ocellus considerably smaller than eye and located closer to eye than to tip of rostrum. Covered everywhere with large deep honeycomb meshes, not organized into any pattern of ridges, collars, or spines.

Shell. About 120 meshes on half the shell, those posterior to midventral bulge and those in posterior portion of head much larger than those toward front (figures 67, 69). Interior of meshes with irregular spiderweb pattern of crinkly ridges of varying height, producing rather coarse and irregular network, radiating outward from centre, with several elongate ridges in almost every mesh (figures 125, 128). Edges of mesh walls, at least on tip of rostrum, along ecdysial line, and along ventral margin, fringed with fine setules (figures 128, 129, 131). Setae of ventral duplicature 24–29 ($n = 15$; mean, 26.7), those in posterior two-thirds connected by a heavy line, those in anterior third being isolated from one another (figure 69). No significant setae along mid-ventral bulge, but row of short setules present not reaching margin (figure 127); posterior to last ventral seta a row of short setules that is about as long as one intersetal distance, ends posteriorly in large and more distinct setule (figure 126).

Head. Posterior portion broadly expanded and rounded (figure 67), in keeping with robust nature of this species. In small specimens meshes project beyond margin of rostrum almost to tip (figure 68), in large a variable expanse of free margin at tip, resulting from bordering meshes being lower and not projecting outward; when viewed from side (figure 129) this free border

largely obscured anterior to fornices by mesh walls arising almost at edge; free margin cross or obliquely striated distally (figures 66, 129, 131). Tip of rostrum finely but bluntly bifid (figures 66, 67, 129, 131) and heavily chitinized, usually appearing very dark in phase optics. The i.p. distance usually greater than p.p. distance (15 out of 19 headshields), with the i.p./p.p. ratio decreasing somewhat with increasing size. Both distances increase with size of headshield, the p.p. distance at a somewhat faster rate.

Antennule (figure 77). Simple fusiform, rather broad, with six rounded scallops at tip. Nine aesthetascs, all terminal, shortest ones about two thirds length of longest, but none much longer than half length of antennule. Antennular seta slender, finely pointed, longer than the aesthetascs; arising slightly distad from middle.

Antenna (figure 76). Formula 0-0-3(1)/0-1-3(1). One of terminal setae of endopodite only about half as long as other six swimming setae. Terminal spine of endopodite very small and delicate, barely visible; that of exopodite somewhat longer and more easily visible. All segments of both branches elongate.

Labrum (figures 95-100, plate 8). Expanded anteriorly as a plate extending between the antennules. Anterior margin evenly convex, sometimes very weakly concave near tip, short, only slightly narrowed tip. Posterior margin evenly convex. Posterior angle markedly acute. Tip reaches or slightly exceeds tip of rostrum in undistorted specimens.

Trunklimb I (figures 86, 87). Conforms to common pattern of morphology in these small *Chydorus* species: two setae on o.d.l. and three on i.d.l., one of latter being long, stout, heavily chitinized, and provided with long setules in distal third. Middle seta in middle group on corm longest, then dorsal seta of this group. Accessory setae of all three groups well developed.

Trunklimb II (figure 90). Conforming to general pattern in relative size and armament of the eight scraping spines and in structure of gnathobasic setae and filter comb. Scraping spine 4 (counting from gnathobase) most heavily chitinized and with stoutest denticles.

Trunklimbs III-V. Setae in gnathobasic filter comb number 8, 6, and 4, respectively, and 'soft' setae on exopodite number 7, 7, and 4, respectively. The general configuration of these trunk limbs among the various *faviformis*-like species seems almost indistinguishable.

Postabdomen. Pre-anal angle sharp, protruding, and very prominent (figures 70-73, 124, 138, plate 5). Distal end of anal groove indicated by sharp angle in contour seen from side. Anal groove subequal in length to pre-anal portion, much longer than postanal portion. Dorsal margin provided with seven to nine long, slender, straight denticles on each side, of which four or five attached to postanal portion and rest to anal portion; latter strongly angled with respect to margin, whereas postanal denticles nearly normal to margin or slightly angled proximally. Denticles generally more or less parallel, except that fourth or fifth from the end angled more strongly, giving impression of two convergent series. Proximal to denticles along anal groove a row of fine setules projecting beyond margin, decreasing in length proximad, followed by second row of coarser, shorter, and more widely spaced setules, strongly angled with respect to margin and not projecting beyond margin. Pre-anal angle provided on each side with three groups of rather stout spinules. Lateral surface provided with submarginal row of eight or nine crescents of fine setules, proximalmost two or three crescents being strongly V-shaped. Farther from, and at a marked angle to, margin, two or three crescents of more delicate setules. Abdominal setae long, but considerably shorter than length of postabdomen. Immature specimens (figure 70) with much shorter postanal portion, making postabdomen almost quadrangular in shape, and with widely spaced, coarse, denticle-like setae along entire length of anal groove.

Postabdominal claw (figures 74, 75). Long, slender, tapered to sharp point; convex margin weakly and somewhat unevenly curved; concave margin with setules throughout length, those in proximal third markedly shorter than others. Subapical 'flagellum' long and distinct. Two basal spines, the larger longer than basal width of claw, curving outward slightly, and tapered uniformly to sharp point; shorter spine very slender and sharp, only about half as long.

Male

The mature male on the slide prepared by G. B. Deevey has many essential details obscured, hence only a partial description can be given. The following are the major points.

(i) The specimen is strongly honeycombed everywhere.

(ii) The postabdomen is not constricted and tapered in the manner of *C. faviformis* sens.st. but instead is elongated, finger-like, and has a distinct postanal angle (figure 116, plate 9). Along the anal and postanal portions are very long, slender, straight, submarginal spines in pairs or triplets, the number of such groups corresponding almost precisely to the number of marginal denticles in the female. This doubling of the setae is reminiscent of the strong doubling tendency in instar-II males of *faviformis*. Proximad from the spines is a row of fine setules, about as in the female. The distal end seems to have a bulge ventrally, on which the genital pores open. The irregularity in the middle of the ventral margin is certainly a distortion from preservation.

(iii) The postabdominal claw is very similar to that of the female, although possibly a little stouter. The large basal spine was distinct, but the smaller one was difficult to resolve. No subapical flagellum was visible using oil phase.

(iv) The rostrum is shorter relatively than in the female. Few details could be made out, but the rostrum seems to be rounded truncate and to have a short, stout spine at the tip.

(v) The socket from which the antennular seta arises is located slightly more than half the distance toward the apex (figure 118). The two-segmented male seta arises about at the same distance. Only five of the aesthetascs are visible, but the socket from which the aesthetascs arise number twelve, three of which are subterminal. The longest aesthetascs are about as long as the antennule, their tips exceeding the tip of the rostrum.

(vi) Trunklimb I (figure 117) was obscured and distorted. The copulatory hook is widely open, with the free limb being elongated, very slender, somewhat irregular toward the tip, and having two curved ridges at the tip. The three i.d.l. setae are markedly reduced in length compared with the female. The male seta on the i.d.l. and the copulatory brush seta could not be resolved.

(c) *Chydorus obscurirostris tasekberae* n.subsp.

Etymology

Genitive case (assuming female gender) of the combined name of the type locality.

Type locality

Tasek Bera in the east-central portion of the Malay Peninsula. Nine samples collected by B. A. G. Idris on 20 April 1982 from four different localities in the marsh yielded a variety of specimens and exuviae, most of which, unfortunately, had been distorted in preservation. Tasek Bera is the only locality in Malaysia from which this taxon is known. It was first reported in the literature from here by Idris (1979) as *Chydorus faviformis*. Earlier (in 1974) Fernando showed me some specimens in Malaysia, and later (1976) he sent me some rough camera lucida drawings of the taxon.

Comments

This taxon agrees very closely with the description of *Chydorus obscurirostris* from Australia. Because the specimens are poorly preserved, and no males are among them, the conspecificity, or otherwise, of the Australian and Malaysian taxa cannot be decided at present. Consequently the taxon, at least for the moment, is listed as a geographical subspecies of the Australian taxon.

Types

Type series. All the specimens (roughly 90) and exuviae from the nine samples collected by Idris in Tasek Bera.

Holotype. A mature parthenogenetic female 0.34 mm long, mounted on a slide in glycerine jelly, has been placed in the Australian Museum (registration number P 35712).

Paratypes. These are as follows.

(i) Australian Museum. Registration numbers: slide of two females in glycerine jelly (P 35713); slide of two females in polyvinyl lactophenol (P 35714); slide of heads, shells, and dissected exoskeleton (P 35715); slide of dissected parthenogenetic females (P 35716).

(ii) United States Natural History Museum. Catalogue numbers: slide of two females in glycerine jelly (227023); slide of two females in polyvinyl lactophenol (227024); slide of heads, shells, and dissected exoskeleton (227025); slide of dissected parthenogenetic females (227026).

(iii) British Museum (National History). Accession numbers: slide of 2 females in glycerine jelly (1985.201–202); slide of two females in polyvinyl lactophenol (1985.203–204); slide of heads, shells, and dissected exoskeleton (1985.205–206); slide of dissected parthenogenetic females (1985.207–208).

All the remaining specimens and exuviae are in the D. G. Frey collection in Bloomington.

Most of the illustrations of the Malaysian taxon are not referred to specifically in the following account, but when considering the description of the Australian taxon, the reader should compare illustrations of corresponding parts of the Malaysian and Australian taxa.

Differences from Australian taxon

In spite of the poor condition of the specimens, which made careful observation difficult, the following differences seem more or less distinct.

(i) Setae in posterior ventral duplicature of shell. Malaysian specimens have more setae here (mean 28.7, range 27–32, $n = 30$) than do the Australian (mean 26.7, range 24–29, $n = 15$). In the Australian specimens there is a cluster of setules posterior to the ventral setae, but the posterior member although the largest is not large enough to be called a seta. In the Malaysian specimens the posterior member of the group is now large enough to be counted, although still considerably shorter than the seta in front of it (figure 141, plate 12). Thus, the number of duplicature setae is increased by one, and the row of setules posterior to them is eliminated. The posterior shell margin of the Malaysian specimens is free of any other setules.

(ii) Fringing setules in mesh edges. Malaysian specimens tend to have such fringing setules more generally distributed than do Australian.

(iii) I.p./p.p. relationships. Measurements made from mounted headshields covering about the same size range show that the i.p. distance averages more and the p.p. distance less in Malaysian specimens, resulting in the i.p./p.p. ratio being considerably larger. Furthermore, both dimensions increase with size of headshield, although the individual variation is great,

especially in the midlength range. In both populations the p.p. dimension increases at a faster rate than the i.p. dimension, resulting in the i.p./p.p. ratio continually decreasing with size. The means and ranges of these relationships, expressed in micrometres, are shown below.

dimension	Australia	Malaysia
<i>n</i>	19	15
i.p.	80 (64–91)	80 (66–95)
p.p.	74 (52–96)	71 (57–86)
i.p./p.p.	1.10 (0.90–1.42)	1.19 (1.02–1.35)
t.l.	324 (282–363)	335 (291–372)

(iv) Setae of inner distal lobe (i.d.l.) of trunklimb I. The largest of three i.d.l. setae in the Malaysian specimens is relatively longer and more slender than in the Australian specimens (figure 88; cf. with figure 86). This relationship has not been quantified.

(v) Postabdomen (figures 110–113, 135, 136, 139). The Malaysian taxon has a somewhat higher count of marginal denticles; these tend to be curved rather than straight as in the Australian taxon, shorter and somewhat stouter. The Malaysian taxon also exhibits a distinct tendency for doubling of the denticles along the anal groove, whereas in the Australian taxon these denticles are nearly always single.

(vi) Postabdominal claw (figures 114, 115, 137). Both basal spines are stouter than in the Australian taxon, and the subterminal flagellum is better developed. The Australian taxon seems to have fewer spinules along the concave margin, both in the short, stubby proximal group and in the longer spinules of the distal group. However, these are scarcely countable with certainty using the light microscope.

Ephippial female

A headshield and an exoskeleton were recovered. The body is narrow and higher dorsally than in the parthenogenetic female. Except for the mesh walls being lower, there is little other change in surface configuration; the ephippium seems to lack any marked pigmentation. In lateral view there is a marked depression in dorsal contour in the region of the minor pores. The anterior part of the shell will be sloughed off on moulting along a line of irregularity in shell pattern; this line of separation extends to the ventral margin of the shell almost at the posterior end of the duplicature (figure 109), thereby affording little likelihood that these anterior pieces would remain attached to the ephippium after moulting. The headshield (figures 107, 108) is more elongate and tapered posteriorly than in the parthenogenetic female in order to accommodate the changed dimensions of the ephippial female. A bluntish lateral expansion on each side posterior to the fornices projects into a notch in the shell at the upper end of the slough line.

Size

Overall length range excluding the honeycomb meshes, 0.23–0.39 mm ($n = 64$); mature parthenogenetic females, 0.28–0.39 mm ($n = 39$); smallest female with embryos, 0.28 mm. Idris (1983) gives the length (total, including the meshes) as 0.36–0.45 mm ($n = 10$), with a mean of 0.41 mm. This obviously includes only the largest specimens, as in my samples the total length of mature females was 0.31–0.43 mm.

(d) *Chydorus opacus* n.sp.*Etymology*

From (L) *opacus*, shaded, dull, referring to the optically dense nature of the carapace.

Localities

Type locality. Ambangbang Lagoon, Kakadu, Northern Territory, Australia. Sample N-73 of B. V. Timms, collected 8 July 1981. Yielded 368 specimens, including ten ephippial females, one instar-II male, and one mature male.

Other localities

(i) F2403. Billabong on Crooked River, south of Couchman Range, ten miles north of Drysdale, Kimberley, Western Australia, May 1965. W. D. Williams sample number 596. Eight specimens, plus fragments.

(ii) Muirella Lagoon, Kakadu, Northern Territory. Sample N-79 of B. V. Timms, 9 July 1981. 39 specimens, including one ephippial female, plus fragments.

(iii) Unnamed billabong near Marakai Crossing, middle Adelaide River, Northern Territory. Sample N-113 of B. V. Timms, 11 November 1982. Three parthenogenetic females.

(iv) Unnamed billabong on Marakai Road beyond the crossing, Northern Territory. Sample N-114 of B. V. Timms, 11 November 1982. 19 parthenogenetic females.

(v) Unnamed lagoon near Six Mile Yard, Coleman River, Cape York, 14° 55' S, 142° 53' E. Sample collected by B. V. Timms, 26 June 1983. 19 parthenogenetic females.

(vi) F6547. Sample NT-179 of R. J. Shiel. Northern Territory. 33 females, plus fragments.

(vii) Sample 724 of R. J. Shiel. Two shells.

Types

Type series. All the specimens and exuviae from Timms' sample N-73 from Ambangbang Lagoon.

Holotype. A mature parthenogenetic female 0.28 mm long, mounted on a slide in glycerine jelly: Australian Museum (registration number P 35717).

Paratypes. Suites of specimens consisting of three mature parthenogenetic females mounted on a slide in glycerine jelly, three on another slide in polyvinyl lactophenol stained with lignin pink, one ephippial female in glycerine jelly, and ten parthenogenetic females in a solution of glycerol and 5% formaldehyde in a 1:1 mixture have been deposited in the museums as follows.

(i) Australian Museum. Registration numbers: slide of mature females in glycerine jelly P 35718; slide of females in polyvinyl lactophenol P 35719; slide of ephippial female in glycerine jelly (P 35720); specimens in liquid P 35721.

(ii) United States Natural History Museum. Catalogue numbers: slide of mature females in glycerine jelly 227027; slide of females in polyvinyl lactophenol 227028; slide of ephippial female in glycerine jelly 227029; specimens in liquid 227030.

(iii) British Museum (Natural History). Accession numbers: slide of mature females in glycerine jelly 1985.209-211; slide of mature females in polyvinyl lactophenol 1985.212-214; slide of ephippial female in glycerine jelly 1985.215; specimens in liquid 1985.216-225.

All the remaining specimens and exuviae are in the D. G. Frey collection in Bloomington.

Short diagnosis

C. opacus is a small, honeycombed species in which the meshes are small, numerous, and have low walls. Possibly the most distinctive feature is the seemingly overlapping layers of irregularly waved and anastomosing striae within the meshes, which generate the characteristic pattern of fine round holes as seen with the light microscope and make the shell opaque. The forward expansion of the headshield over the eye creates a marked change in curvature as seen from the side, giving the animal a distinctive appearance. Rostrum with a clear marginal strip not covered by any honeycombs, and with meshes along strip having low walls. Tip of labrum rather broad, convex on both sides, and with angle behind the tip very narrow; small keel on labrum projects forward between the antennules. Ehippium with little pigmentation. Postanal portion of postabdomen very short, strongly tapering toward base of claws. Anal and post-anal series of marginal denticles converging in their direction of elongation. Postabdominal claw with two basal spines, the proximal one slender and more than half the length of the long distal spine.

Size (figure 285)

Overall length range (minus the honeycomb meshes), 0.20–0.32 mm ($n = 299$); parthenogenetic females with eggs, 0.26–0.32 mm ($n = 87$); ehippial females, 0.28–0.31 mm ($n = 10$); instar-II male, 0.21 mm ($n = 1$); mature male, 0.22 mm ($n = 1$). Some of the 374 specimens recovered were too distorted to be measured.

Parthenogenetic female

Shape. Resembles that of *C. sphaericus* sens. str. but considerably broader (figure 148, plate 13). Head with a distinct bulge over the eye that produces a marked change in dorsal contour (figures 144–146). Posterior-dorsal angle rather sharp and protruding. Posterior-ventral angle obscure, almost lacking. Prominent mid-ventral bulge. Covered everywhere with small meshes having low walls. Type population from Ambangbang Lagoon heavily plastered posteriorly with a sessile unicellular alga (?).

Shell. About 190 meshes on each half shell. Interior of meshes (figure 181) consists of several layers (?) of short, irregular, branching and anastomosing lines, producing characteristic pattern of round, light spots in phase contrast, and making shell so dark that details of trunk limbs, postabdomen, and labrum, difficult to resolve even in cleared specimens. Ventral duplicature with 24–27 submarginal setae ($n = 22$), of which posteriormost scarcely shorter than those in front; all attached to prominent solid line that continues dorsad along posterior margin (figure 165, plate 14). No setules visible under s.e.m. along this line posterior to duplicature (figure 176, plate 16) nor along mid-ventral bulge. Anterior to bulge some long, very slender setae, difficult to see and enumerate even under s.e.m.

Head. Headshield covered with shallow honeycomb meshes (figures 155, 156), smallest and lowest in height over eye (figure 168, plate 15). Headshield broad posteriorly and broadly rounded. Rostrum with margin free of meshes, but with irregular patterning of same kind as occurs within meshes, resulting in transverse or oblique striae near tip, and in irregular longitudinal striae toward fornices (figures 171, 172). Tip of rostrum most commonly weakly bifid with rounded tips, sometimes asymmetrically bifid, sometimes with just a single point (figures 157–159, 171–172). The i.p. distance usually greater (six out of ten instances) than

p.p. distance, both measurements increasing irregularly with headshield length. Ocellus distinctly smaller than eye (figures 144–146); much closer to eye than to tip of rostrum.

Antennule (figures 152, 173). Short and broad. With nine aesthetascs, all arising close together at tip; much shorter than antennule, shortest being less than half as long as antennule. Antennular seta slender, arising beyond middle of antennule, longer than any aesthetasc.

Antenna (figure 151). Formula 0-0-3 (1)/0-1-3 (1). Spines on terminal segments very small, that on exopodite slightly larger. Swimming setae of exopodite equally long, matching two of terminal setae of endopodite plus that arising from middle segment. Third terminal seta of endopodite less than half as long as other two.

Labrum (figure 173). Broad from side to side, but provided with flattened keel projecting forward between antennules. Bowed outward prominently in front, with slight concavity toward tip. Tip convex on both edges. Post-tip angle constricted and much less than 90°.

Trunk limb I (figures 149, 175). Two o.d.l. setae, one of which is very small, and three i.d.l. setae, one of which is large, heavily chitinized, and sharply angled in distal half, and provided with coarse setae. Middle seta of middle group on corm longest, then dorsal seta of this group. Accessory setae of middle and dorsal groups well developed and readily visible. As the illustration is of the lateral surface, it does not show the accessory setae well.

Trunk limb II (figures 150, 177). With four typical gnathobasic setae and eight setae in the gnathobasic filtering comb. First five spines with countable transverse setules along distal half, those of spine 4 being stoutest. The curved spine beyond scraping spine 8, though present was not visible in the specimen drawn.

Trunk limbs III–V. Seem not to differ appreciably from those of *C. faviformis*.

Postabdomen (figures 160, 161, 163). Dorsal and ventral margins roughly parallel for some distance anterior to sharp postanal angle. Postanal portion short and tapered strongly toward base of claw. Pre-anal angle large, prominent, and protruding in typical *Chydorus sphaericus*-group fashion. Seven to eight long, slender denticles, arranged in two converging groups, with convergence most commonly occurring between third and fourth denticles from distal end, occasionally between fourth and fifth. Three sequential series of setules along anal groove between marginal denticles and pre-anal angle, becoming progressively finer and more delicate proximad. Typical clusters of setules along sides, and two clusters of coarser setules at pre-anal angle.

Postabdominal claw (figures 162, 174). Two basal spines, larger slender, curved outward slightly, and about as long as basal width of claw, smaller very slender but more than half length of larger. Concave surface with series of setules, about seven beginning just beyond larger spine, short, stout, and rather widely spaced, followed by about 14 longer, at first stout but then become more slender distad. Subapical 'flagellum' arising from convex side of tip prominent.

Ephippial female

Single ephippial egg (figure 164) considerably larger than parthenogenetic eggs. Brood pouch expanded dorsally and contracted in width from side to side to accommodate egg. Headshield with triangular lateral expansions immediately posterior to fornices (figures 166, 178, 180), which project between ephippium and anterior portion of shell that, in typical *Chydorus* fashion, peels off ventrally and laterally on moulting (figure 165). Posterior portion of headshield elongated and tapered to rather narrowly rounded tip. Very little pigmentation in egg locule region. Surface sculpturing very similar to that of parthenogenetic female except for lower honeycomb walls.

Males

Only one instar-II and one mature male were recovered from the voluminous sample. These were studied first via temporary mounts in glycerol, with camera lucida drawings being made of the lateral view. Then the left shell of each specimen was dissected away, and the specimens were processed for s.e.m. examination. Not all the desired details could be observed clearly in any of the preparations.

Instar-II. Small, being in length range of instar-I females (figure 285). Dorsal margin flattened and irregular (figure 153), especially over head pores. Marked change in curvature over eye, with rostrum bending sharply ventrally, then posteriorly at tip. Posterior-dorsal angle protruding slightly, but posterior-ventral angle essentially absent, as in female. Eye and ocellus both large; ocellus somewhat closer to eye than to tip of rostrum. Rostrum considerably shorter and broader than in female; tip weakly bifid. Antennule larger and more robust than in female, but all nine aesthetascs still terminal. Postabdomen very similar to that of immature females, in that postanal portion very short, resulting in short, subquadrangular shape for anal and post-anal portions. Copulatory hook J-shaped, rather blunt at tip, with one or more short rows of very fine denticles producing serrated ridges (figure 182, plate 17). Anlage of male i.d.l. seta well developed, with broad, stout base and much narrower second segment (?) that tapers to bluntish point.

Mature. Small; only slightly longer than instar-II and barely longer than biggest instar-I female (figure 285). Height of mesh walls greatly reduced compared with female, especially low over compound eye and distal quarter of rostrum (figure 154). Dorsal margin irregularly flattened, with even more marked change in curvature over compound eye than in instar-II male; posterior-dorsal angle protruding somewhat; posterior-ventral angle lacking as any detectable change in curvature. Head shorter and more robust than in female; rostrum tapered to blunt, roundly bifid point (figure 183); lateral margins broadly scalloped; eye and ocellus both large, ocellus about equidistant between eye and tip of rostrum. Details of antennule and aesthetascs not visible. Postabdomen elongate (figures 154, 186–188); pre-anal portion less wide than in female, which reduces prominence of pre-anal angle; anal portion not appreciably narrower than instar-II, about half as long as postabdomen from abdominal setae to insertion of claws; postanal portion with three or four long slender sometimes double denticles; no denticles along anal portion; submarginal row of crescents of setules along postanal and anal portions, a small cluster of setules immediately anterior to pre-anal angle; genital pore not visible. Postabdominal claw scarcely distinguishable from that of female, except possibly that setules on concave margin somewhat longer and stouter; subapical flagellum not visible on s.e.m.s. Copulatory hook widely open (figure 184); free portion long, slender, tapering distally to slender point, with finely toothed (dentate) ridge on medial side of concave margin for almost half its length, and toothed ridge near tip of lateral margin (figure 185).

Comments

In Australia *C. obscurirostris* and *C. opacus* can occur in the same waterbodies, but are easily distinguishable by the characters summarized in table 2. *C. opacus* seems more frequent in its occurrence, based on the limited material available.

(e) *Chydorus sinensis* n.sp.

Comments

When Jiang Xie-zhi (= Chiang Sieh-chih) came to Indiana University in 1980, he brought with him splits of samples containing various species of *Chydorus*. One of these from a ricefield in Yunnan Province contained specimens of the taxon then called *Chydorus faviformis* in the

DESCRIPTION OF PLATES 13–17

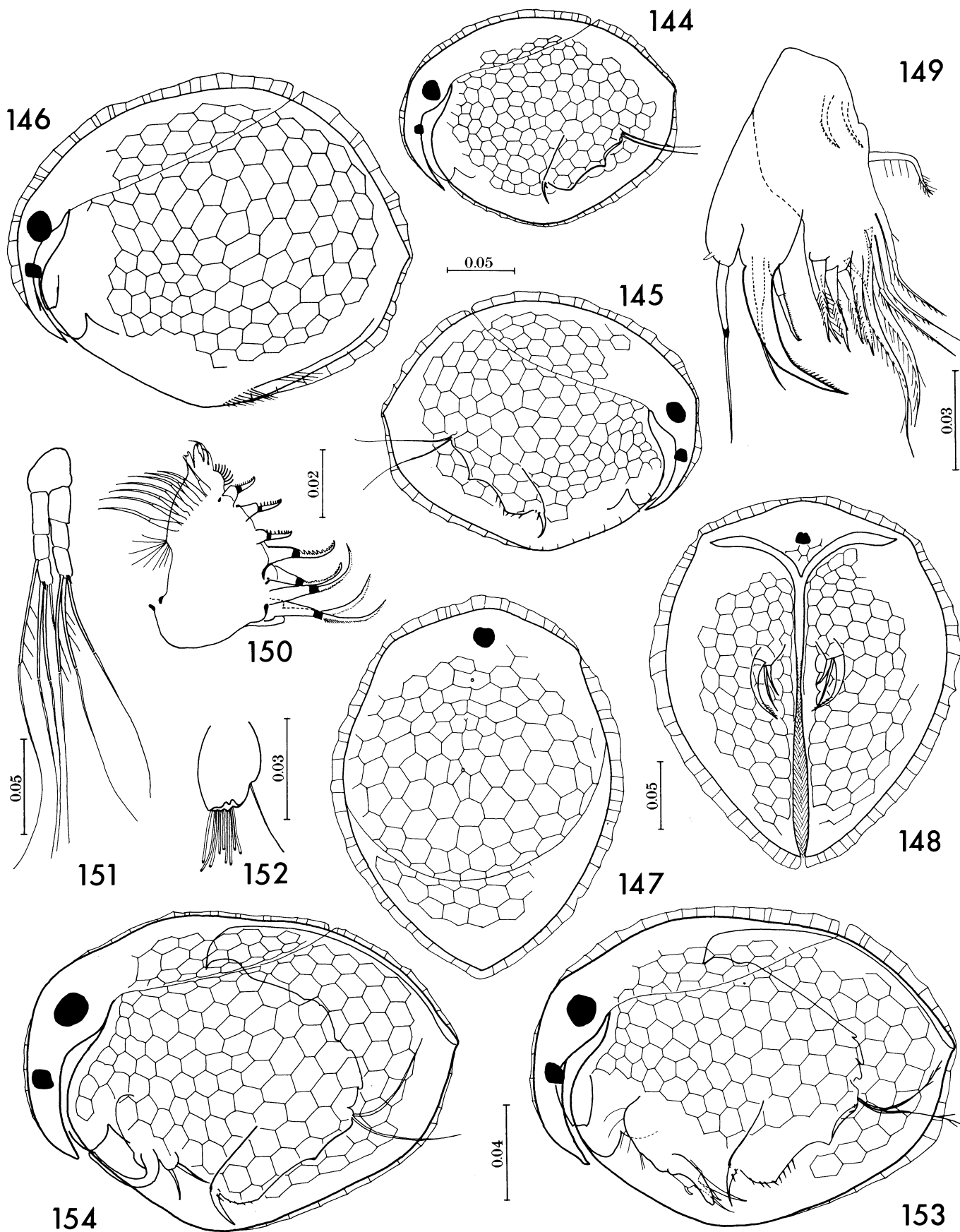
PLATE 13. *Chydorus opacus* n.sp. Figures 144–150 and 154 are of specimens from B. V. Timms' sample N-73 from Ambangbang Lagoon, Northern Territory, Australia. Figures 151–153 are of specimens from R. J. Shiel's sample from Northern Territory. (144–146) Lateral views of instar-I, instar-II, and mature females, respectively; (147, 148) top and bottom views, respectively, of mature parthenogenetic females; (149) Trunklimb I of ephippial female, showing the strongly chitinized hook-like seta on the i.d.l.; (150) trunklimb II of parthenogenetic female; (151) antenna, and (152) antennule of mature parthenogenetic female; (153) instar-II male; (154) mature male: note the broad postabdomen and the prominent pre-anal angle. In most of these specimens the marked change in curvature near the compound eye is distinctive.

PLATE 14. *Chydorus opacus* n.sp. Figures 155–159 and 164–166 are of females from B. V. Timms' sample N-73 from Northern Territory; 160 and 162 are from W. D. Williams' sample from Western Australia; and 161 and 163 are from R. J. Shiel's sample from Northern Territory. (155, 156) Headshields of parthenogenetic females; (157–159) tips of rostra of parthenogenetic females, showing the variable nature of the tip from weakly and vaguely emarginate to finely rounded; (160, 161, 163) postabdomens of mature females; (162) postabdominal claw of mature female; (164) ephippial female; (165) shell of ephippial female, with anterior portion having pulled away from ephippium along slough line; (166) headshields of ephippial female, showing the narrowing and elongation posteriorly that is necessary to conform to the changed shape of the ephippial female.

PLATE 15. *Chydorus opacus* n.sp. Figure 168 is of a female from the W. D. Williams sample from Western Australia; all the rest are females from B. V. Timms sample from Northern Territory. (167–170) Side, front, rear, and ventral views of parthenogenetic females; (171, 172) tip of rostrum, showing weak emargination, dense reticulation within meshes, and marginal strip completely free of meshes, the latter also shown to be completely free of meshes in figure 168; (173) anterior end of dissected specimen, showing particularly the labrum and the antennule (a., antennule; l., labrum; m., mandible); (174) postabdominal claw of mature female, showing the proximal and distal rows of denticles visible from the outside and the at least five clusters of denticles attached to the inner surface.

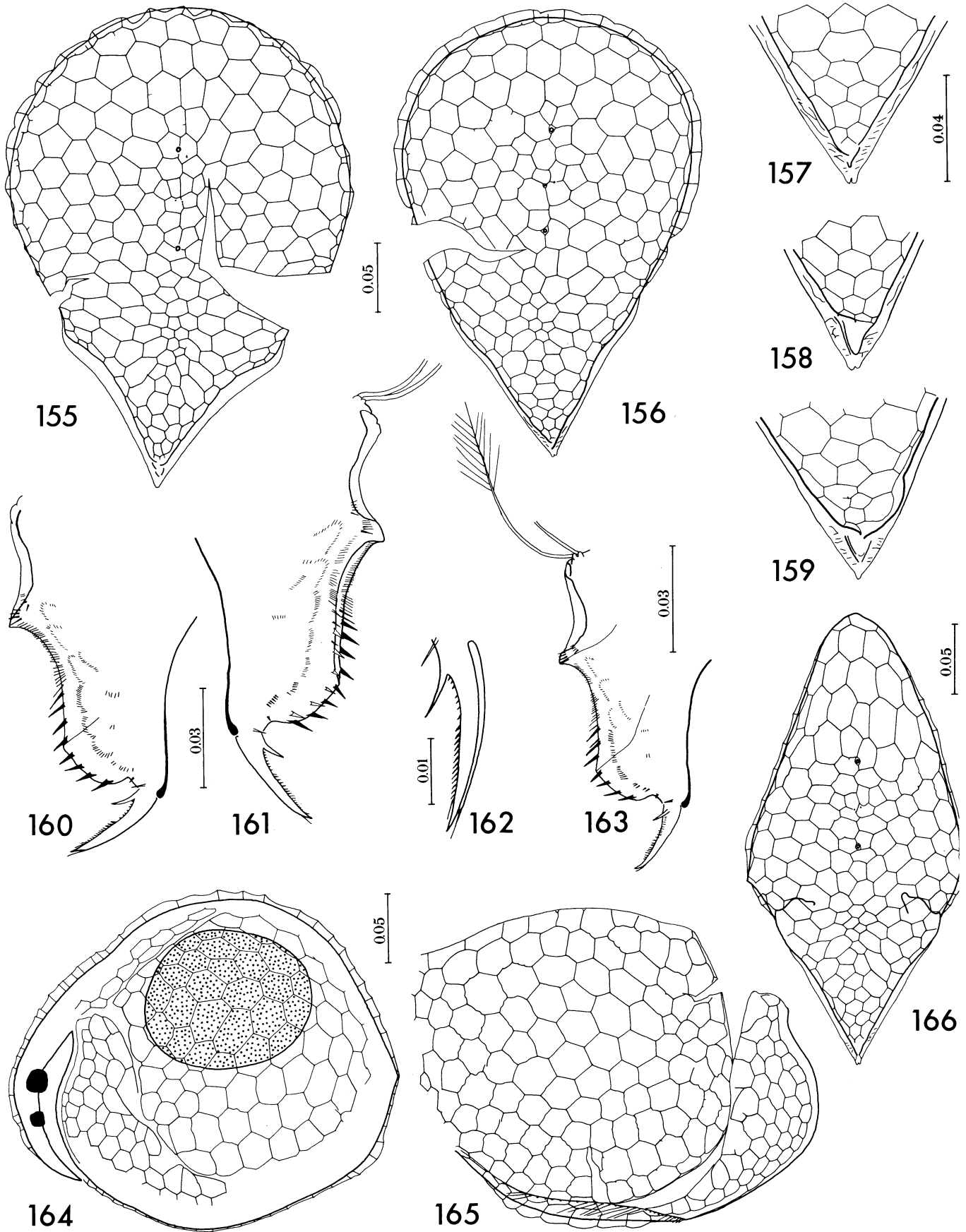
PLATE 16. *Chydorus opacus* n.sp. All figures are of females from B. V. Timms' sample N-73 from Northern Territory. (175) Basal portion of i.d.l. from inside and of o.d.l. partly obscured (o.d.l., outer distal lobe; i.d.l., inner distal lobe), showing a pore of unknown function, although possibly for some 'entangling secretion' (Fryer 1968); (176) margin of shell posterior to setae in ventral duplicature, showing complete lack of any setules along posterior margin; (177) gnathobase of trunklimb II from the inside, showing the three gnathobasic setae usually visible with the light microscope, plus a fourth seta attached somewhat laterally and usually obscured by the other three setae; (178) ephippial female from the front, showing the slough line, dense pattern of spider-web markings within the meshes, mesh-free margin of rostrum, and the very weakly emarginate tip; (179) ephippial female from side, showing the double nature of the ecdysial line, the marked indentation in the head outline over the minor pores, and the well developed slough line; (180) enlargement of same specimen to show the dip at the junction of the slough line with the ecdysial line and the corresponding development of the headshield to fill the notch (e.l., ecdysial line; s.l., slough line); (181) meshes along the ecdysial line.

PLATE 17. *Chydorus opacus* n.sp. Instar-II males and mature males, from Timms' sample N-73 from Northern Territory. (182) I.d.l. of instar-II male, showing elongating copulatory hook with minute denticles near tip, and the Anlage of the male seta (c.h., copulatory hook; m.s., Anlage of male seta); (183) tip of rostrum of mature male, showing crenulated margin near tip; (184) dissected front end of mature male, showing copulatory hook and other setae of the i.d.l. and o.d.l. (c.h., copulatory hook; m.s., male seta; o.d.l., outer distal lobe; i.d.l., inner distal lobe); (185) tip of copulatory hook, enlarged to show its tapered nature and the two longitudinal rows of fine denticles, the medial row being much longer than the lateral; (186) postabdomen of mature male, discouragingly obscured by setae of the various trunk limbs; (187) anterior end of postabdomen enlarged, showing four slender denticles along the postanal portion, various clusters or crescents of setules laterally, and the structure of the postabdominal claw being very similar to that of the female (figure 174); (188) enlarged proximal portion of anal groove, showing projecting pre-anal angle, crescents of setules laterally from margin but no setules projecting beyond margin except at pre-anal angle.

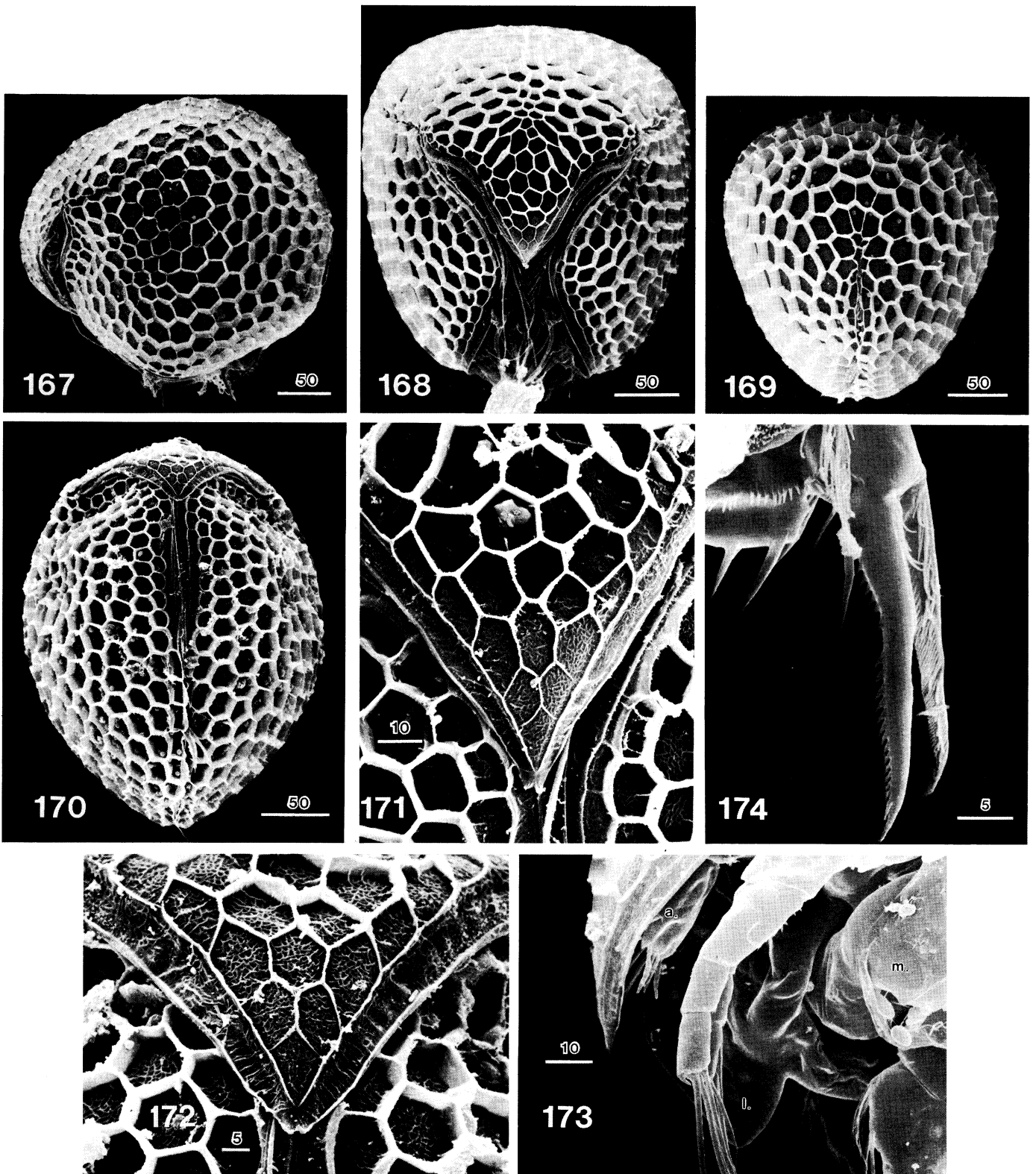


FIGURES 144-154. For description see opposite.

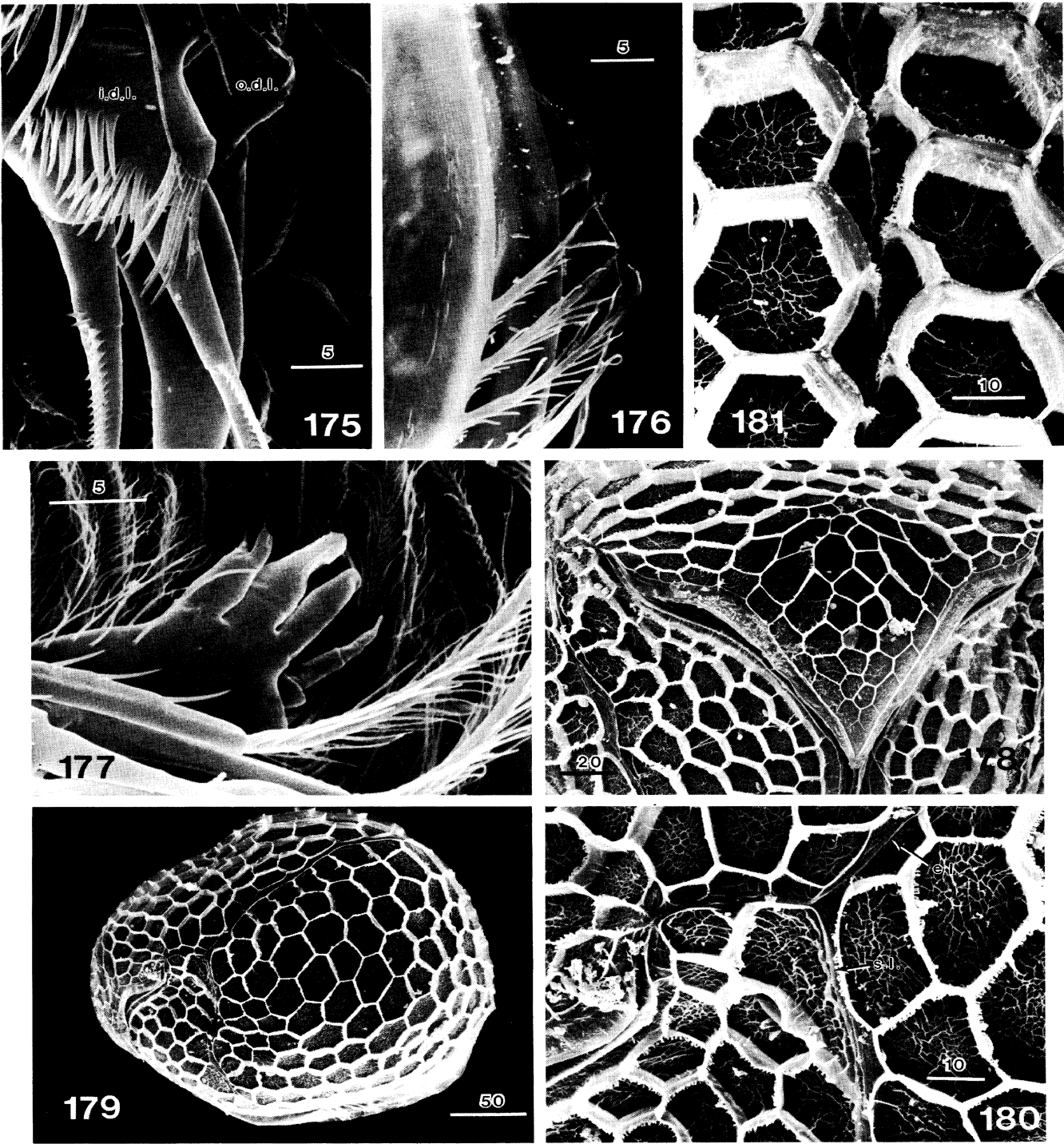
(Facing p. 376)



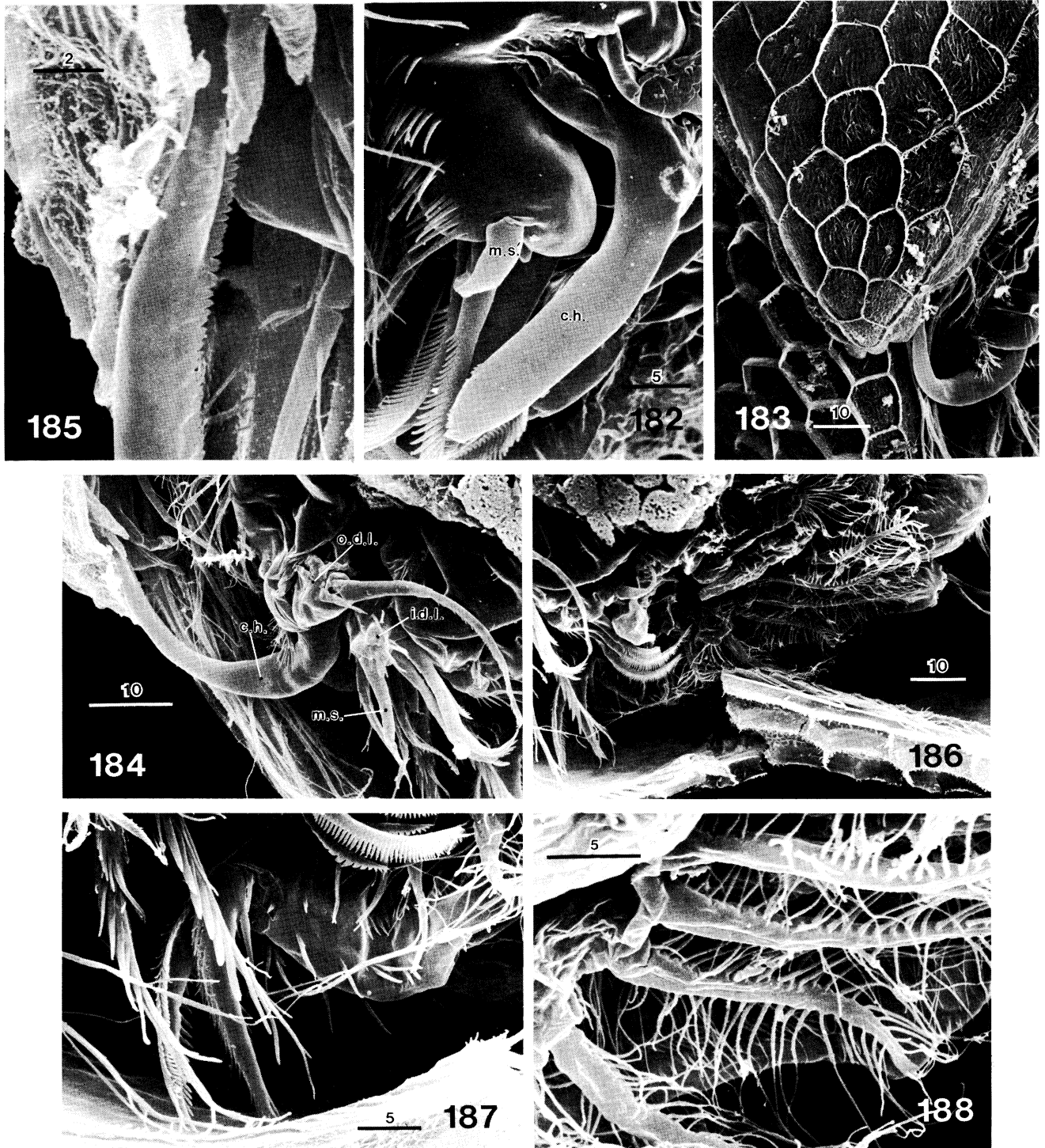
FIGURES 155-166. For description see p. 376.



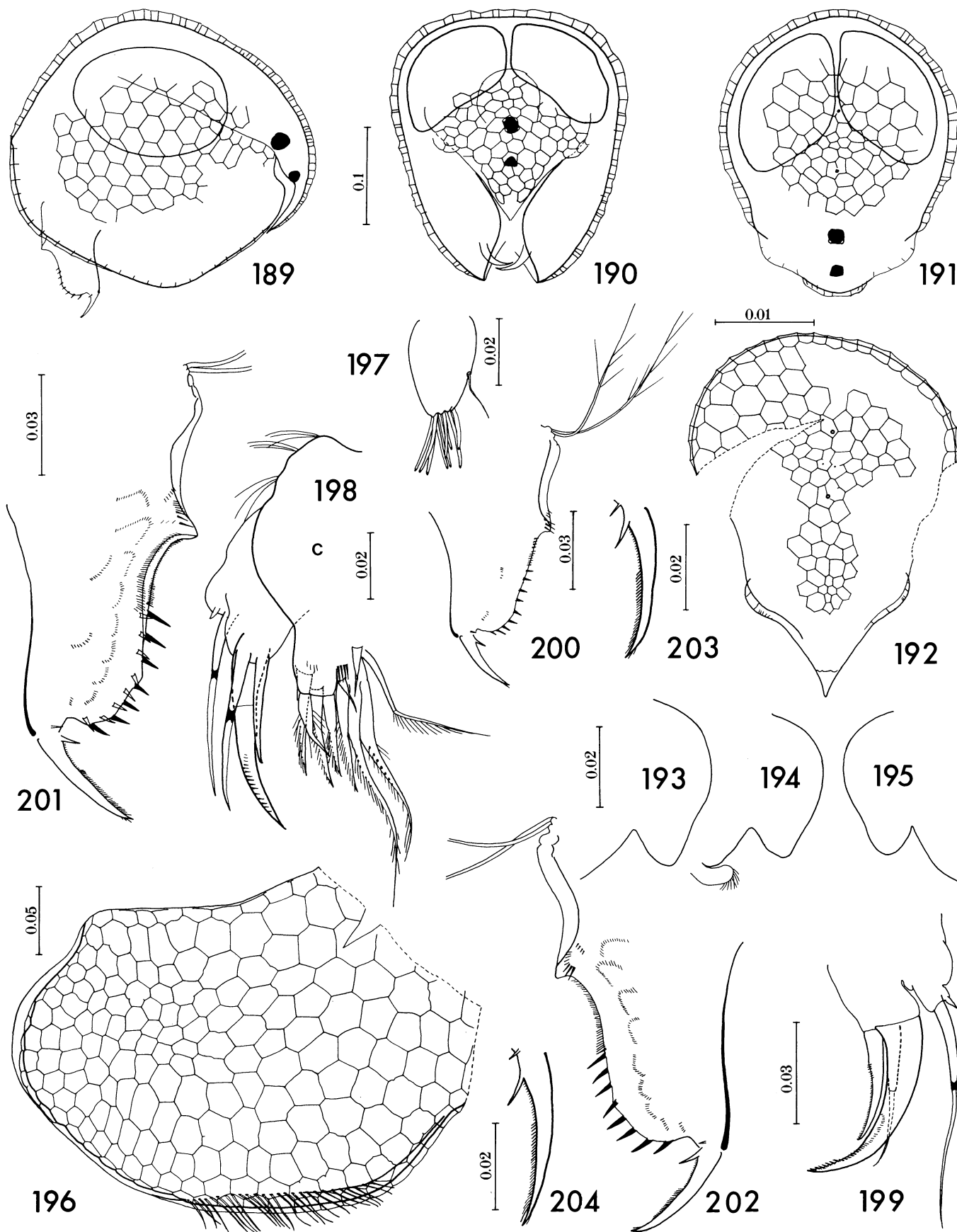
FIGURES 167-174. For description see p. 376.



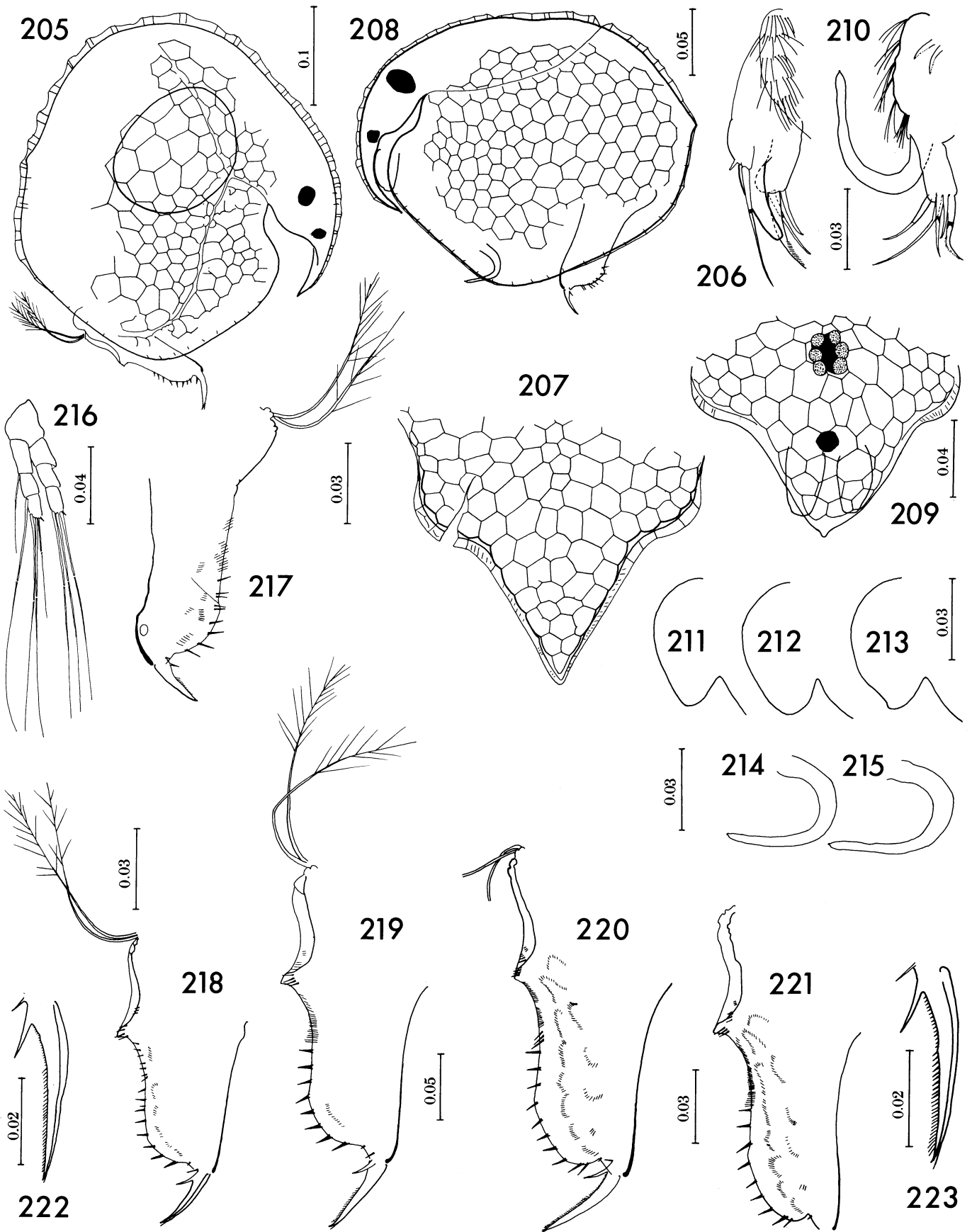
FIGURES 175–181. For description see p. 376.



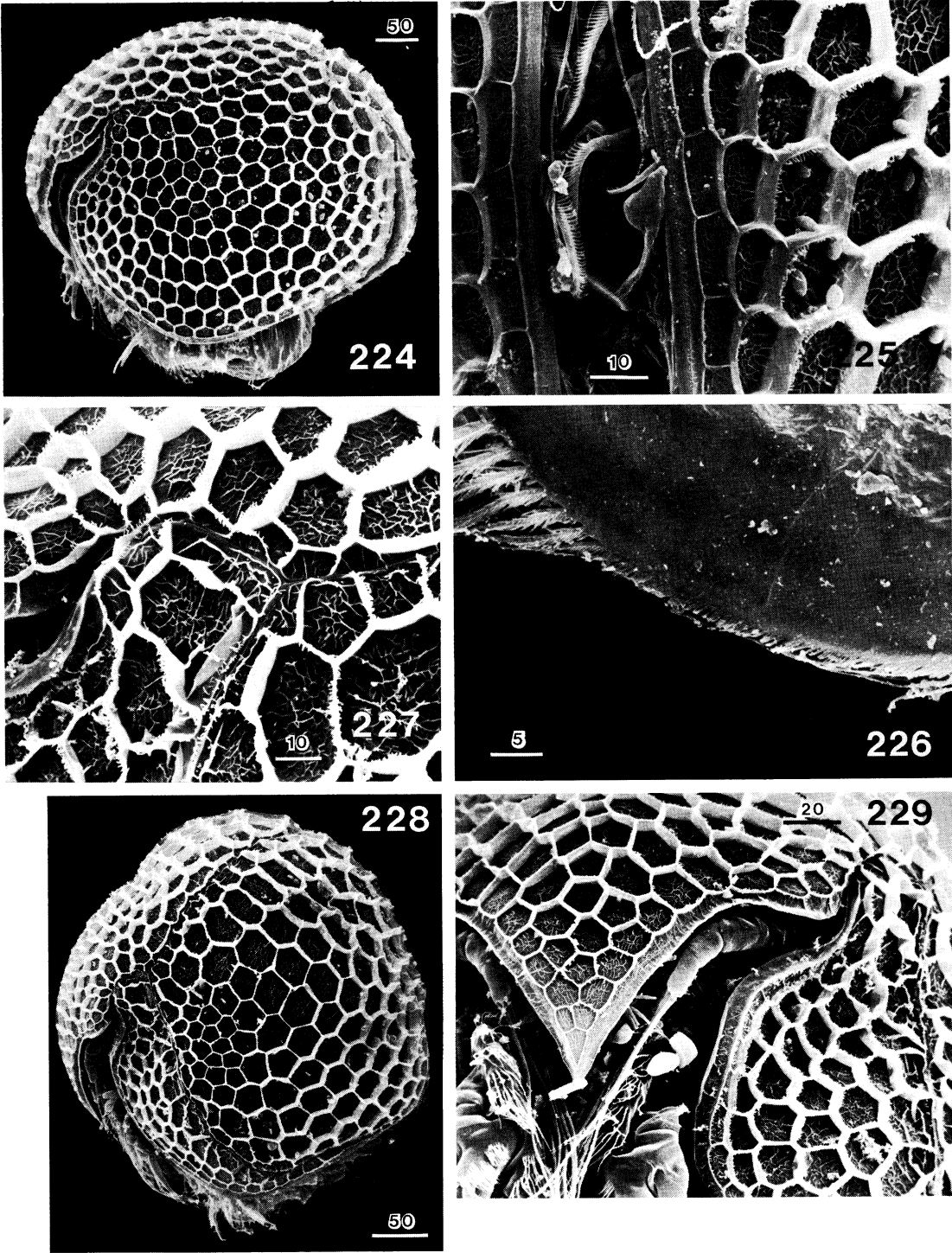
FIGURES 182–188. For description see p. 376.



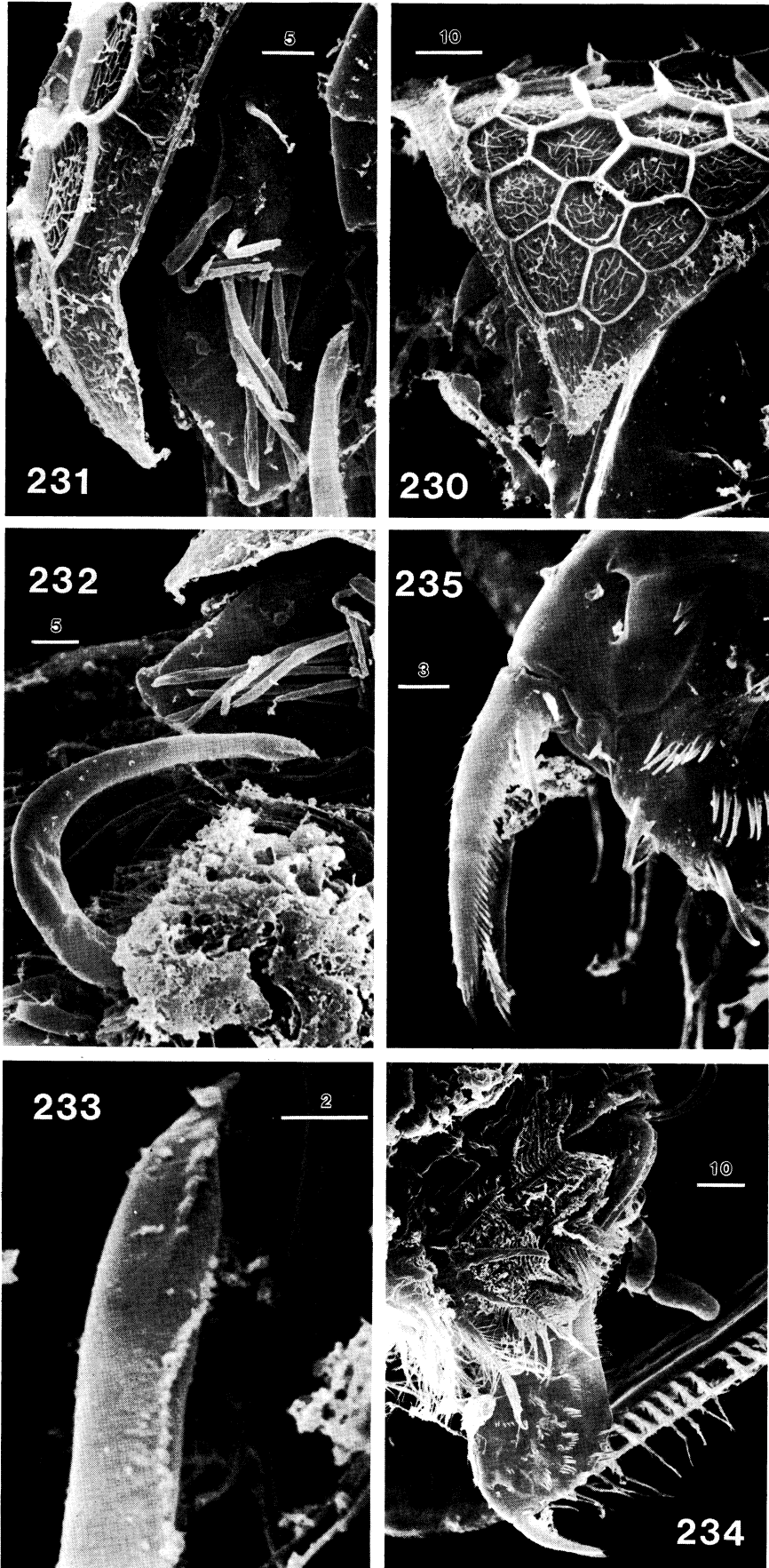
FIGURES 189-204. For description see p. 377.



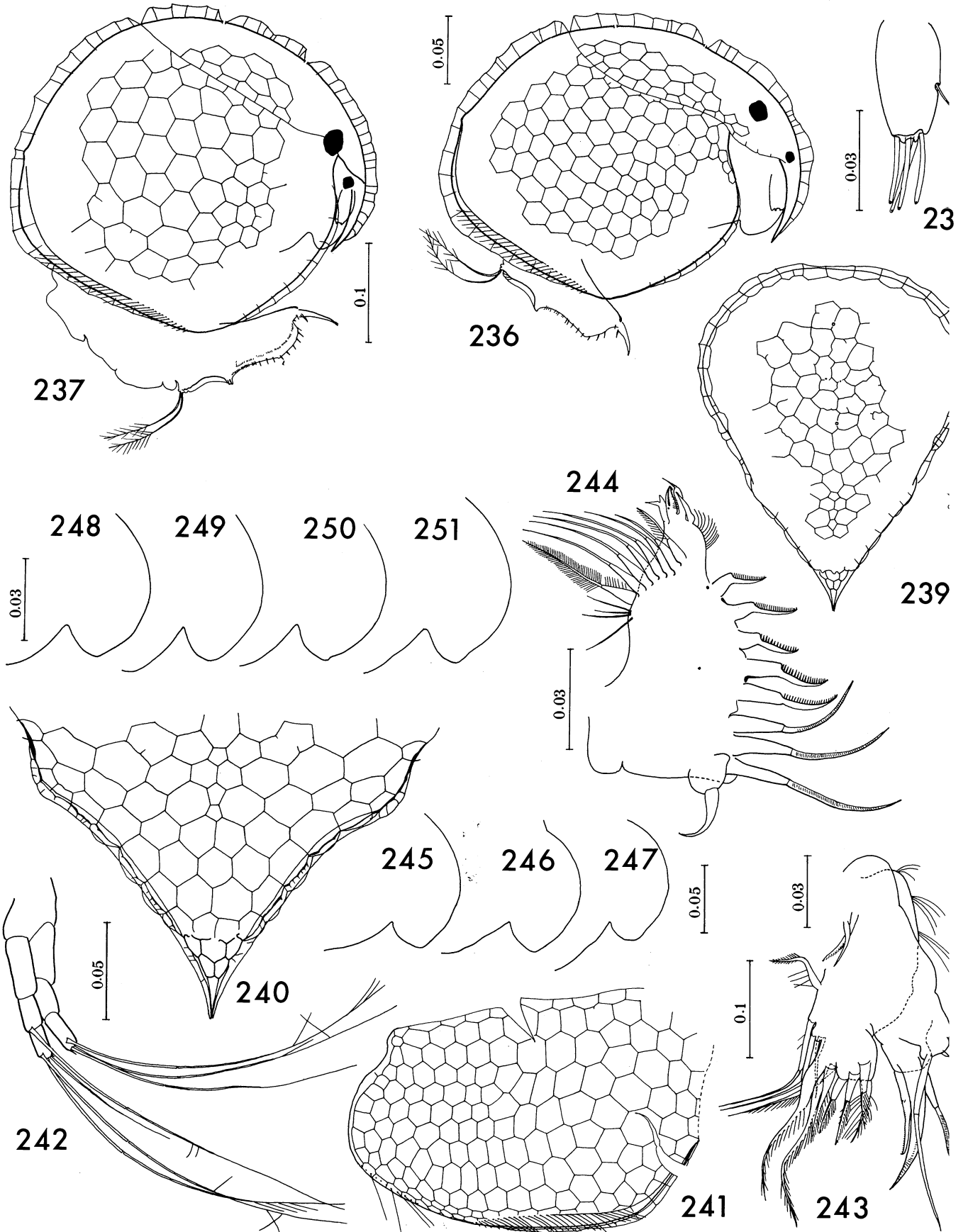
FIGURES 205-223. For description see p. 377.



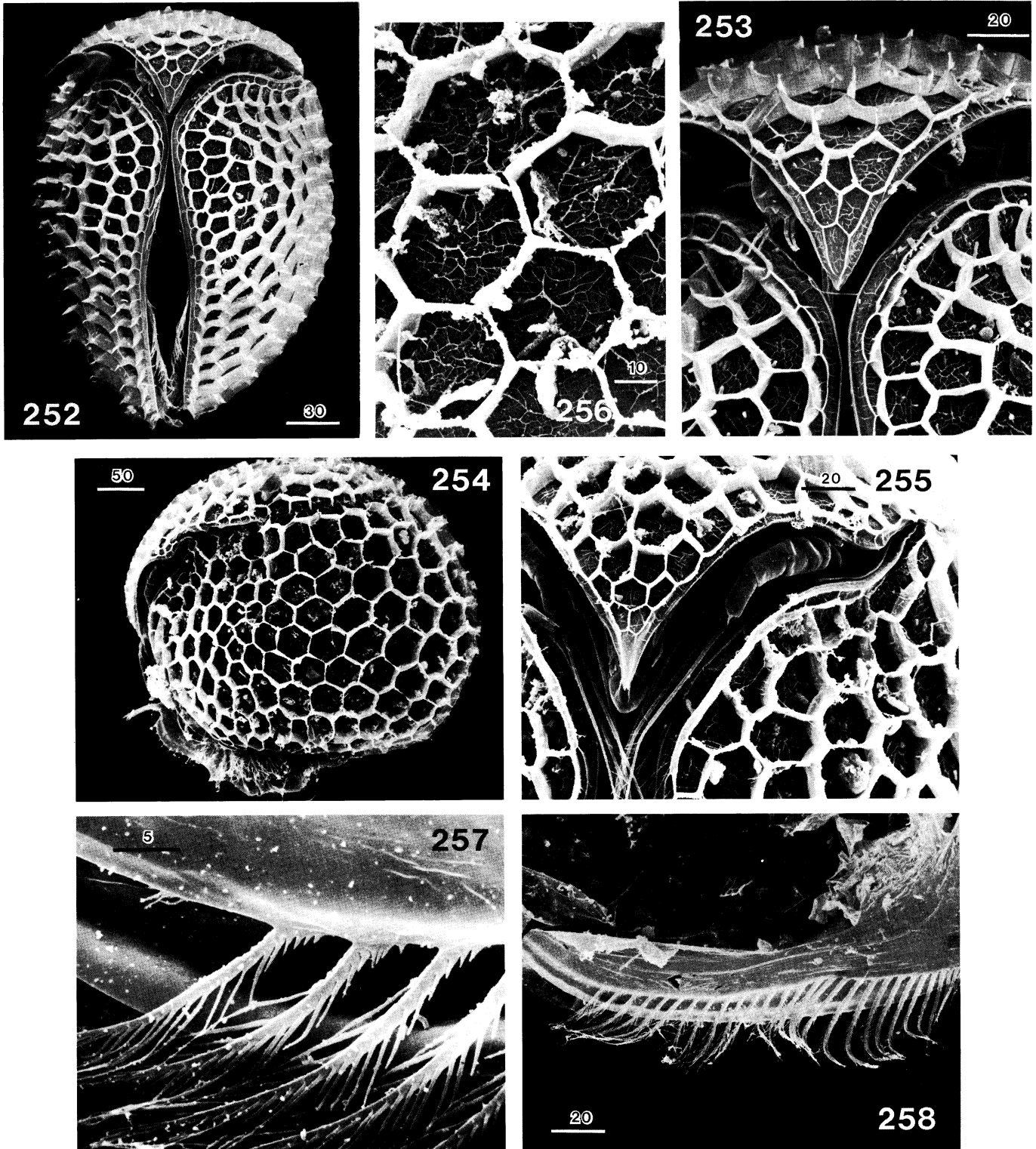
FIGURES 224–229. For description see p. 377.



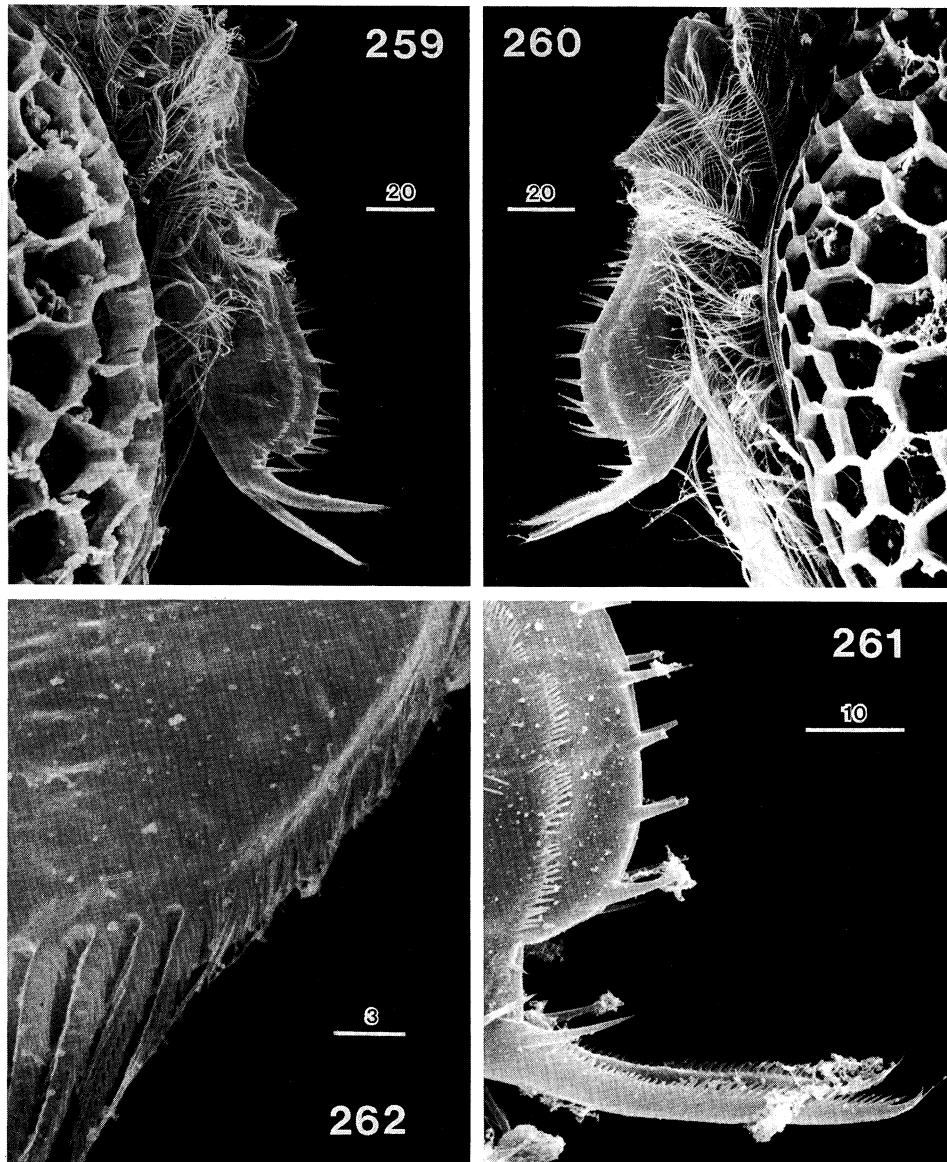
FIGURES 230–235. For description see p. 377.



FIGURES 236-251. For description see p. 377.



FIGURES 252–258. For description see p. 377.



FIGURES 259–262. For description see opposite.

literature, which included all three instars of males plus one ephippial female. The specimens were mostly distorted and were densely covered with sessile organisms including many bacteria, making it difficult to observe fine details satisfactorily. Nevertheless, the taxon can be described reasonably well.

DESCRIPTION OF PLATES 18–24

- PLATE 18. *Chydorus sinensis* n.sp. All figures are of specimens from a ricefield sample collected by Jiang in Yunnan Province, China. (189–191) Mature parthenogenetic females from side, front, and top, respectively, 190 and 191 being of the same specimen; (192) headshield from dissected female; (193–195) labra from dissected females; (196) shell; (197) antennule; (198) trunklimb I from dissected female (c., corm; o.d.l., outer distal lobe; i.d.l., inner distal lobe); (199) enlarged i.d.l. and o.d.l., showing stout hook-like seta on i.d.l.; (200) postabdomen of immature female; (201, 202) postabdomens of mature females, showing a virtually continuous row of setules projecting beyond margin of anal groove; (203, 204) postabdominal claws of mature females.
- PLATE 19. *Chydorus sinensis* n.sp. All figures are of specimens from Jiang's ricefield sample from Yunnan Province, China. (205) Ephippial female, showing ecdysial line and slough line; (206) part of trunklimb I of instar-II male; (207) rostrum of instar-II male; (208) lateral view of mature male; (209) rostrum of dissected mature male; (210) part of trunklimb I of mature male; (211–213) labra of mature males; (214, 215) copulatory hooks of different specimens of mature males; (216) antenna of mature male, showing the short seta arising from the basal segment of the endopodite; (217) postabdomen and postabdominal claw of another mature male, showing particularly the much elongated anal groove and the absence of a protruding pre-anal angle.
- Chydorus angustirostris* n.sp. All figures are of females from the pond at Jalalpur, India. (218) Postabdomen of instar-I female; (219) postabdomen of instar-II female; (220, 221) postabdomens of dissected mature females; (222, 223) postabdominal claws of dissected mature females.
- PLATE 20. *Chydorus sinensis* n.sp. All figures are of females from Jiang's ricefield sample in Yunnan Province, China. (224) Immature female; (225) ventral view of shell, showing mainly the sculpturing within the meshes and the trended presence of a fringe along the edge of the mesh walls; (226) inner ventral margin of shell anterior to large setae of duplicature (at left), showing the presence of submarginal setules all of roughly the same length, extending as an almost continuous band (although vaguely grouped) across the mid-ventral bulge; (227) side view of ephippial female at junction of slough line and ecdysial line; (228) side view of same ephippial female, showing the marked prolongation of the slough line posteriorly; (229) front-end view of same ephippial female.
- PLATE 21. *Chydorus sinensis* n.sp. All figures are of males from Jiang's ricefield sample in Yunnan Province, China. (230) Front end of dissected instar-II male; (231) front end of dissected mature male, showing antennule, labrum, and tip of copulatory hook; (232) somewhat different view of same specimen, showing all of copulatory hook; (233) tip of copulatory hook, showing its pointed nature and the presence of two rows of small denticles, the longer more posterior one of which moves from a lateral position to a sharp ridge along the inner surface; (234) postabdomen of mature male, showing the lack of a pre-anal angle and the presence of long slender denticles only on the postanal portion except for a single denticle about midway along the anal groove; (235) enlarged terminal portion of postabdomen, showing the location of the genital pore and the fine structure of the claw.
- PLATE 22. *Chydorus angustirostris* n.sp. All figures are of parthenogenetic females from the pond at Jabalpur, India. (236) Side view of instar-I female; (237) side view of mature female; (238) antennule, with fewer than half of the aesthetascs visible; (239) headshield of mature female; (240) rostrum of mature female, showing the elongation or attenuation of the tip; (241) cast shell of mature female; (242) antenna; (243) trunklimb I; (244) trunklimb II, showing four teeth on the gnathobase, as in figure 177 of *C. opacus*; (245–247) labra of instar-I females; (248–251) labra of mature females.
- PLATE 23. *Chydorus angustirostris* n.sp. All figures are of parthenogenetic females from the pond at Jabalpur, India. (252) Ventral view of instar-I female; (253) enlargement of anterior end of same specimen, showing edge of rostrum without meshes but with bordering mesh walls being rather high; (254) lateral view of instar-II female; (255) front view of mature female, showing attenuated and finely emarginate tip of rostrum; (256) pattern of shell reticulation and of finer armament within the meshes; the latter is more like striae arising from a smooth surface, with little suggestion of any dimension of depth; (257) posterior end of the ventral duplicature from inside, showing an insignificant cluster of three setules beyond the last ventral seta, but nothing more; (258) inside view of dissected shell, showing setae of ventral duplicature.
- PLATE 24. *Chydorus angustirostris* n.sp. All figures are of adult females from the pond at Jabalpur, India. (259, 260) Postabdomens; (261) distal tip of postabdomen, showing postabdominal claws with their long subterminal 'flagellum'; (262) anterior end of ventral duplicature from inside, showing the fine slender setules in distinct groups along the mid-ventral bulge.

TABLE 2. MAJOR DETAILS OF MORPHOLOGY DISTINGUISHING *C. OBSCURIROSTRIS* FROM *C. OPACUS*

character	<i>C. obscurirostris</i>	<i>C. opacus</i>
reticulation	(1) meshes relative few, those in posterior half much larger than others	(1) meshes more abundant, smaller, those in posterior half not much larger than others
	(2) walls quite high	(2) walls relatively low
	(3) coarse pattern of fine striae inside, some of which are elongate and thickened; pattern transparent	(3) fine pattern of overlying layers of fine striae; no elongation or thickening; makes shell opaque
shell	(4) posterior-ventral angle reasonably distinct	(4) posterior-ventral angle almost absent
	(5) 26.7 setae (range 24–29, $n = 15$) in ventral duplicature	(5) 25.6 setae (range 24–27, $n = 22$) in ventral duplicature
	(6) setae in posterior two thirds of duplicature attached to solid line; anterior ones separated	(6) all setae in duplicature attached to solid line
	(7) duplicature setae more or less evenly spaced	(7) duplicature setae more widely spaced posteriorly, more narrowly spaced anteriorly
head	(8) short row of submarginal setules posterior to ventral setae (in Australian specimens)	(8) no setules along posterior margin
	(9) narrower posteriorly	(9) broader posteriorly
	(10) only distalmost two or three rows of meshes do not overhang edge of rostrum; meshes in middle part arise at edge	(10) entire margin of rostrum free of meshes; bordering meshes have low walls
i.d.l.	(11) i.p. distance \geq p.p. distance	(11) i.p. distance \leq p.p. distance
	(12) only slight outward bulge over eye; meshes not greatly reduced in height	(12) marked outward expansion over eye; meshes greatly reduced in height
postabdomen	(13) large seta longer, more slender, more easily deformed	(13) larger seta shorter, stouter, less deformable
	(14) postanal portion longer	(14) postanal portion shorter
	(15) two rows of setules along anal groove, distal one projecting beyond margin, proximal one strongly angled and not projecting	(15) three rows of setules along anal groove, all projecting beyond margin

Synonymy

Chydorus faviformis Birge 1893: Yeh 1956: pp. 56–57, plate 3, figure 24, 24a–b; Chiang & Du 1979: pp. 258–259, figure 183.

Yeh acknowledges that Chiang drew the illustrations of *Chydorus faviformis* in his paper. The same figures are given in Chiang and Du, to which has been added only a drawing of the surface sculpturing within the meshes. The drawings are good, although the postabdomen does not have all the setules known to be present from my study.

Etymology

(NL) *sinensis* of, belonging to China.

Localities

Type locality. Ricefield, Dongwacungang, Danli County, Yunnan Province, China. Sample collected in 1957.

Other localities. The species was originally listed by Yeh (1956) from Lake Tung-Tsien-Hu (or Dongchien Hu). Chiang and Du list it from the provinces of Zhejiang, Hubei, Sichwan, and Yunnan. These localities are all south of 31° latitude and range at least 1500 km from east to west. Thus is widely distributed in southern China.

Types

Type series. The 39 specimens and the several exoskeletal parts recovered from Chiang's sample.

Holotype. A mature parthenogenetic female 0.29 mm long, mounted on a slide in glycerine jelly; Australian Museum, registration number P 35722.

Allotype. A mature male 0.27 mm long, mounted on a slide in glycerine jelly; Australian Museum, registration number P 35723.

Paratypes.

(i) Australian Museum, registration numbers: slide of mature female in glycerine jelly P 35724; two mature females in formalin/glycerol mixture P 35725.

(ii) United States Natural History Museum. Catalogue numbers: slide of mature female in glycerine jelly 227031; two mature females in formalin-glycerol mixture 227032.

(iii) British Museum (National History). Accession numbers: slide of mature female in glycerine jelly 1985.226; two mature females in formalin-glycerol mixture 1985.227-228.

All the remaining specimens are in the Frey collection in Bloomington.

Diagnosis

Covered everywhere with mostly small honeycomb meshes, which persist in mature male; mesh walls variably fringed with setules along free margins of shell and head, on rostrum, and along ecdysial line; internal pattern of fine, irregular striae, some of which sometimes thickened. The i.p. distance of mature females greater than p.p. distance; minor pores very small but distinct, three to four major-pore diameters apart; rostrum evenly tapered, roundly pointed, with no tendency toward emargination. Labral keel convex anteriorly, but weakly concave ventrally, producing narrow tip. One i.d.l. seta large, heavily chitinized, hook-like, relatively rigid in shape. Postabdomen with subparallel margins; pre-anal portion only slightly longer than anal portion; generally four denticles on postanal portion, three to four on anal portion, direction of elongation roughly parallel; continuous row of setules between denticles and pre-anal angle, projecting at right angle from margin. Both basal spines on postabdominal claw relatively short and slender; very weak submarginal flagellum, often not visible. Ephippial female with same height of mesh walls and same internal spiderweb pattern as parthenogenetic female and no marked pigmentation over egg locule; body expanded dorsally and contracted in width, with meshes of posterior head and adjacent shell elongated to accommodate modified shape. Mature male with tapered rostrum, somewhat shorter than in female, bluntly pointed at tip with no emargination; copulatory hook large, free portion slender and tapering to fine blunt point, provided with two ridges distally, formed by very small and short spinules; postabdomen finger-like, without distinct pre-anal angle; about four long, slender denticles in postanal portion, and variable crescents of setules on lateral surface; postabdominal claw similar to female, but shorter and somewhat stouter.

Parthenogenetic female

Shape. High, broad (figures 189–191, plate 18, 224, plate 20); flattened transversely at top; dorsal margin rather evenly curved, but with greatest curvature in posterior part of headshield. Posterior-dorsal angle sharp; posterior-ventral angle indistinct; ventral bulge pronounced. Completely reticulated; meshes with low walls, which decrease still further in height toward free edges of shell and head, ecdysial line, and tip of rostrum; edges commonly fringed with fine setules (figure 225); interior of meshes filled with striae at different levels, anastomosing irregularly and forming a rather coarse pattern, with some members elongate and thickened (figures 225, 227).

Shell. Meshes mostly small, about 200 on each side. Posterior duplicature with 27–30 setae (figure 196); anterior setae stouter and longer than posterior and more closely spaced; those in posterior third attached to stout line, continuing submarginally toward posterior-dorsal angle; on line beyond last seta is row of indistinct setules, ending in stouter setule at distance from last seta greater than any intersetal distance; setae in anterior two thirds of duplicature arising independently from prominent rounded tubercles. Continuous row of very fine setules across mid-ventral bulge, visible with s.e.m. but not phase microscopy (figure 226). Ecdysial line appears double, resulting from bordering meshes having complete but unraised edges close to line.

Head. Rostrum short (figure 192); tip more or less bluntly pointed, with seemingly no tendency toward emargination. Strip at edge of rostrum clear of meshes, but with low transverse supports from bordering meshes to edge of rostrum and irregular transverse striae (figure 229); fine striae of same pattern as in meshes also present. Eye small (figure 189); ocellus about half the size of eye or slightly greater, and located considerably closer to it than to tip of rostrum. The i.p. distance (76 μm in a mature specimen) less than p.p. distance except in immature females and in males. Minor pores very small but distinct; widely separated, located about four median-pore diameters apart. Headshield broadly rounded posteriorly.

Antennule (figure 197). Short and broad; tip reaches about half way between ocellus and tip of rostrum. Nine terminal aesthetascs, all much shorter than antennule; longest only about three-fifths as long, and two shortest only two-thirds as long as longest. Antennular seta arises slightly beyond middle; slender, sharply pointed, only about half as long as antennule.

Antenna. Formula 0-0-3 (1)/0-1-3 (1). One of terminal swimming setae of endopodite about half as long as other two. Terminal spine on each branch very small and indistinct. No spine arising from basal segment of exopodite.

Labrum (Figures 193–195). Expanded forward as a keel between antennules; anterior margin mostly convex but variably concave ventrally near tip, making tip less broad than in other species. Angle behind tip considerably less than 90°.

Trunklimb I (figures 198, 199). Two setae on o.d.l., three on i.d.l. Largest i.d.l. seta stout, curved, heavily chitinized, and hook-like; longest of three setae on i.d.l. almost as long as o.d.l. seta; provided in distal half with stout, blade-like setules.

Trunklimb II. Four gnathobasic setae, and eight in filter comb. First five scraping spines with countable setules, varying from about 19 in spine 1 to about 25 in spine 5; spine 4 with largest setules, with good spacing, producing comb-like appearance.

Postabdomen (figures 201, 202). Dorsal and ventral margins subparallel proximad to sharp and protruding postanal angle; then dorsal margin bends markedly toward peduncle of claw.

Most commonly seven or eight marginal denticles, usually four on postanal portion; stout and usually slightly curved; direction of elongation of all similar, sometimes with weak convergence near postanal angle. Continuous row of conspicuous setules along anal groove between pre-anal angle and first denticle; oriented roughly at right angle to margin and projecting beyond margin. Pre-anal angle sharp, protruding; accompanied by two groups of setules. Lateral surface with eight or nine crescents of fine setules arranged in submarginal row, plus several less distinct crescents farther from dorsal margin. Pre-anal portion only slightly longer than anal groove. Abdominal setae about as long as distance to postanal angle. Postabdomen of immature female (figure 200) shorter and broader, with no fringe of fine setules along anal groove but with several isolated, rather coarse setules; crescents on lateral surface not detected.

Postabdominal claw (figures 203, 204). Elongate, slender; shallowly curved to sharp point. Both basal spines short and slender, longer being shorter than basal width of claw, shorter only about half as long. Concave margin with two sequential rows of fine setules; proximal third with about 14 very short setules; distal two thirds with about 25 longer setules somewhat coarser in middle third, then decrease in thickness and visibility toward tip. Subapical flagellum present, but very delicate and not always distinct under phase optics.

Size (excluding meshes). Parthenogenetic females, 0.20–0.35 mm ($n = 29$); smallest female with eggs, 0.28 mm; ephippial female, 0.32 ($n = 1$); instar-I males, 0.21–0.22 mm ($n = 2$); instar-II male, 0.23 mm ($n = 1$); mature males, 0.25–0.27 mm ($n = 6$).

Ephippial female

Body expanded dorsally and narrowed to produce ephippium, headshield elongated and narrowed, and meshes of posterior part of head and of adjacent shell enlarged to accommodate change in shape. Distinct transverse notch in dorsal contour of head in region of minor pores (figures 205, plate 19, and 228). Anterior part of shell that peels away on moulting separated from ephippial portion by a distinct interruption of mesh pattern along slough line (figures 205, 227–229). No major differences from parthenogenetic female in surface sculpturing of shell; possibly shell pattern in meshes slightly coarser or more heavily chitinized, but nothing more; no changes in wall height, and no appreciable pigmentation over egg locule.

Males

Although all three male instar were present in the sample, the details of morphology of some characters could not be resolved satisfactorily. Hence, the description will be chiefly of the adult, with features of the two immature instars, especially of trunklimb I, brought out when available.

General aspects. Contour seen from side flattened dorsally (figure 208), with weak depression over minor pores; head bent strongly ventrally in region of eye. Rostrum shorter (figure 209) than in instar-II male (figures 207, 230, plate 21) and in female (figure 192); tapered and more bluntly pointed than in female, with no suggestion of emargination. Eye large; ocellus less than half its diameter, located about midway between eye and tip of rostrum. Labrum (figures 211–213) much as in female. Head and shell completely honeycombed as in female; meshes with low walls and dense pattern of striae inside.

Antennule (figure 231). Enlarged; 12 aesthetascs, longest of which project beyond tip of rostrum; well developed male seta arising from medial side about midway and extending beyond tip of antennule; antennular seta short, slender, and pointed as in female, arising about midway on outer-lateral surface.

Antenna (figure 216). Similar to female, but endopodite has small seta arising from basal segment, yielding formula 0-0-3(1)/1-1-3(1); one terminal seta on endopodite only half as long as other two; terminal spine of both branches very small and difficult to see.

Trunklimb I. Goes through ontogenetic changes typical of chydorids generally in development of copulatory hook and male accessory seta on i.d.l., in elongation of seta-bearing lobe, and in reduction in size of i.d.l. and o.d.l. setae. Limb similar to female in instar I except for Anlage of copulatory hook; by instar III (= mature), i.d.l./o.d.l. lobe much elongated and setae much reduced in size compared with female. Copulatory hook peg-like in instar I, more elongate and tapered in instar II (figure 206), long and slender in instar III (figures 210, 214-215); gape wide to accommodate meshes of female; free arm somewhat irregular in width and tapering to bluntish point at tip; latter has two ridges formed by very small and very short, bluntly pointed denticles; shorter ridge arises laterally and moves forward to tip; longer arises somewhat lateral of midline, then moves medially at about level where shorter line begins (figures 232, 233). Details of copulatory brush not completely clear; seems to consist of a sparse cluster of long setae. Copulatory brush seta not visible, nor is Anlage of male seta on i.d.l. in instar II.

Postabdomen of mature male (figures 217, 234). Elongate, finger-like; no protruding pre-anal angle; postanal angle distinct as in female, with postanal portion tapering to very short peduncle of postabdominal claw. Marginal denticles long, straight, slender, with some tendency toward doubling; confined largely to postanal portion. S.e.m. specimen shows four long denticles in postanal portion and 1 in anal portion separated by considerable distance (figure 234). Anal groove with at least two or three clusters of long setules distally, projecting beyond edge. Lateral surface of postabdomen with row of at least six crescents of setules, located farther from margin than in female, plus irregular clusters scattered distally. Ventral margin somewhat irregular distally and expanded. Distal bulbous expansion contains genital pores, opening near ventral midline close to base of claw (figure 235).

Postabdominal claw (figure 235). Similar to female except shorter and stouter; same development of spinules along concave margin. Two basal spines even more delicate than in female, especially shorter one. Subapical flagellum seemingly absent, or at best indecisively visible with 50 × phase objective.

(f) *Chydorus angustirostris* n.sp.

Synonymy

Chydorus faviformis Birge, 1893: Khan *et al.* (1978): p. 81.

Etymology

(L) *angusti* narrow, (L) *rostrum* beak, snout.

Localities

Type locality. Pond at Jabalpur in Madhya Pradesh, India. Collected by P. Rane in 1978. From the two samples borrowed from C. H. Fernando, approximately 100 parthenogenetic females plus various exuvial components were recovered. No males or ephippial females were present.

Other localities. Surinsar Lake (30° 47' N, 75° 0.2' E) in the strike valley of the lower Siwaliks, Jammu Province, India. Collected about 1977 by Khan *et al.* (1978). None of these specimens were available for examination.

Types

Type series. All the specimens and exoskeletal parts from the type locality. These are mostly distorted and covered with a tenacious detritus that cannot be removed easily with detergents.

Holotype. A mature parthenogenetic female 0.33 mm long, mounted on a slide in glycerine jelly has been deposited in the Australian Museum, registration number P 35726.

Paratypes. Suites of specimens consisting of a mature parthenogenetic female mounted on a slide in glycerine jelly, another on a slide in polyvinyl lactophenol, and four in a glycerol-5% formaldehyde 1:1 mixture have been deposited in the following museums.

(i) Australian Museum. Registration numbers: slide of female in glycerine jelly P 35727; slide of female in polyvinyl lactophenol P 35729; specimens in liquid P 35728.

(ii) U.S. National Museum of Natural History: Catalogue numbers: slide of female in glycerine jelly 227033; slide of female in polyvinyl lactophenol 227034; specimens in liquid 227035.

(iii) British Museum (Natural History). Accession numbers: slide of female in glycerine jelly 1985.229; slide of female in polyvinyl lactophenol 1985.230; specimens in liquid 1985.231-234.

All the remaining paratypes and exoskeletal parts are in the Frey collection in Bloomington.

Diagnosis

Meshes mostly small (about 150 per half shell) and hexagonal; walls weakly and variably fringed; interior with variably coarse spiderweb pattern, usually with one or more members thickened and raised. Headshield of mature females broad behind; rostrum attenuated to fine tip not or only very weakly and obliquely bifid; clear strip at edge of rostrum without meshes but overhung by walls of meshes along the strip; medial pores small; minor pores very small and far apart (about three to four diameters of major pores), indistinct at best, sometimes not visible with certainty at 40 × phase objective; i.p. distance always greater than p.p., ratio, 1.23 ($n = 6$). Labrum expanded anteriorly; tip short and broad, both edges convex; angle behind plate under 90°. Pre-anal portion of postabdomen about as long as anal portion; postanal portion short in instar I, longer in instar II, and still longer and tapered in matures; marginal denticles slender, straight, single; isolated denticle-like setules along proximal half of anal groove in instar I, replaced by single row or by three groups of setules in instar II and matures. Larger basal spine on postabdominal claw about as long as basal width of claw or a little longer; smaller spine very slender, about half as long; subterminal flagellum small but distinct, projecting slightly beyond tip of claw. Gamogenetic stages unknown.

Parthenogenetic female

Shape (figures 236, 237, plate 22, 252, 254, plate 23). Dorsal margin evenly arched and without marked increase in curvature near eye; posterior-dorsal angle sharp and protruding; posterior-ventral angle reasonably distinct, rounded; ventral bulge narrow and well formed. Meshes small to moderate in size, about 150 per half shell; walls low; edges mostly straight; weakly fringed toward front of head and near free edges of shell; interior of meshes with spiderweb pattern with variable development from mesh to mesh of thickenings that project from shell and sometimes intersect with mesh walls (figure 256); transverse extensions of mesh

walls along ecdysial line (figure 254); bordering meshes not complete, hence ecdysial line single. Body broad from side to side (figure 252) flattened at top.

Shell. About 29 setae in posterior duplicature (figure 258), of which posteriormost 14–16 attached to continuous line, those in front arising from distinct, isolated tubercles (figure 241). Setae do not decrease in length appreciably, posteriormost being three quarters or four fifths as long as the longest. Line to which setae of duplicature attached continues submarginally to posterior-dorsal angle. No, or very few, setules on line behind last duplicature seta, typical groups of short setules across ventral bulge in front of duplicature (figure 262, plate 24).

Head. Headshield broadly expanded posteriorly in mature females (figure 239), much less so in immatures. Rostrum narrowly tapered and attenuated (figures 239, 240, 255), usually not bifid but sometimes very weakly and obliquely so; free edge of rostrum without meshes but overhung by walls of bordering meshes and interrupted by transverse connections from meshes to edge of headshield (figure 255); transverse striae also present; elongate narrow mesh at tip with very low mesh wall or none, occasionally one or two mesh-rows immediately posterior lack high mesh walls (figures 239, 240, 255). Rostrum of instar-I female much less attenuated (figures 252, 253). Ocellus about half diameter of eye, somewhat closer to eye than to tip of rostrum (figure 237). I.p. distance in mature females 95–99 μm ($n = 6$), always greater (ratio = 1.25) than p.p. distance. Major pores small but distinct; minor pores minute, not always visible at 40 \times phase objective, separated by three to four diameters of major pores.

Antennule (figure 238). Width somewhat greater than half length. Tip with series of small broad lobes or scallops at edge. Antennular seta arises just beyond middle; very slender and tapered to sharp point; seemingly slightly shorter than aesthetascs. Nine aesthetascs, all terminal, about three fifths as long as antennule, not reaching tip of rostrum.

Antenna (figure 242). Formula 0-0-3 (1)/0-1-3 (1). One of terminal setae of endopodite only about half as long as other two, which are subequal in length to remaining four. Terminal spine on exopodite very small; that on endopodite smaller still and less stout, visible with difficulty.

Labrum. Anterior margin strongly and evenly convex, sometimes with weak concavity near tip. Tip short, convex on both edges, giving labrum a broad and expanded appearance. Angle posterior to tip narrowed, almost sharp, distinctly less than 90°. No appreciable change in shape between immatures (figures 245–247) and matures (figures 248–251).

Trunklimb I (figure 243). Two setae on o.d.l., three on i.d.l.; one of latter stout, elongate and heavily chitinized, with a row of setules in distal half. Middle seta of middle group slightly longer than dorsal seta of this group. All three accessory spines well developed.

Trunklimb II (figure 244). Four gnathobasic setae; eight setae in gnathobasic comb. Eight scraping spines, first five counting from gnathobase with prominent denticles, those of spine 4 longest and stoutest.

Postabdomen. Pre-anal portion about as long as anal groove. Postanal portion varies in appearance with instar, short and almost truncate in instar I (figure 218), a little longer and less sharply angled in instar II (figure 219), still longer in matures (figures 220, 221, 259, 260). Mature specimens with eight or nine marginal denticles, occasionally ten; five to seven denticles on postanal portion of instar II and matures, four to five on instar I; denticles nearly always straight, short, and very slender; convergence in direction of orientation between proximal and distal denticles much less prominent than in some other species. Anal groove of instar I bordered by small number of thickened, denticle-like setules well separated from one another; in instar

II and matures anal groove proximad from marginal denticles bordered by fine setules sometimes forming almost continuous row, or arranged into three distinct groups, those of middle and distal groups projecting well beyond margin. Peduncle of claw always with distinct small spine near angle.

Postabdominal claw (figures 222, 223, 261). Weakly and evenly curved to sharp point. Large basal spine slender, evenly tapered to point, curving outward slightly, about as long as or slightly longer than basal width of claw. Smaller basal spine very slender, only about half as long. Subterminal flagellum distinct, projects somewhat beyond tip of claw. Concave margin with about 15–18 short, slender setules proximally and about 20 larger (especially in middle third of claw) setules distally.

Size. Overall length without honeycomb, 0.22–0.37 mm ($n = 77$); instar I, 0.22–0.26 mm ($n = 20$); instar II, 0.26–0.29 mm ($n = 18$); matures (beginning with smallest size containing eggs), 0.29–0.37 mm ($n = 39$) (see figure 285). Khan *et al.* (1978) give the length as 0.5–0.6 mm, which is the same as Birge (1893) gives for the North American *faviformis*. This is quite certainly too large, as the biggest *C. angustirostris* from Jabalpur measured just 0.39 mm including the honeycomb.

(g) *Chydorus parvireticulatus* n.sp.

Synonymy

Chydorus faviformis Birge, 1893: de Ferrato (1966): pp. 401–402, figures 8 and 9; Brandorff *et al.* (1982): p. 76 (only mentioned in a list of species).

Comments

Working with this taxon has been frustrating because of the few specimens available and their generally poor condition. There are just two records for South America in the literature, the first by de Ferrato (1966) from two localities in the middle Paraná basin of Argentina, but these specimens no longer exist (*fide* J. C. Paggi). More recently Smirnov (in Brandorff *et al.* 1982) listed the taxon as being present in the Amazon region. He graciously sent me his extant material, which consisted only of two specimens, two shells, and an exoskeleton. These have been used mainly to produce the s.e.ms.

The only specimens available for study originally were from a collection made by H. Kleerekoper near Porto Alegre, Rio Grande do Sul, Brazil, in September 1941. In the 1940s Kleerekoper submitted this and other samples from the region to the U.S. National Museum for identification, which then engaged Rufus Kiser to study them. Kiser mounted three parthenogenetic females of the *faviformis*-like taxon, each on a separate slide, and he made a similar mount for his own collection, which was turned over to the National Museum in 1983. Besides these four slides I was able to borrow from the museum the rest of the bulk sample Kiser had used. Disappointingly, it yielded only one immature specimen in poor condition, plus four shells, one complete headshield, and one partial headshield. The specimens mounted by Kiser are distorted and hence do not show clearly many details of morphology that are needed. The remains from the bulk sample did not yield much additional information. Yet, the taxon is so different from the others in this paper, and especially from *C. faviformis* in North America, that I had no hesitation about describing it as a new species. The description originally was based only on this very inadequate material from the Kleerekoper sample.

Subsequently, other specimens were discovered, the study of which has required a revision

of the description. The first records of this taxon from South America are unpublished, but specimens are available. Many slides in the Birge collection are indicated only by numbers, with no way at all to interpret them until the notebooks of Harriet Bell Merrill and her letters to Birge fortuitously turned up in 1986. Merrill collected extensively in South America, briefly in 1902 and continuously from 1907 into 1909. Her notebooks give details of all this activity and enable all the slides to be identified positively as to place and date. Three samples containing the taxon are from near Manáos, Brazil, and one from Santarem downstream on the Amazon. Merrill mounted one specimen from each sample in a drop of glycerol on a slide but without a cover. Over seven decades the glycerol had gradually seeped away, leaving the specimens covered with only a thin film of dirty glycerol. The specimen on one slide could not be found, but the other three were remounted in glycerine jelly. Not much is left of the specimens except the head and shell, with occasional appendages or postabdomen visible dimly with phase optics. However, enough details of morphology are evident in these several deficient specimens to indicate that they probably belong to the same taxon as do the specimens from southern Brazil.

A final sample also received after this section had been written originally is from near Corrientes City in Corrientes Province, Argentina, collected by J. C. Paggi in 1971. This sample contained nine dirty specimens, three of which were used for s.e.ms.

Etymology

From (L) *parvi* small, and (L) *reticulatus* network, referring to the small size (and hence large number) of honeycomb meshes covering the head and shell.

Localities

Type locality. Temporary pool on grassland near Porto Alegre, Rio Grande do Sul, Brazil. Sample collected by H. Kleerekoper in September 1941.

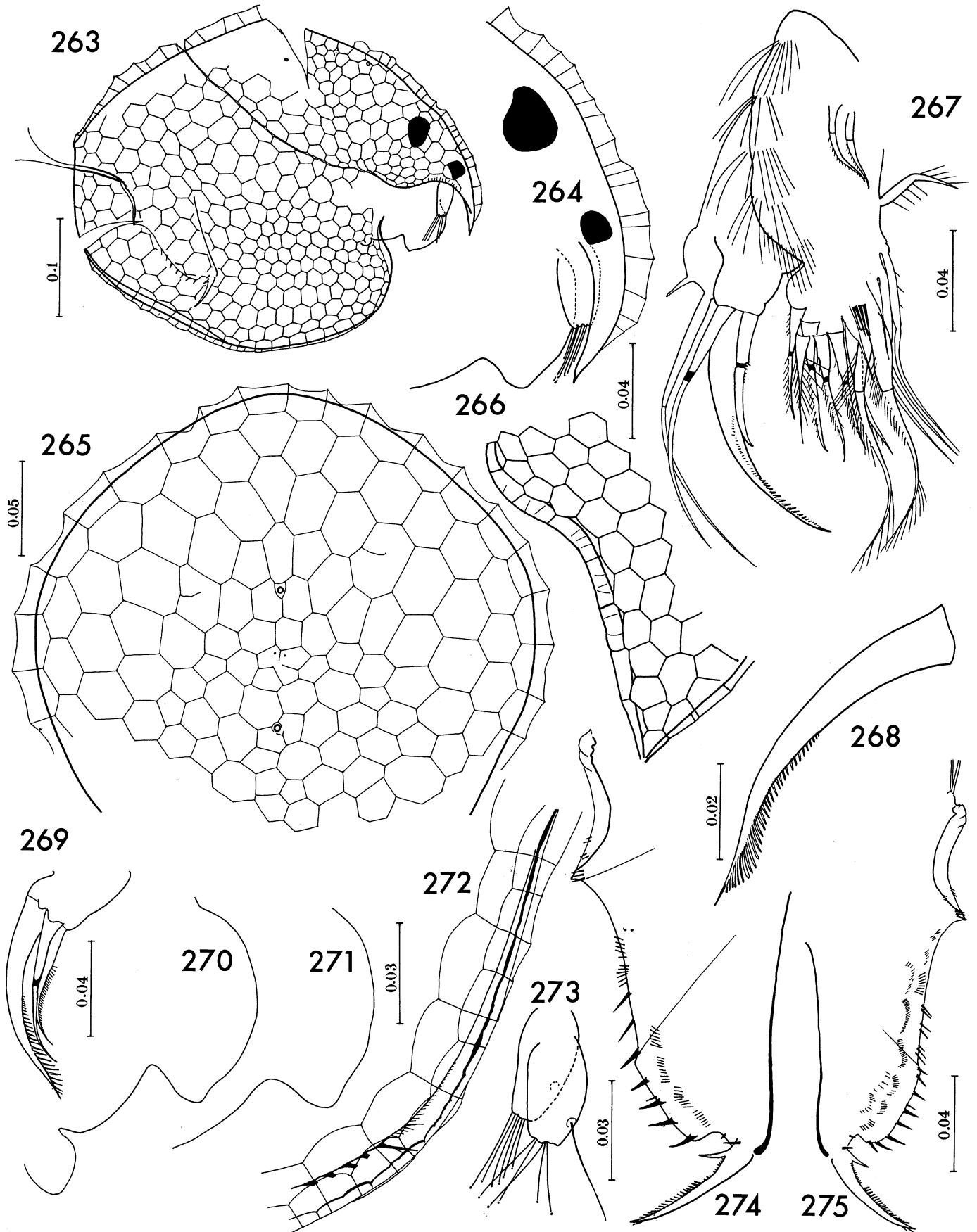
Other localities.

(i) Among macrophytes in an arroyo on the island Sirgadero and in laguna Los Espejos, both in the middle Paraná basin, Argentina (de Ferrato 1966).

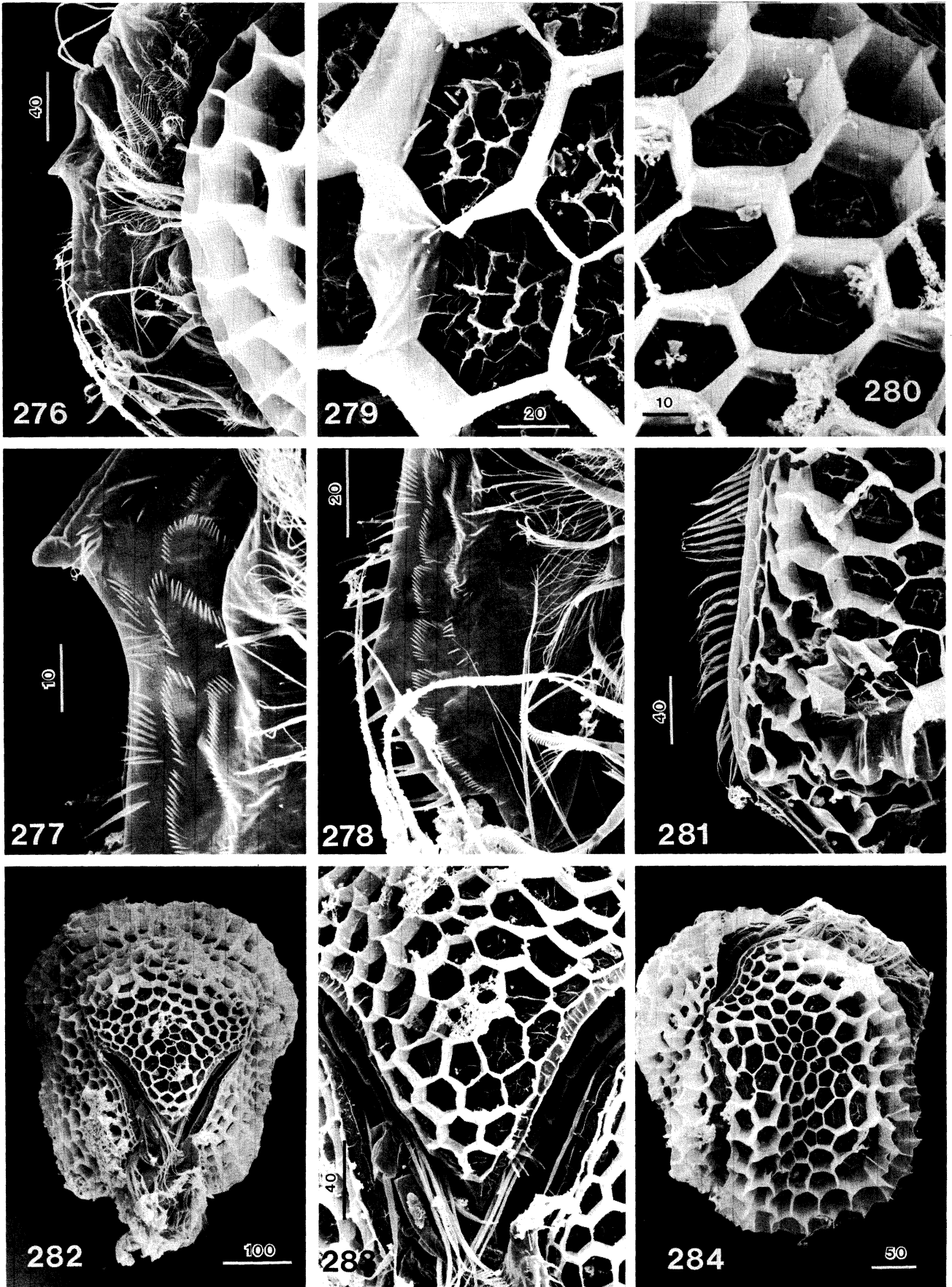
(ii) The upper course of the Rio Xuedá, Brazil, among flooded trees (Brandorff *et al.* 1982). This is in the lower Rio Nhamunda region between the states of Pará and Amazonas. Smirnov's meagre sample is from here.

DESCRIPTION OF PLATE 25

PLATE 25. *Chydorus parvireticulatus* from near Porto Alegre, Brazil. All drawings are of parthenogenetic females. Figures 263, 270, 273, and 274 are of the Holotype; 267, 268, 272, and 275 of Paratype I; 264 and 271 of Paratype II; 266 and 269 of Paratype III (= specimen from Kiser collection); and 265 from the exoskeletal remains. (263) Holotype, from the right side; (264) head end; (265) posterior part of headshield, showing shape and pore configuration; (266) part of rostrum, showing the transversely striated free border (tip of rostrum could not be seen clearly in this specimen, but other specimens and remains show that the mesh-free border continues around the tip, which is not emarginate); (267) trunklimb I, showing the large size of the hook-like seta on the i.d.l.; (268) enlargement of hook-like seta on i.d.l., showing the long setules distally; (269) i.d.l. of trunklimb I; (270, 271) labral plates; (273) antennules, showing mainly the shape, the origin and length of the antennular seta, and the lengths of the aesthetascs, not all of which were visible; (274, 275) postabdomens and postabdominal claws, showing the elongated shape, the shortness of the pre-anal portion, and the great length of the anal groove.



FIGURES 263-275. For description see opposite.



FIGURES 276–284. For description see opposite.

(iii) The samples collected by H. B. Merrill near the Amazon River, Brazil, are roughly comparable to Smirnov's sample as to general location:

- (a) Sample 107. Rio Machado, near Manáos, 9 May 1908. (The specimen on this slide had disappeared.)
- (b) Sample 109. An igarape connected with Rio Machado, near Manáos, 9 May 1908.
- (c) Sample 213. Open water of Rio Machado, near Manaos, 3 June 1908.
- (d) Sample 292. Lake in sand at Santarem, on Amazon River downstream from Manáos, 12 October 1908.

(iv) Laguna la Brava, near Corrientes City, Corrientes Province, Argentina. Collected by J. C. Paggi on 25 August 1971, his sample 642.

Types

Holotype. A parthenogenetic female about 0.44 mm long on one of the four slides in the U.S. National Museum, which were all labelled U.S.N.M. Accession number 164520, catalogue number 93362. It has been labelled Holotype to distinguish it from the specimens on the other slides. The numbers given above now apply to this specimen only.

Paratypes. The other three mounted specimens in the U.S. National Museum, and four slides of the exoskeletal components recovered from the bulk sample. The specimens measure roughly 0.38, 0.41, and 0.42 mm, with the smallest specimen having two parthenogenetic eggs. Slides of the exoskeletal components are in the Frey Collection in Bloomington.

Parthenogenetic female

Diagnosis. The four most useful characters for distinguishing this species from the other *faviformis*-like taxa are (i) the large number (over 200 per half shell) of small meshes on the shell and on the head, almost to the tip of the rostrum; (ii) the rostrum bordered by a mesh-free strip with transverse striations; (iii) the tip of the rostrum being tapered and pointed, not emarginate; and (iv) the elongate postabdomen, in which the anal groove is considerably longer than either the pre-anal or postanal portions, the dorsal margin of the pre-anal portion is strongly concave, and the postanal portion tapers markedly toward the claws, almost as a straight line. In addition, the ecdysial line is double, the interior of the meshes contains a delicate spiderweb pattern, usually with a small group of thickened striae centrally, and the large i.d.l. seta is very long, heavily sclerotized, and has long setules that become longest in the distal third of the seta. The two figures in de Ferrato (1966) emphasize (i) and (iv) above, and also the fine interior pattern of the meshes.

DESCRIPTION OF PLATE 26

PLATE 26. *Chydorus parvireticulatus*, all parthenogenetic females. Figures 276–279, 281, and 284 are from specimens in the Smirnov sample from Rio Xuedá, Brazil. Figures 280, 282 and 283 are from the sample collected by J. C. Paggi near Corrientes City in Argentina. (276–278) Postabdomen; (279–280) meshes on shell, showing the nature of the internal sculpturing; (281) posterior-ventral margin of shell, showing the number and size of the setae in the posterior duplicature and the fact that the mesh walls on the shell vary greatly in height; (282) front-end view, showing the areas of low wall height laterally on the shell and across the headshield in the pore region; (283) enlargement of head, showing the pointed, non-emarginate tip of the rostrum, the marginal strip along the rostrum that is free of meshes but has transverse striations, and the low height of the mesh walls; (284) side view, showing the low height of mesh walls in anterior and central parts of shell and in a band across the headshield from one fornix to the other.

Comment. The description based on the Kleerekoper specimens stated that the head and shell were completely covered with many small meshes having low margins and no appreciable pattern of relief over the animal. The new specimens, which being free could be looked at from any angle, showed that the small specimens, presumably immature, had this pattern, but that the larger mature specimens had a somewhat different pattern. Here the meshes on the shell had low walls in the anterior and central portions but much higher walls along the ecdysial line and also posteriorly and ventrally. Furthermore, there was an arc of low-walled meshes across the headshield in the general vicinity of the head pores. Also, the surface markings within the meshes were not always a fine honeycomb with a central cluster of long, coarse ridges, because some of the specimens used for s.e.ms had only the coarse markings. The significance of these differences cannot be resolved from the material at hand. Possibly these are ontogenetic differences, as all specimens that could be examined closely enough showed the same pattern of other characters, such as a non-emarginate rostrum and a postabdomen having the shape, proportions, and armament as in the population from Porto Alegre described originally. If at some future time it is decided that two species are present, then *C. parvireticulatus* will be the one with the uniform fine meshes, such as found in the Rio Grande do Sul specimens and as illustrated in figures 263–275, plate 25.

Shape. Dorsal margin (excluding the meshes) uniformly and rather weakly curved, with only a slight change in curvature over the eye (figures 263, 264), but with rostrum bent rather sharply backward near its tip (figure 284, plate 26); posterior-dorsal angle sharp and protruding (even more so than in figure 263); posterior-ventral angle broadly rounded; mid-ventral bulge weak. Meshes on shell small and with uniformly low walls in some specimens; more numerous (over 200 per half shell) than in any other honeycombed species considered here; larger specimens have somewhat fewer meshes, with walls low anteriorly and centrally, but high dorsally, posteriorly, and ventrally (figures 276, 281–284); head with an arc of low-walled meshes running between the fornices and through the central region containing the head pores (figures 282, 284); interior of meshes sometimes with a fine spiderweb pattern of striae and a clump of raised, thickened striae in the middle (figure 280), at other times with only the larger units centrally (figure 279); edges of mesh walls sometimes smooth, but more commonly fringed with extremely fine setules (figure 280). Ecdysial line double in specimens from Rio Grande do Sul (figure 263), resulting from all meshes on either side being complete and arising closely parallel to the line; ecdysial line of specimens from Manáos and Corrientes not double (figure 284).

Shell. Ventral duplicature shallow, containing 27–30 setae (figure 281) most of which are attached to a prominent continuous line posteriorly, only those in the anterior third being partly separated from the line. This line continues submarginally beyond posteriormost ventral seta to posterior-dorsal angle (figure 272); row of fine setules along ventral quarter of posterior margin, those toward bottom being considerably longer and somewhat stouter than those farther dorsad.

Head. Broadly expanded posterior to fornices, and then markedly tapered posteriorly to a rather narrow tip (figure 265); i.p. distance considerably shorter than p.p. distance in all specimens (measuring 78 μm and 109 μm , respectively, in one specimen). Minor pores small but quite distinct, about one and a half major pore diameters apart, somewhat closer to posterior pore (figure 266). Rostrum rather short, tapered to a pointed tip that is not at all emarginate, bordered by a rather broad strip that is free of meshes (figures 266, 283), although meshes adjacent to strip are attached to it by transverse support walls, causing the strip to be

transversely and irregularly striated. Ocellus about half diameter of eye, located roughly midway between eye and tip of rostrum (figures 263, 264).

Antennule. All aesthetascs terminal, unequal in length, with longest about three quarters length of antennule and shortest less than half its length (figure 273); tips reach tip of rostrum or possibly exceed it somewhat (figures 263, 264, 283); number of aesthetascs could not be counted, but undoubtedly nine. Antennular seta a third to a quarter distance from tip, about as long as antennule (figure 273).

Antenna. Antennal formula 0-0-3(1)/0-1-3(1). Terminal spines short and delicate, almost invisible at high phase magnification (figure 283), the one on the endopodite being much smaller. Of the seven swimming setae, one of the terminal ones on the endopodite is only about half as long as the two others, which are subequal in length.

Labrum (figures 263, 264, 270, 271). Expanded and rounded anteriorly, but only slightly concave near tip; posterior margin weakly convex; ventral tip short and quite narrow; angle behind tip variable in size, mostly about 90°.

Trunklimb I (figures 267–269). Largest i.d.l. seta very large, heavily sclerotized, evenly curved, tapered to a sharp point, and provided with conspicuous denticles that increase in size distally. All three accessory setae on corm well developed (figure 267). Middle seta of middle group somewhat longer than dorsal seta of this group. Specimen drawn had four setae (plus accessory setae) in ventral group, which is abnormal, as each group typically has just three setae plus an accessory seta.

Postabdomen (figure 274–278). Elongate, with anal groove considerably longer than either pre-anal or postanal portions. Dorsal border of pre-anal portion markedly concave. Pre-anal angle sharp and strongly protruding (figure 277). Postanal angle prominent, formed by a conspicuous break in dorsal contour of postabdomen (figure 278). Postanal margin almost straight, tapering strongly toward base of claws. Dorsal margin with eight to ten long, slender denticles, of which five or six arise from postanal portion and remainder from distal part of anal groove. Between these denticles and pre-anal angle are two to several row-like groups of setules (figure 277). Two or three groups of setules occur at pre-anal angle. Lateral surface with a row of well-developed arcs of setules marginally, with a second parallel row along the anal groove (figure 278). Single seta arising from peduncle of claw (figures 274, 275, 278). Postabdominal setae considerably shorter than postabdomen.

Postabdominal claw (figures 274–276). Long, slender, evenly curved or rather straight, tapered to a fine point; subapical flagellum rather conspicuous but does not reach tip of claw; one or two secondary flagellar setae can also be present proximal to flagellum. Distal two-thirds of concave side provided with about 20 denticles that are long and stout in middle third of claw, becoming less stout and shorter toward tip; proximal third with 11 or 12 much shorter and more delicate setules. Row of flexible setae along ventral convex margin, and dense row of setae along median side. Larger basal spine long and very slender, longer than basal width of claw; lesser spine very slender, about half as long as larger spine or possibly even a little longer. Spine distinctly longer in specimens from Amazon region than in those from southern Brazil.

Size. The length (excluding the meshes) of the four Kleerekoper females in the National Museum ranges from 0.38 to 0.44 mm, with the smallest specimen carrying two parthenogenetic eggs. Mature, egg-bearing females from Corrientes ranged in length from 0.36 to 0.44, immature females from 0.27 to 0.31 mm. No males or ehippial females were present in the samples.

3. KEY TO WORLD SPECIES OF FAVIFORMIS-LIKE *CHYDORUS*

- (1a) Postabdomen of mature male with prominent pre-anal angle and strongly narrowed distally in manner characteristic of taxa in *C. sphaericus* complex; honeycombing completely lost in mature male: North America *C. faviformis* Birge, 1893.
- (1b) Postabdomen of mature male finger-like, with pre-anal angle obscured, and anal and postanal portions not appreciably narrowed relative to female; mature male fully honeycombed 2
Note: Males of the taxa from Malaysia, India, and Brazil or Argentina are not yet known, but the morphology of their parthenogenetic females suggests a closer relationship to the Australian and Chinese taxa than to the North American.
- (2a) Free edge of rostrum bordered by meshes with high walls, which overlap and obscure marginal strip 3
- (2b) Free edge of rostrum bordered by meshes with low walls, even no walls at all, leaving marginal strip not overhung, and freely visible from any direction 4
- (3a) Apex of rostrum conspicuously bifid, with tips blunt and dark; meshes relatively few in number (about 120 per half shell), large, and with high walls: Australia *C. obscurirostris* n.sp.
Note: The new geographical subspecies *C. o. tasekberae* from Malaysia is tentatively assigned here. The morphology of its parthenogenetic females differs somewhat from the nominate Australian females, but the complete absence of males from Malaysia prevents any reasonable assessment concerning conspecificity.
- (3b) Apex of rostrum elongate, not bifid; meshes moderately abundant (about 150 per half shell), small, and with low walls: India *C. angustirostris* n.sp.
- (4a) Anal portion of postabdomen considerably longer than either pre-anal or postanal portions; more than 200 meshes per half shell: Brazil-Argentina *C. parvireticulatus* n.sp.
- (4b) Anal portion of postabdomen shorter than pre-anal portion; meshes likewise small, but fewer than 200 per half shell. 5
- (5a) 24-27 setae in duplicature, all attached to prominent solid line; postabdominal claw with roughly seven short setules proximally and about 14 longer setules distally; surface pattern within meshes consisting of several overlapping layers of fine, curved, anastomosing striae, making head and shell opaque: Australia *C. opacus* n.sp.
- (5b) 27-30 setae in duplicature, only those in posterior third attached to solid line; postabdominal claw with roughly 14 short and slender setules proximally, about 25 longer but still slender setules distally; surface pattern within meshes of fine, irregular striae, some of which typically thickened: China *C. sinensis* n.sp.

4. DISCUSSION

Whereas previously there was considered to be only one species of honeycombed *Chydorus* in the world (excluding the more elaborate *bicornutus* and *bicollaris* confined to North America), now there are six, possibly seven, depending on further study of the Malaysian taxon. Thus here is another instance among an ever increasing number (see Frey 1987 for a review) in which chydorid taxa from different continents that were regarded originally as the same species have been shown to be different by careful analysis. Previous examples are *Eurycerus lamellatus*, *Chydorus sphaericus*, *Disparalona rostrata*, *Oxyurella tenuicaudis*, and *Alonopsis elongata* described originally from Europe, and *Chydorus reticulatus* from southern Asia. In a few instances the differences reported thus far between the taxa are not only morphological but also genetic, as indicated by the failure to cross populations from North America and Europe. Moreover, even on a single continent, such as North America, we are finding that the situation is still more complicated, because a 'species' may include a number of different morphotypes (= species) even within a single lake at the same time. In the case of the common *Eurycerus* species in North America, separation of a northern (= *longirostris*) species from a southern (= *vernalis*) species is based on the morphology of the populations, electrophoresis, and the time of year when

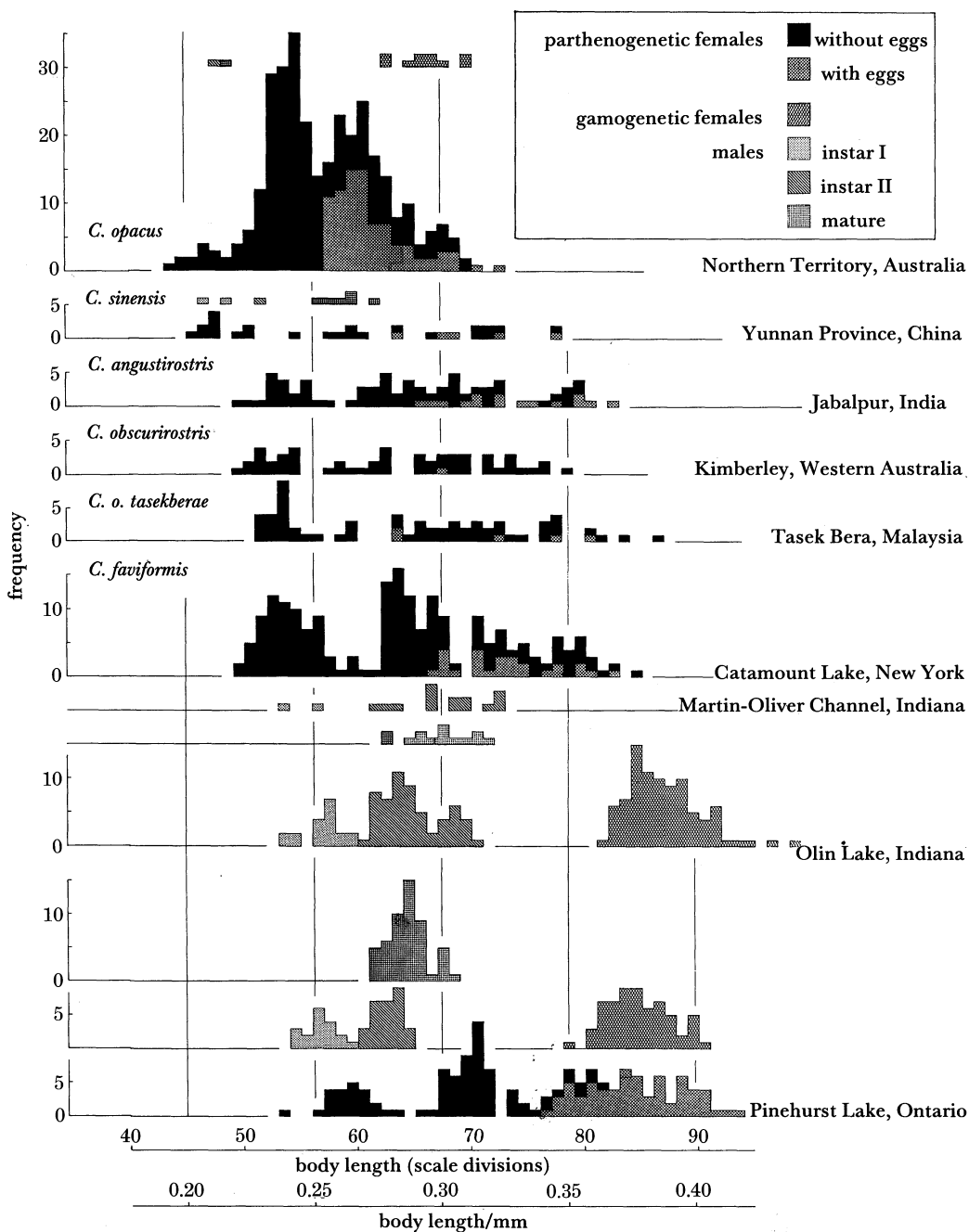


FIGURE 285. Size-frequency distributions of the populations of the various taxa included in this study. The diagrams are based either on all the specimens recovered from a particular sample or else in the case of the Catamount Lake population on a representative subsample, except for the three samples of *C. faviformis* at the bottom. As these were searched for males and ephippial females, the latter are present almost exclusively in the mature size range. In the immature size range from Pinchurst Lake, both the two instars of immature females and the three instars of males are present, because the small specimens had to be sorted into males and females with a compound microscope. All these specimens were measured.

gamogenetic reproduction occurs (Hann 1980, 1982). Ranges of morphological characters in these two species overlap so extensively that individual specimens cannot be identified with certainty without knowing their geographical origin, but populations can be separated easily by differences in regressions of the various characters against size of the animals.

The labelling of all honeycombed species as *Chydorus faviformis* arose from Birge's grossly inadequate description of the taxon from North America, and the subsequent compliant assignment of his name *faviformis* to apparently similar taxa from the other continents, on the assumption, no doubt, that the species of Cladocera are cosmopolitan in distribution. Besides, as there had been no adequate original description there could be no meaningful comparison. Consequently, any honeycombed taxon, from whatever continent, was called *C. faviformis* without compunction.

This illustrates the present unsatisfactory state of cladoceran systematics. Few species from anywhere in the world have been described closely enough that some concerned scientist would be able to judge matters of conspecificity using published descriptions alone. The earliest descriptions of Cladocera are mostly very vague and indecisive, and usually no specimens are available that the authors used. Subsequent investigators have merely expanded the descriptions as necessary without paying too much attention to the morphological limits of the taxa and hence to their geographical extent. Geographical distribution in Europe was a major concern through the late 1800s (Frey 1982*d*), but decisions regarding it were based purely on gross morphology, not on the fine details that today give us an intimate feeling of comfort with the few species that have been described well. The geographical distribution of many of the species in Europe was first expanded to include all of Europe, then the rest of the world. Everyone was looking mainly at gross features that could be observed without too much difficulty. Consequently, descriptions remained inadequate, and the original illustrations, often from distorted or even uniquely anomalous specimens, did not help really to resolve any important matters. Differences between populations, even from different continents, were regarded as infraspecific. Cladoceran resting eggs were known to remain viable for many years in a dried condition, hence it was assumed they could 'easily' be distributed virtually everywhere by air movements and migratory birds. Oceans, mountain ranges, and deserts posed no real barriers. The concept of cosmopolitanism seemed a logical consequence.

The honeycombed species of *Chydorus* reported on in this paper represent the most complex situation tackled to date. The conclusion that everything is different, except possibly the large-meshed species in Australia and Malaysia, was not anticipated at the start, because everything looked the same, grossly. However, *Chydorus faviformis* from North America is now known to be uniquely different from all the other taxa, chiefly because of distinctive characters of its males and ephippial female. *Chydorus parvireticulatus* from South America, even though no males are available, is likewise significantly different from the North American taxon and also from the others in Australia-Asia. It is certain there has been no transport of either New World species into the other continent. *Chydorus faviformis*, for example, is a northern species, presently confined to the glaciated portion of northeastern North America (Frey 1987). It seems unlikely from present evidence that it was ever forced far enough southward during the glacial ages for its resting eggs to reach South America. The differences between these two species are so striking that a single specimen of one in a population of the other could easily be recognized.

Southern China, the Malay Peninsula, and India are presently part of the same land mass, Australia rather far removed, but their honeycombed *Chydorus* are all different from one

another. They seem much more closely related to one another than to *C. faviformis* in North America. The postabdomens of their males, so far as known from the few specimens available, are reasonably congruent among themselves and different from *faviformis*, and all the species in varying degree have the edges of the honeycombs fringed with fine setules. The latter character, like the 'hairs' in *Chydorus pubescens*, may be highly variable from one population to another or even in the same population at different times, but yet in examining many populations of *C. faviformis* from North America, we have never detected that first suggestion of fringing. Obviously these taxa, like the two in the Western Hemisphere, have been isolated from one another for very long periods of time, demonstrating again that transfer of resting eggs from one continent to another, or even between major parts of a continent, probably does not occur. Water is not just water, but it has a highly diverse set of chemical, physical, and biological factors that help mould the environment and make each waterbody almost unique. The various species have become adapted to different suites of these conditions, hence for successful displacement to another region they must find another waterbody with closely similar conditions.

Now that this study is momentarily completed and the honeycombed species are realized to be vastly different from one another, it would be interesting to tackle one of the other presumably cosmopolitan species, especially those occurring in the lower latitudes. Two good examples would be *Alona karua* and *Ephemeroporus barroisi*, both of which are common everywhere in the tropics and subtropics. Another with reputedly much wider distribution is *Alona affinis*. My impressions from examining many populations of these is that although they look similar in gross morphology, they are probably differentiated from one another at the species level, as there are many differences in details of structure. And I believe that many other chydorids, including most of those in Europe that are claimed to occur on other continents, probably are also differentiated at the level of species.

We know the Cladocera is a very old group, probably having originated some time in the Palaeozoic. Smirnov (1970) has found some peculiar microfossils from the Permian in Kazakhstan that he believes are Cladocera, and Fryer (personal communication) has found a good ehippium from the Cretaceous of Australia. Thus, the Cladocera were certainly well developed and well differentiated by the time the primordial land mass began separating into the present-day continents and subcontinents. An hypothesis to explain the occurrence of apparently similar Cladocera on the various continents without any genetic exchange having occurred through the intercontinental transfer of resting eggs is that the species occurring now differentiated from the primordial species present throughout the original land mass before its separation into the continents. Even without this hypothesis having been substantiated yet, all species of Cladocera must be examined closely, especially those reported from widely separated regions. Our task is to work out the means for interpreting evolutionary pathways. We cannot do this by the careless transfer of specific names to taxa that are really different, even though they appear to be the same grossly. The correctness of this hypothesis can only be guessed at now, because the various species around the world have not been studied and differentiated from close relatives.

This deplorable lack of good systematics today has resulted from innumerable, unintended, and mostly injudicious decisions by many investigators in the past. To change this to a suitable base for taxonomic judgements will require much effort even to get the various species already described sorted out reasonably well. Not only morphology will be needed for this but also

knowledge about ontogeny, life history, and genetics based on breeding attempts, electrophoresis, chromosome counts, DNA content, etc. The task is big but necessary. We have many species that are difficult to distinguish, even on the basis of very fine morphological details. Without any coordinated action we shall continue to muddle along in complete frustration.

My recommendations include the following.

1. We need to work with *populations, not isolated specimens*. Because there may well be a seasonal replacement or succession of species in a waterbody, one cannot, without detailed study, regard all specimens from the same waterbody but collected at different times of the year as necessarily being the same species. Needed are large samples collected in one waterbody over several seasons. Ideally the main sample studied should contain at least several hundred specimens and should be from the time of year when gamogenesis is likely to occur. At middle and high latitudes this will be in the autumn, at low latitudes probably most likely in spring, although gamogenesis of 'southern' species here will probably still be in autumn (Frey 1982a).

For the most part the samples need to be collected where the animals occur, which for the chydorids is mostly in beds of macrophytes, on sticks, stones, and other items on the bottom, and in the sediments themselves. The latter habitat is particularly important and one that has not been sampled adequately to date. It seems that sediment-associated chydorids may provide the only instances of true endemism among the ancient lakes of the World (Vasil'yeva & Smirnov 1969, 1975) in Lake Baikal; Petkovski & Flössner (1972) in Lake Ohrid; and Frey (personal observations) in Lake Malawi). Samples from offshore collected for studying the limnetic plankton will generally yield only isolated specimens of the substratum frequenting Cladocera, except for certain species, such as *Chydorus sphaericus sens. lat.*, which may become abundant in the true plankton during episodes of high productivity, and in the tropics certain species of *Ephemeroporus* and occasionally other chydorids. If one works only with such offshore samples for chydorids he will be using the specimen approach to species, not the population approach, and even if he finds enough specimens he will not have the instar-frequency distribution of the producing population.

2. *All specimens should be examined*. If several hundred specimens of what seem to be the same species are removed and examined closely with a compound microscope, it should be possible to determine quite easily if they are all the same species from the details of their morphology. Each specimen, even the smallest, can be identified as being either male or female from characteristic morphological features. Males of all chydorids known to date, from the smallest *Alonella* or *Ephemeroporus* to the largest *Eurycercus*, have only two pre-reproductive instars and seemingly only one reproductive instar. Mature males are smaller than mature females, usually very markedly so. Ehippial females can usually be recognized easily by characteristic changes in structure of the part of the shell that will enclose the egg, or eggs (= the ehippium), by the dark pigmentation often present in addition, and by the thickening of the dorsal margin, which provides the tension needed to keep the ehippium tightly closed around the egg, or eggs. Usually there is only one resting egg in chydorids, although at least three species of Chydorinae (*Chydorus ovalis* and *Chydorus biovatus* (Fryer & Frey 1981); *Chydorus piger* (Frey 1985)) regularly have two. Species in the subfamilies Eurycercinae and Sayciinae have a variable number, which increases with size of the females.

3. From such a sample a *size-frequency distribution* can be constructed. The three instars of males sort out readily on morphological grounds, which enables the curtailment in growth rate between instars II and III to be observed easily. The instars of parthenogenetic females do

not sort out from one another in size–frequency distributions, except for the first and possibly the second instar in small chydorids, and up to instar III or even IV in *Eurycercus*. Species in the subfamilies Aloninae and Chydorinae seem to have just two prereproductive instars, although a population of *Monospilus dispar* collected in Florida in February had three (Frey & Hann 1985). Species of *Eurycercus* and *Saycia*, the largest chydorids, have more than two immature instars, the number increasing with size of the species (Frey 1973; Bottrell 1975). Among all Cladocera there is a constantly changing population composition as the cohorts of offspring produced on successive days progress through the various instars in their ontogeny. In the population of *Monospilus* mentioned above (291 individuals, mostly immature), the instar of each individual could be determined by the number of nested shells of previous instars on the carapace, hence the frequency distribution of each instar could be plotted. Reproduction began in instar IV and continued through VII, with just single specimens present of older specimens up to instar X. In summer the full population of seven instars would be completely changed about every two weeks, with maturation from egg to reproducing female taking less than a week. Other small chydorids probably have similar time relationships, although at present no way exists for studying this in unrestricted populations.

4. *Males change in morphology* over their three instars. Instar-I males can be recognized by the peg-like Anlage of the copulatory hook on trunklimb I, sometimes by a slightly larger antennule containing an Anlage of the male seta, and by a small genital pore on the postabdomen, which is usually located more proximad than in the reproductive male. In instar II these changes have become greater, and in addition there is now an Anlage of an extra seta on the inner distal lobe and the Anlage of the copulatory brush seta. The antennule is bigger, but it still has only the nine aesthetascs characteristic of the female. The mature male is completely different. The copulatory hook is fully developed, varying in the variety of its shapes and of structures near the tip, the extra i.d.l. seta and the copulatory brush seta are fully developed, as is the copulatory brush that enclosed the latter. The antennule has become much larger in many species, with the male seta and the now usually 12 aesthetascs fully developed. The rostrum, which typically has been shortening since instar I, now reaches its final form, often being at this stage very different from that of the female. And the postabdomen and claw, which in instars I and II closely resemble those of the female, except for the developing reproductive pores and sometimes the tendency in instar II for the lateral denticles to be multiple instead of single, now are often strikingly different from those of the female. These changes in morphology of the male from instar to instar are highly important for detecting evolutionary relationships and patterns. Males are so important in revealing differences and similarities among chydorid species that any description without full attention to them is woefully incomplete. This is indicated clearly by the large differences in morphology of males between the North American and Australo-Asian taxa in the present study.

5. Of importance almost equal to the males in evolutionary study are the *ephippial females*. All species of chydorids produce ephippia, but the variety among them greatly exceeds that in the Daphniidae, where each of the two subgenera of *Daphnia* produces a unique kind of ephippium, and each of the genera *Ceriodaphnia*, *Scapholeberis*, *Simocephalus* and *Daphniopsis* a distinctive kind. In each of these genera there is variation in details from one species to another, but always within the generic pattern. In the chydorids things are different, in that there are no general patterns of ephippium morphology associated with one genus or another. In small chydorids the pattern ranges from some species (for example *Disparalona rostrata* and *D. leei*

(Michael & Frey 1984)) in which the entire shell is used without any different sculpturing or even pigmentation, to those in which the ephippium is highly sculptured and pigmented and the excess shell is sloughed off along lines of weakness, leaving an egg capsule that bears no morphological resemblance at all to the species that produced it. All one can see is a resting egg enclosed by a highly modified and often highly pigmented part of the shell that has been closely trimmed in shape and size to the egg.

Modifications of the shell for production of the ephippium and the changes in body proportions this has required are really the only structural differences between an ephippial and a parthenogenetic female. There are no changes in the postabdomen, the postabdominal claw, setation, or any structures associated with the head. Usually there is a barren instar between two successive instars that produce a resting egg. The ovaries seem to require more time to produce the larger resting egg than parthenogenetic eggs, where every instar can be reproductive under favourable conditions. The barren ephippial female resembles the reproductive ephippial female closely in structure of the shell but generally has much less intense pigmentation. Details of morphology, however, enable the animal to be recognized positively as being in the ephippial condition, and thus one can determine the ratio between barren and reproductive ephippial females in a sample. Rammner (1929) in his work on *Scapholeberis* found that the barren instar normally lasts about three days and the reproductive instar only about one. The reproductive ephippial female is heavily pigmented, which should make it more vulnerable to predation by a sight-feeding predator, such as a fish. Having it in the population for only a short period of time should increase the likelihood that the female will survive to successful moulting and the release of the resting egg into its protective ephippium.

6. Even the *ontogeny of parthenogenetic females* should be understood, as often there are marked morphological changes between immature and mature specimens. Body proportions are different, resulting from the brood pouch being expanded to receive the parthenogenetic eggs. In immature females the postanal portion of the postabdomen is often relatively much shorter than in the mature female, and the anal groove is bordered by spaced single denticles rather than by groups or rows of fine setules. Furthermore, the surface patterns of the carapace are often much more distinct than in reproductive specimens, so that one sometimes wonders if he is looking at just one species. All this emphasizes the need to base a primary description not only on mature females, along with males and ephippial females, but to have in addition a description of any ontogenetic changes that occur from instar I to maturity.

7. The International Code of Zoological Nomenclature (Stoll *et al.* 1964) requires a *detailed comparison* between the new species being described and the most closely similar taxa that have already been described. Because few species in the literature have been described adequately for the morphology of males and ephippial females, for the ontogenetic morphology of females, and for the detailed morphology of adults, no real comparisons can be made. Here is the real bottleneck in cladoceran systematics and the origin of much of the improper acceptance of cosmopolitanism around the world. We cannot make decisions about conspecificity or evolutionary relationships at the species level until we know what the species are. I formerly thought that Europe was the only geographical region in which the Cladocera were well known, because of its rather restricted size and because of the intensive study of these animals by scientists in many countries during the past 200 years. But I have decided that even here the taxa are imperfectly known, mainly because the scientists looked chiefly at gross features and considered all variation from whatever continent as being infraspecific.

What is needed is a *close redescription* of the European taxa as a best first start, the *establishment of new type populations* if no specimens exist from the original collections, and the *placing of a diversity of specimens in strategic museums* around the world, so that they can be used for direct comparison with specimens from any country or region other than the original one.

8. Because of all these difficulties and uncertainties, it is impossible to construct the distribution of any major species from names in the literature. The only aspect that might emerge from such an endeavour is the geographical distribution of a species-group or a species-complex, but only if the various taxa around the world have been identified closely enough. The latter seems unlikely because of the carelessness with which names have been transferred from one continent to another. Real distributions can be worked out only through the comparison of populations from different localities, as only by such means can cosmopolitanism be demonstrated for any taxa. Our studies to date suggest that it does not occur in the chydorids.

I am indebted to many persons for information and specimens used in this study, without which the study could not have been done. C. H. Fernando made available R. P. Lim's magnificent series of samples from Pinehurst Lake, Ontario, and also the two samples from the pond at Jabalpur, India, collected by P. Rane. R. Rajapaksa carefully picked out this latter material and sent it to me. D. P. Zutshi attempted without success to collect additional samples from India. B. A. G. Idris collected fresh samples for me from Tasek Bera. W. D. Williams provided splits of his Australian sample to me and to G. B. Deevey, who turned her material over to me, and more recently R. J. Shiel and B. W. Timms have provided additional samples from Australia. Chiang Sieh-chih brought the Chinese taxon to Bloomington in 1980. For the material from South America, I am indebted first to Rufus Kiser for permitting me to look over his personal material, and to T. E. Bowman of the U.S. National Museum of Natural History for the loan of the three specimens Kiser had mounted and for the loan of the bulk sample from which these had been removed. J. C. Paggi made available his specimens from Corrientes Province, Argentina and N. N. Smirnov his from near Manáos in Brazil. The three specimens (or four including the one lost) from South America in the Birge collection were finally specifically identified as to locality and date by means of the laboratory notebooks of Harriet Bell Merrill and her letters to Birge discovered in Florida quite accidentally by H. W. Binford. Dr F. R. Turner at Indiana University produced the excellent s.e.m.s in this paper, which are marred only by poor quality of some of the specimens and the difficulty of removing all the detritus and organisms attached externally. This research has been variously supported by a number of grants from the National Science Foundation, most recently by BSR 82-14600.

APPENDIX 1. DISTRIBUTION OF *C. FAVIFORMIS*

Newfoundland

Avalon Peninsula: Daggett Pond no. 2 (3558); three ponds and lakes in LaManche Marsh region south of St John's (7062, 7075, 7076, 7080, 7081); lake (no. 14) southwest of St John's (Daggett 1973); pond on Highway (Hgy) 1, 7.2 miles east of Hgy 80 (7074); pond just north of Markland on Hgy 81 (7113).

Terra Nova National Park west to Badger: lake 9.3 miles south of Charlottetown exit, Terra Nova National Park (7196); Jonathan Pond, 12 km north of Gander (5737 = C 230); four unnamed

ponds and lakes on Hgy 1 from 16 km west of Gander to 6 km west of Glenwood (5739 = C 232, 5740 = C 233, 5741 = C 234, 7203, 7205); two lakes near Notre Dame Provincial Park (7044, 7045, 7206); Rushy Pond, 15.4 miles east of Badger (7043).

Gros Morne National Park: pond just south of Parsons Pond and north of the Park (7039).

Nova Scotia

Annapolis County: Big Dam Lake East (7286, 7287); Big Dam Lake West (7285); Kejimkujik Lake (5768 = C 261).

Cumberland County: lake on Hgy 104, 1.4 miles west of Oxford exit (7339).

Guysborough County: lake on west side of Hgy 7 south of Lochaber (7239); lake 0.3 miles further south (7240).

Halifax County: Papermill Lake, near Bedford (7331); Sandy Lake, near Bedford (7333).

Lunenburg County: Wentzell Lake, on Hgy 10 (7258); Williams Lake, on Hgy 10 (7259); lake at northern outskirts of New Germany (7260); Fancy Lake, south of Bridgewater (7302); small lake, 1.0 miles off Hgy 103 near Conquerall Mills (7304); Crooked Lake, in same general region (7305); Spectacle Lake, in same general region (7306); Island Lake near Middlewood (7307).

Queens County: Beaverhead Lake (7271); Beaverskin Lake (7278); Grafton Lake (5767 = C 260, 7284); Harmony Lake (7291); Hilchemakaar Lake (5763 = C 256, 7279); Kempton Lake (7274); McGinty Lake (7282); Minard Lake (7270); Pat Kempton Pond (5761 = C 254, 7269).

Quebec

La Mauricie National Park: Ruisseau Brodeur Pond (5800 = C 292); small lake near St Mathieu entrance (5804 = C 296); Lac Soumire (5805 = C 297).

Ontario

45 localities (not specified) in all regions of Province except distal half of peninsula between Lakes Huron and Erie (Hann 1975, 1981); Georgian Bay (Bigelow 1922); Lake Erie (Wilson 1960).

Eastern Ontario: Beaver Pond (6448); Bond Lake, just north of Toronto (Bigelow 1922); Brewer Lake (6444); Costello Lake (6447); Cranberry Bog near Galt, Youtha Lake, and Timagami Lake (Brandlova *et al.* 1972); Devil Lake (6492–93); Loughborough Lake (6491); Lake Muskoka (Adamstone 1928); Lake Opeongo (6445); Lake Opinicon (6459–6469); Pinehurst Lake (Lim 1976); Pond on Opeongo Road (6446); Round Lake (6500); Silver Lake (6487–6489); South Buck Lake (6494, 6495); Sydenham Lake (6490); Tea Lake (6454); Upper Rock Lake (6470, 6473); Warner Lake (6474); West Smith Lake (6443).

Algoma County: Bog Pond (3674) and Spruce Bog Pond (3675), both east of White Lake.

Essex County: Pond on Pt Pelee (Bigelow 1922).

Frontenac County: limestone quarry near Kingston (Klugh 1926, 1927); mouth of Little Cataraqui River (Klugh 1926).

Thunderbay County: Beartrap Lake (3672); Lake Nipigon (Bigelow 1923, 1928); Shaker Pond (3673).

Kenora Region: Lake 99 (3313), Lake 119 (3311), Lake 302 (3306–7); lake east of Kenora (3664–5); Justice Lake (C 347).

Manitoba

Riding Mountain National Park: Lake Whirlpool (5542 = C 3).

Minnesota

Aitkin County: Bass Lake (3936); Wakefield Lake (3939, 3942).

Becker County: Bad Medicine Lake (Quade 1969); Missouri Lake (3920; Synerholm 1979).

Clearwater County: Elk Lake (Whiteside 1974); Lake Itasca (DeCosta 1964); Lake Mary (Quade 1969); Squaw Lake (3904, 3908; Quade 1969; Synerholm 1979); Tower and Twin Lakes (Synerholm 1979).

Cook County: Road, Squint, and Clearwater Lakes (Synerholm 1979); Mary (Quade 1969).

Crow Wing County: Big Pelican Lake (DeCosta 1964).

Itasca County: Small Lake (3946); Surprise Lake (3947).

Lake County: Lakes Kylan, Little Springs, Tony, and Railroad (Synerholm 1979).

Mahnomen County: Faith and Ballard Ponds (Synerholm 1979).

Sherburne County: Briggs Lake (DeCosta 1964).

Wisconsin

Dane County: Lake Wingra (Frey 1960).

Oneida County: Baker Lake (6086); Lake Julia (Birge 1893); Lake Madeline (6015, 6017); Minocqua–Tomahawk Channel (6008–9, 6125–6); Tomahawk Lake (6153).

Shawano County: White Clay Lake (DeCosta 1964).

Vilas County: Lake Kawaguesaga = *type locality* (Birge 1893); Allequash Lake (5992, 6080–1); Escanaba Lake (6102); Grassy Lake (6106); Mann's Creek Lake (6121–23); Mystery Lake (5996, 6134–6); Palette Lake (6141); Tomahawk Lake (6153, 6154); Tomahawk–Minocqua Channel (6125–27); Wild Rice Lake (6160).

Michigan

Barry County: Lawrence Lake (1860; Keen 1976).

Cheboygan County: Douglas Lake (293–302, 679; Moore 1939); Lake Sixteen (311); Lancaster Lake (264–6, 324); Twin Lake (312).

Emmett County: Goose Pond (331).

Gogebic County: Lake Gogebic (Birge 1893).

Presque Isle County: Clear Lake (329); Francis Lake (271); Orchard Lake (330); Shoe Pac Lake (270).

Indiana

Kosciusko County: Lakes Winona and Wyland (Mueller 1964).

Lagrange County: Eve Lake (6074); Martin Lake (2341, 2880, 3803, 4463, 4858, 5443); Martin–Oliver Channel (2502, 2515, 2524); Olin Lake (2874).

Marshal County: Lawrence Lake (Mueller 1964).

Noble County: Crooked Lake (195, 2292).

Steuben County: James and Pleasant Lakes (DeCosta 1964).

Pennsylvania

Wayne County: Lake Lacawac (6225-6, 6228-30, 6891-97).

New York

Franklin County: Saranac Lake (1949); Saranac Flowage (2557); Simond Lake (2562-4).

Hamilton County: Lake Ahanakee (3380); cedar swamp near Raquette Lake (2572, 2574, 3363); Charley Lake (3388); Little Tupper Lake (3374); Lower Brown Tract Pond (3364, 3366); Mason Lake (3386); Raquette Lake (1950, 2573); Sabbatis Boy Scout Camp (3373).

Herkimer County: Panther Lake (3355); Utowana Lake (2568).

St Lawrence County: Catamount Pond (2548-9); Cranberry Lake (2536); Tupper Lake (2550-1, 2565).

Warren County: Loon Lake (2581).

Connecticut

New Haven County: Linsley Pond (Deevey 1942).

Massachusetts

Barnstable County: Goodwill Pond (604).

Berkshire County: North Pond (Crisman 1976).

Hampden County: Three ponds near Hampton (3407-10).

Plymouth County: Maquen Pond (600); New Long Pond (6970).

Vermont

Caledonia County: Bald Hill Pond (2593, 2599); *Essex County*: Island Pond (2596); Lodo Pond (3376); *Orleans County*: May Pond (2585).

New Hampshire

Carrol County: Lake Winnepesaukee (2001).

Grafton County: Big Squam Lake (1988-9); Little Squam Lake (1986); Newfound Lake (1981); White Oak Pond (1998).

Merrimack County: Eagle Pond (1973); Horseshoe Pond (1972).

Sullivan County: Little Sunapee Lake (1966); Swamp Creek (1968).

Maine

Androscoggin County: Sabbatus Pond (592).

Aroostook County: Conroy Lake, south of Monticello (7361); Logan Lake, on north Holton Twp Line (7364).

Cumberland County: Crescent Lake (595); mill pond at south end of Little Sebago Lake (593, 1919); Panther Pond (1902-04); Parker Pond (1880); Saturday Pond (1886); Sebago Lake (specimens in E. A. Birge collection from A. A. Doolittle); Trickey Pond (1935-36).

Hancock County: Aunt Betty Pond, Mt Desert Island (7373); Burnt Pond (7444); Dubec Pond (7442); Echo Lake, Mt Desert Island (7380); Fox Pond, east of Ellsworth (7359); Harriman Pond, south of East Holden (7435); Little Long Pond, east of Ellsworth (7352); Long Pond, east of Ellsworth (7356); Lower Hadlock Lake, Mt Desert Island (7377); Moulton Pond, south

of East Holden (7433); Salmon Pond, east of Ellsworth (7354); Spring River Lake, east of Ellsworth (7357); Tilden Pond, east of Ellsworth (7351); Tunk Lake, east of Ellsworth (7358); Upper Hadlock Lake, Mt Desert Island (7378); Williams Pond, north of Bucksport (7439).

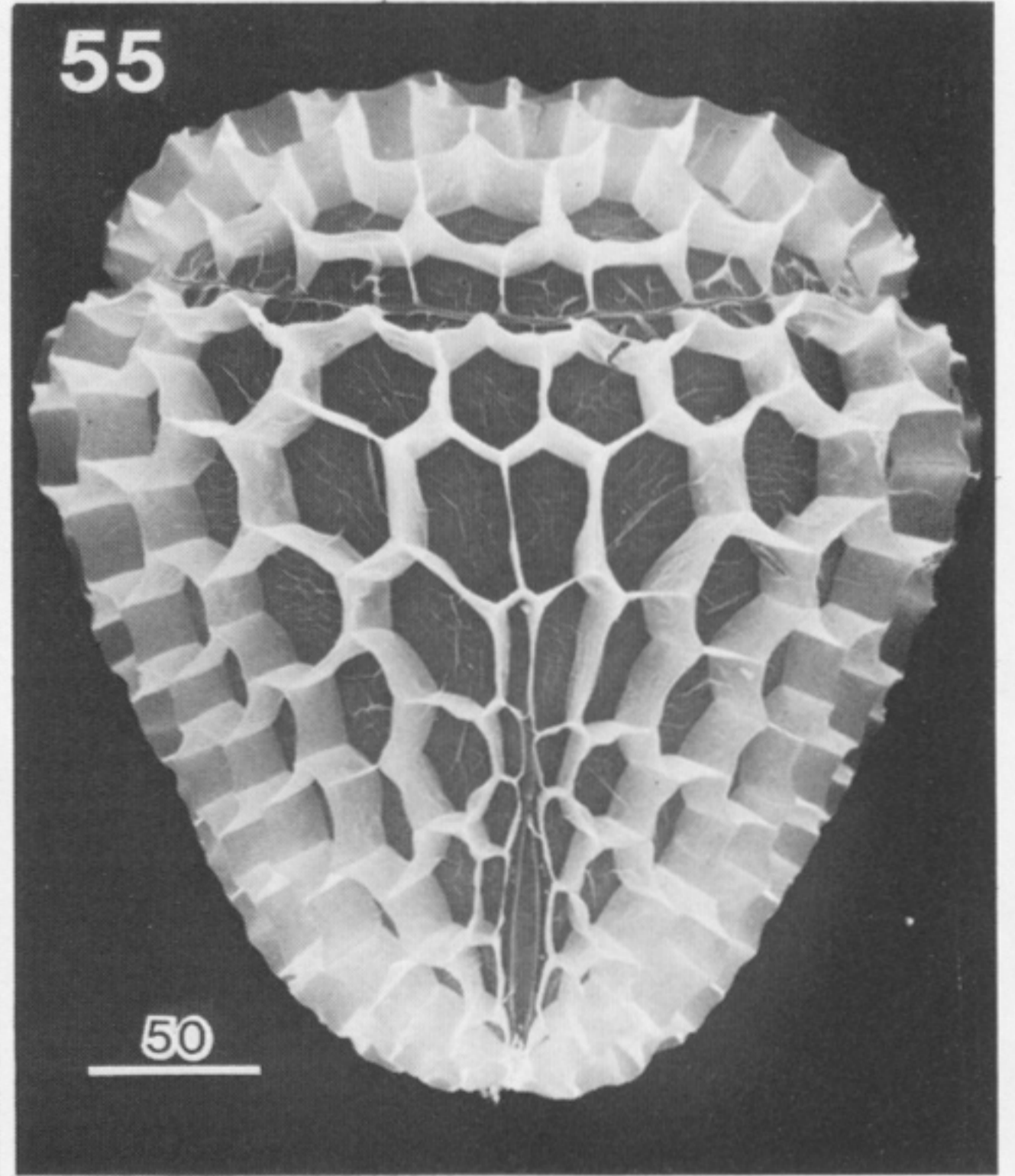
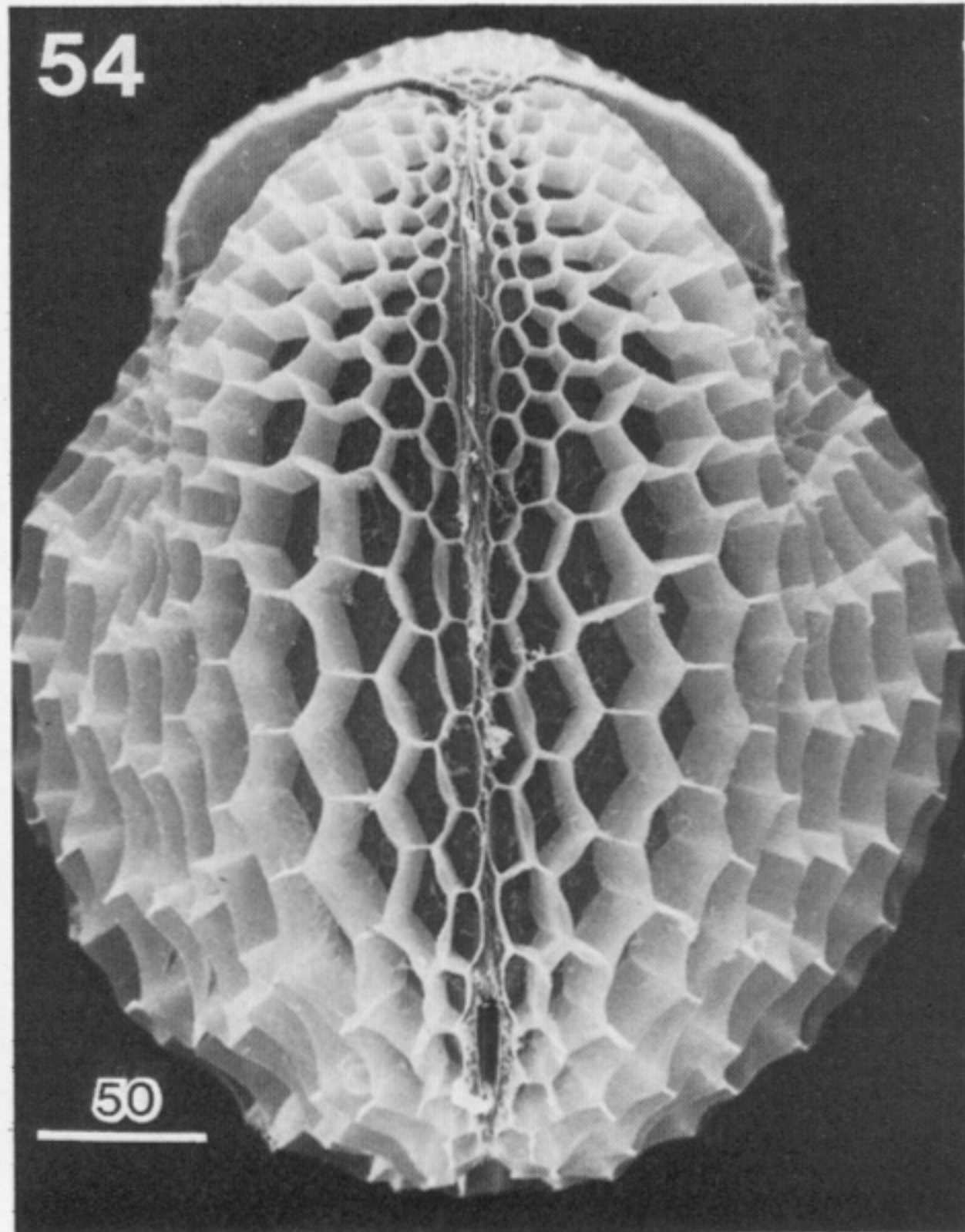
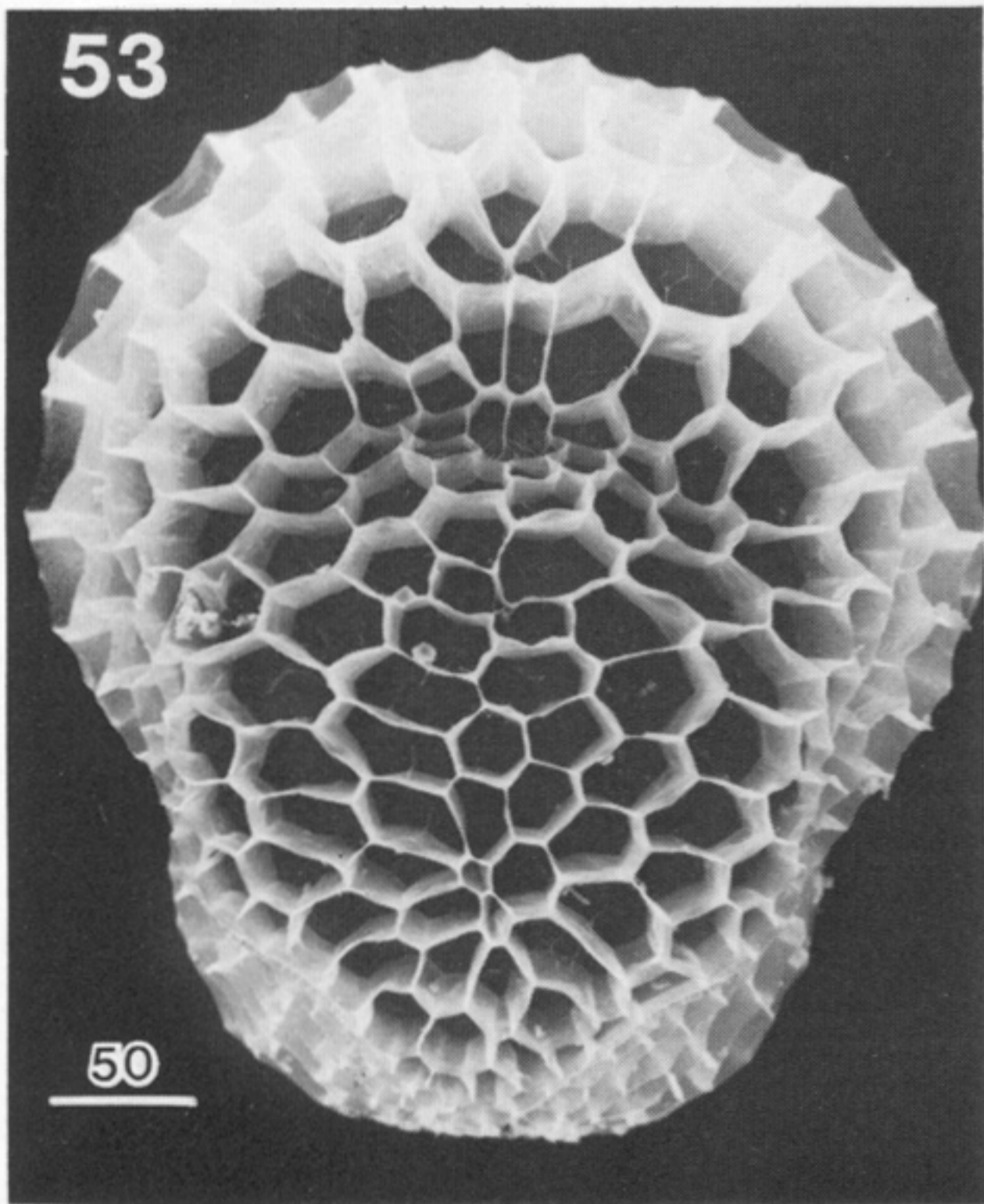
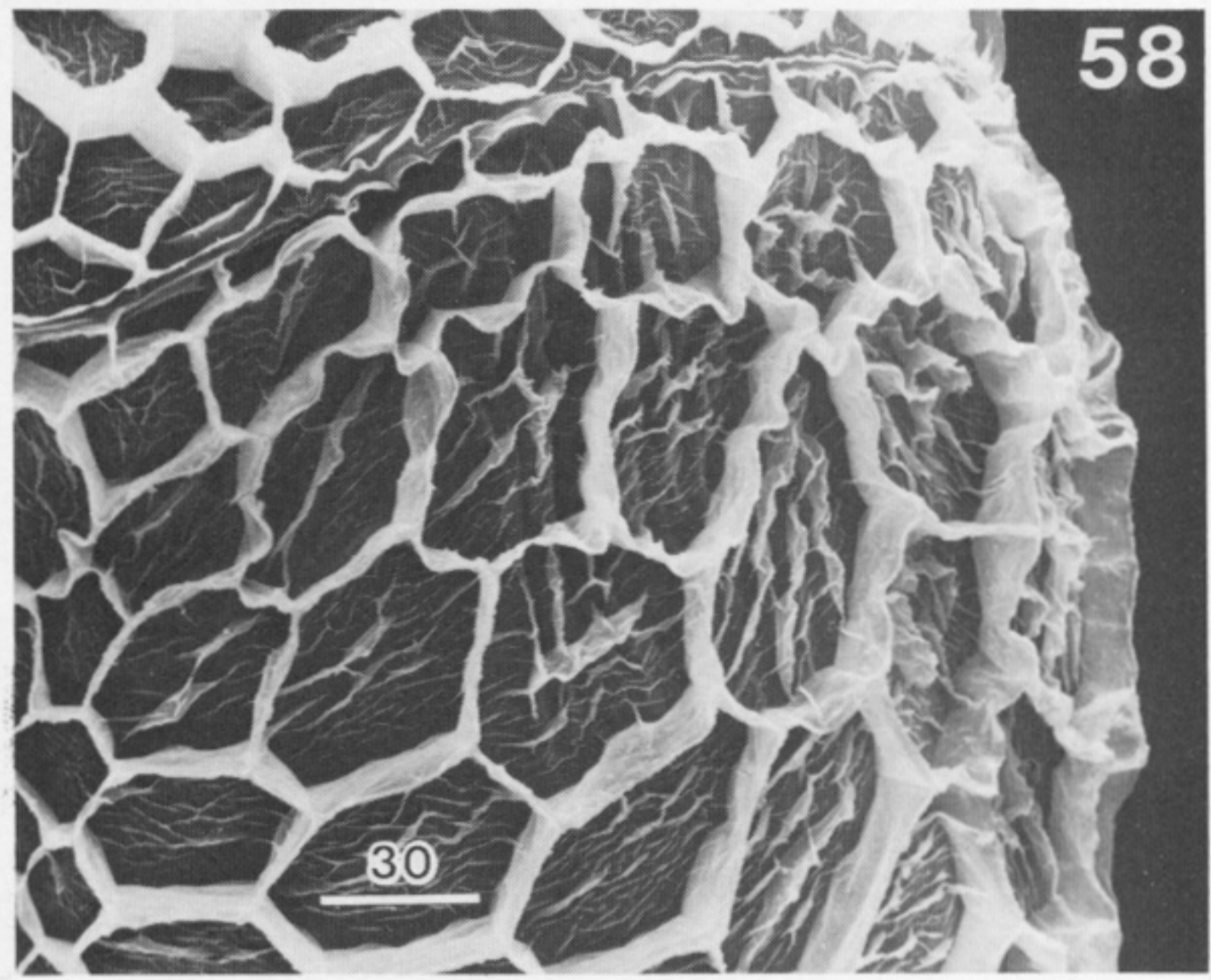
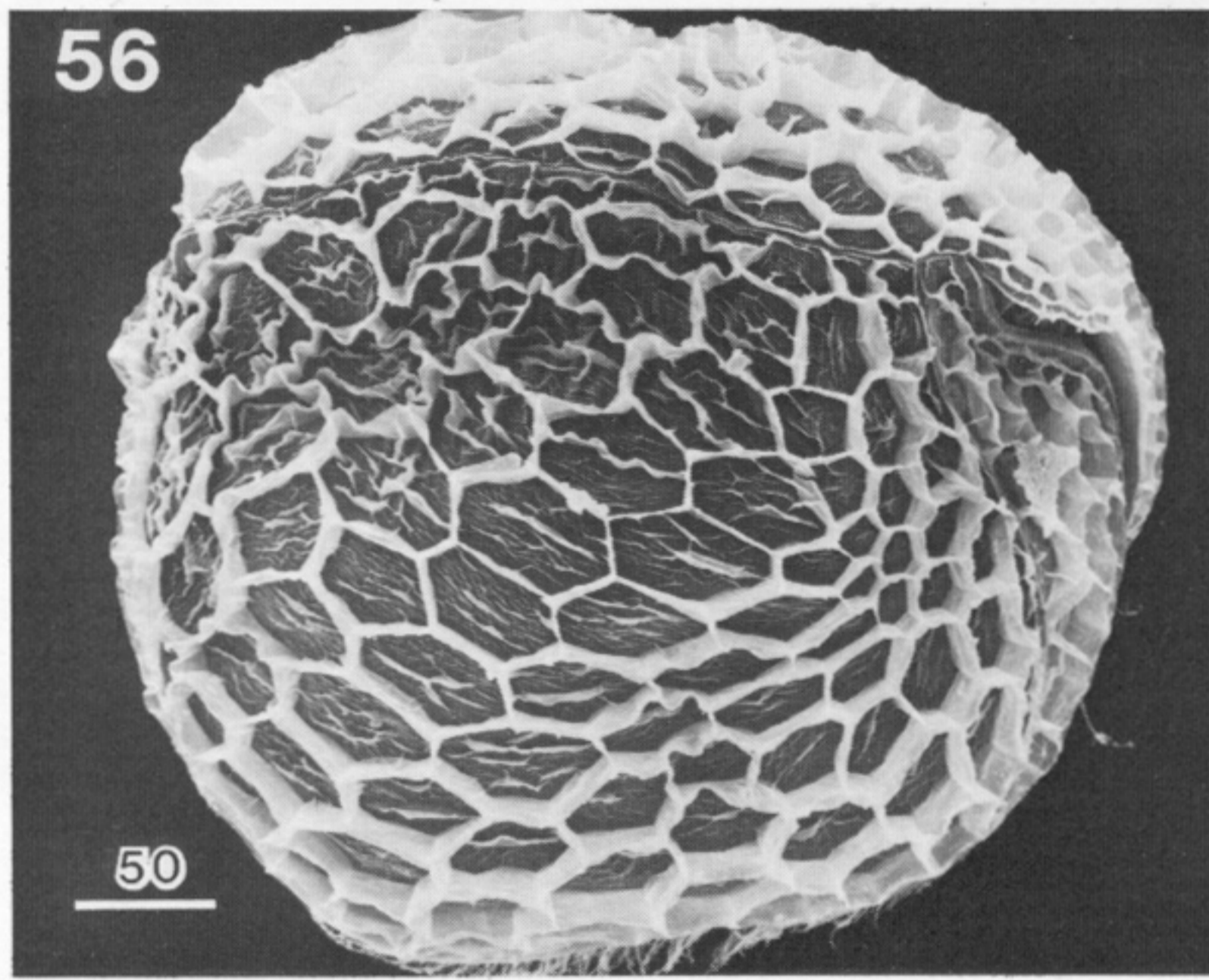
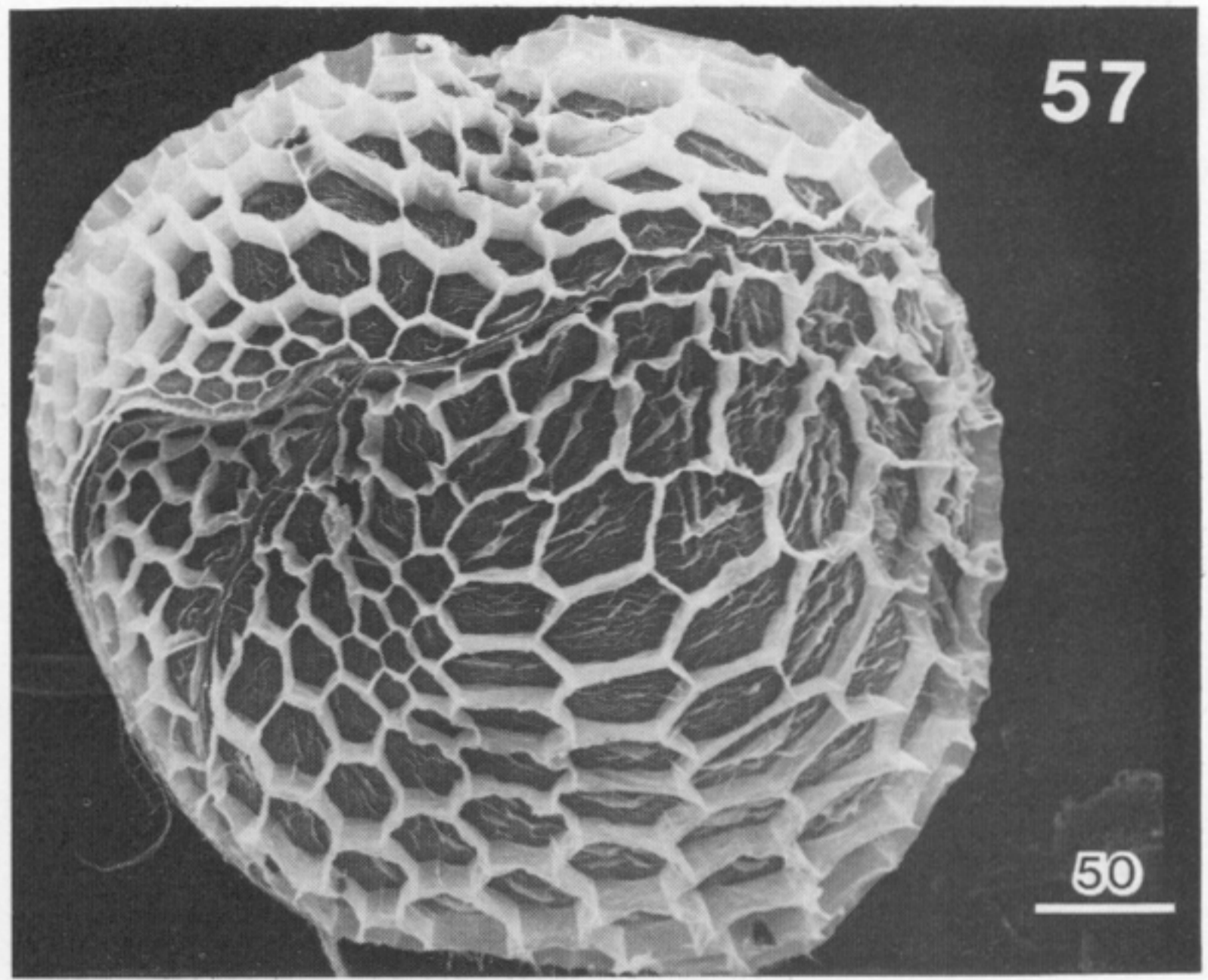
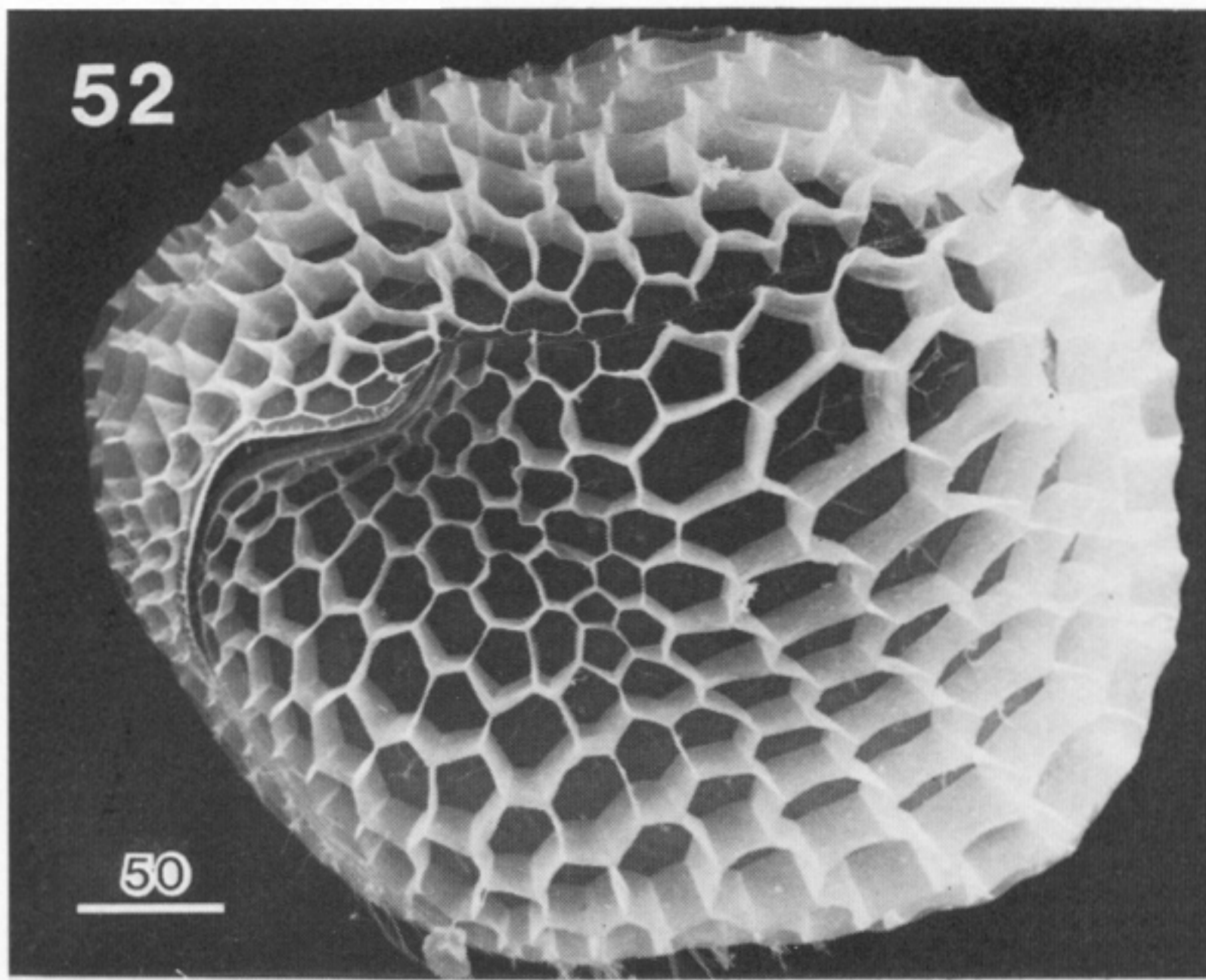
Penobscot County: Chemo Pond (7443); Holbrook Pond, near East Holden (7387); Snowshoe Pond, on road to Floods Pond (7407).

Washington County: Patrick Lake, on Hgy 89, 1.3 miles east of Hgy 101 (7349). Information in parentheses after each record is either documentation from the literature or the accession numbers from our collection in Bloomington. The additional C numbers for some records from Canada indicate collections by Chengalath (1980), from which the Frey numbers are splits.

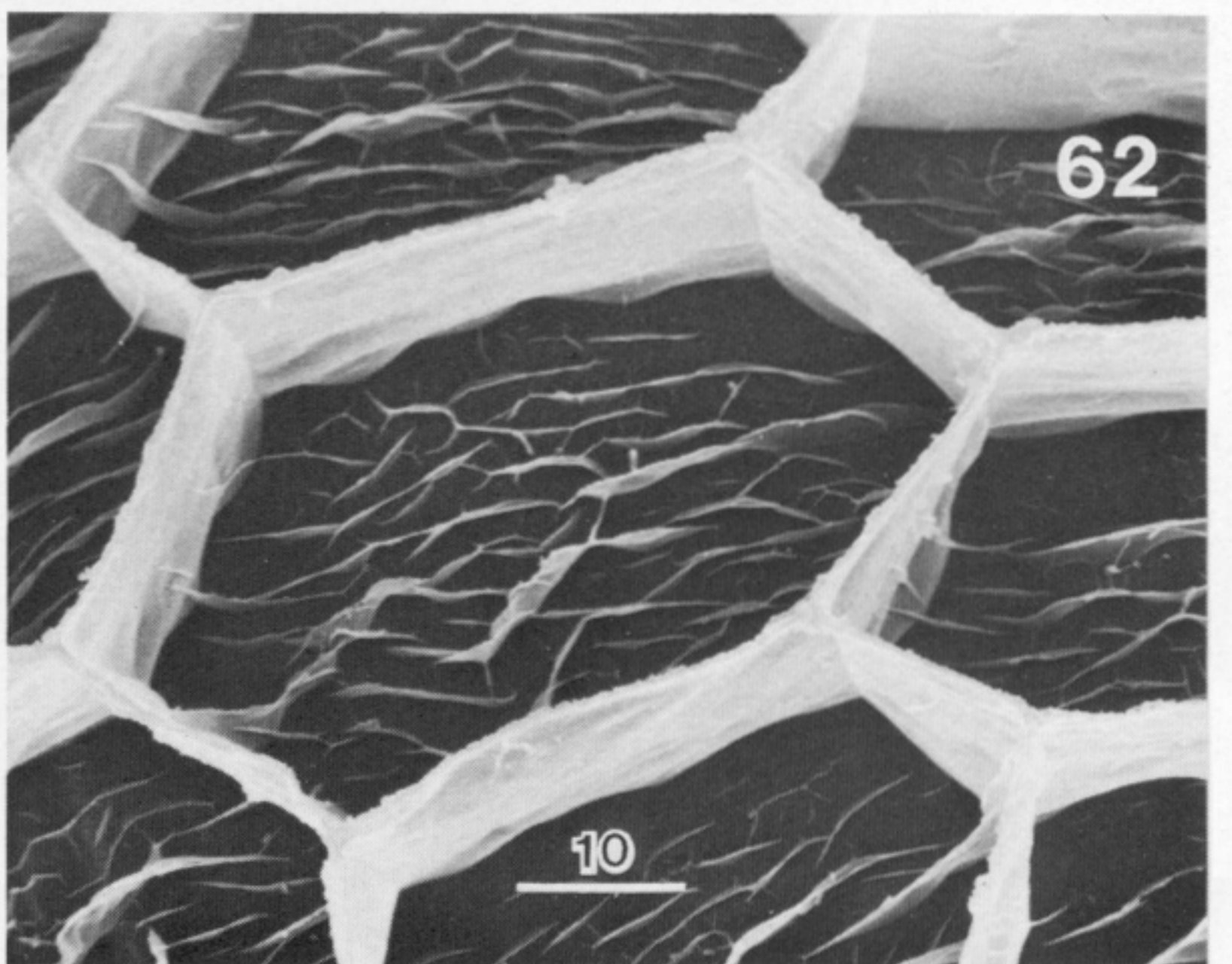
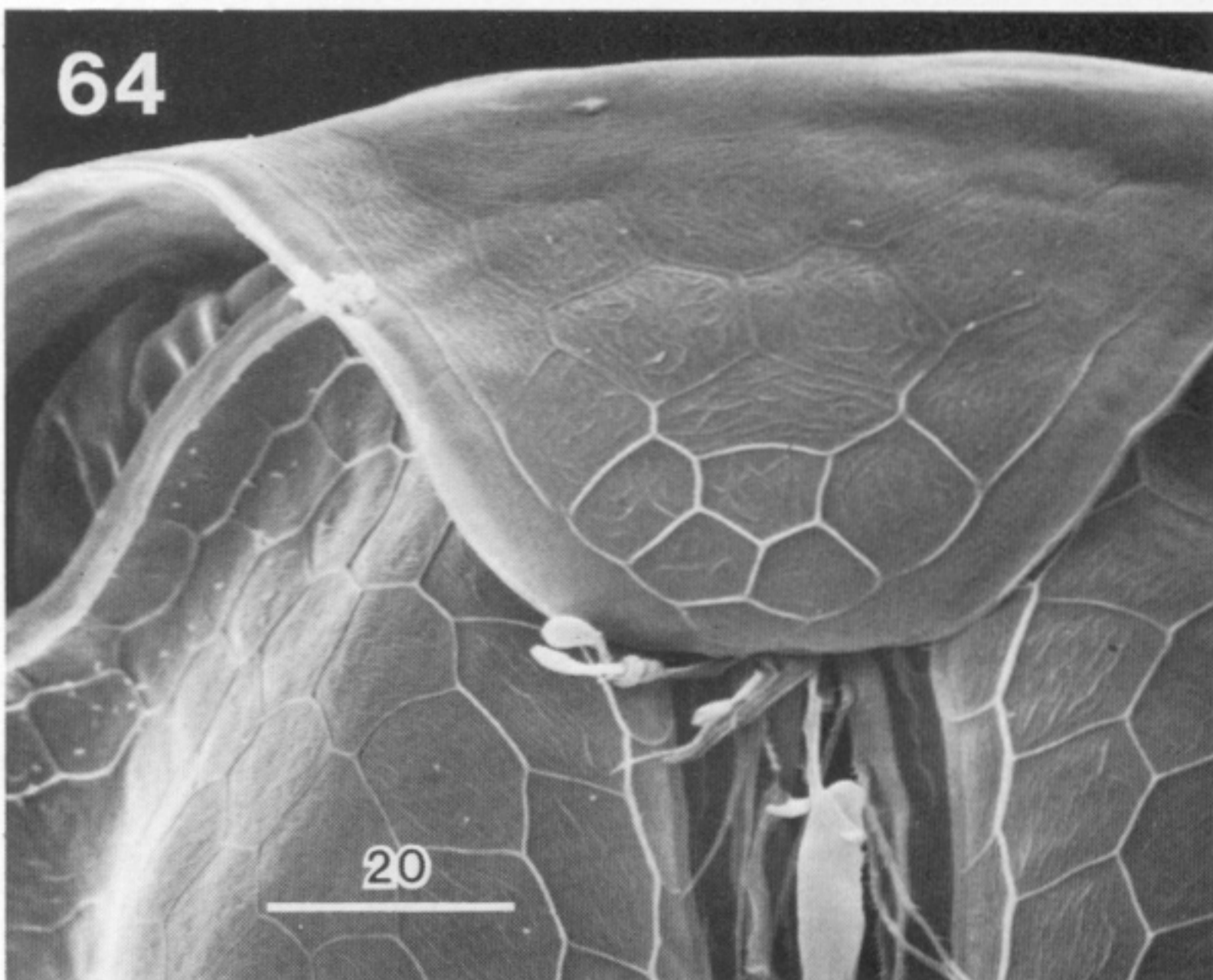
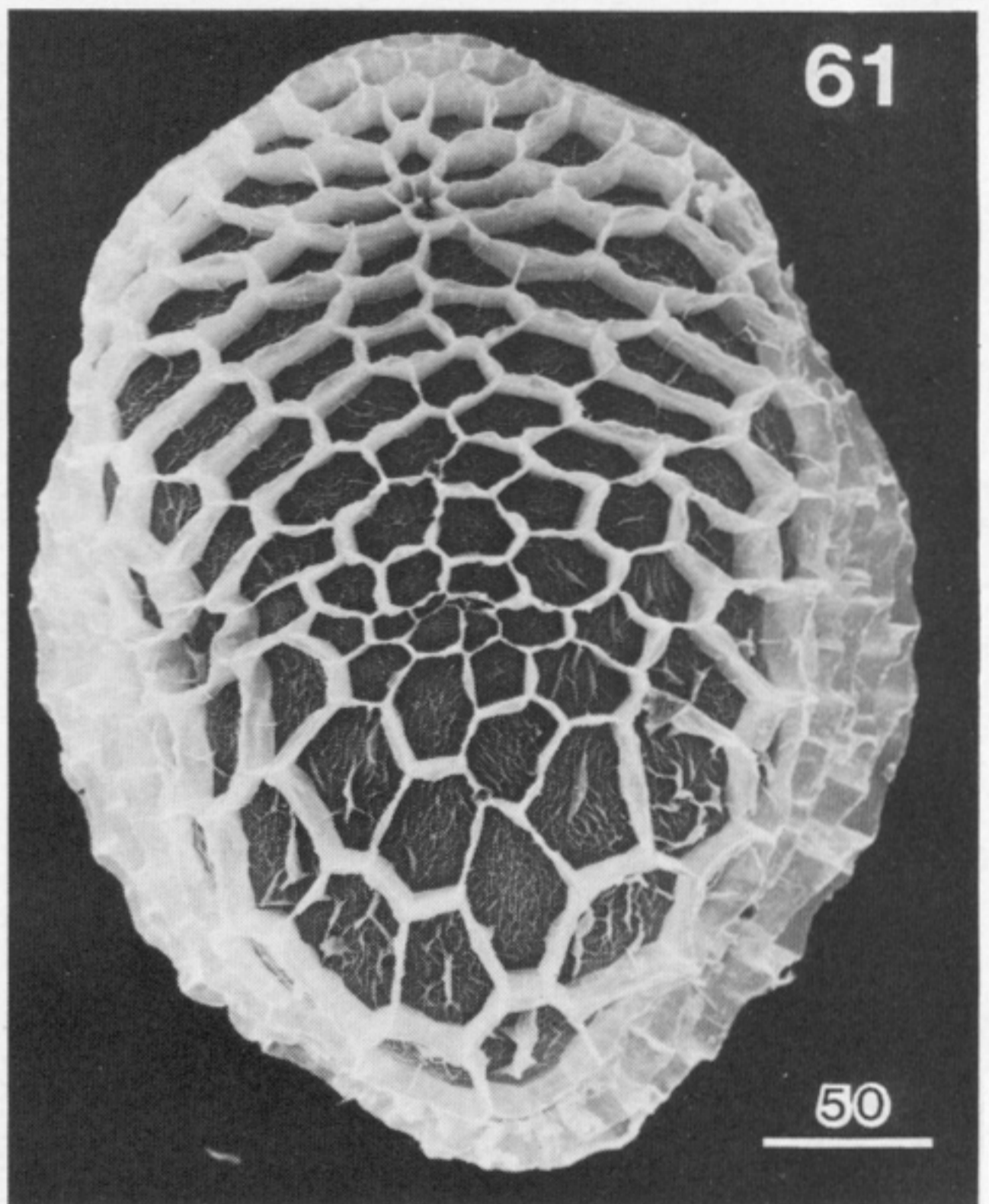
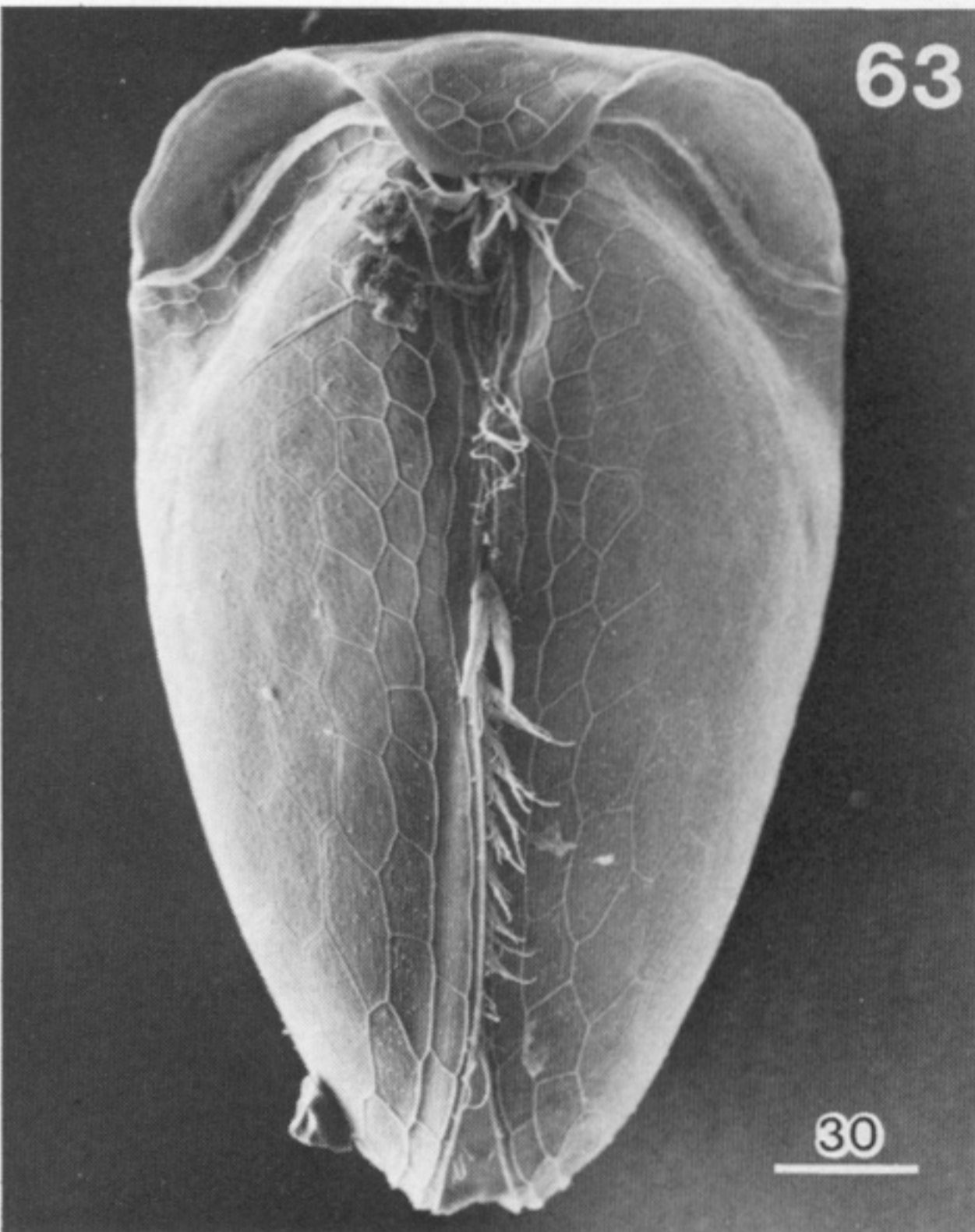
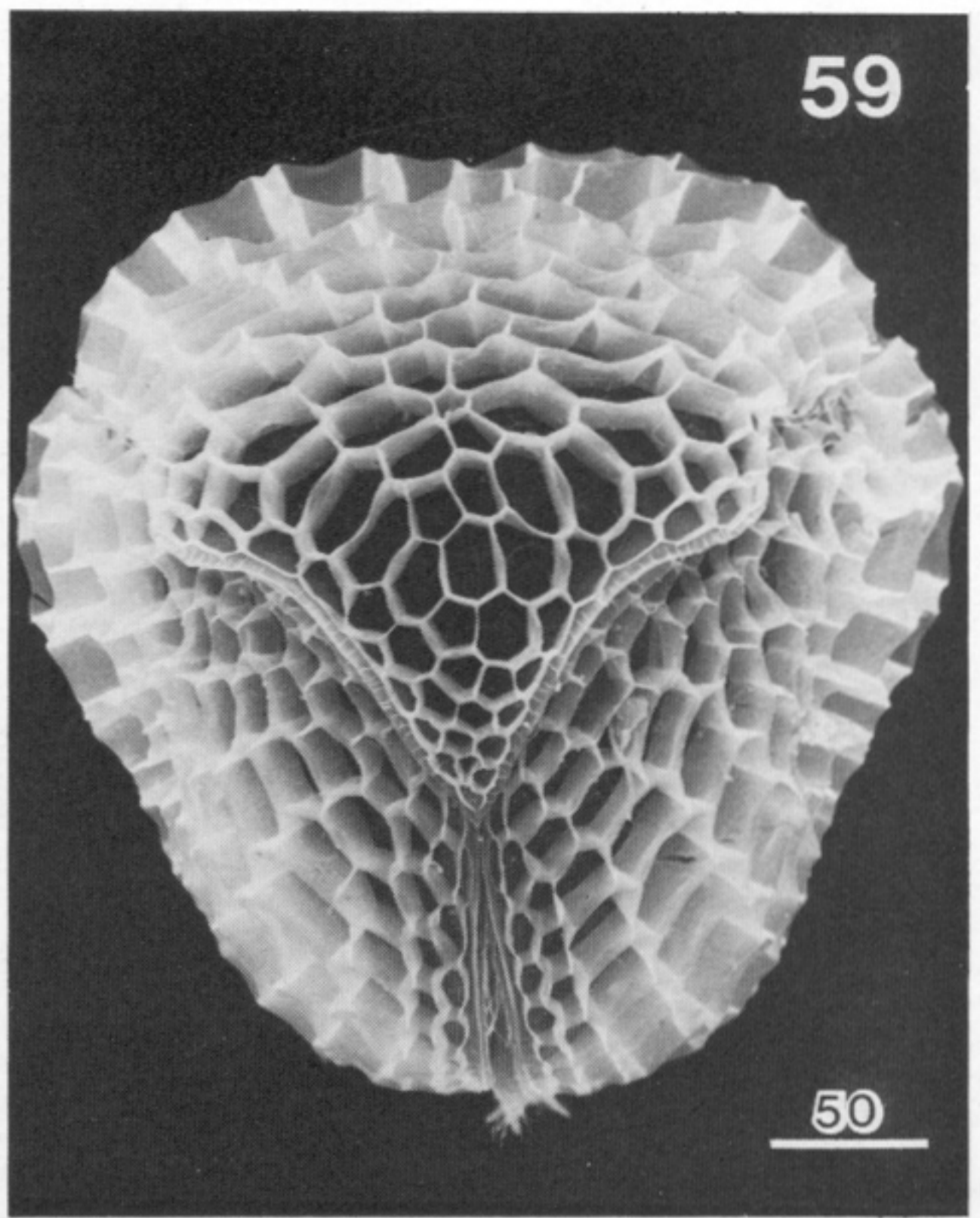
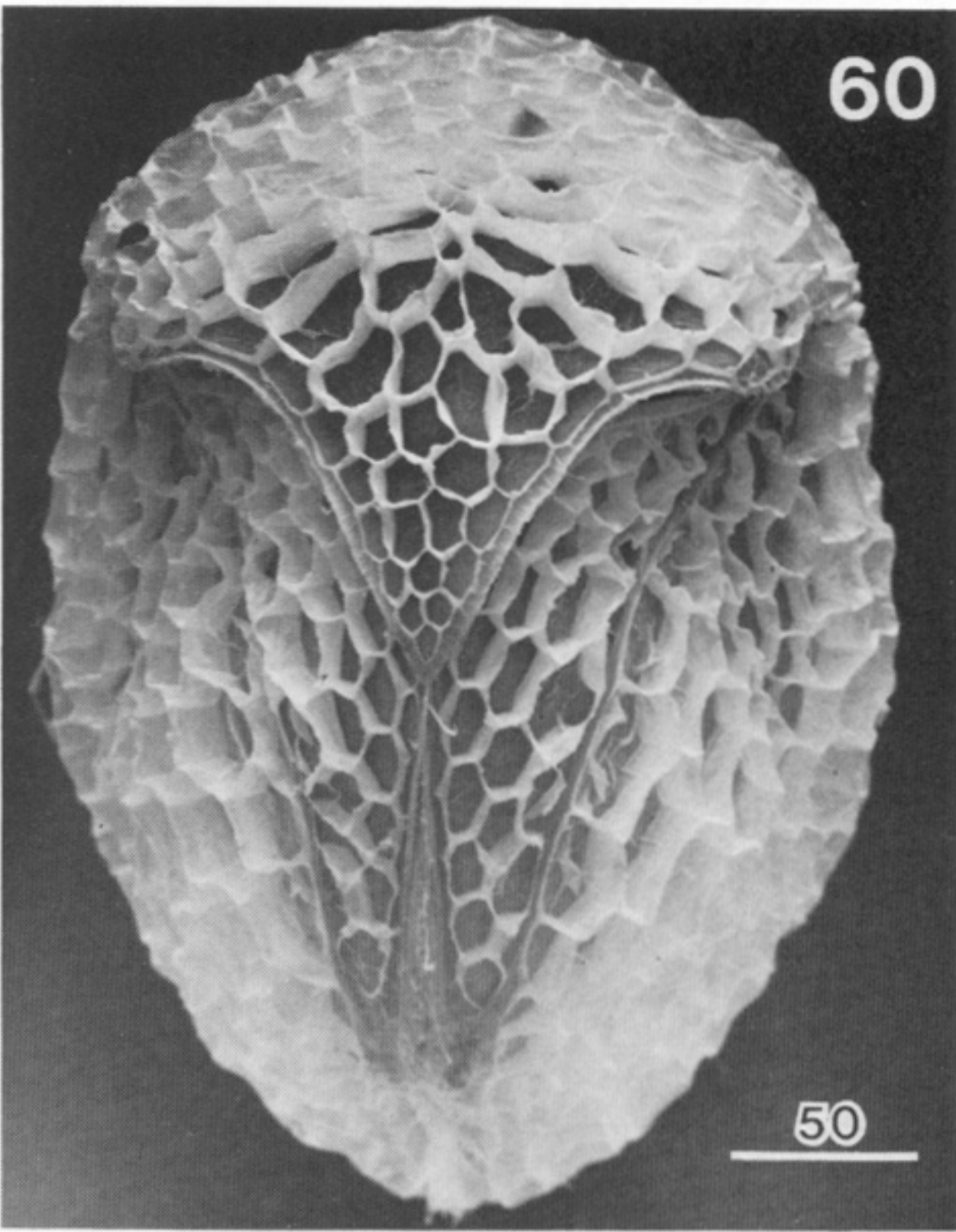
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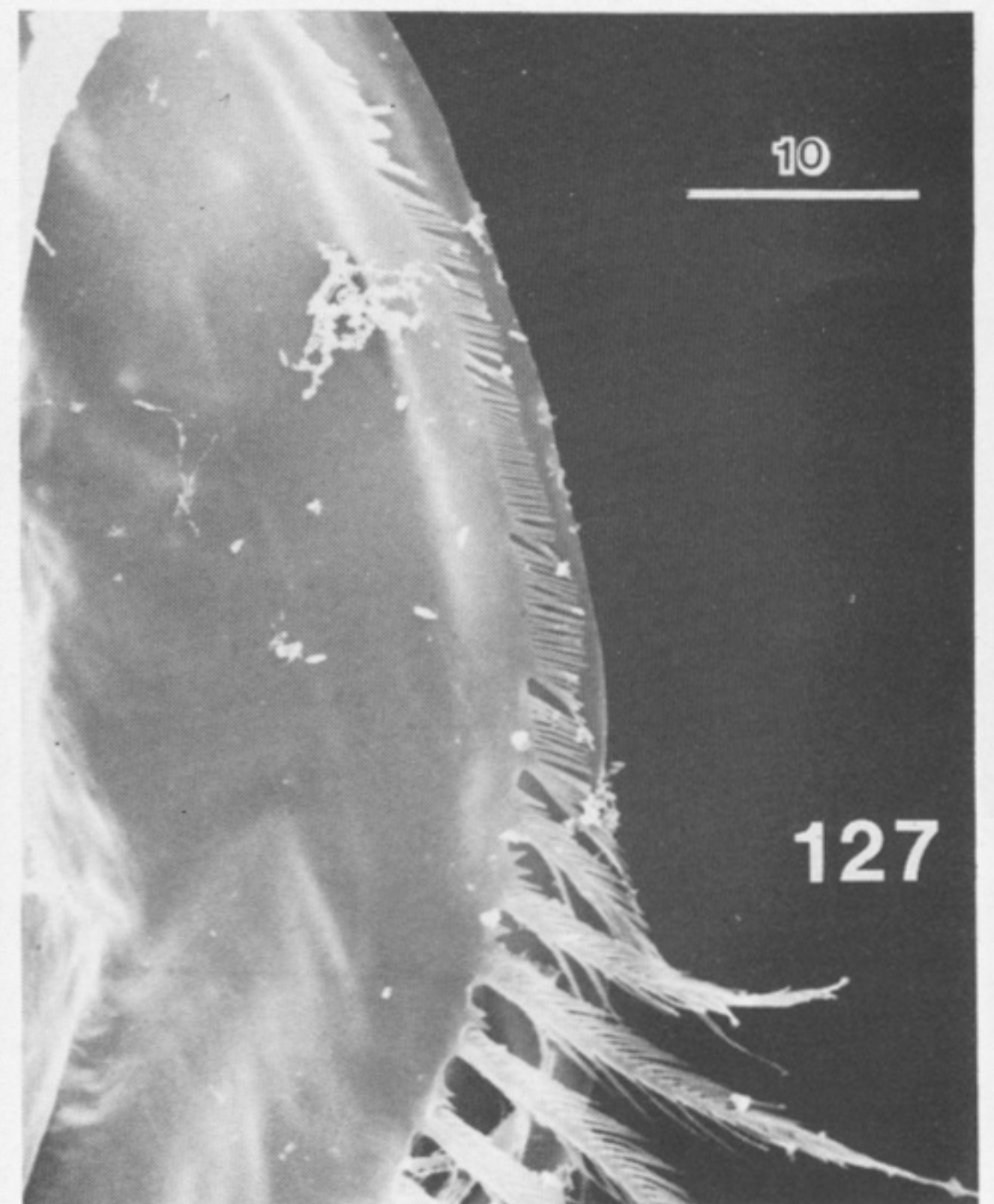
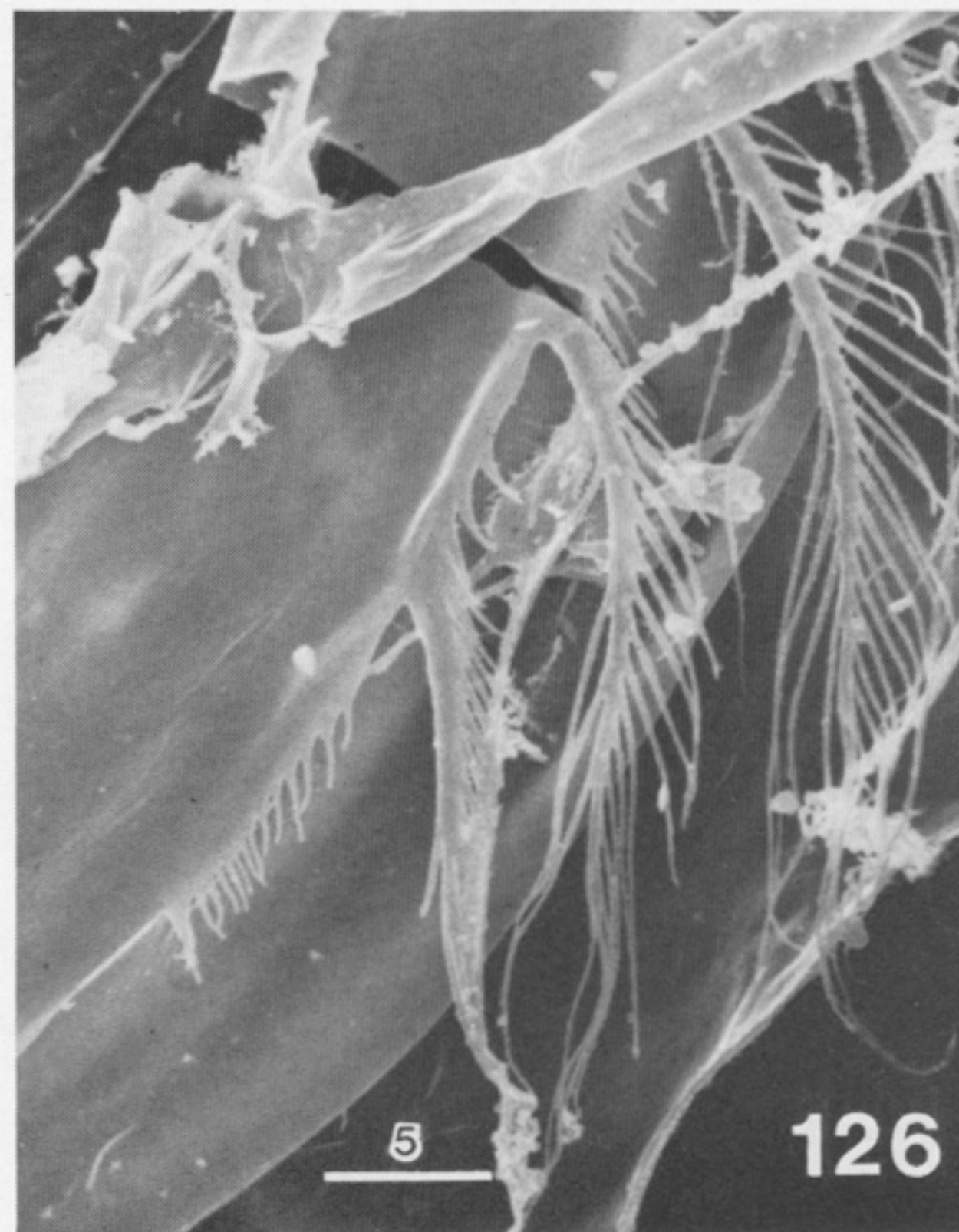
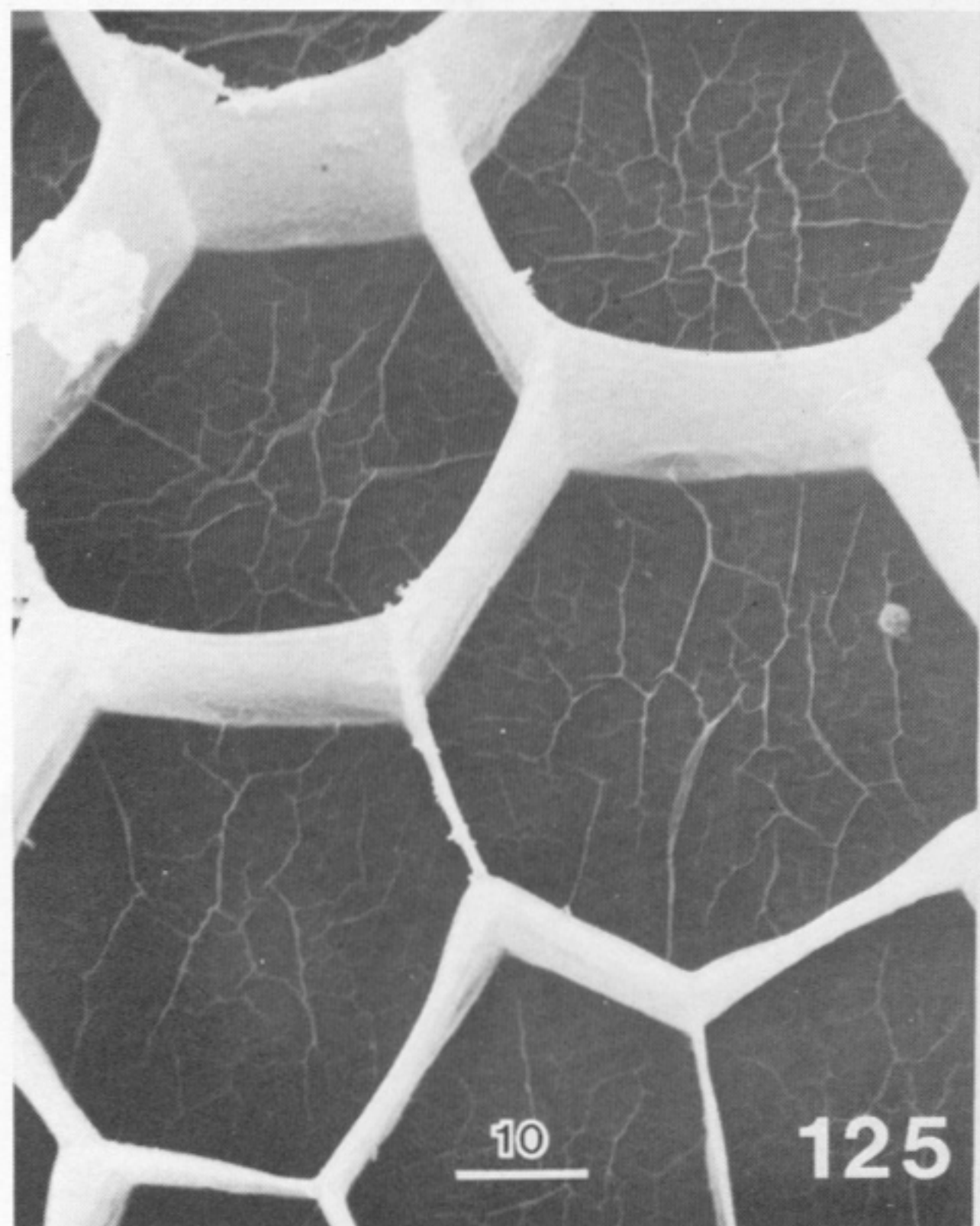
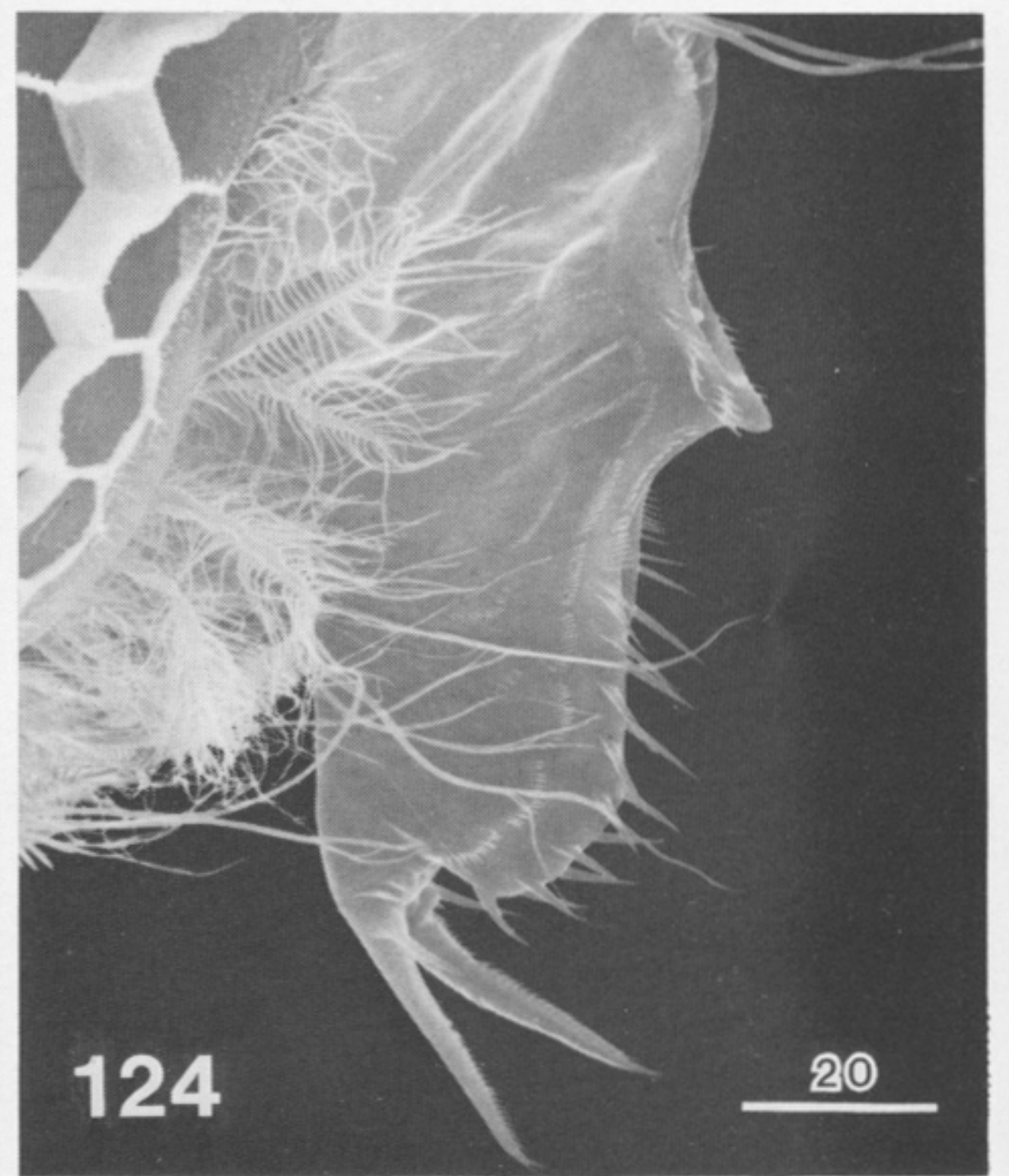
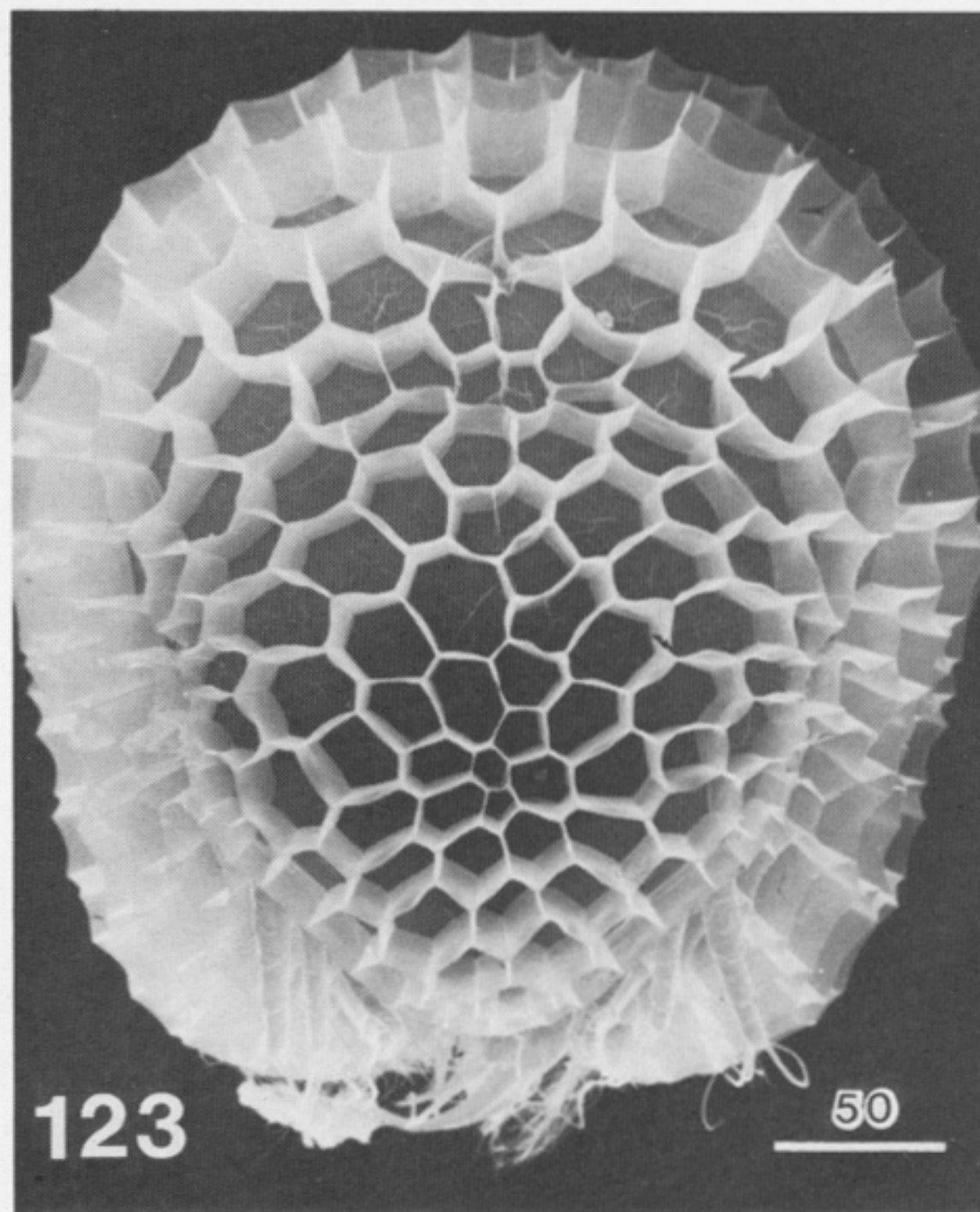
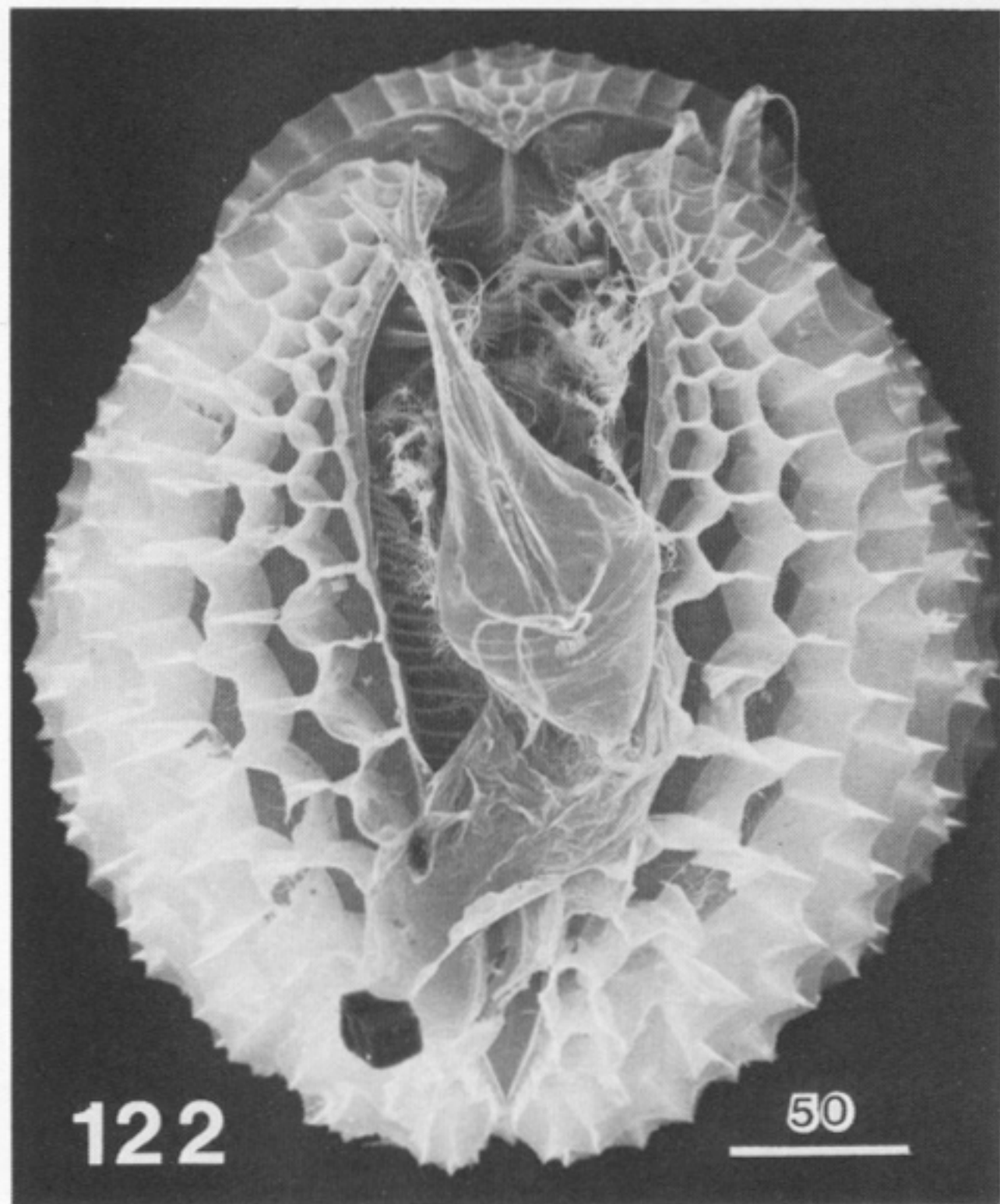
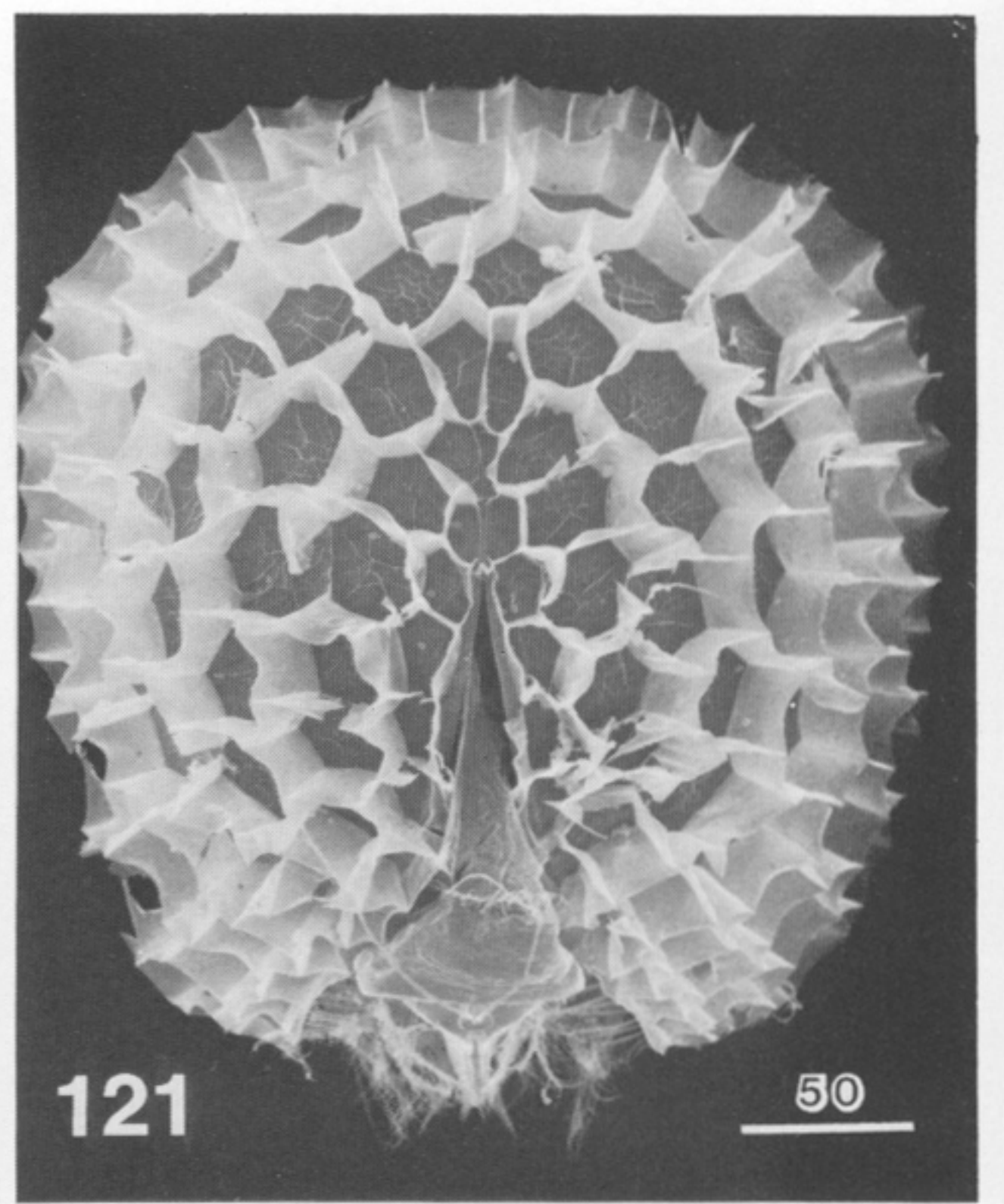
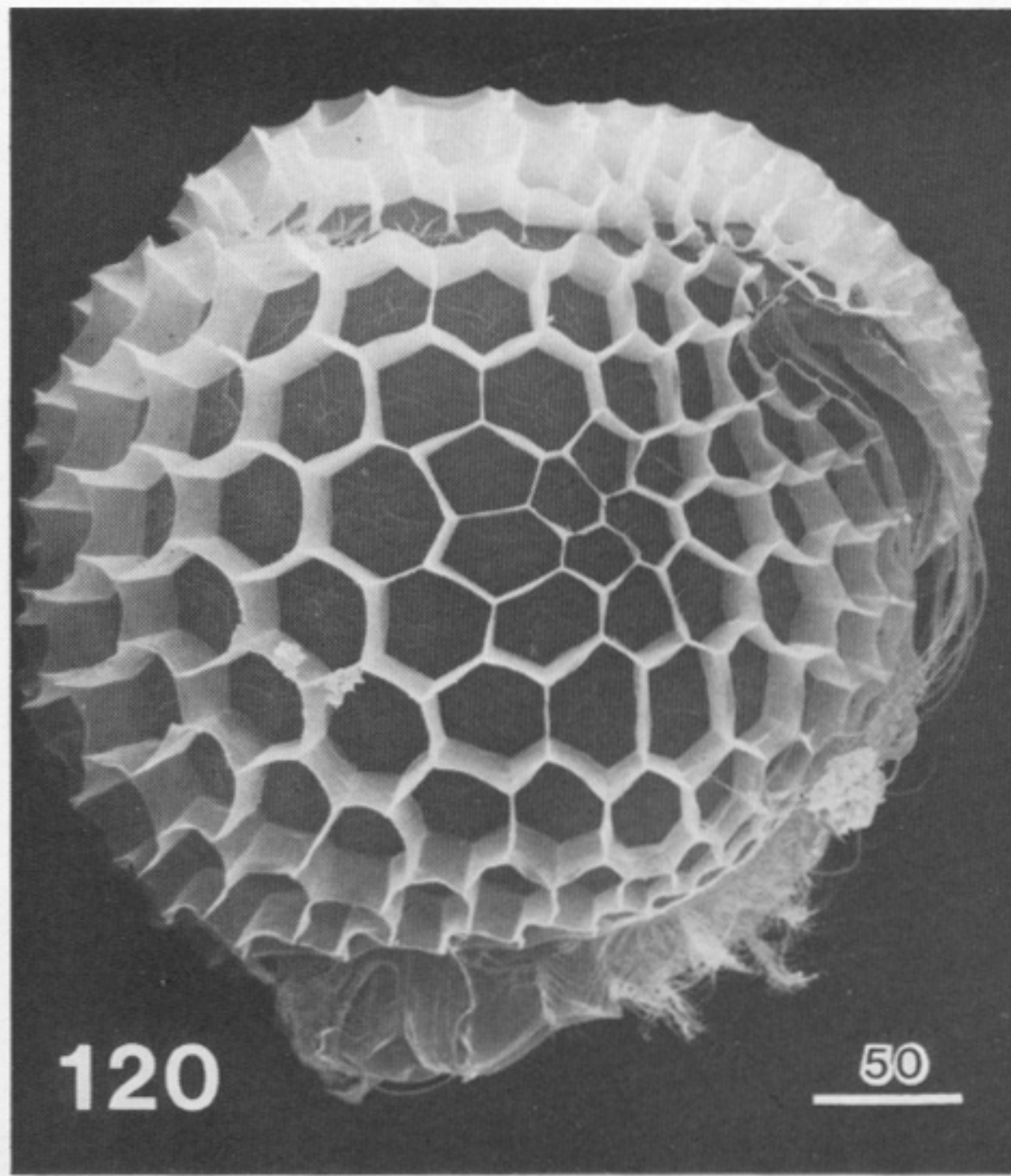
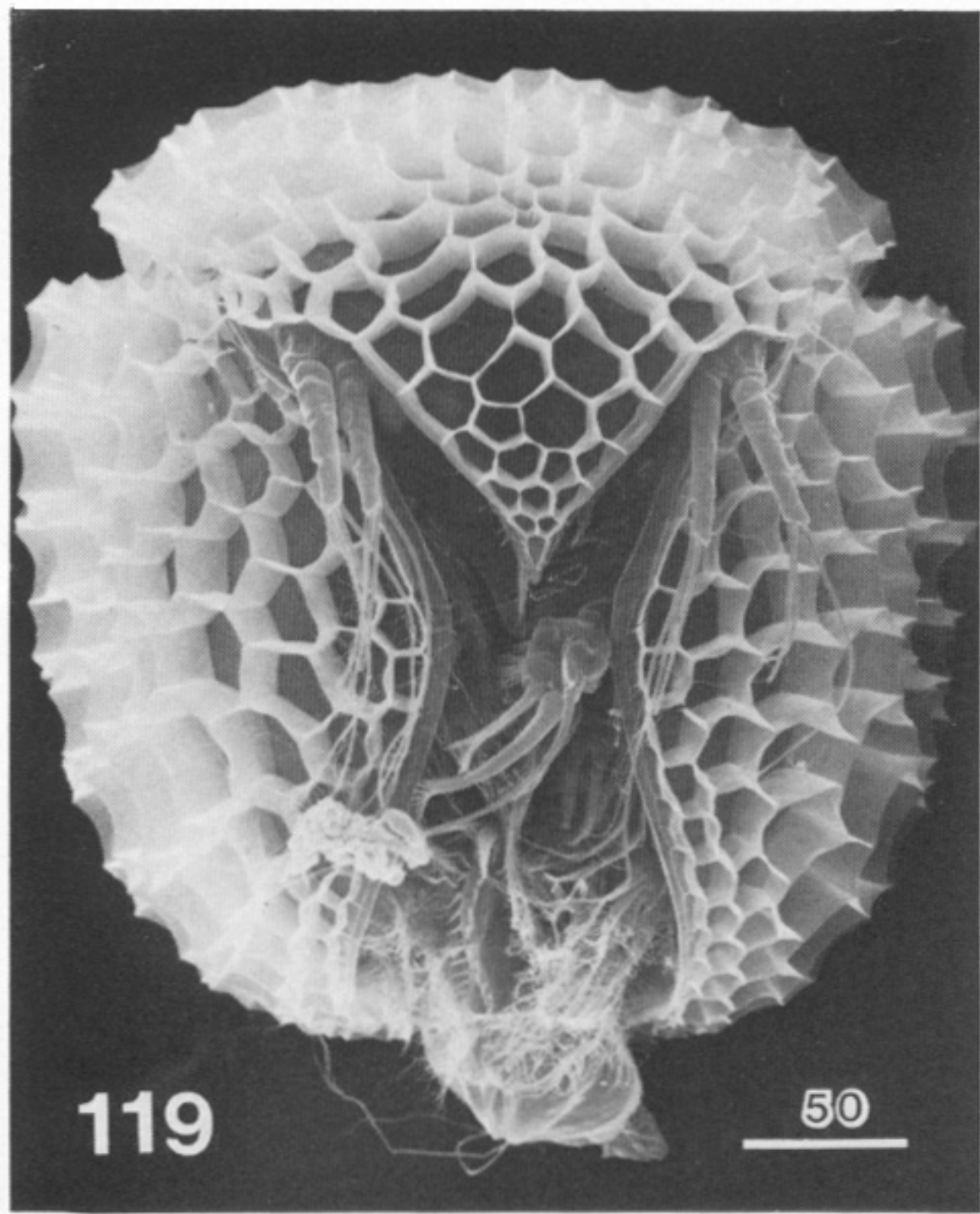
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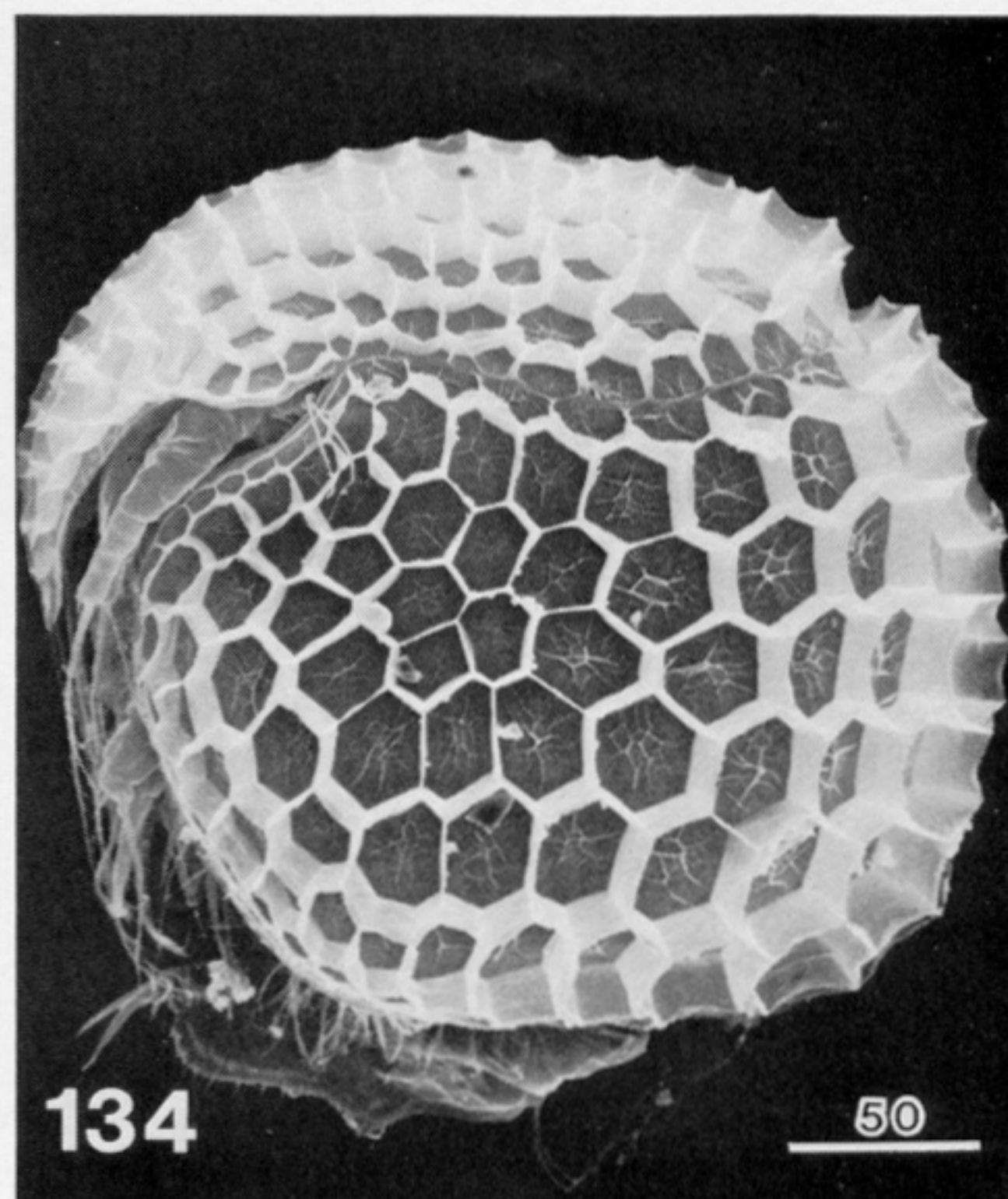
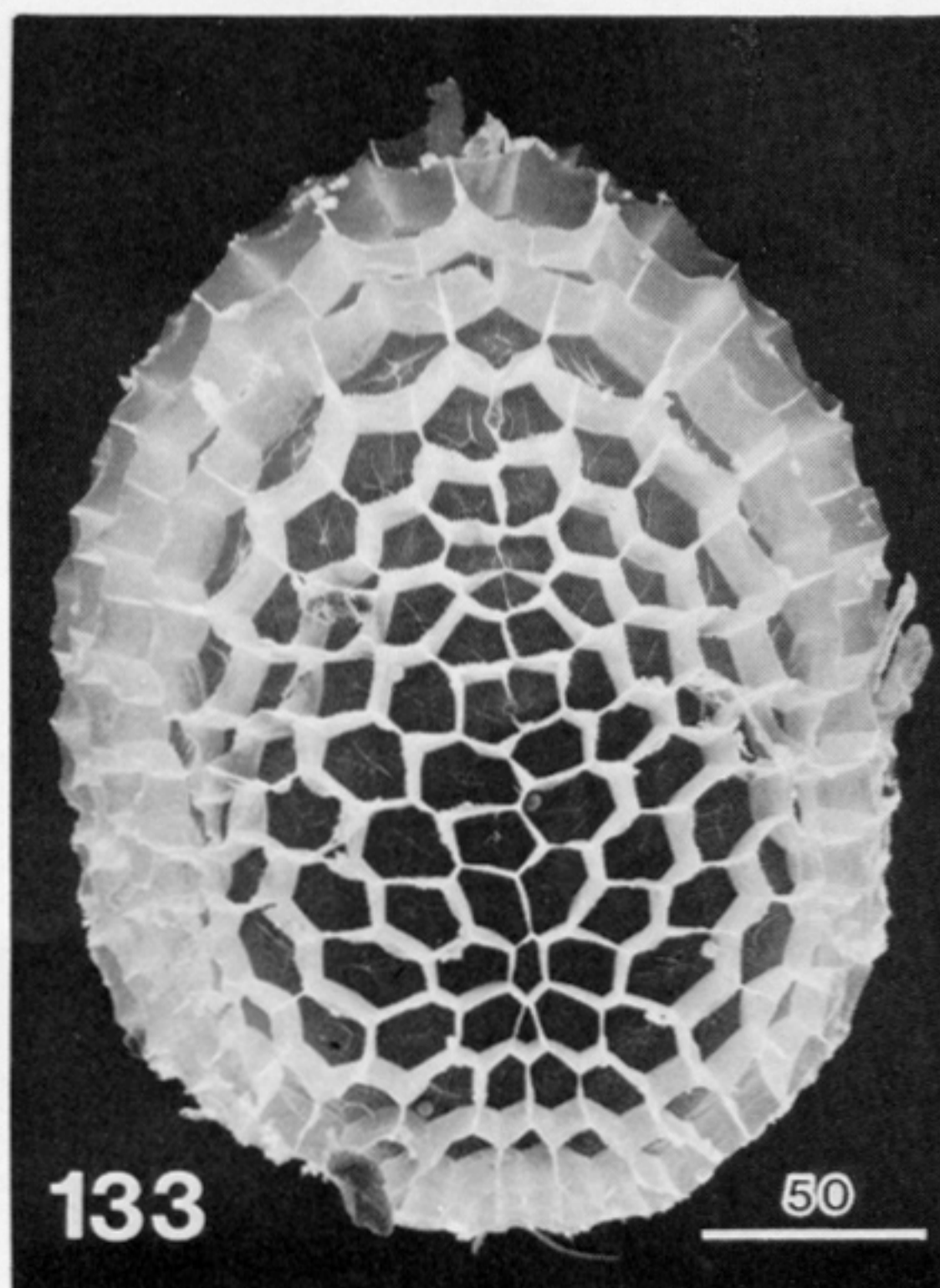
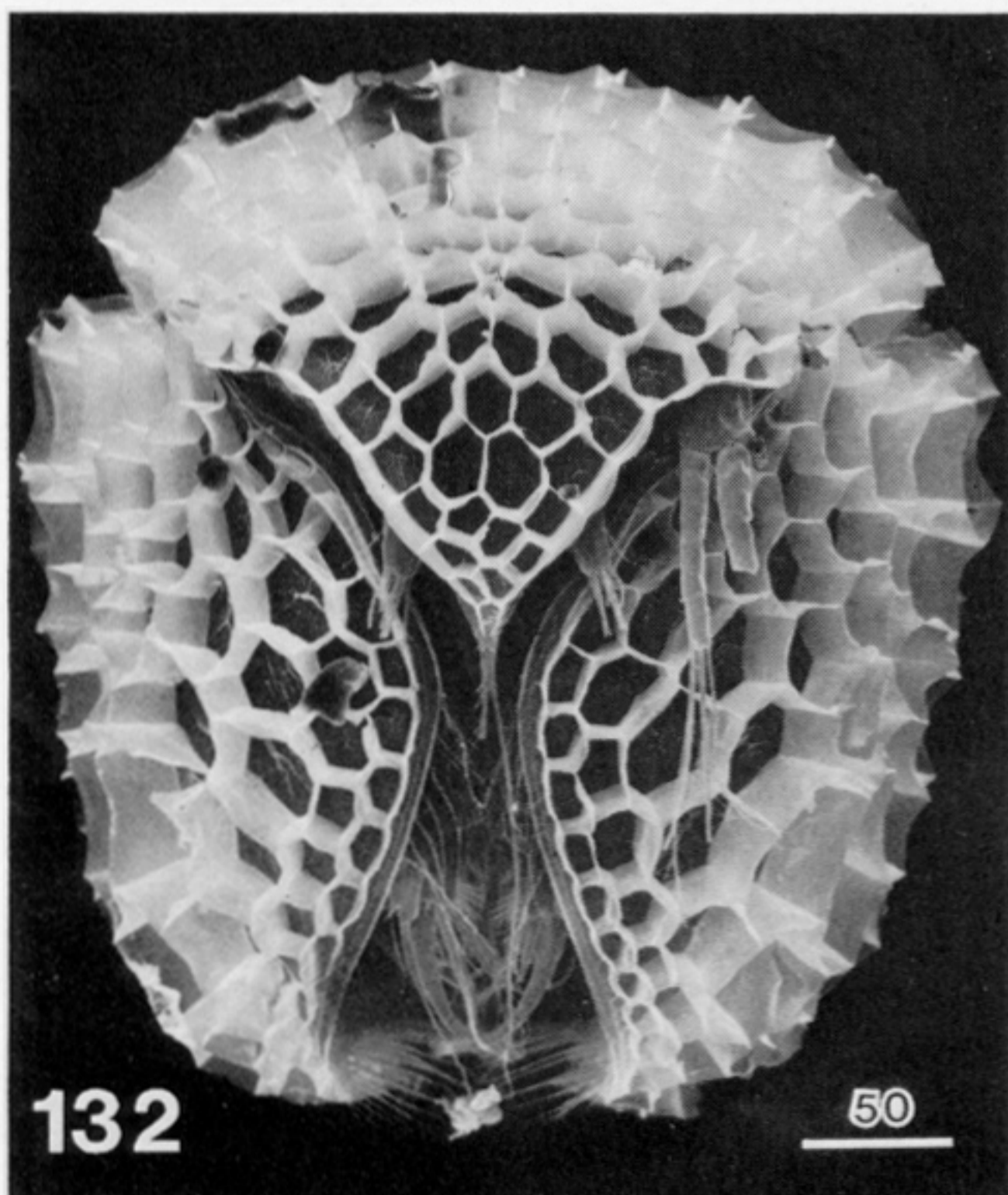
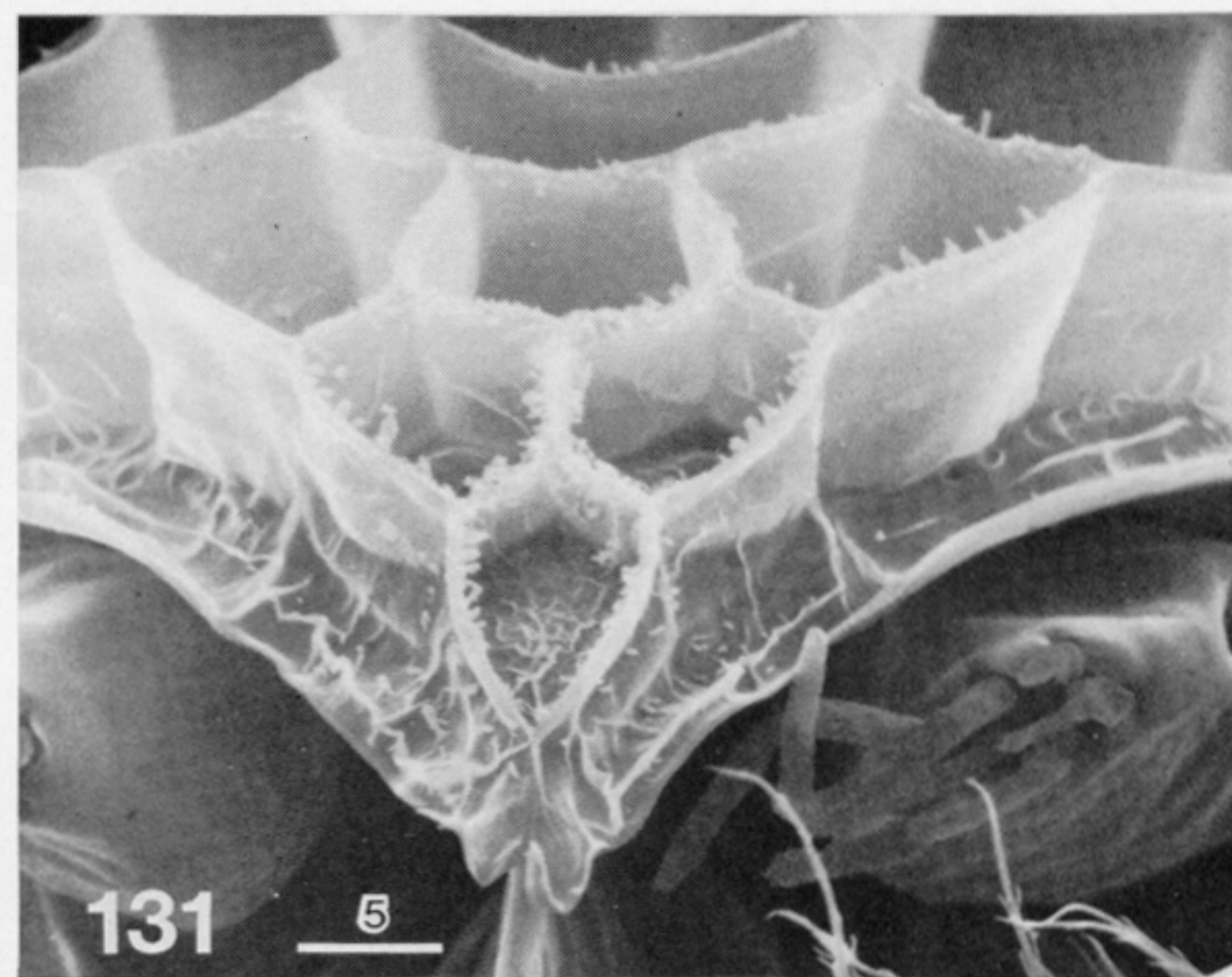
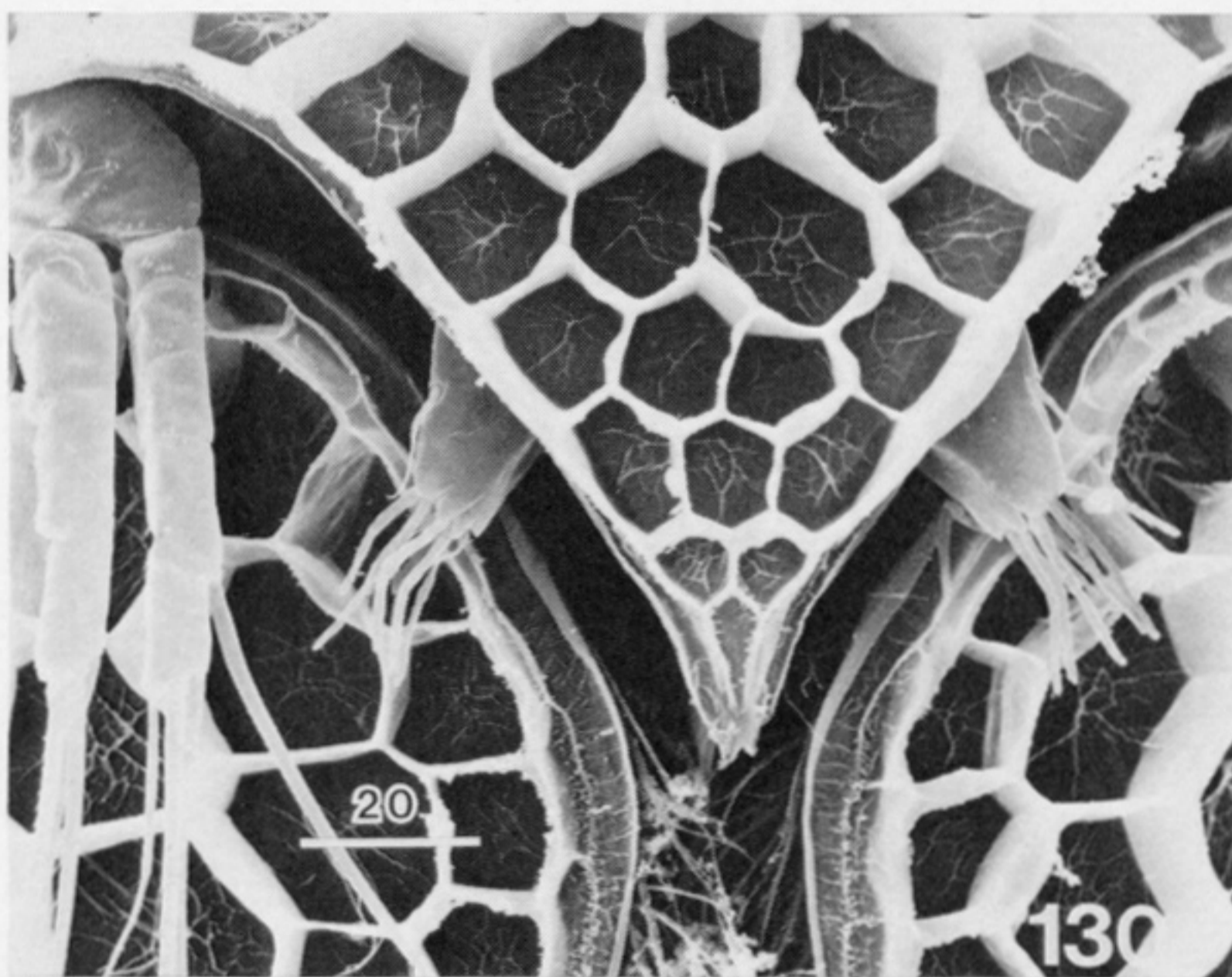
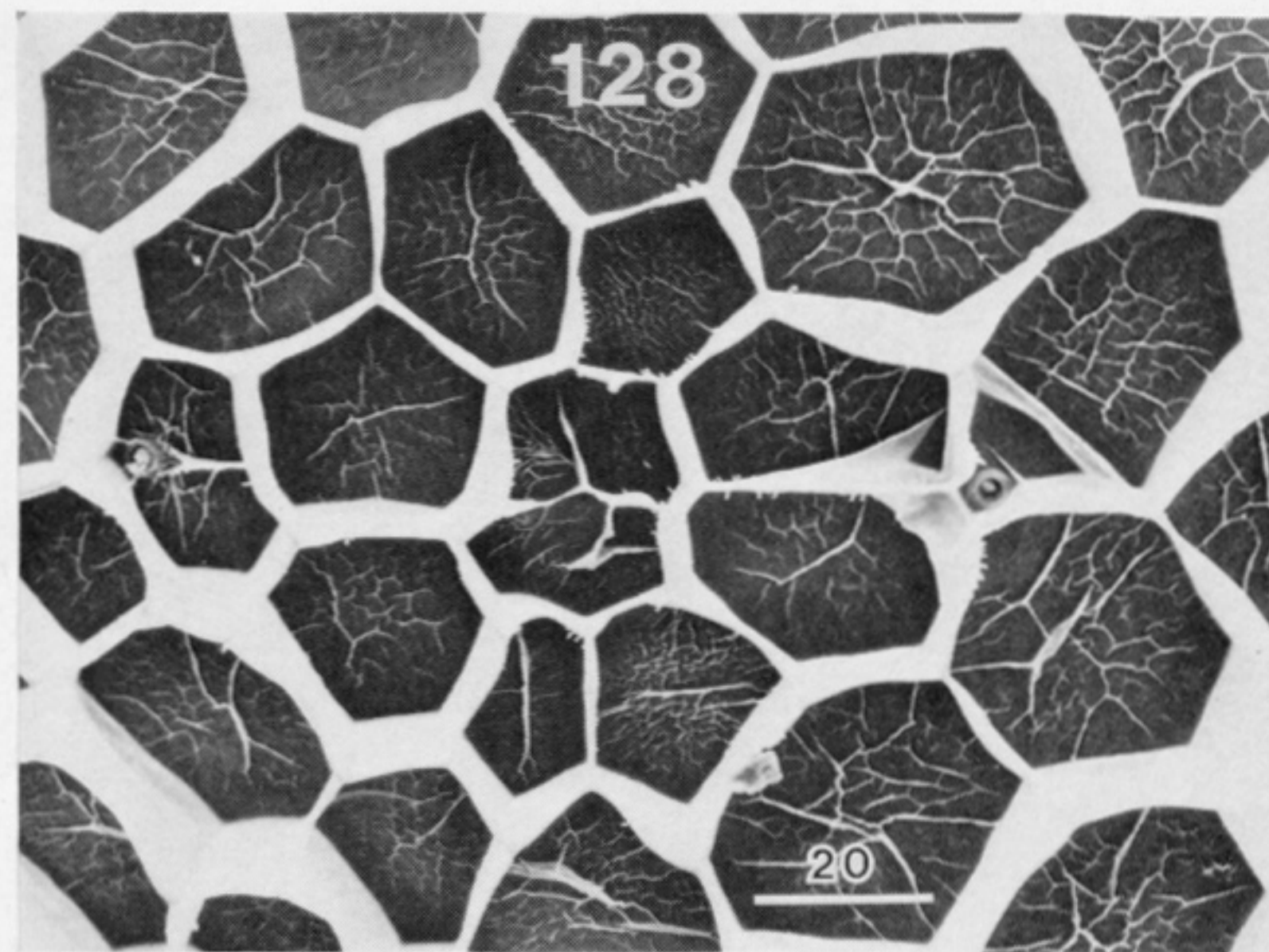
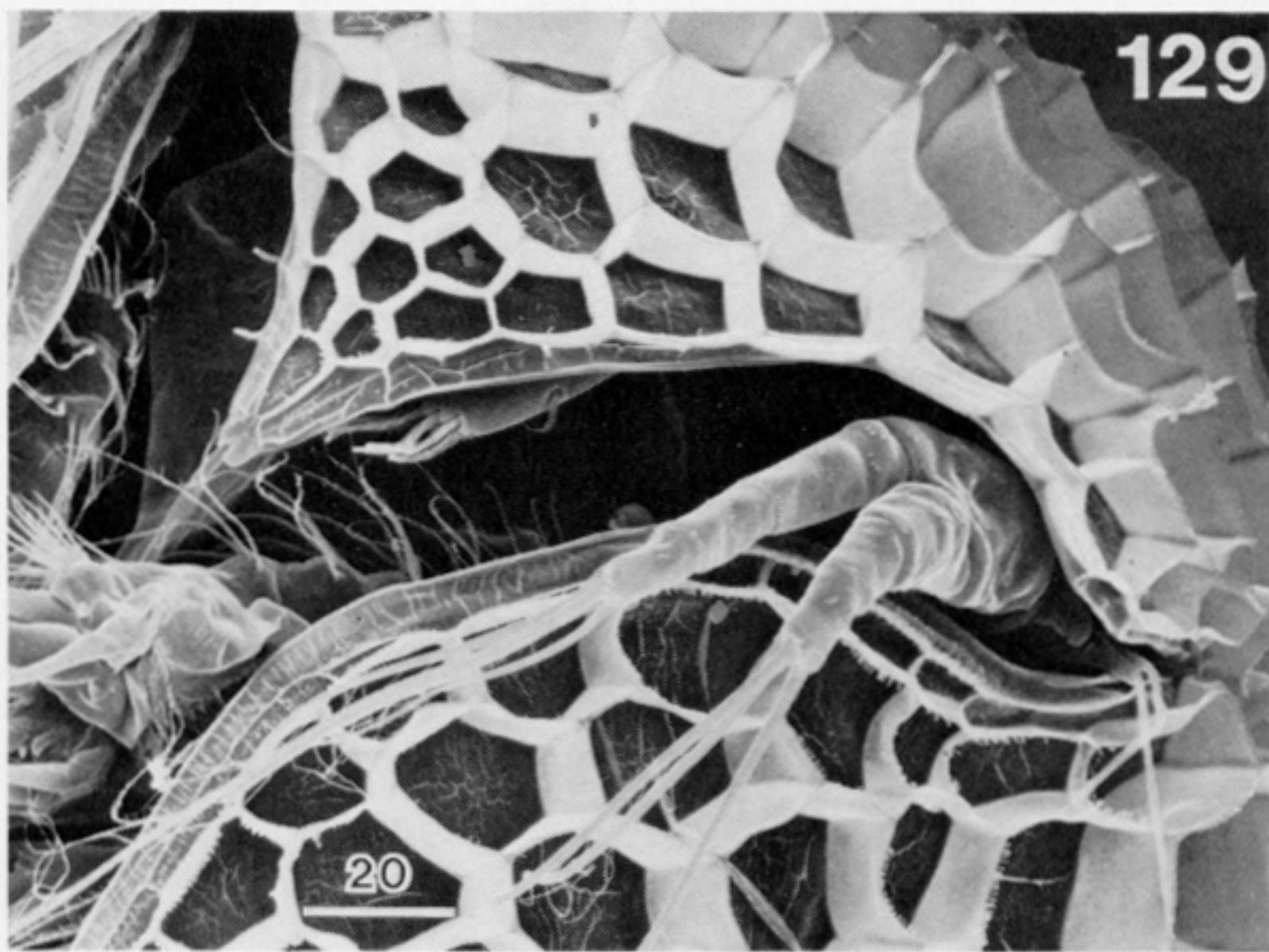
FIGURES 52-58. For description see p. 364.



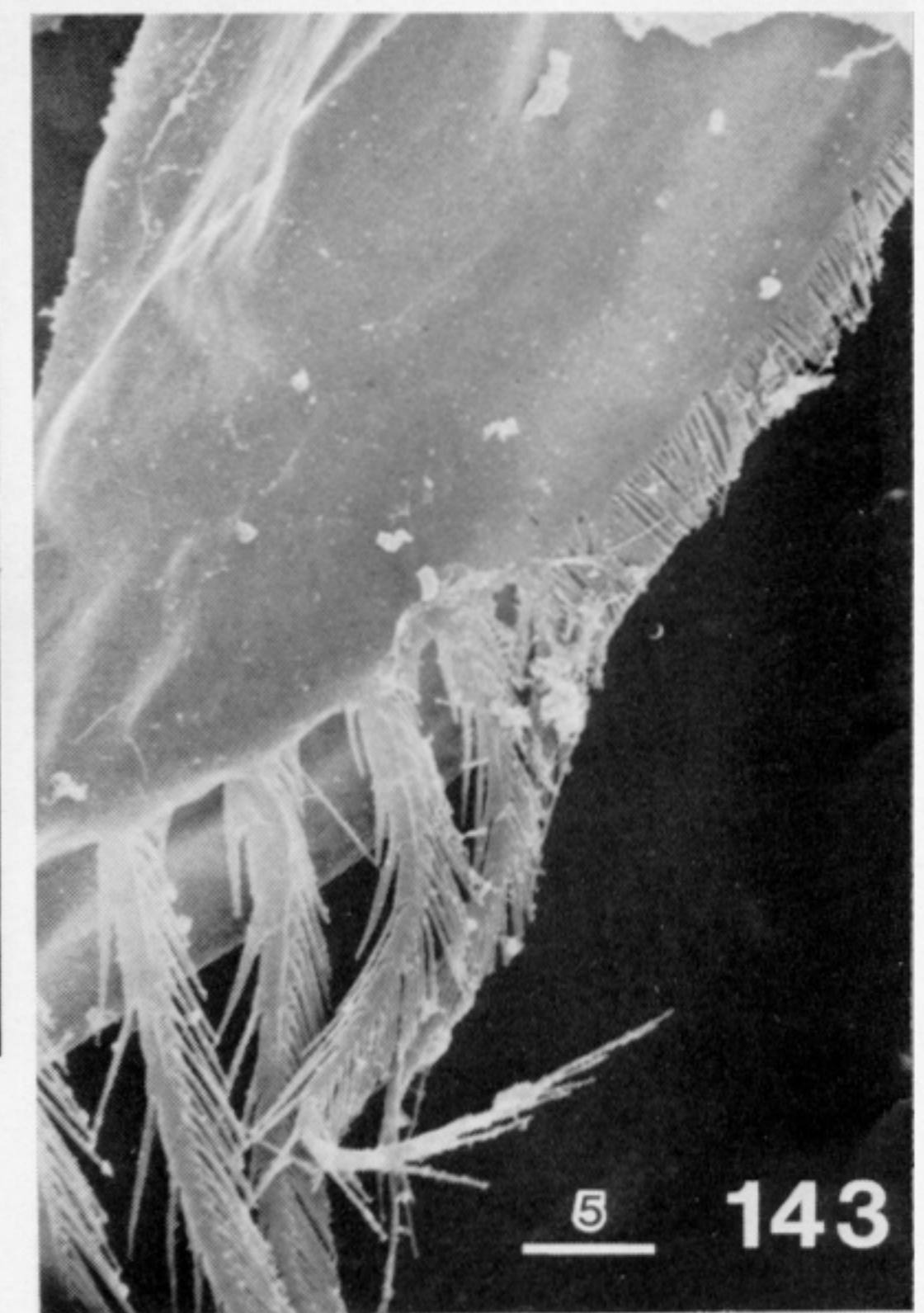
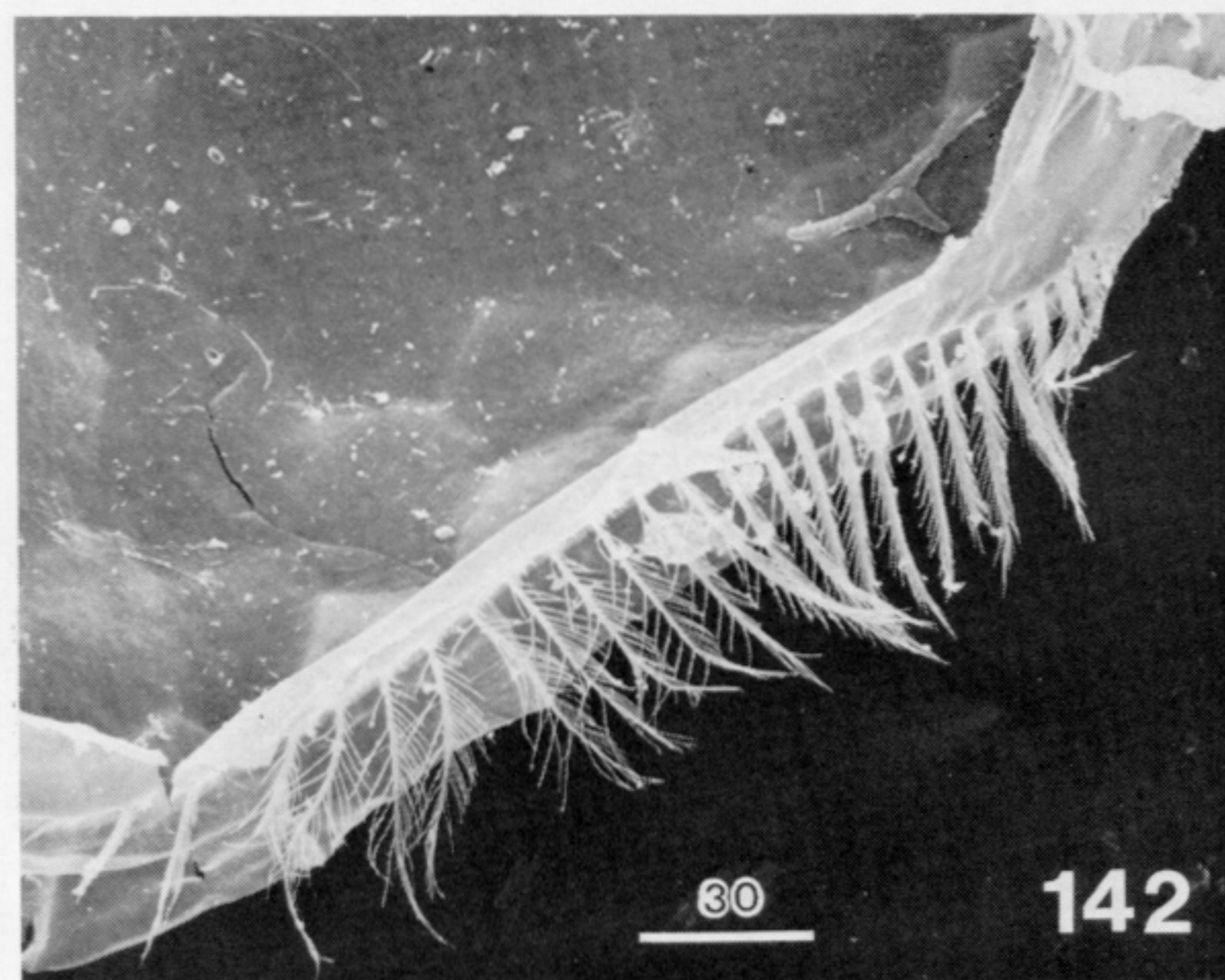
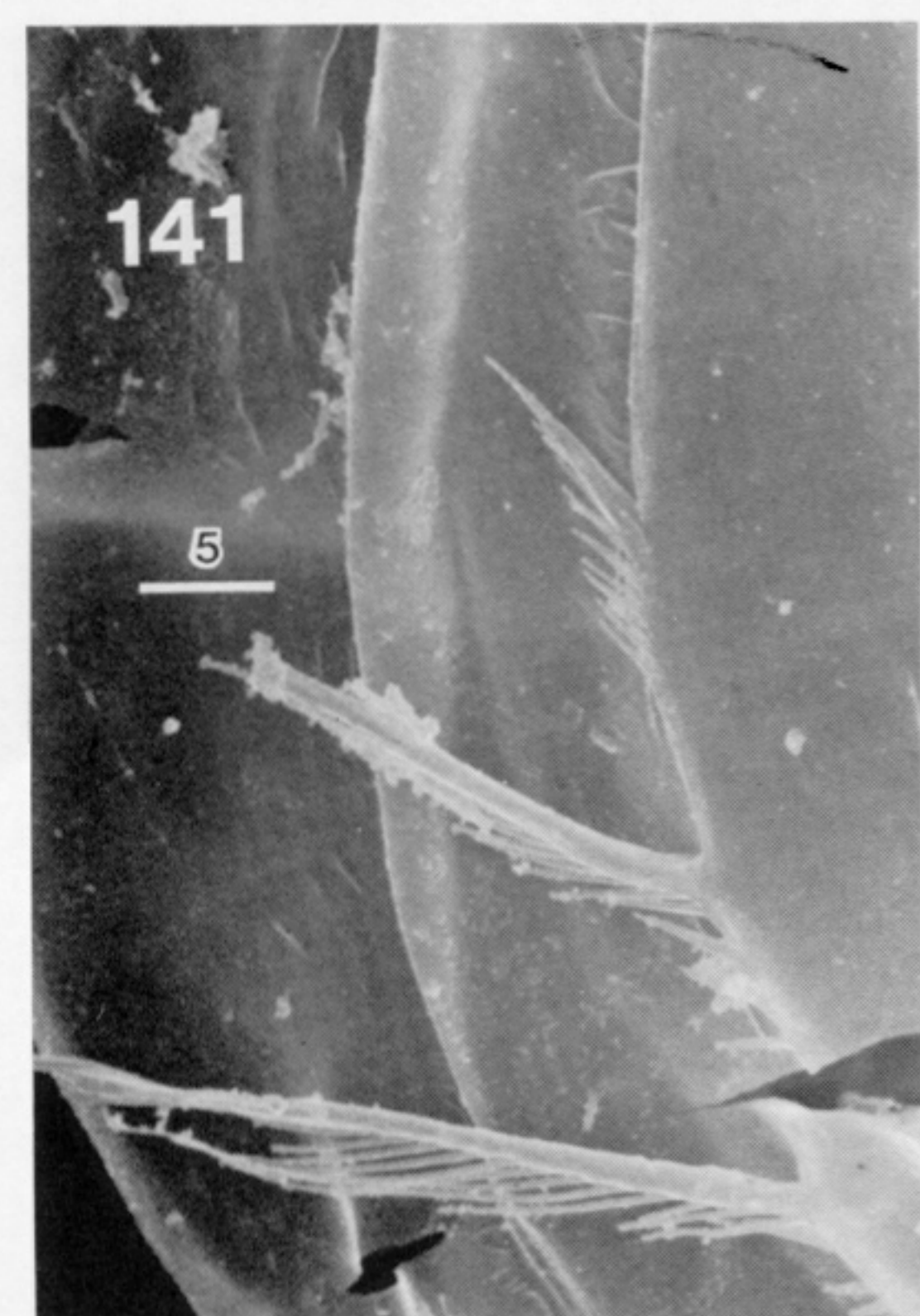
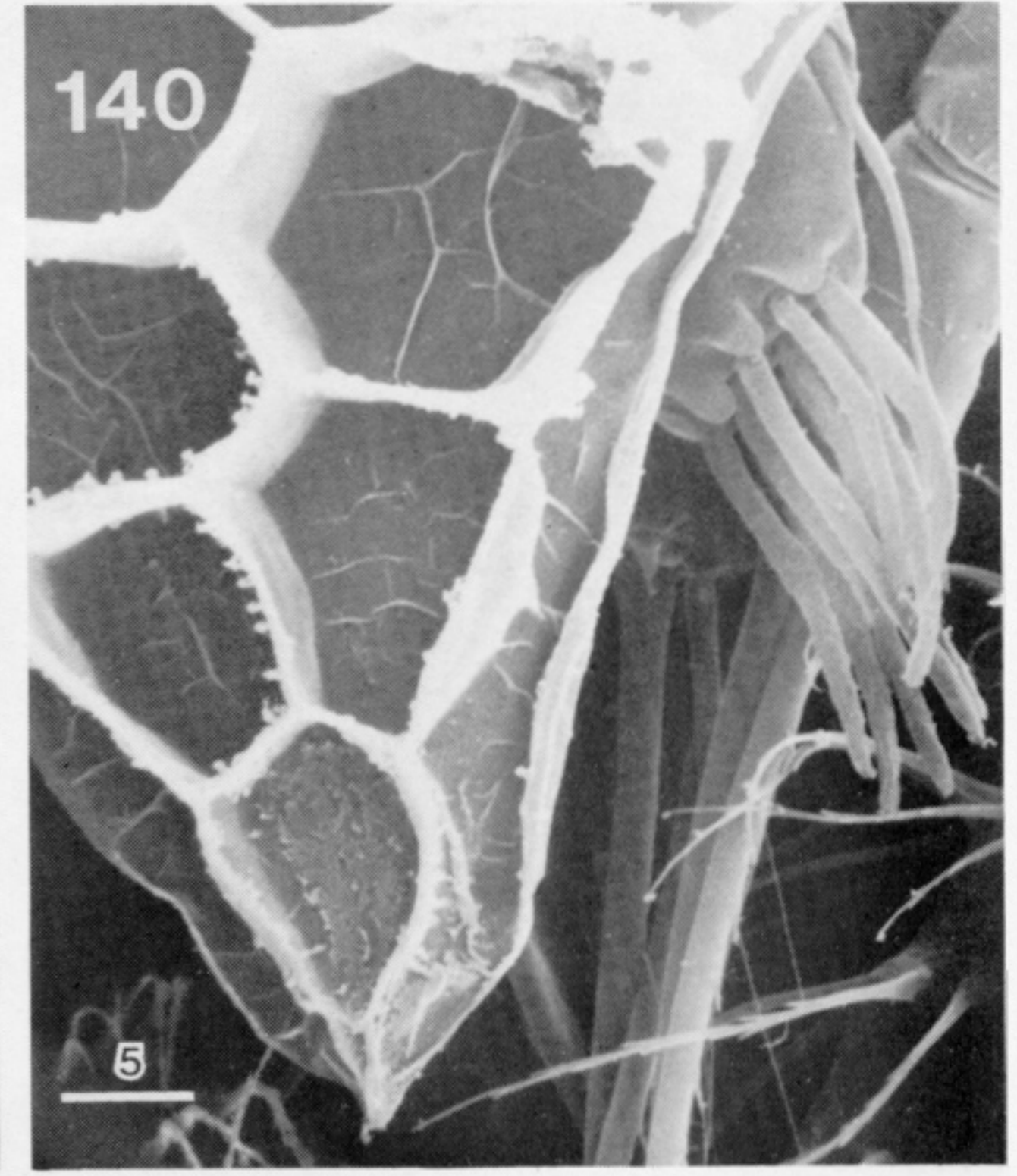
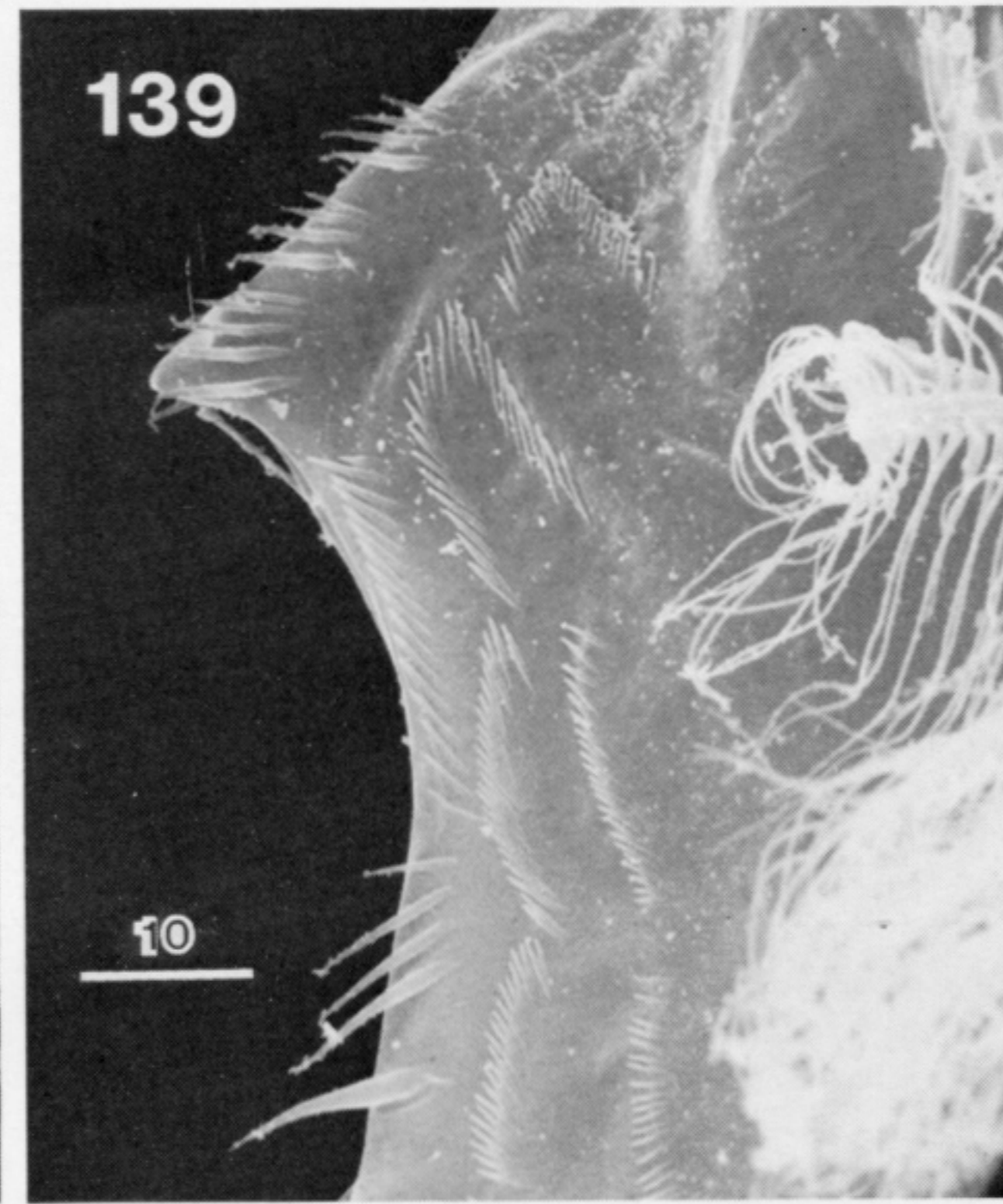
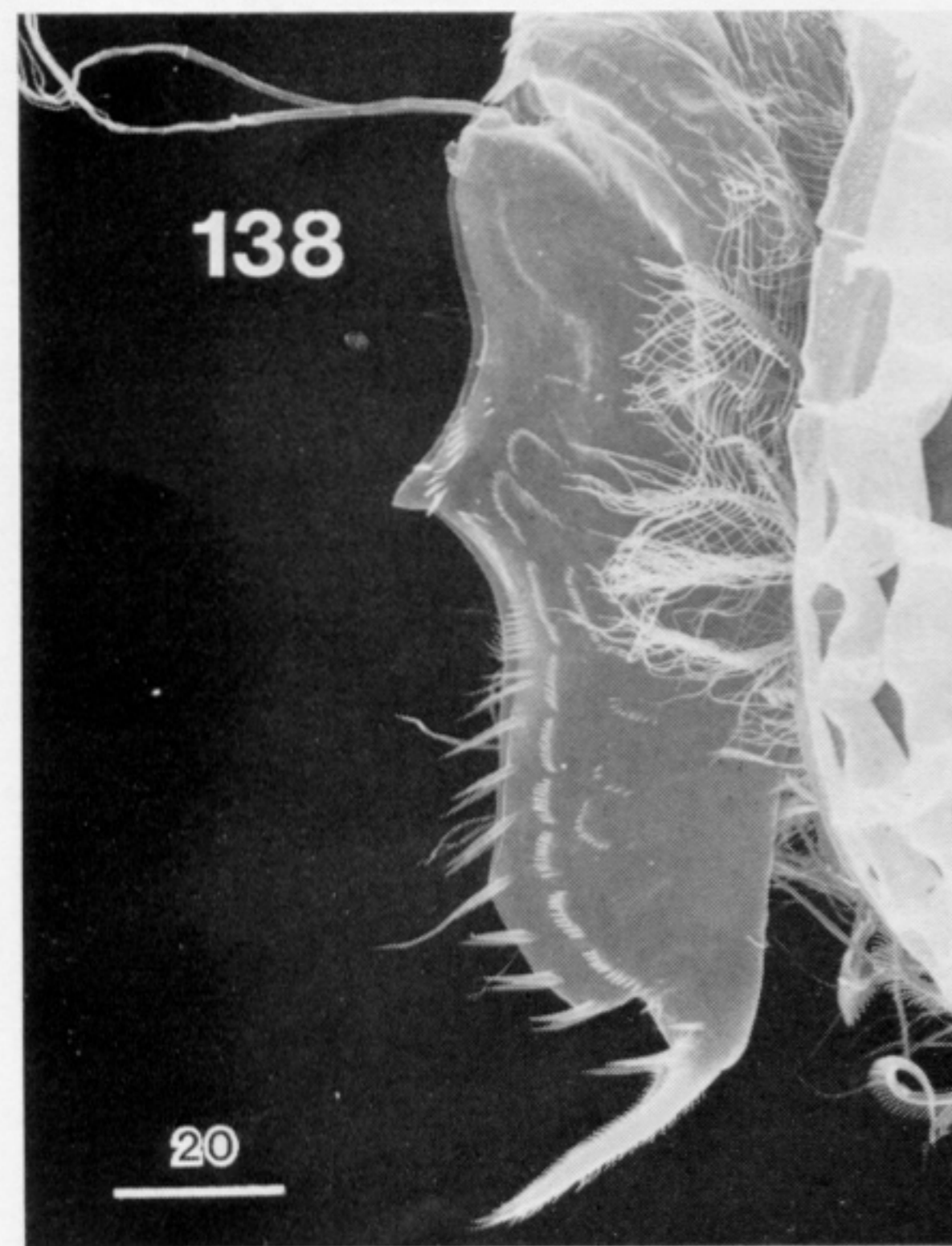
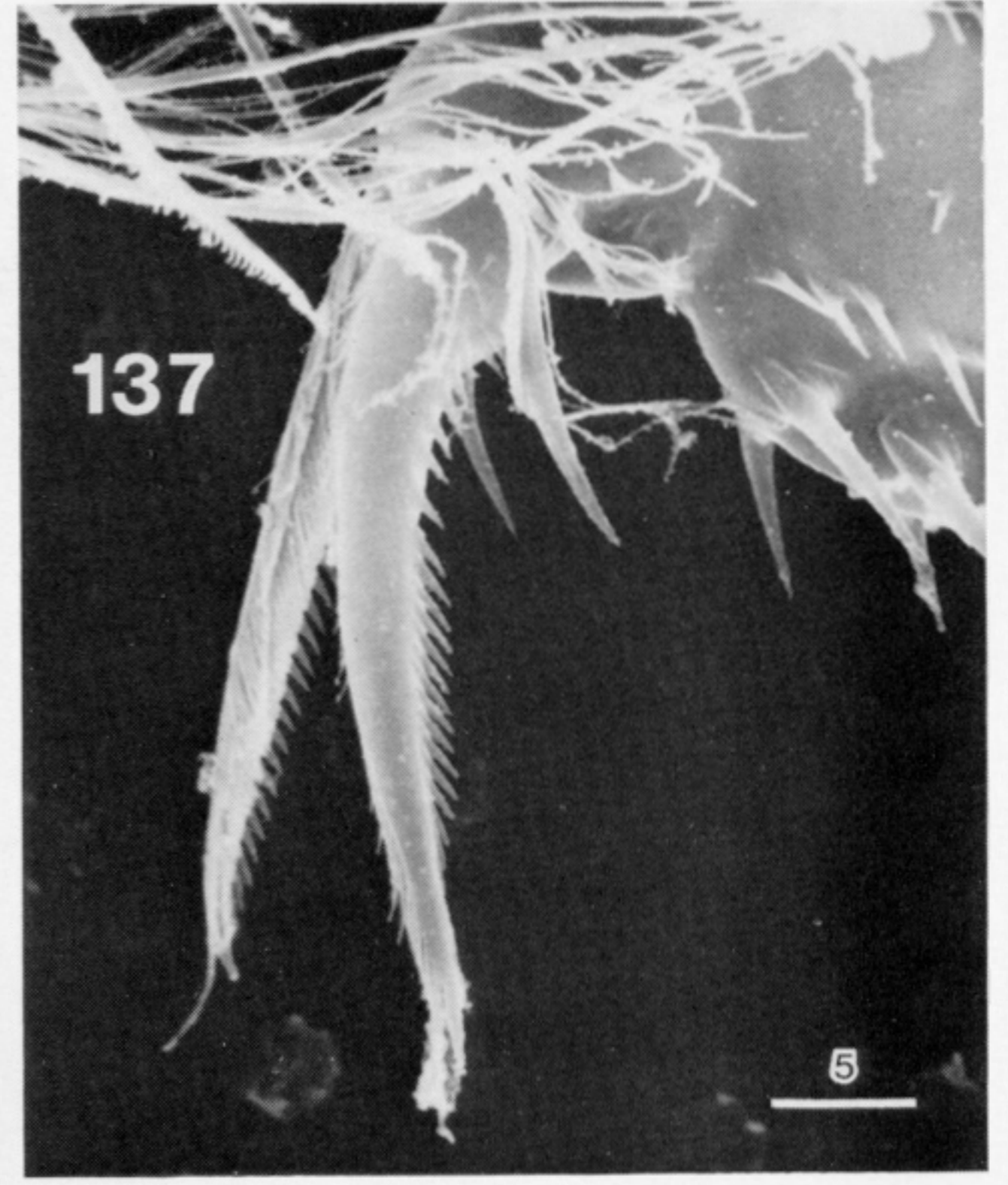
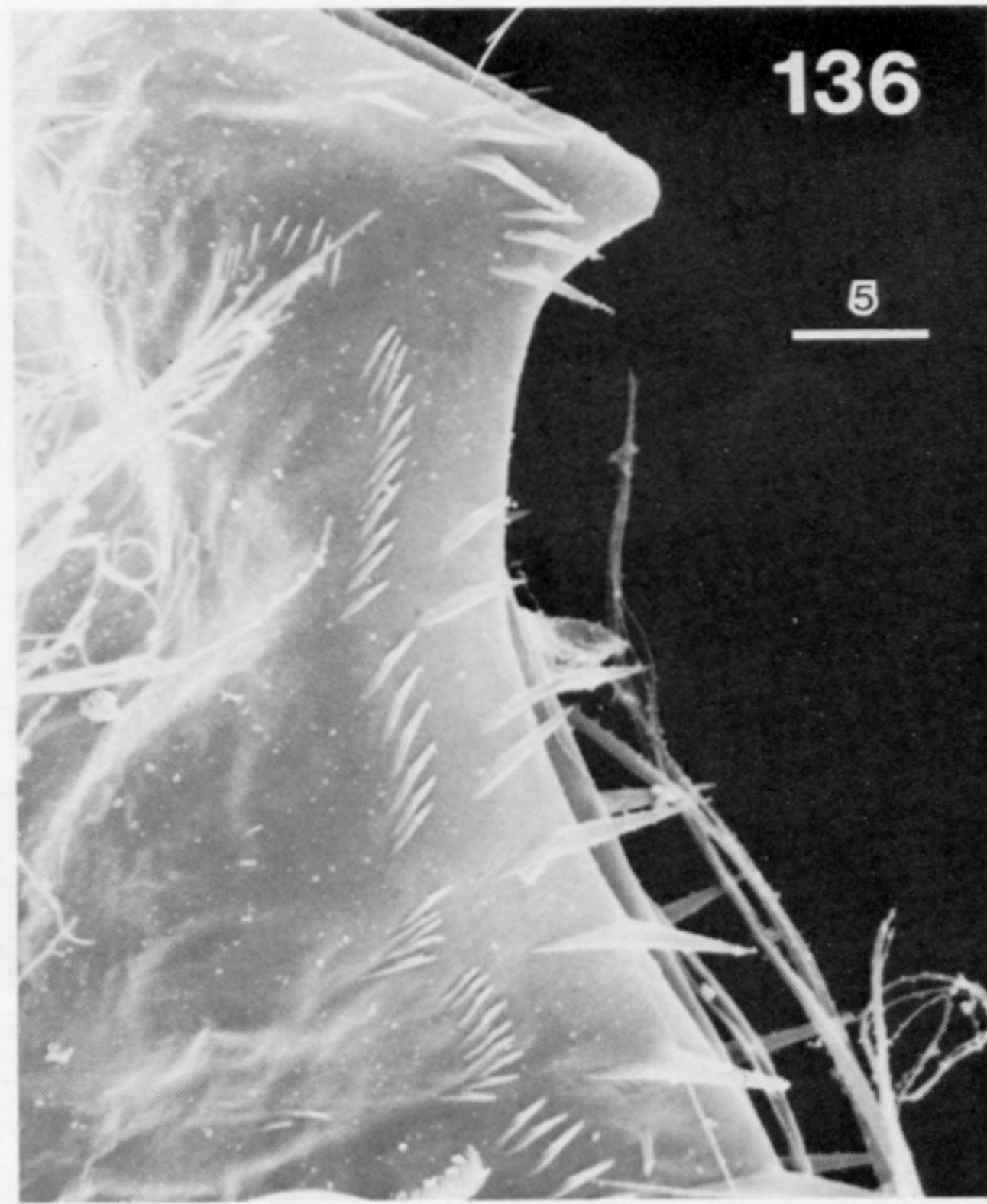
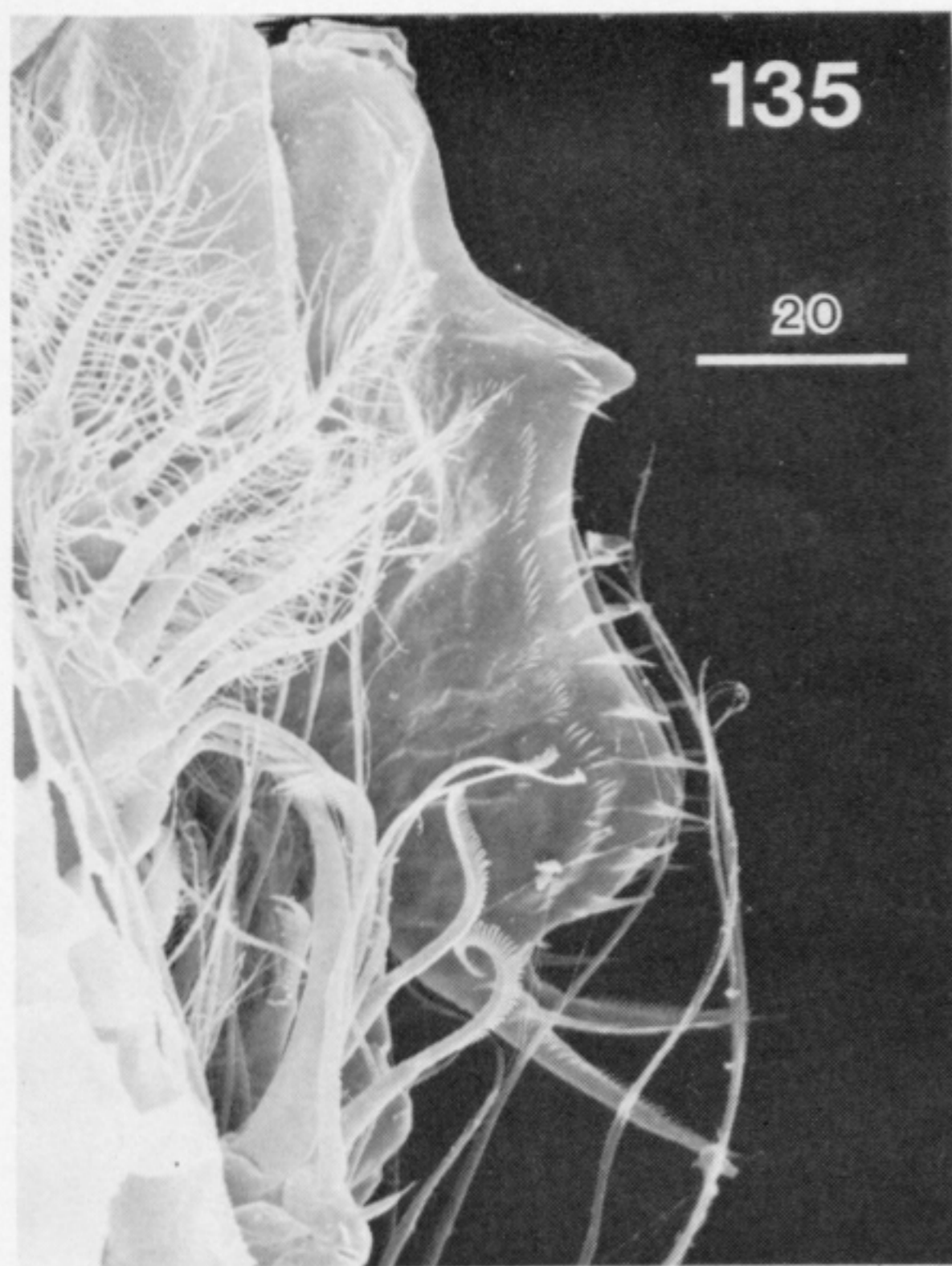
FIGURES 59–64. For description see p. 364.



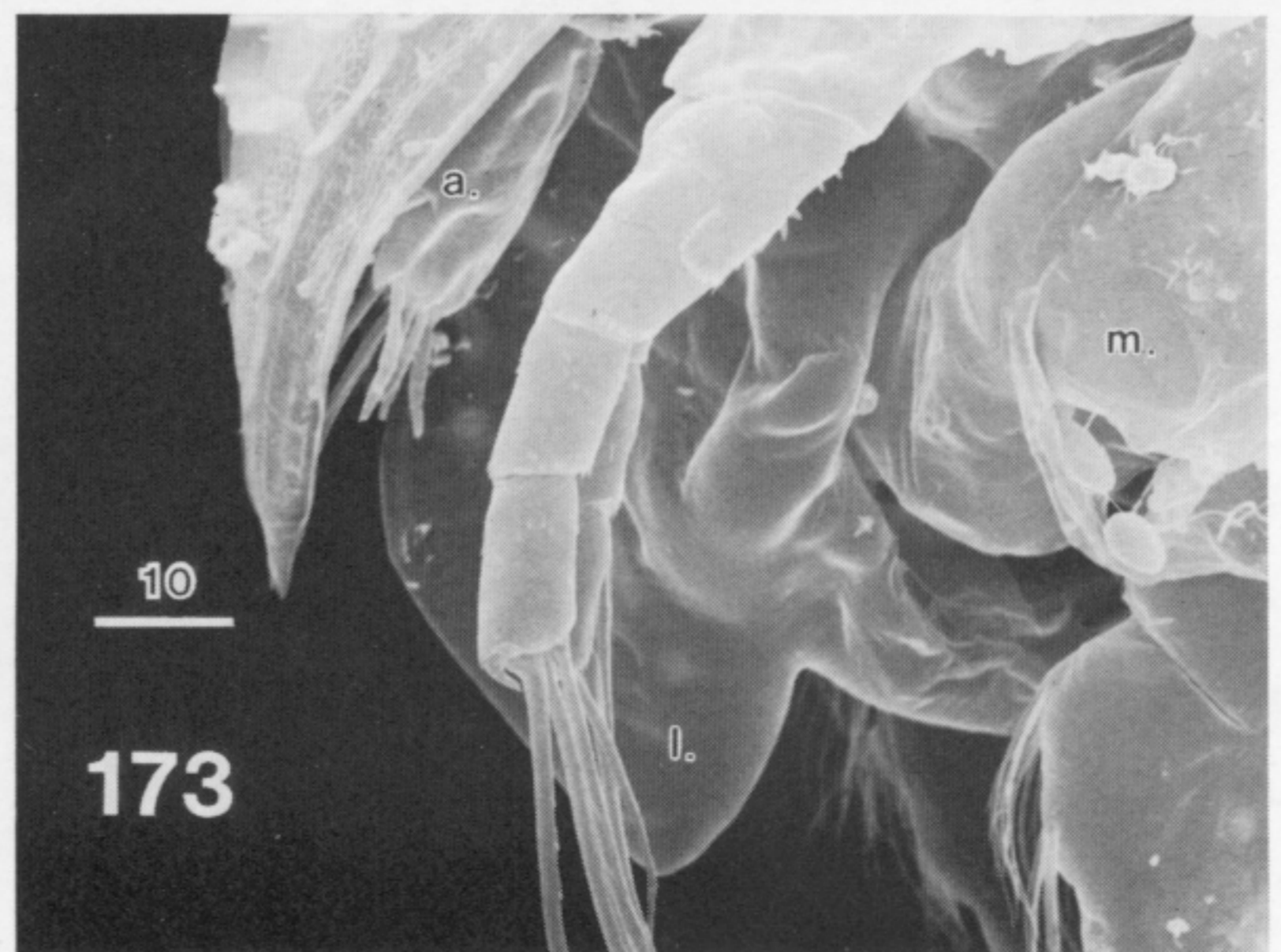
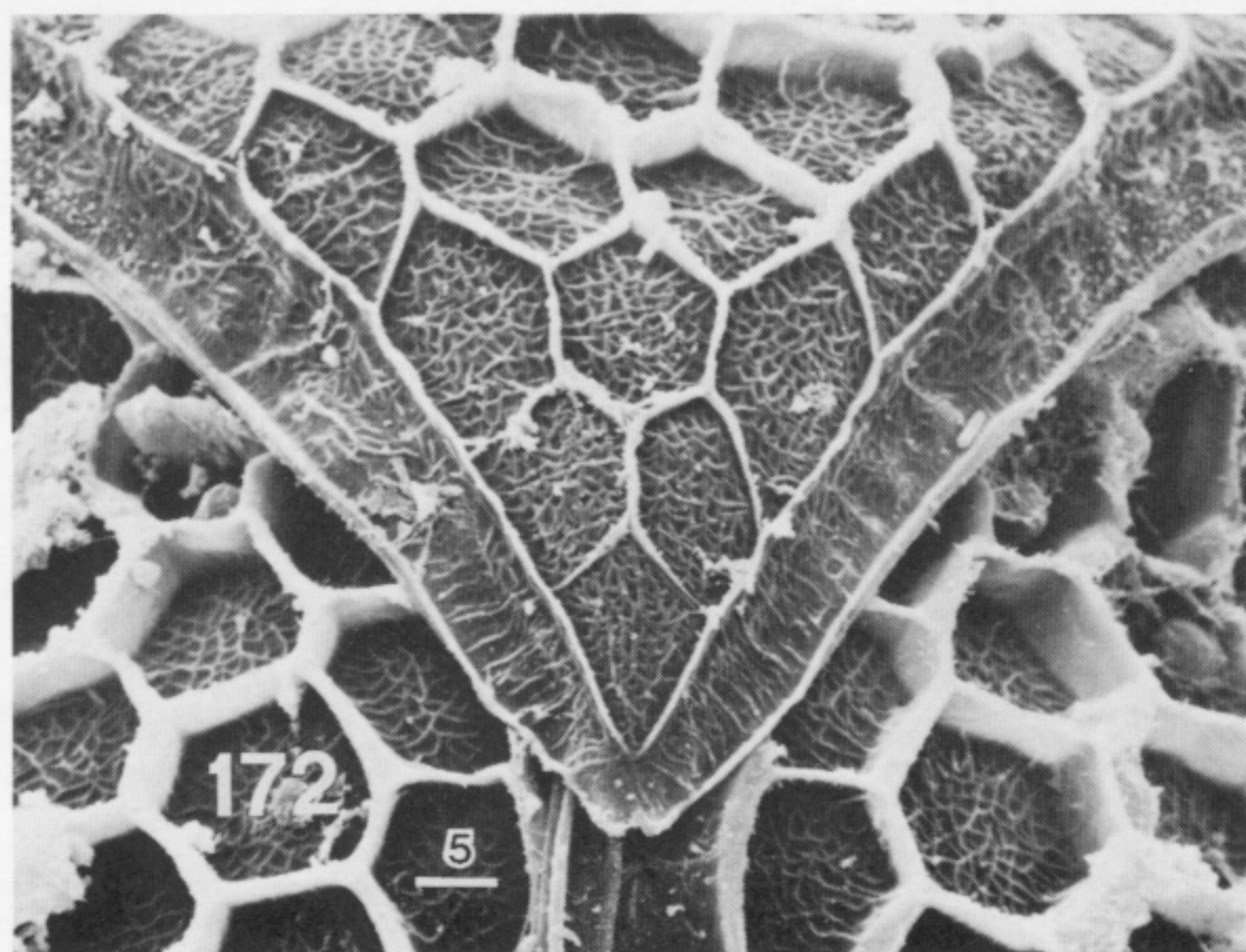
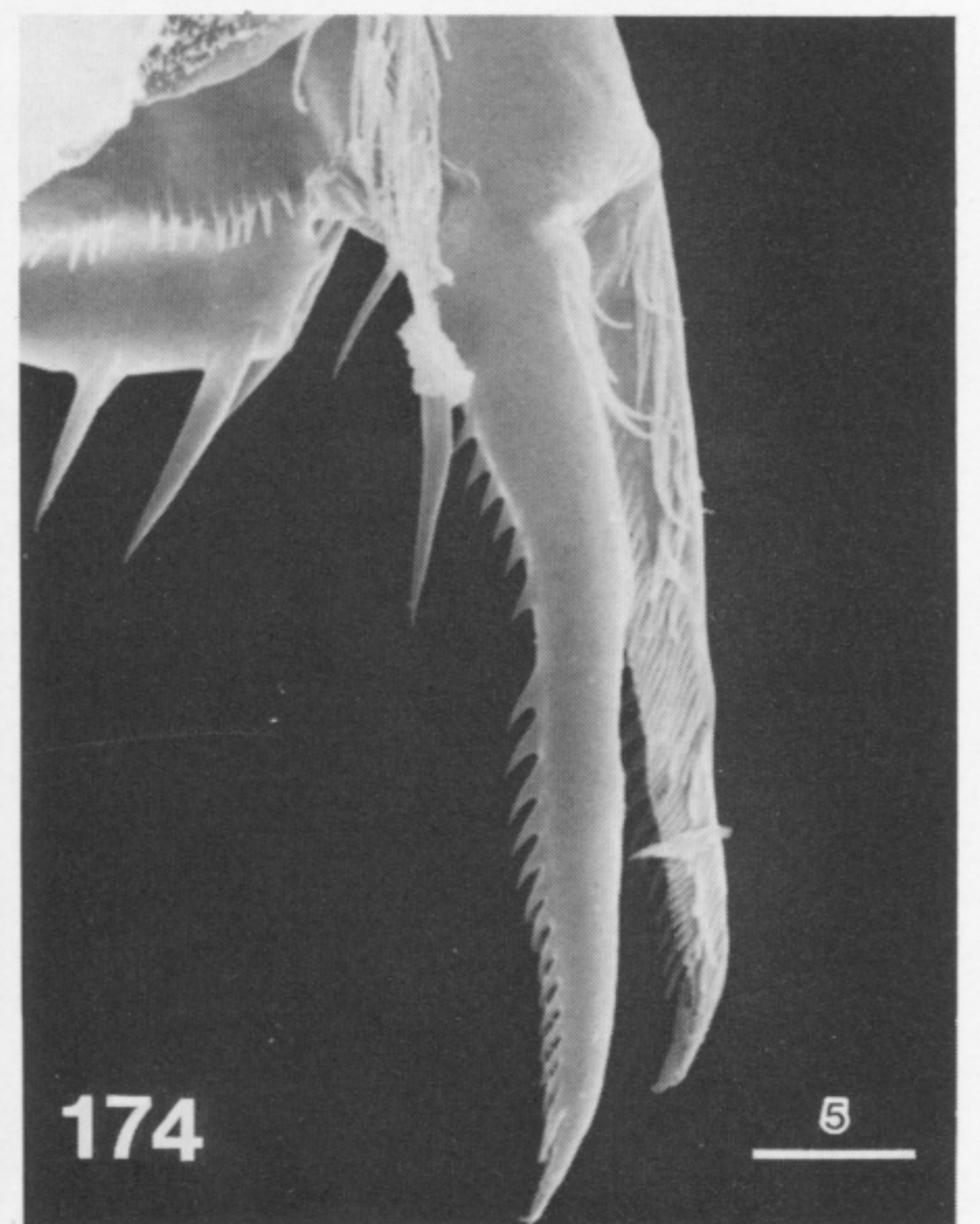
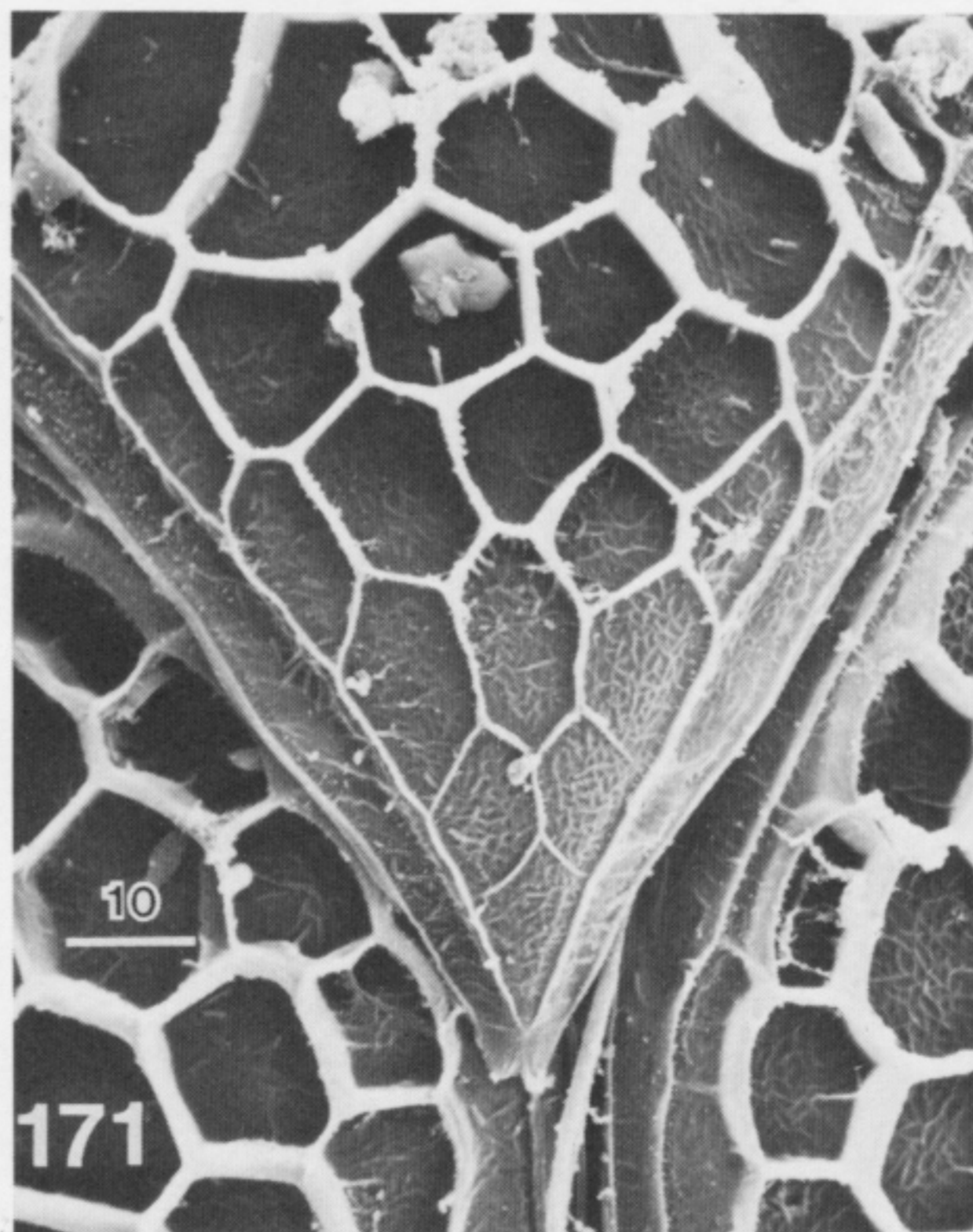
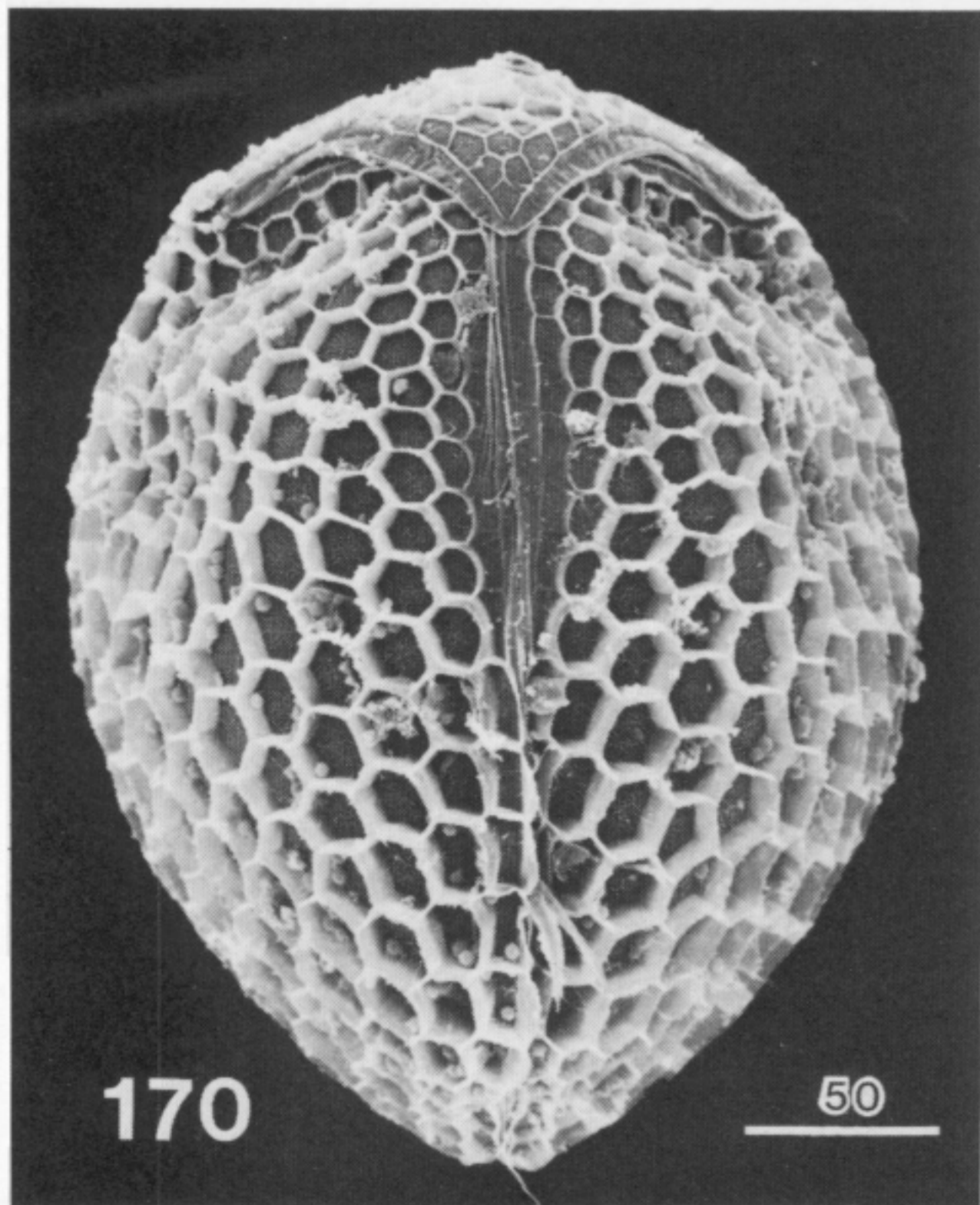
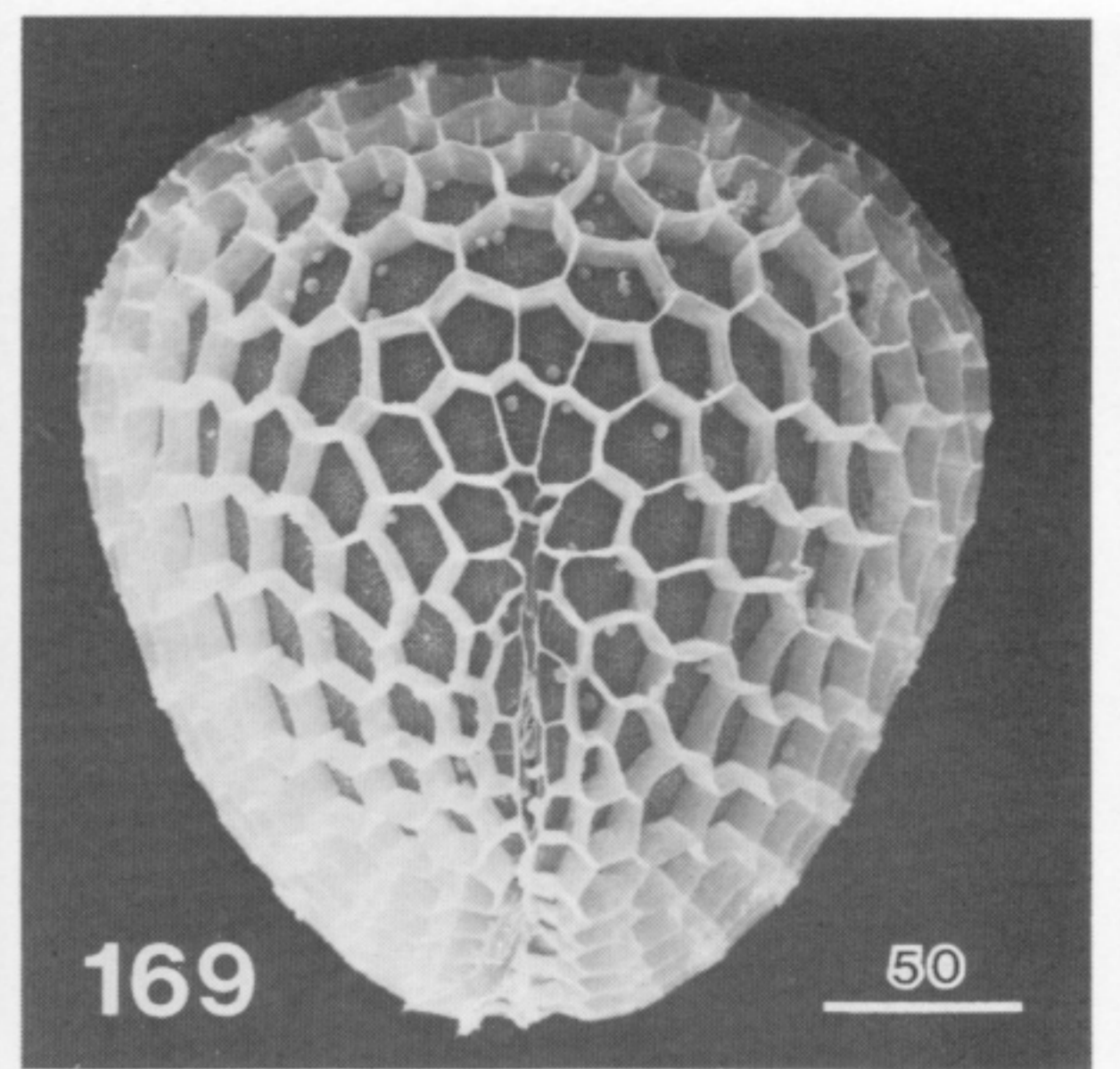
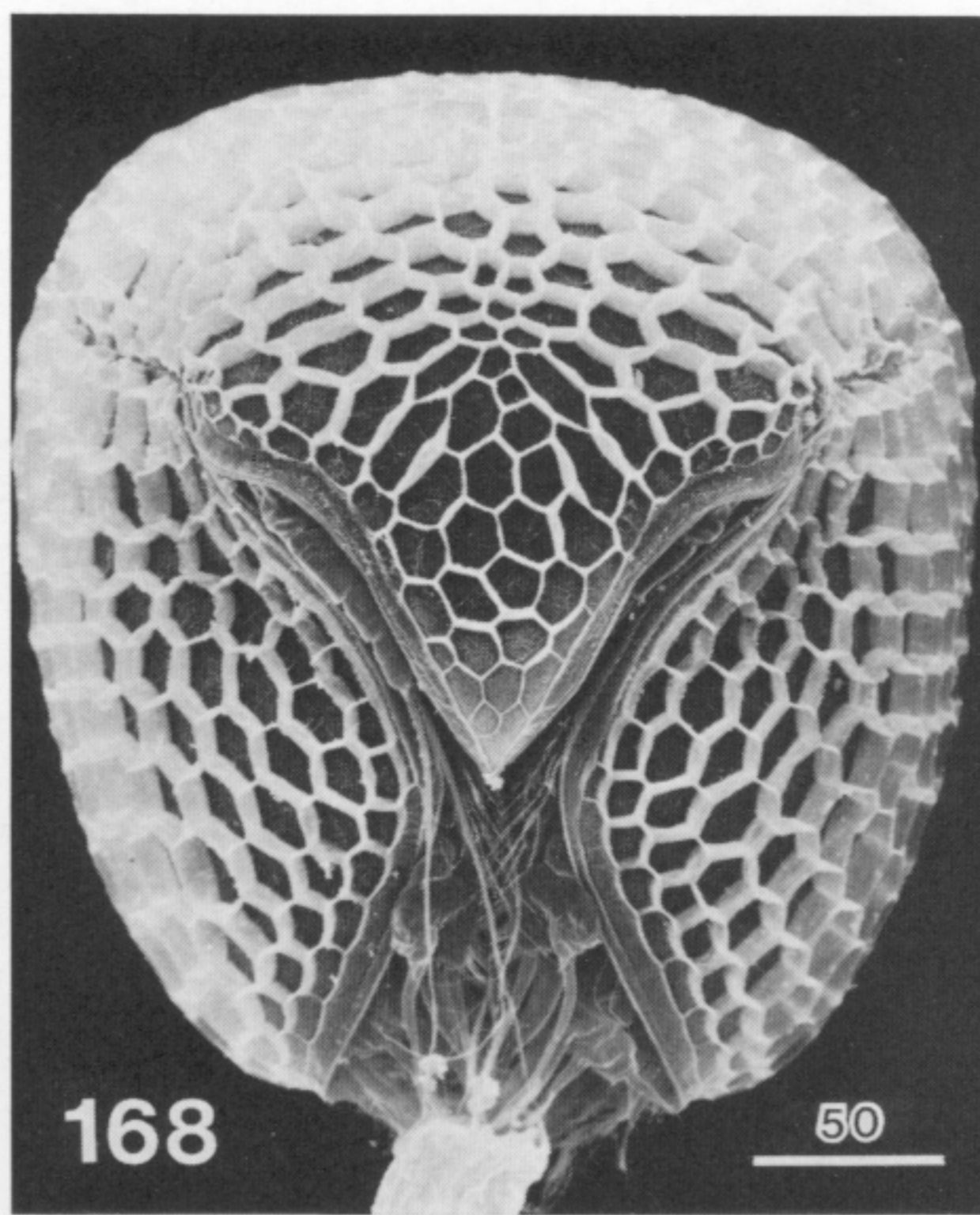
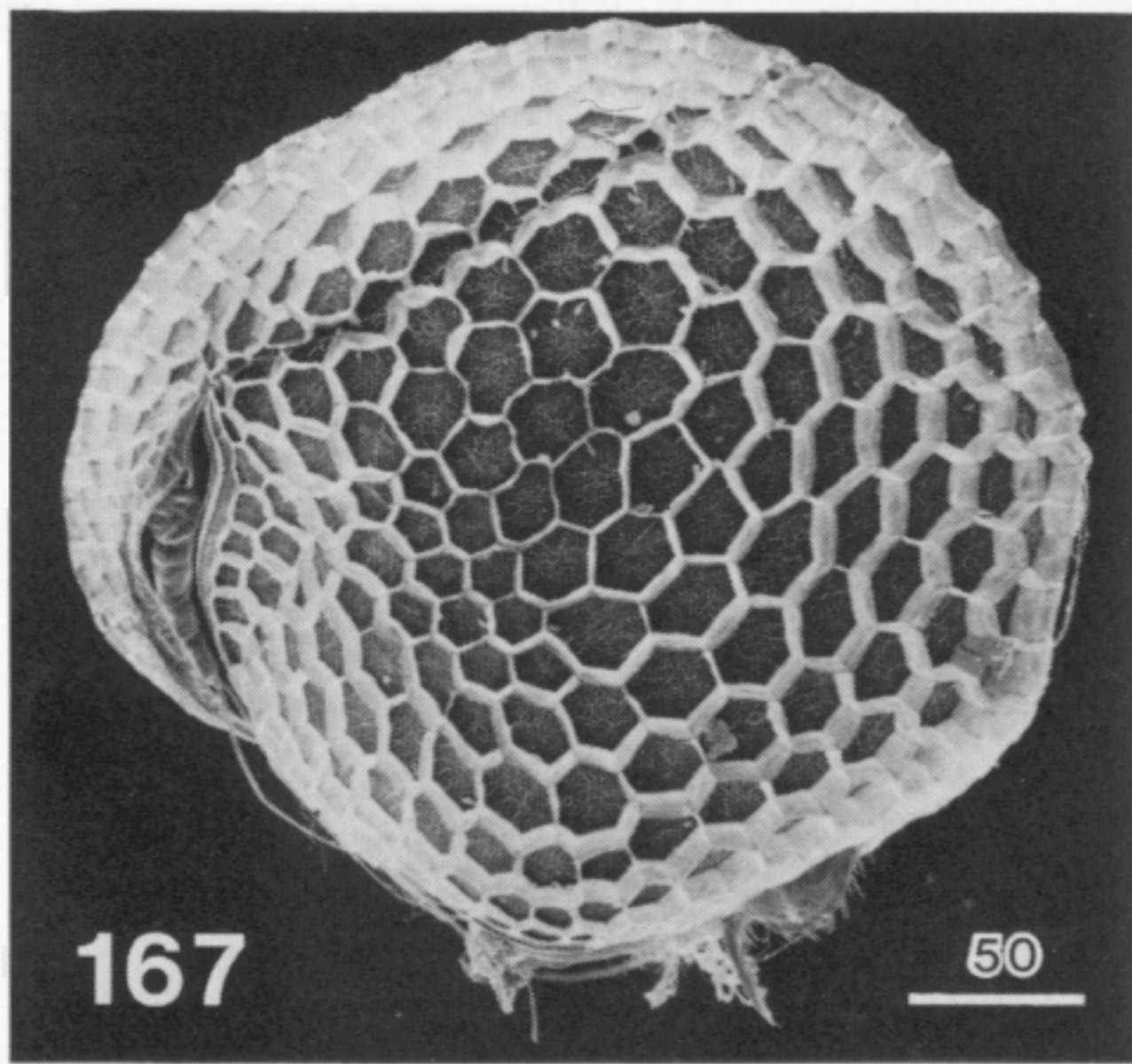
FIGURES 119-127. For description see p. 365.



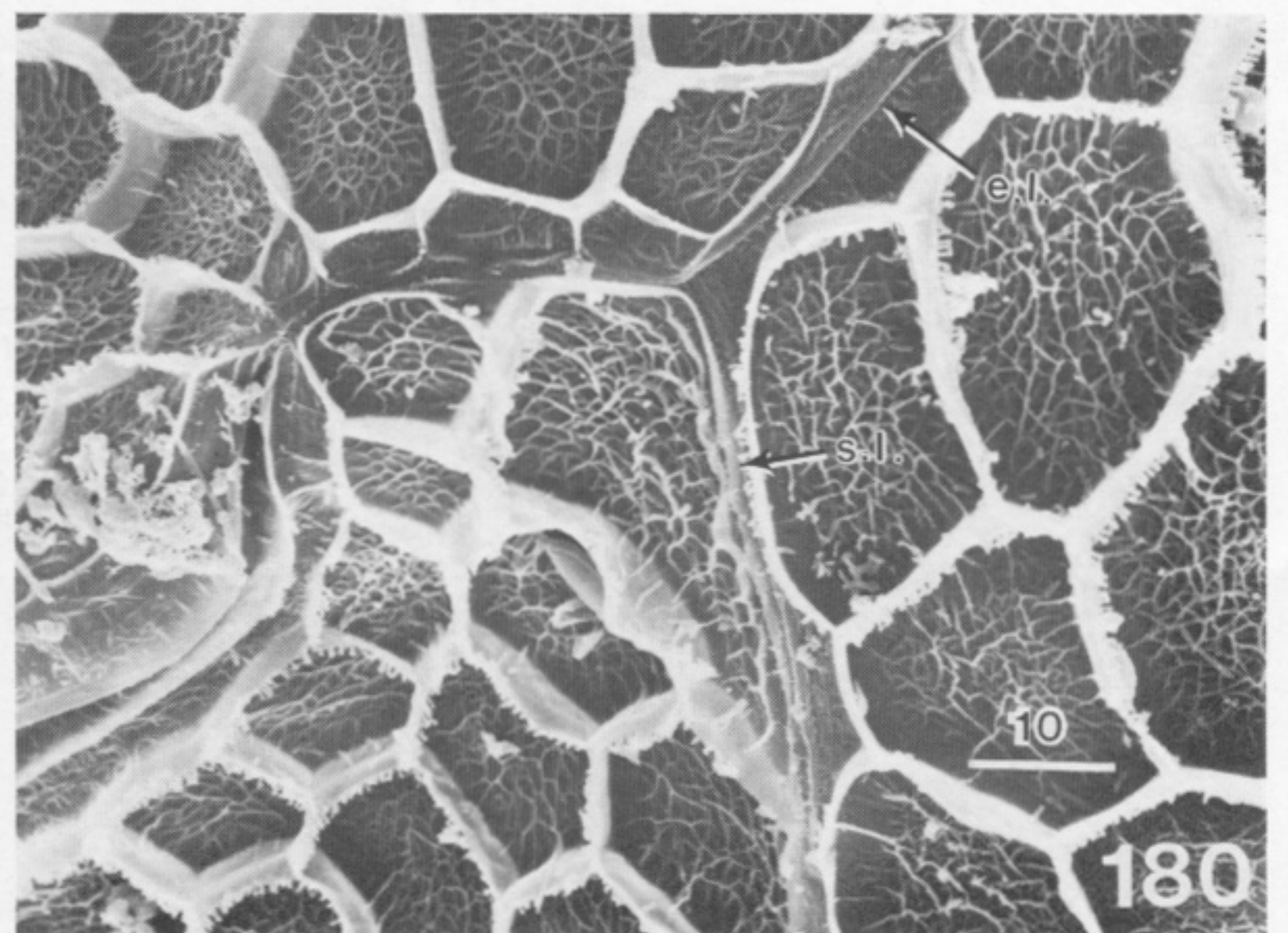
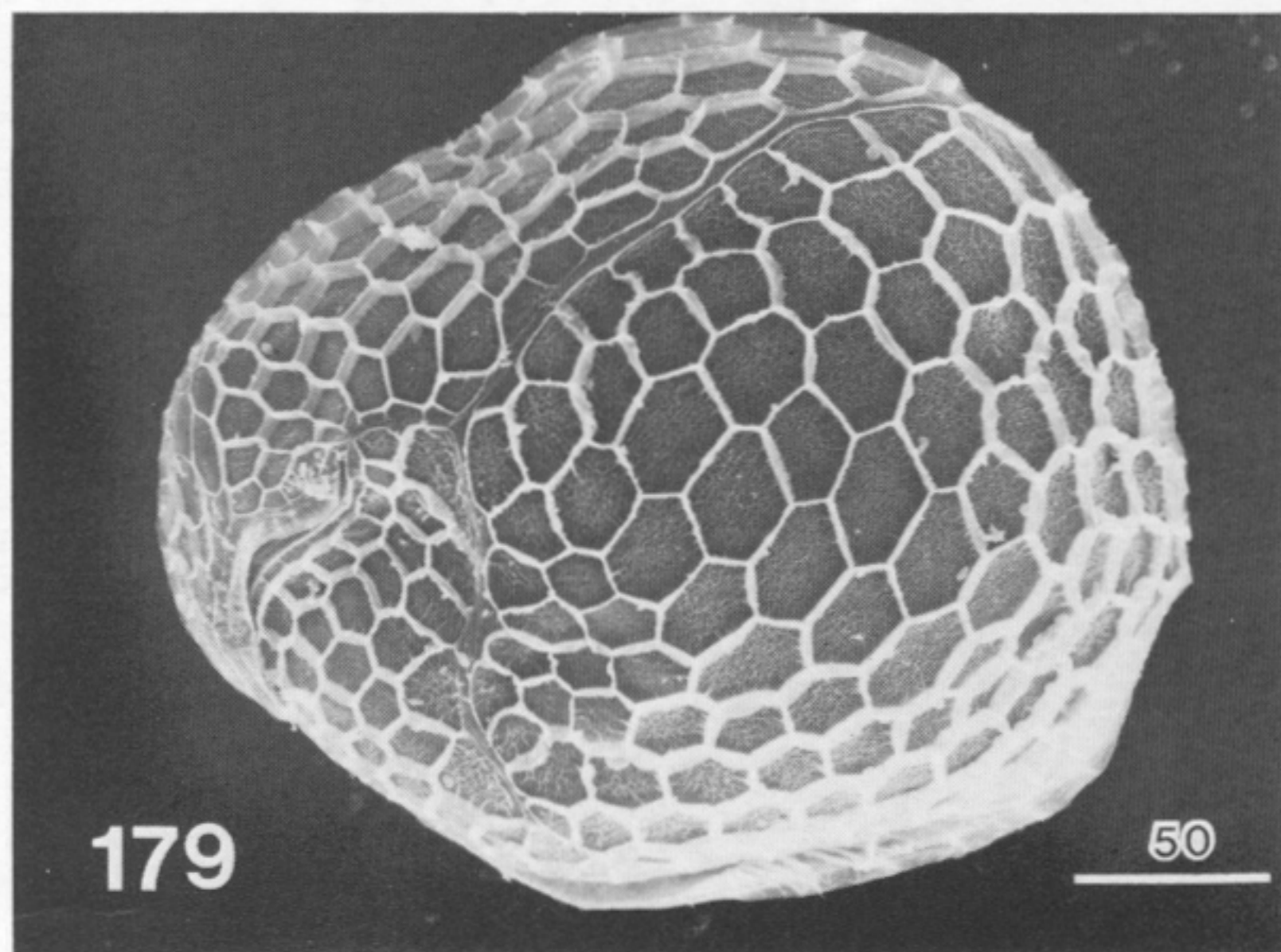
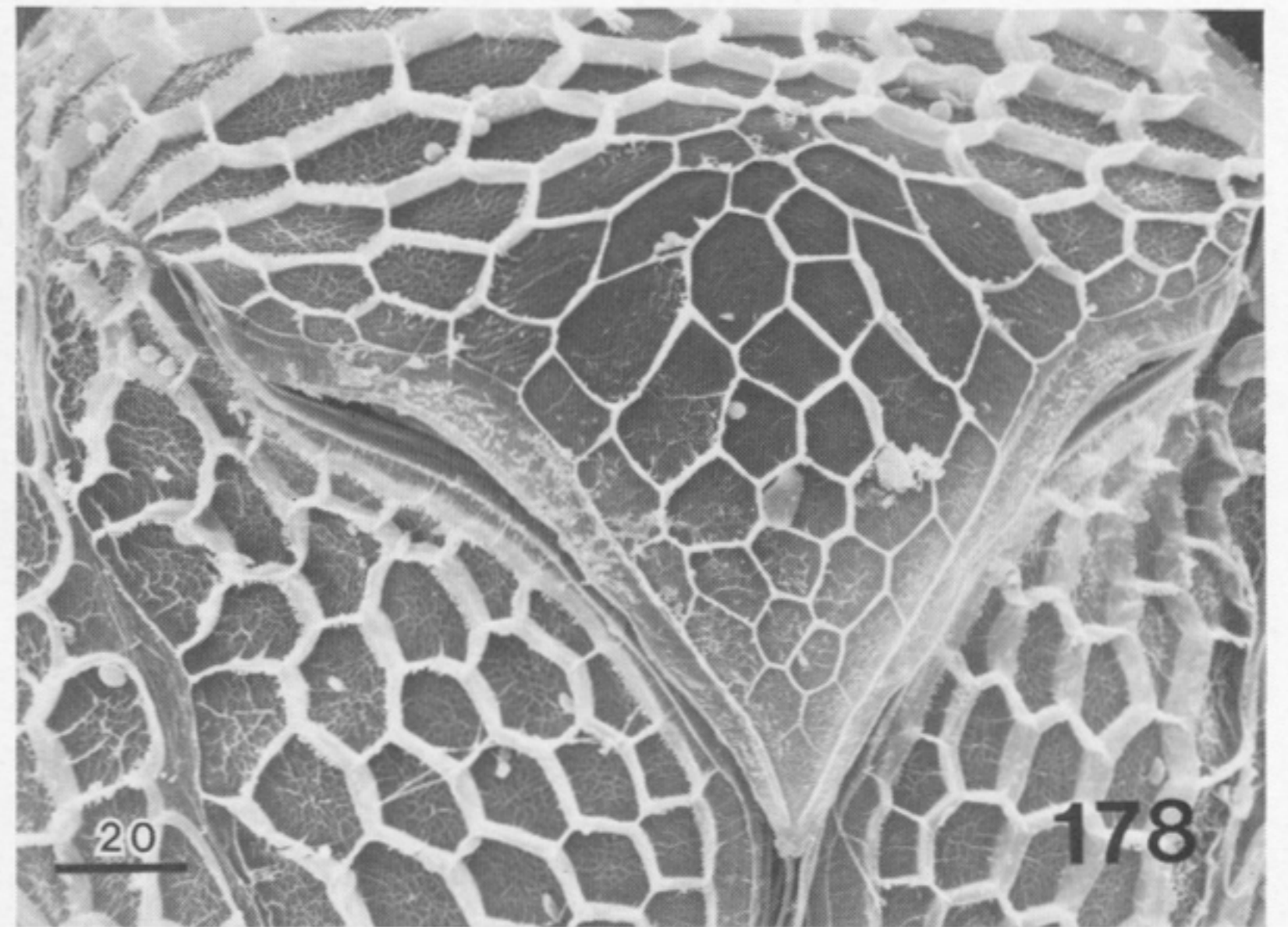
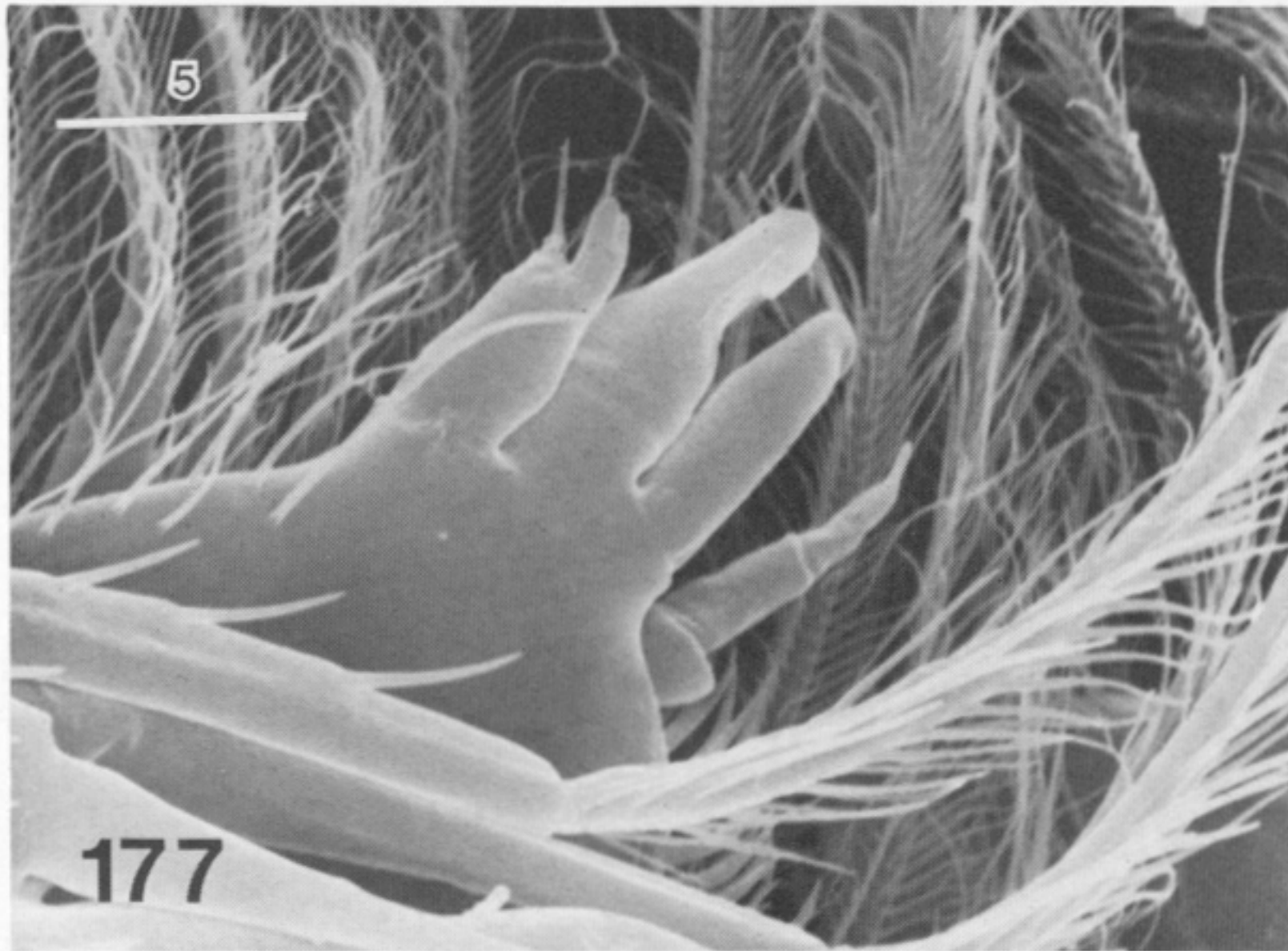
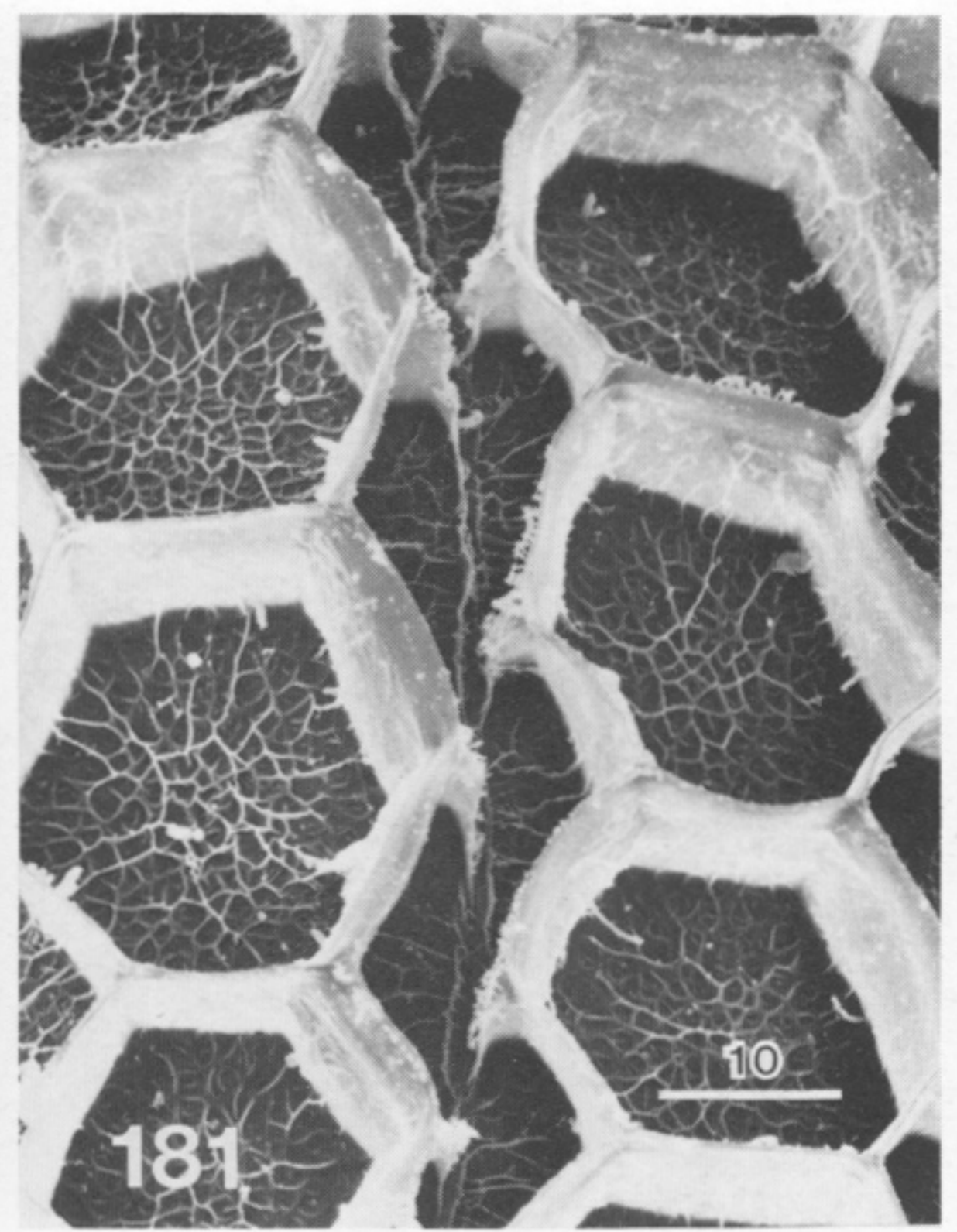
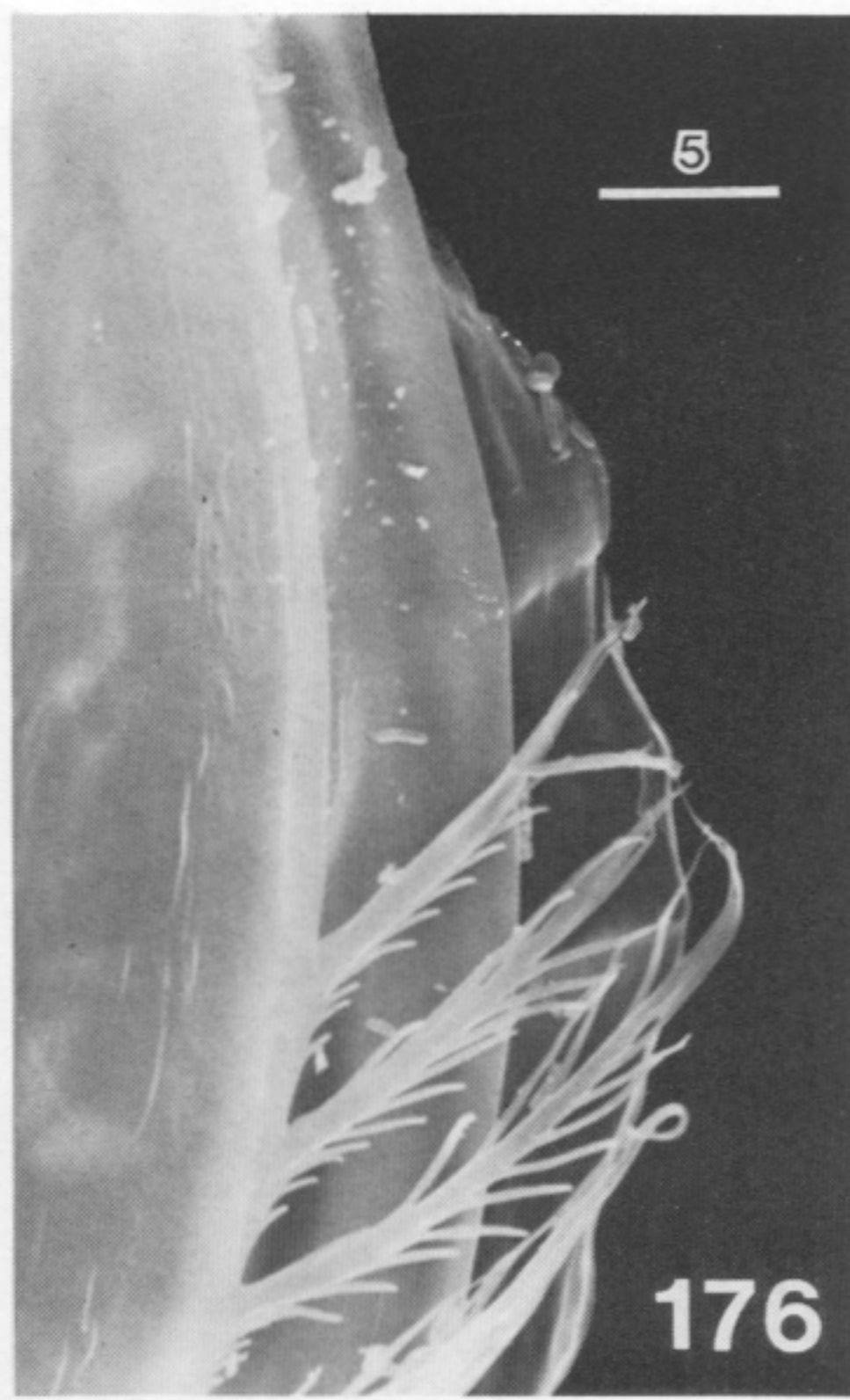
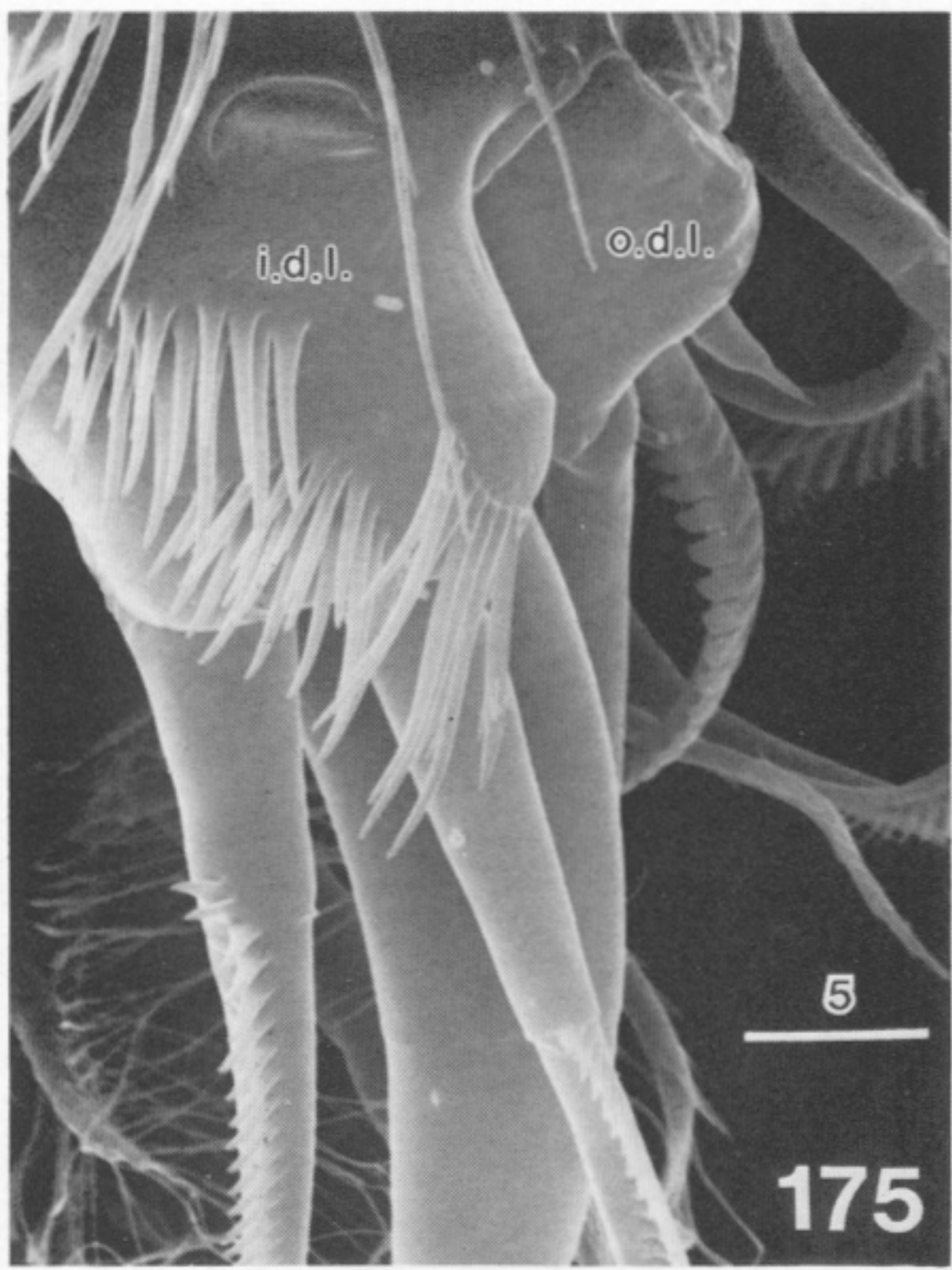
FIGURES 128-134. For description see p. 365.



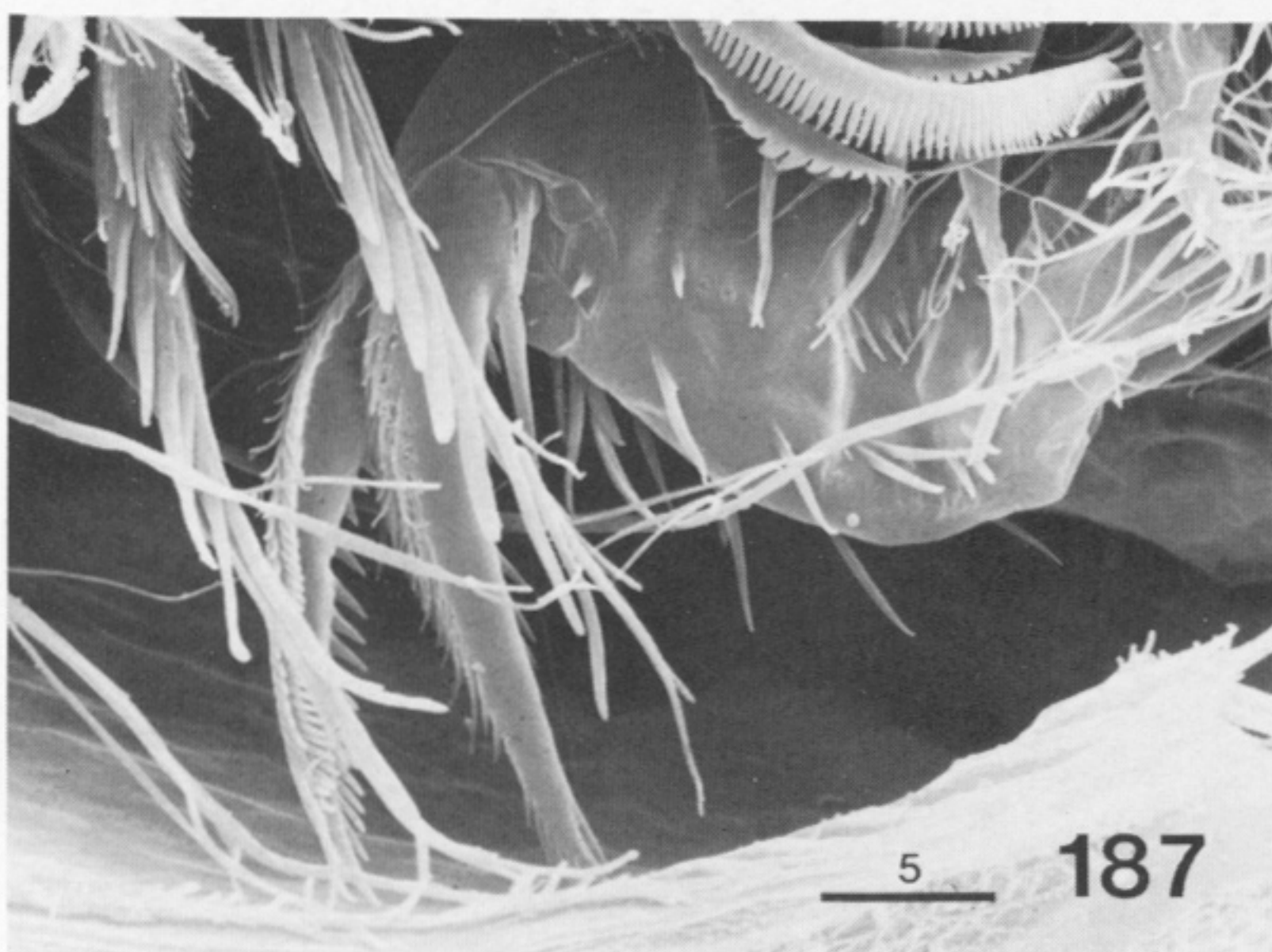
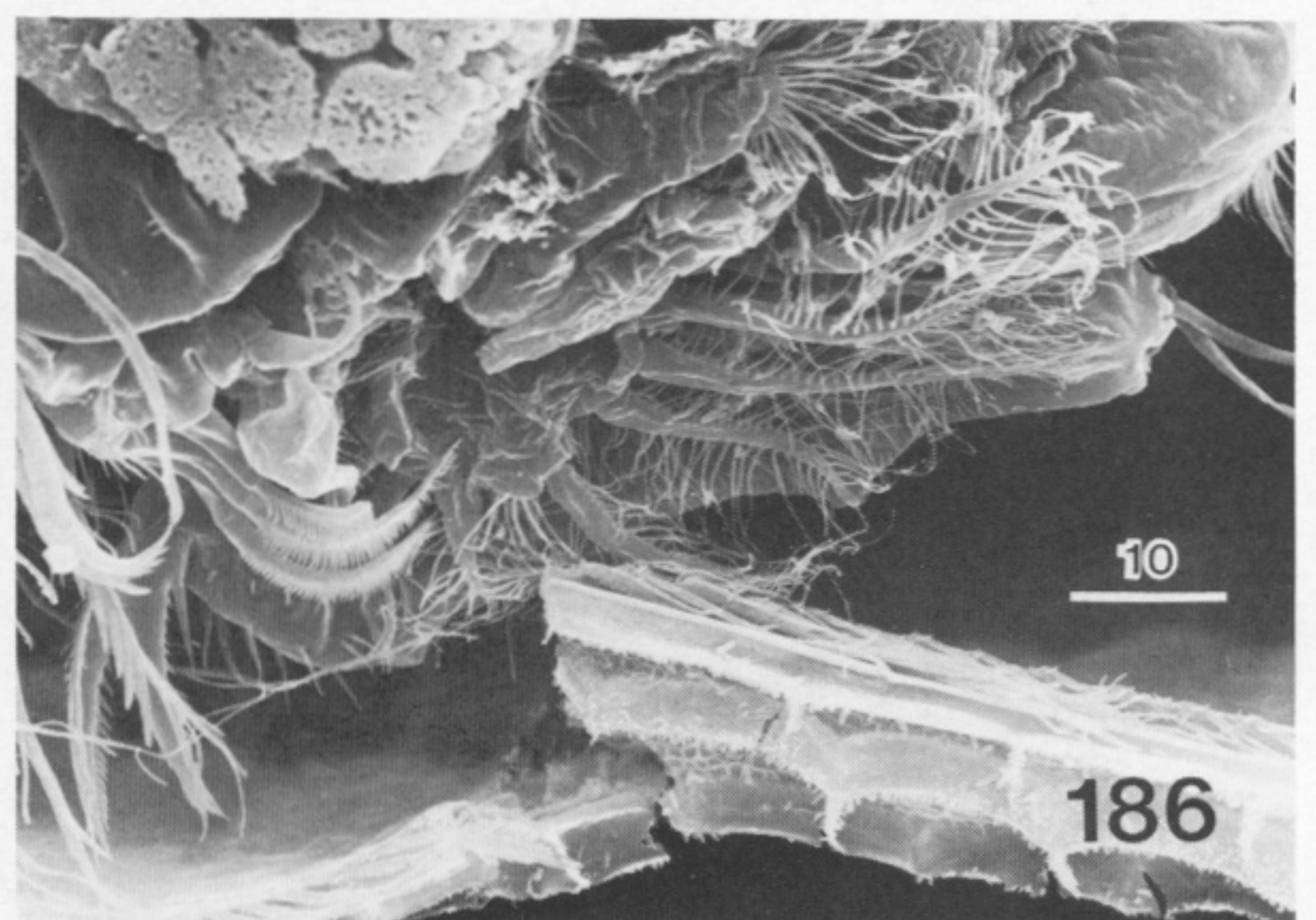
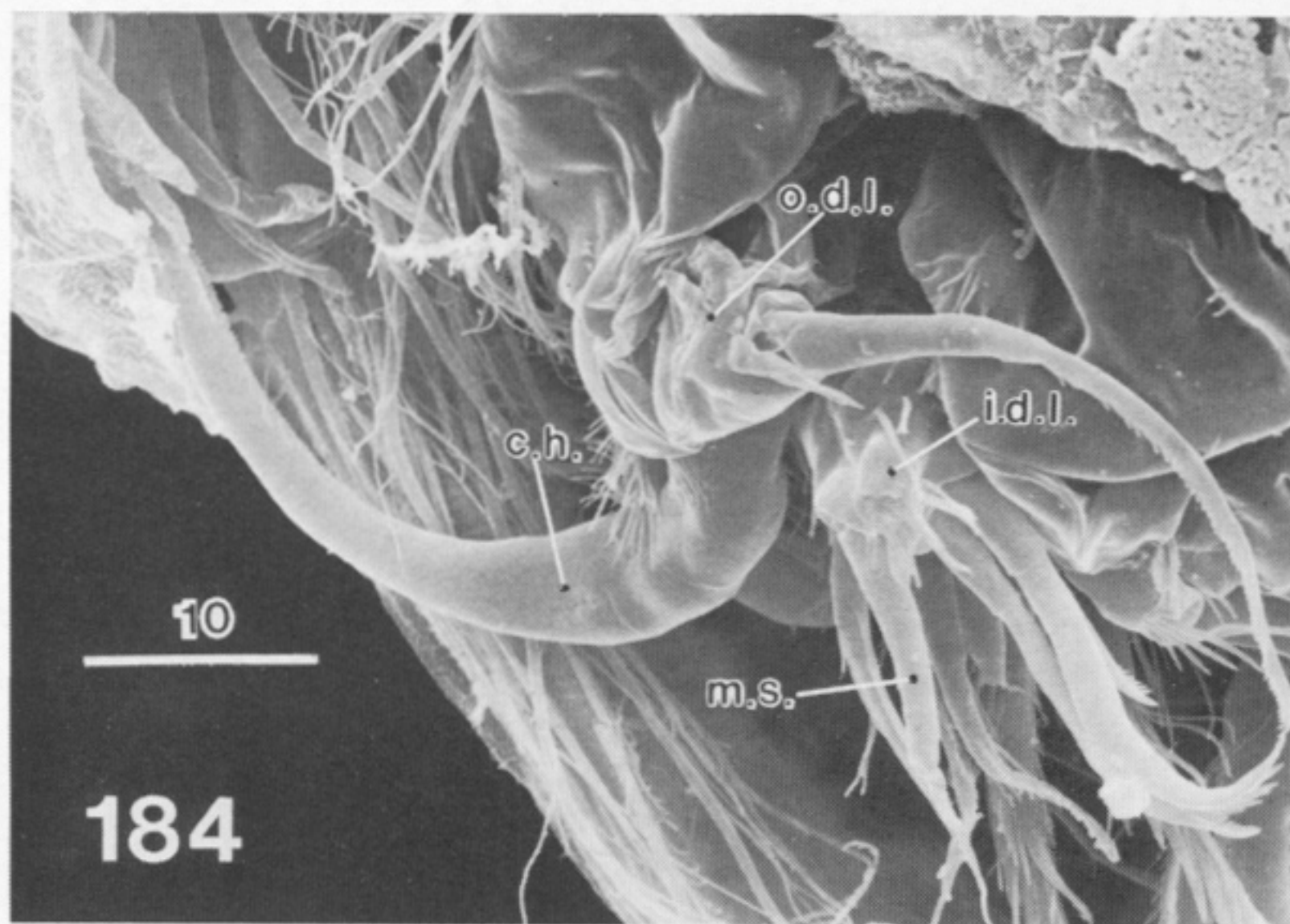
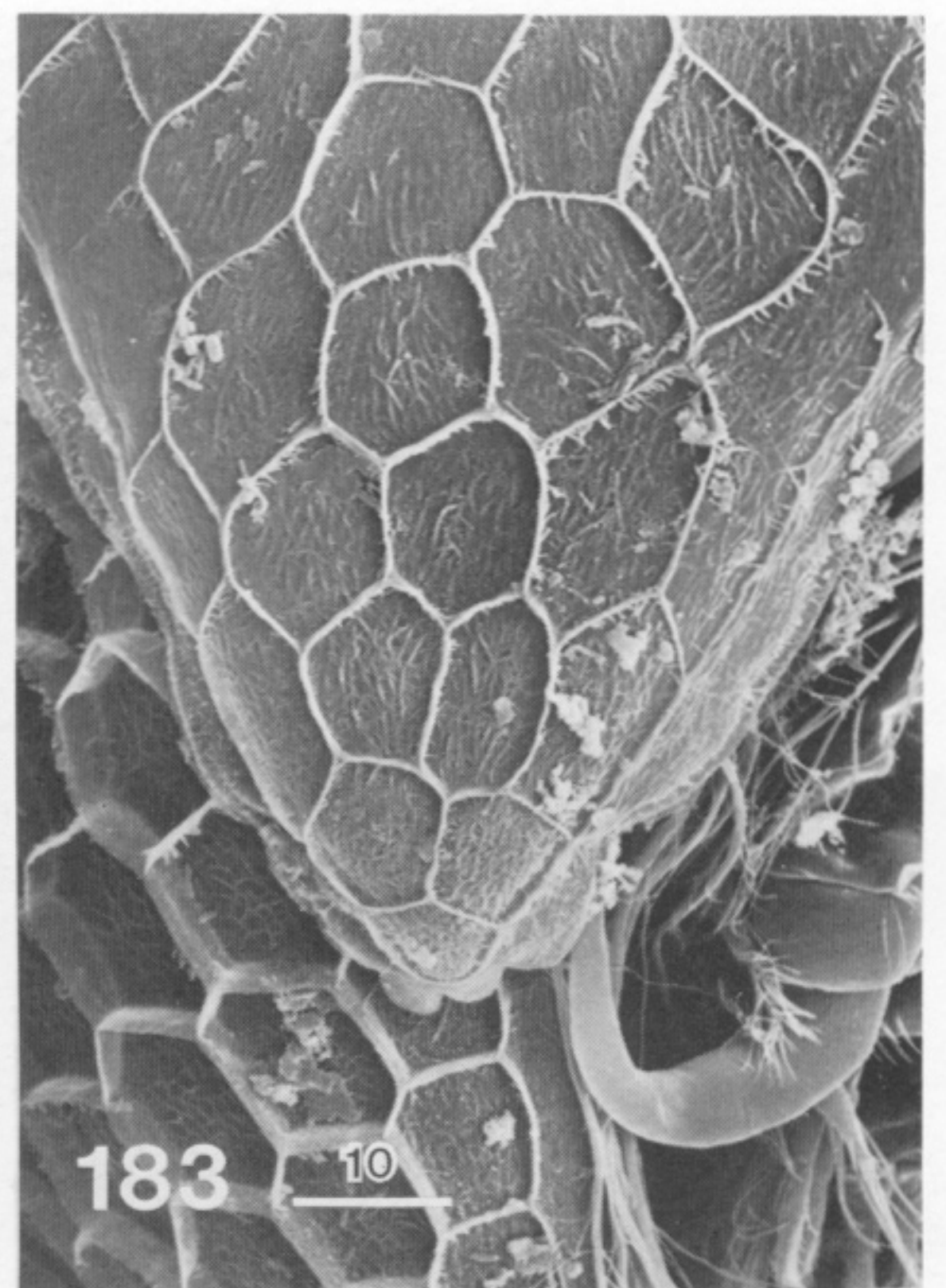
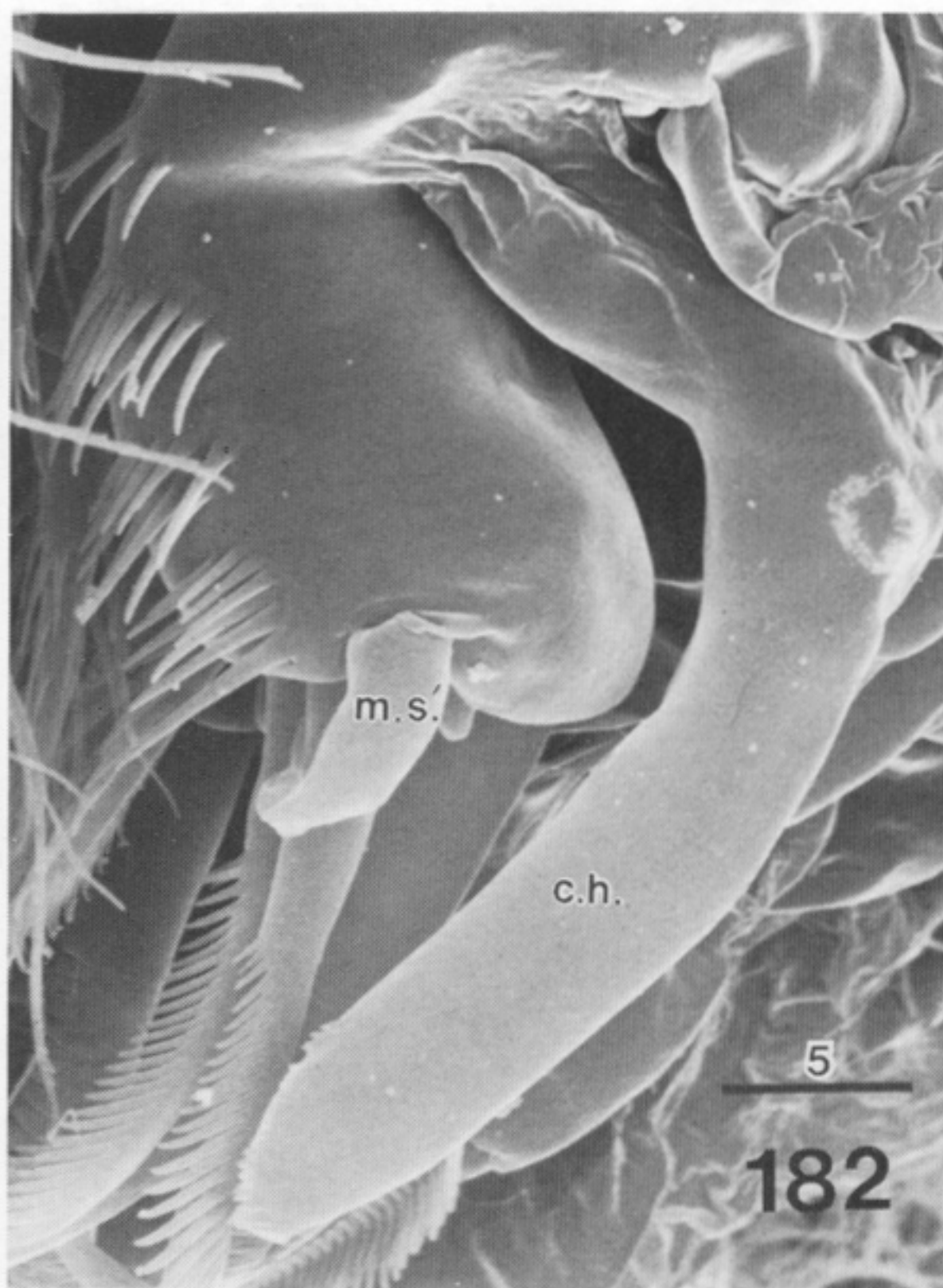
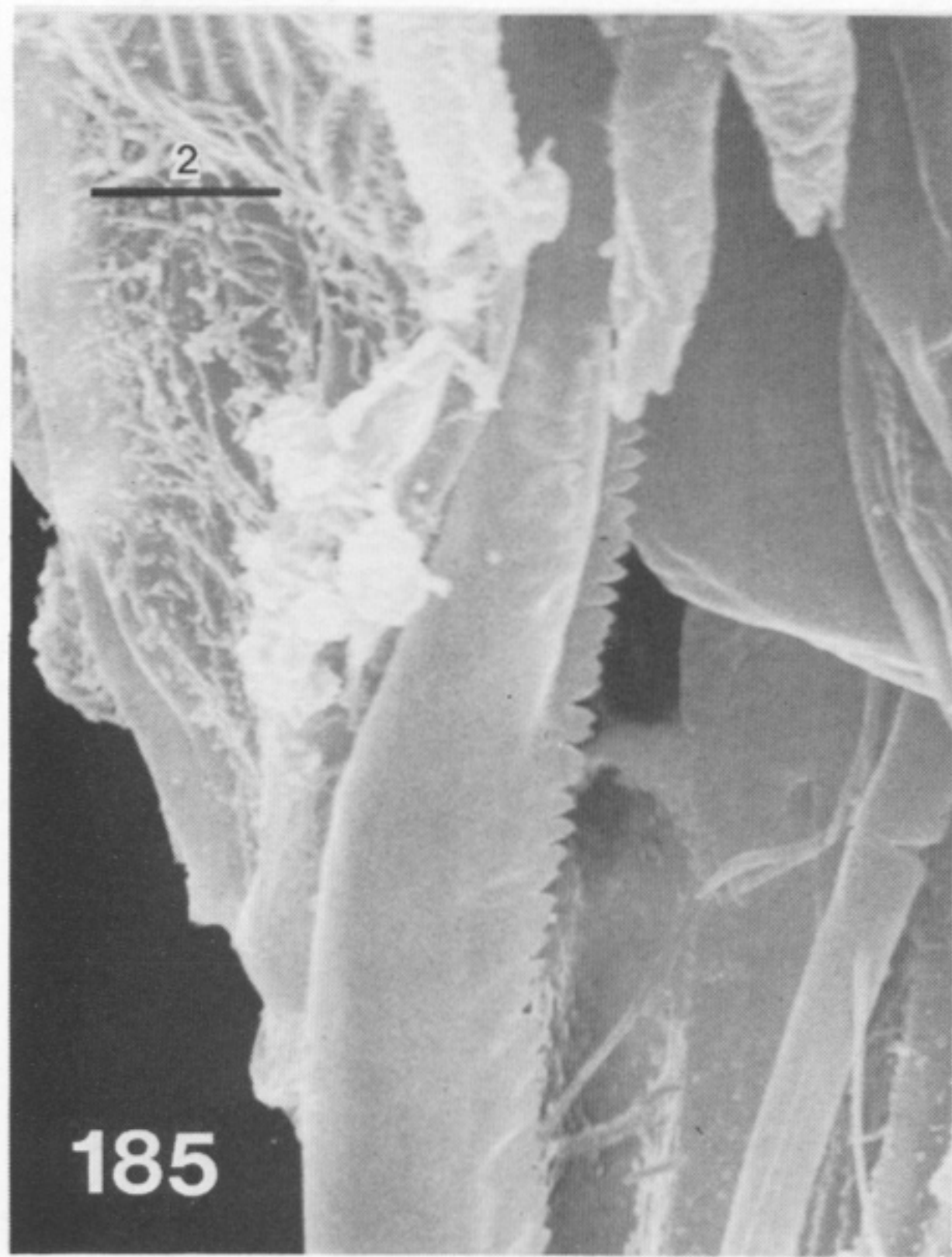
FIGURES 135-143. For description see opposite.



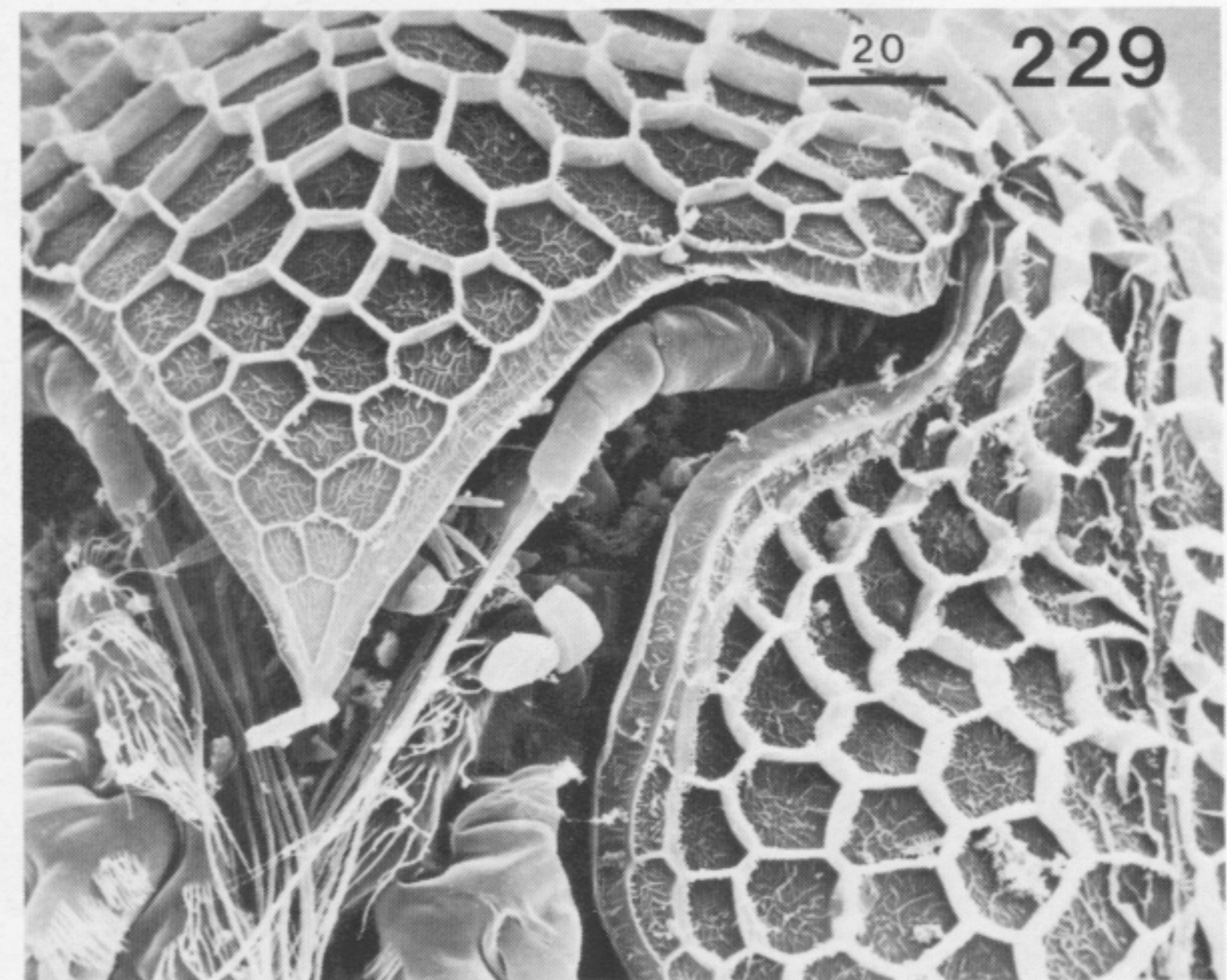
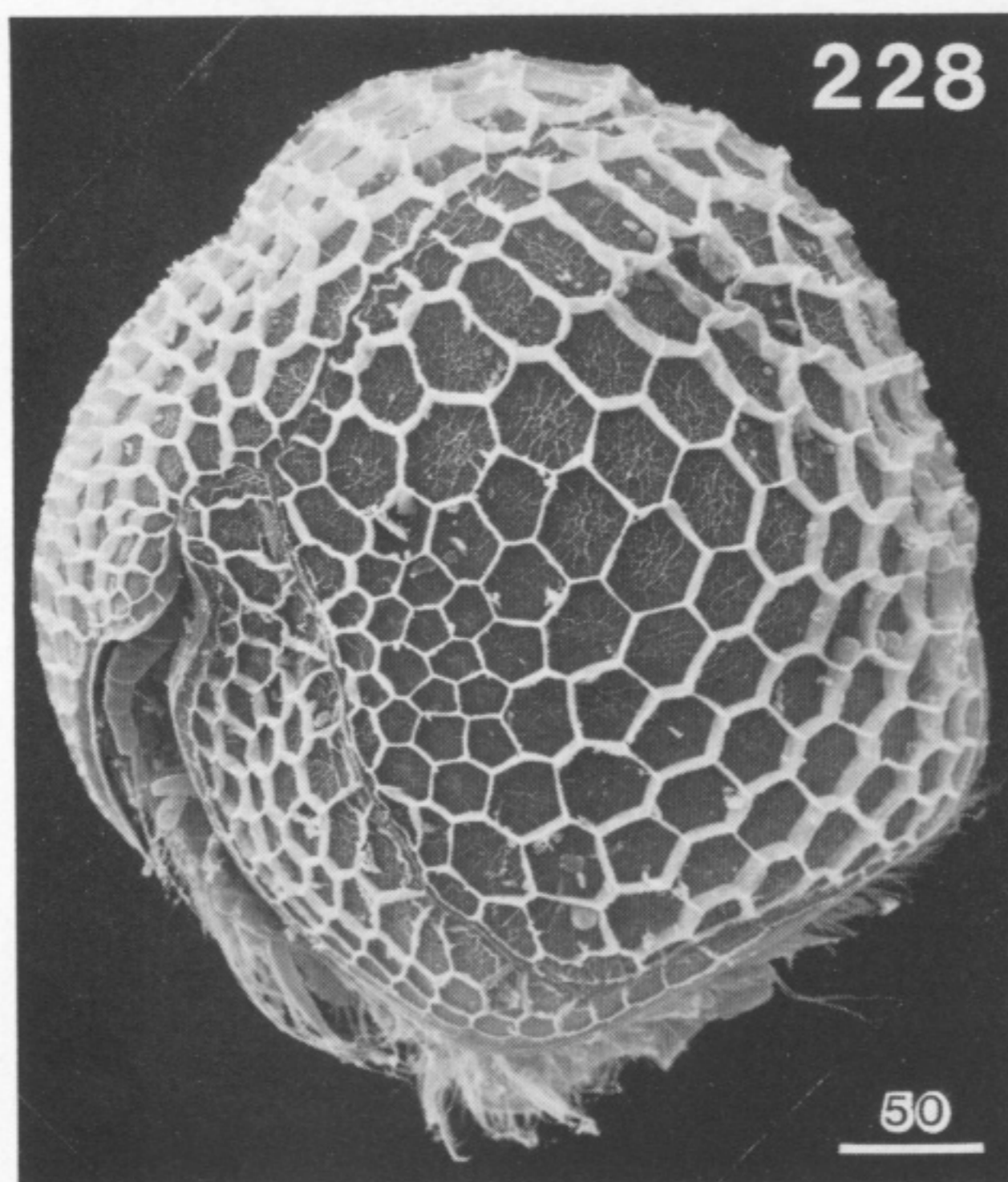
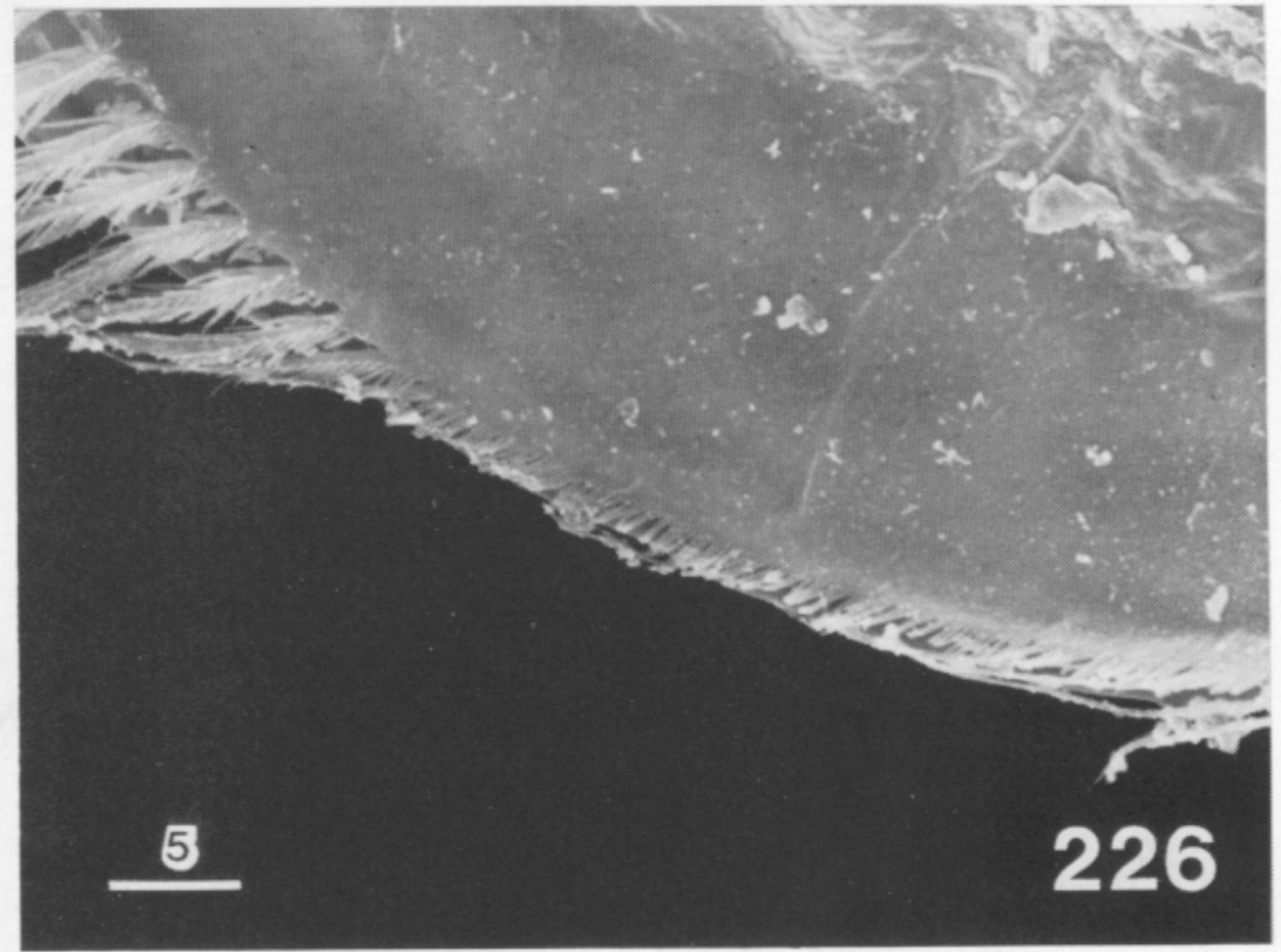
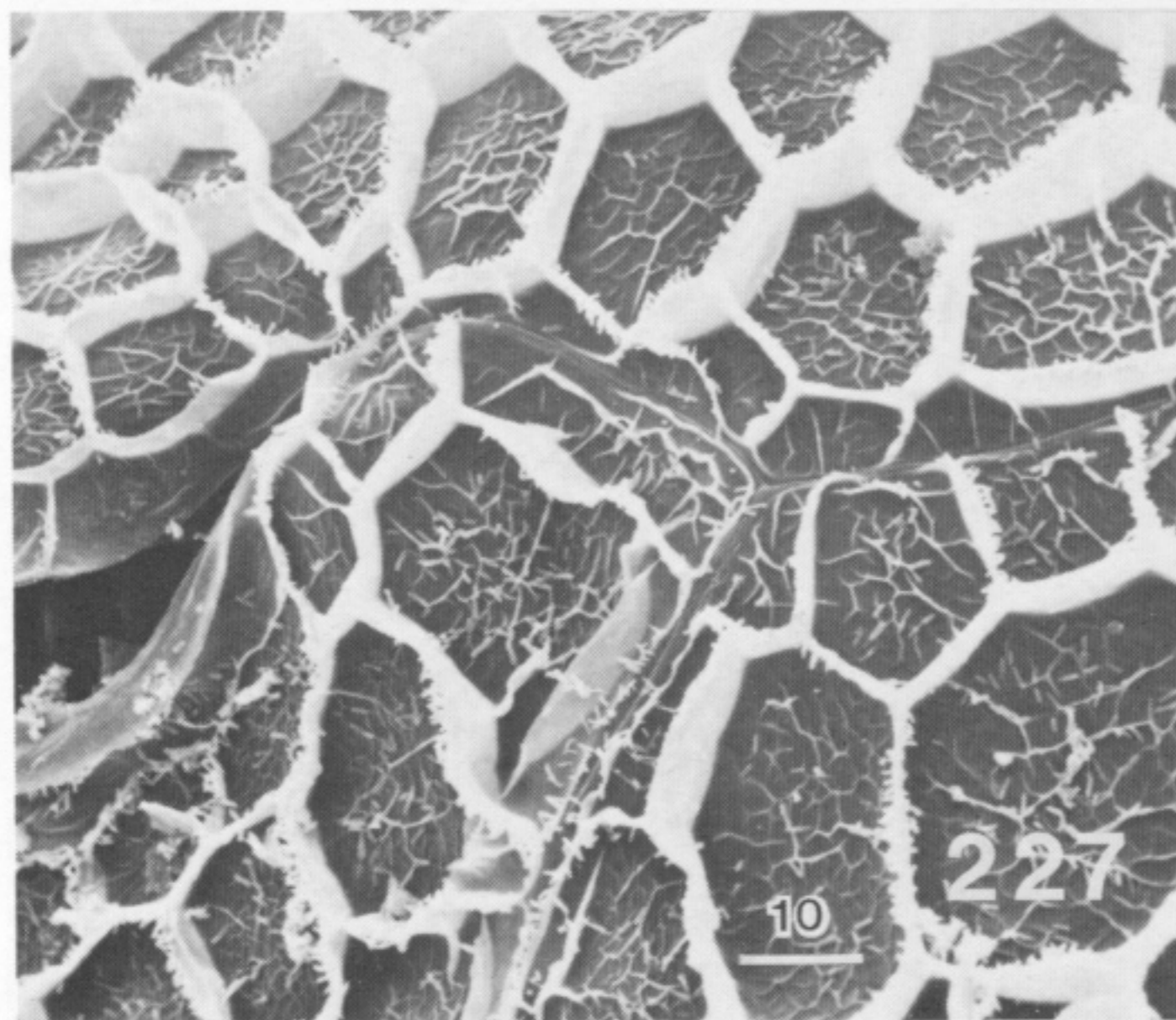
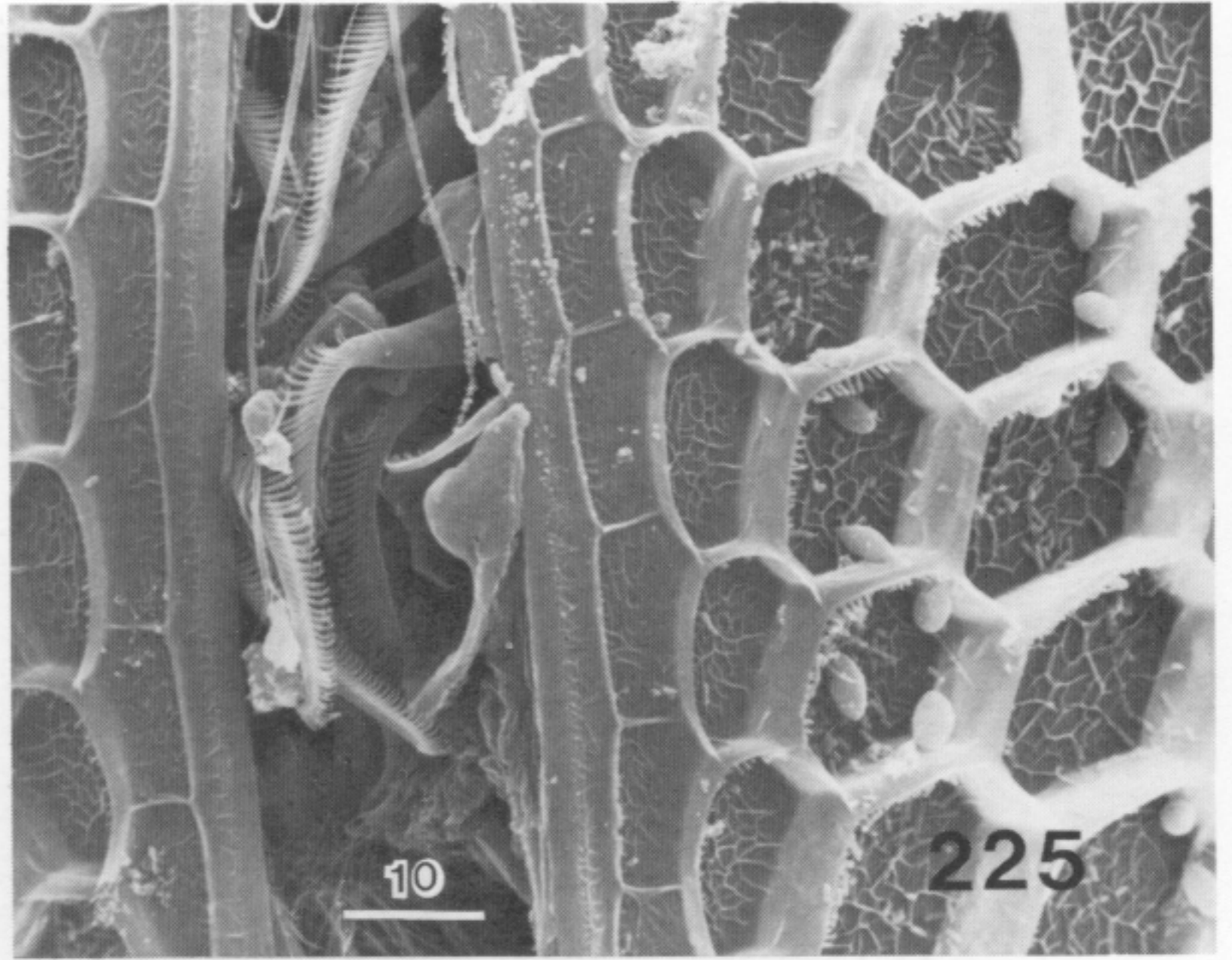
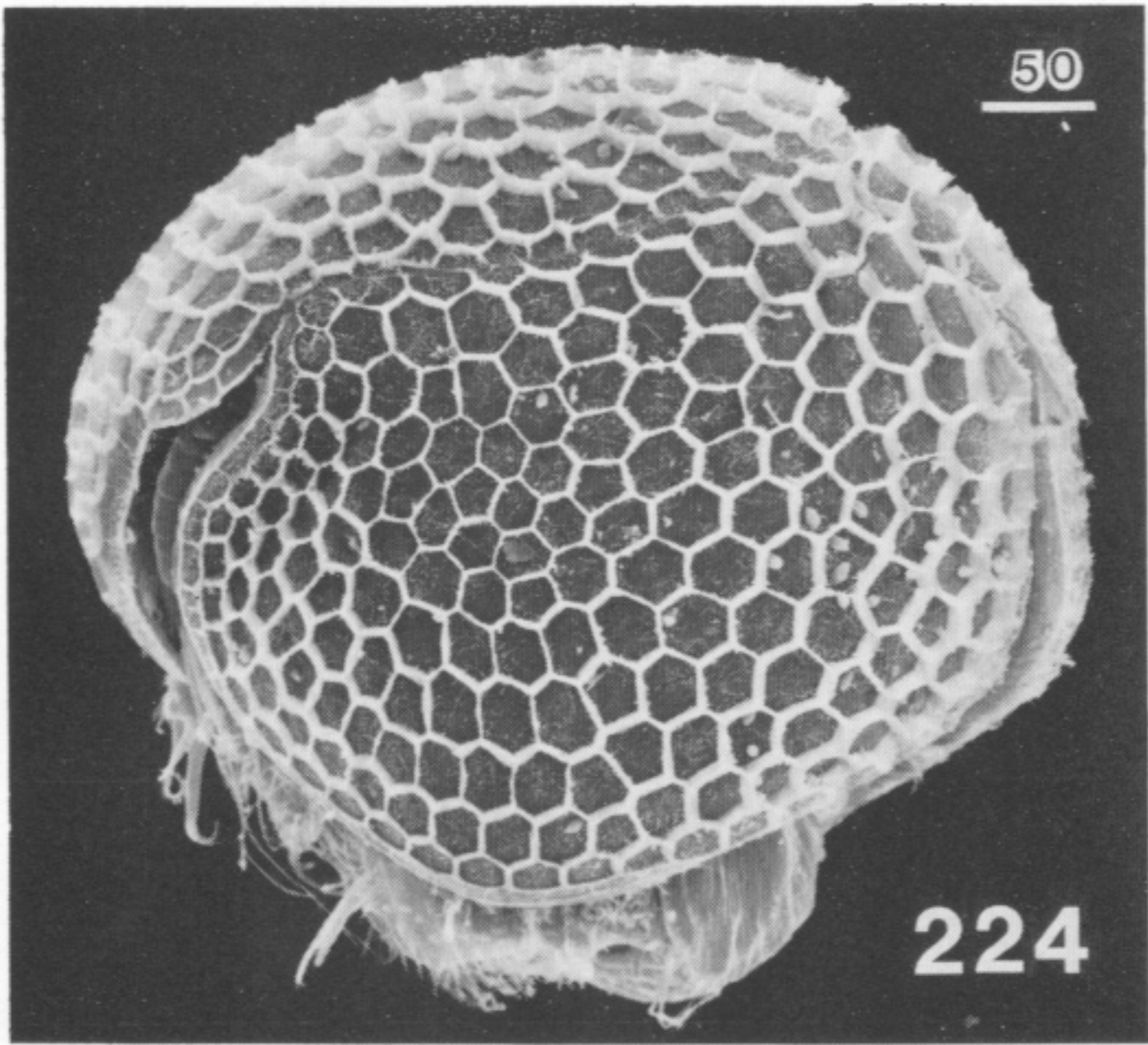
FIGURES 167-174. For description see p. 376.



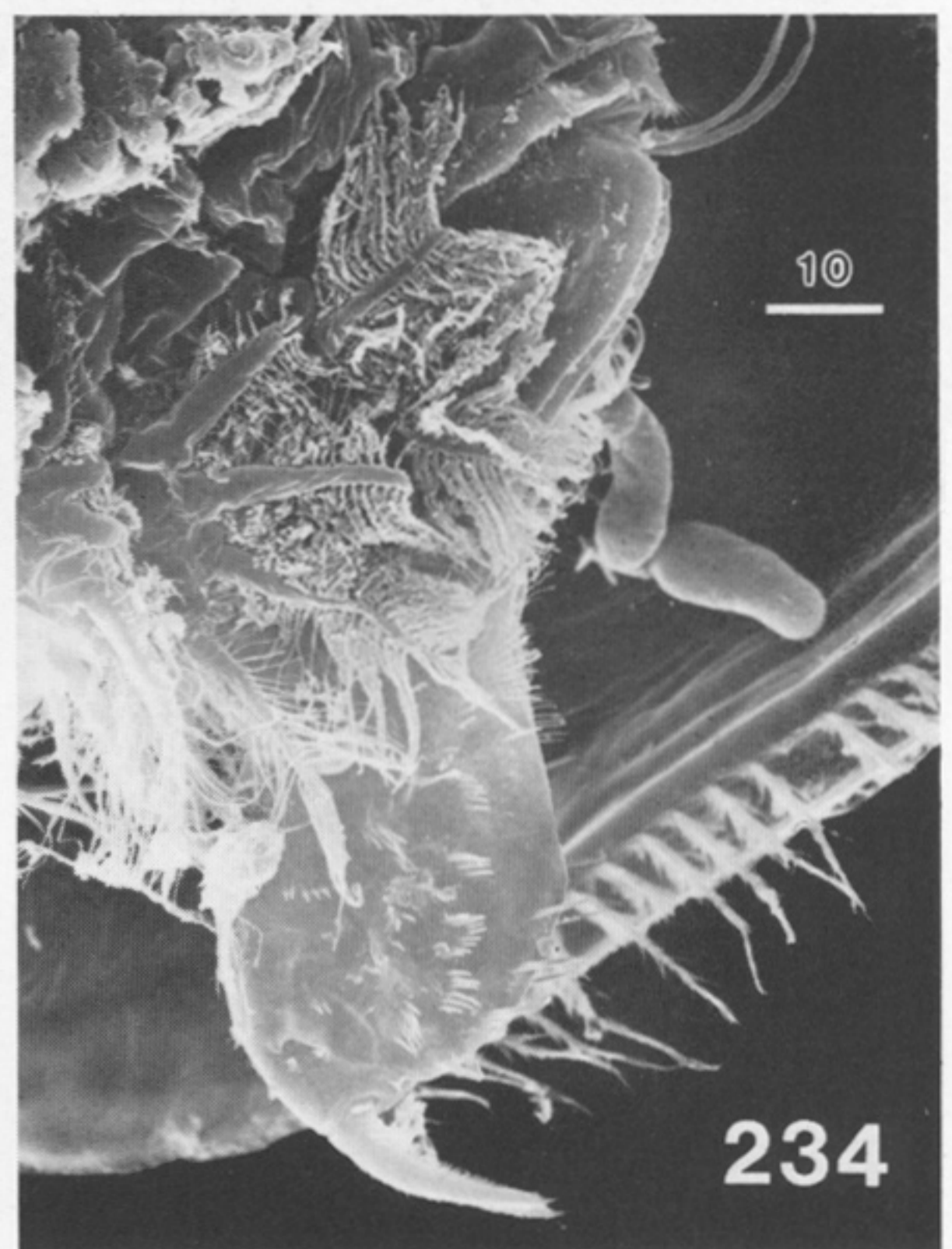
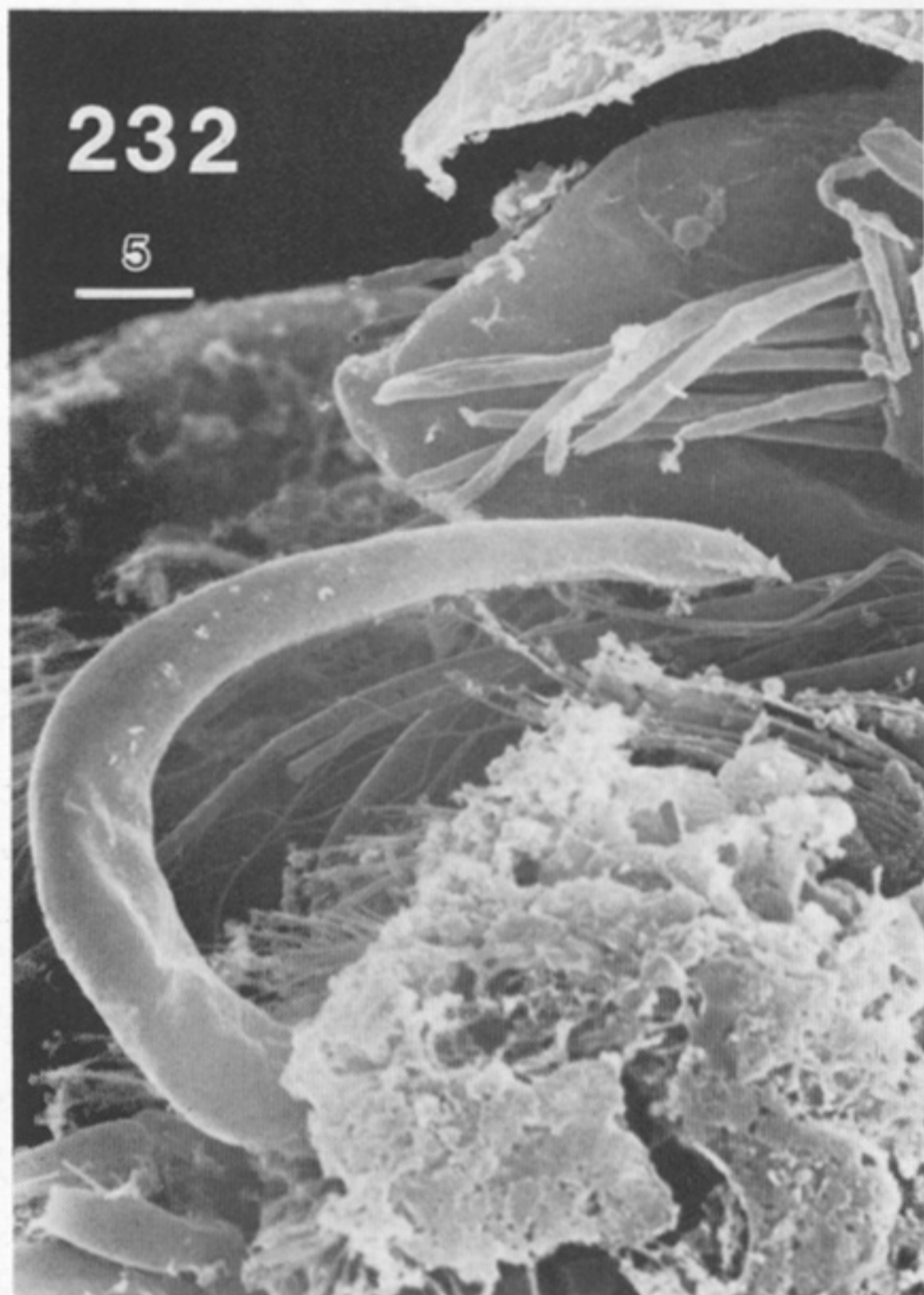
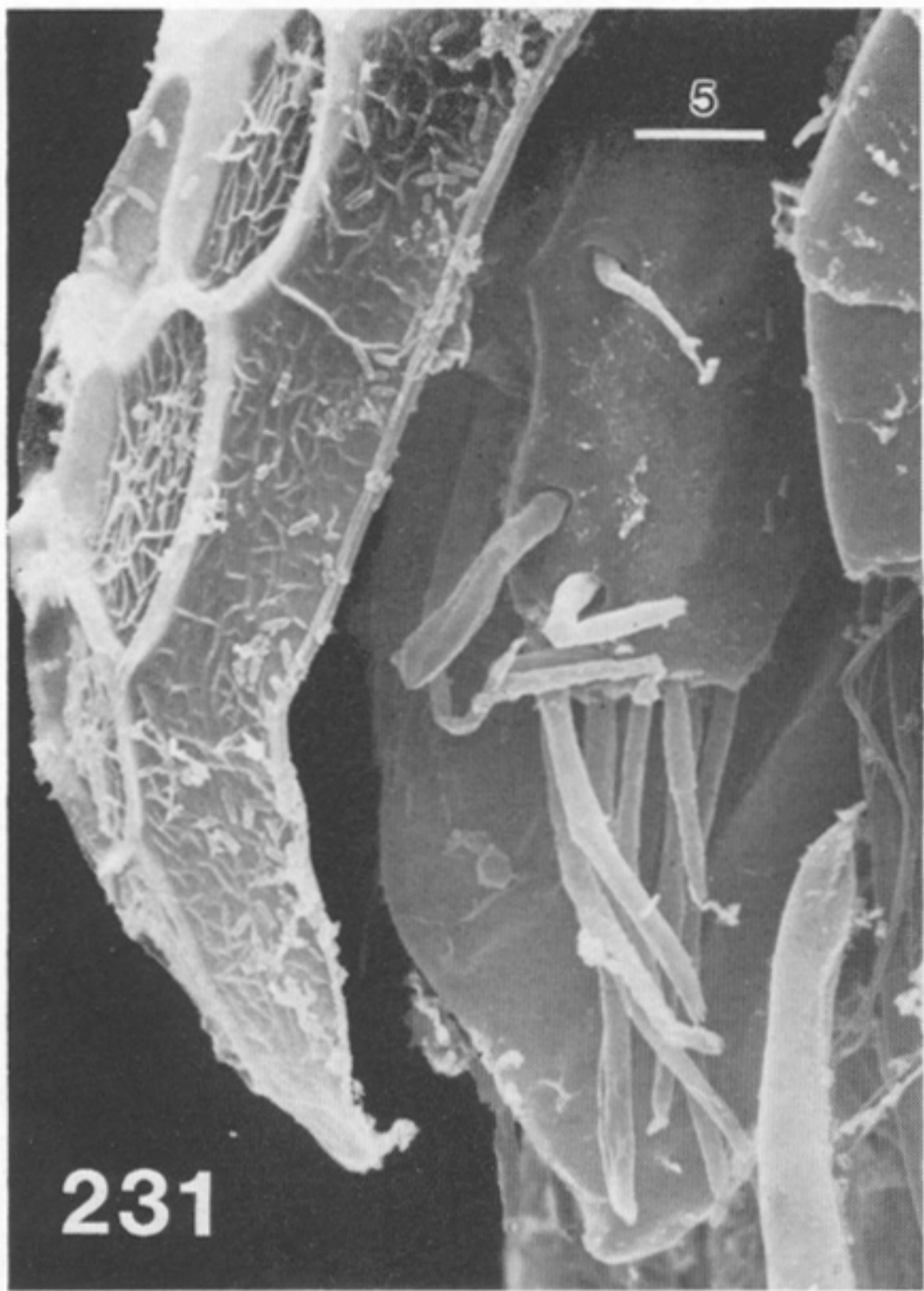
FIGURES 175-181. For description see p. 376.



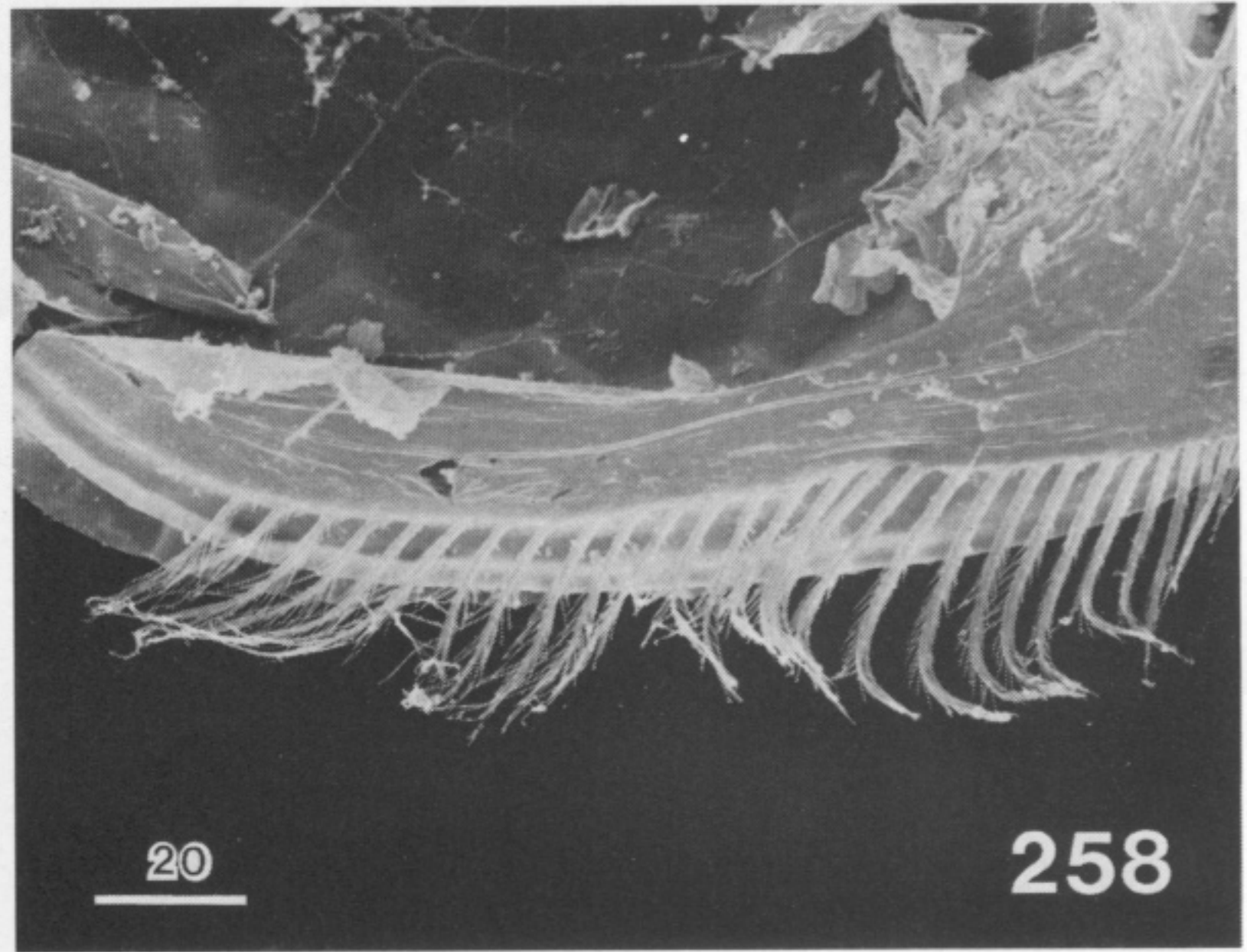
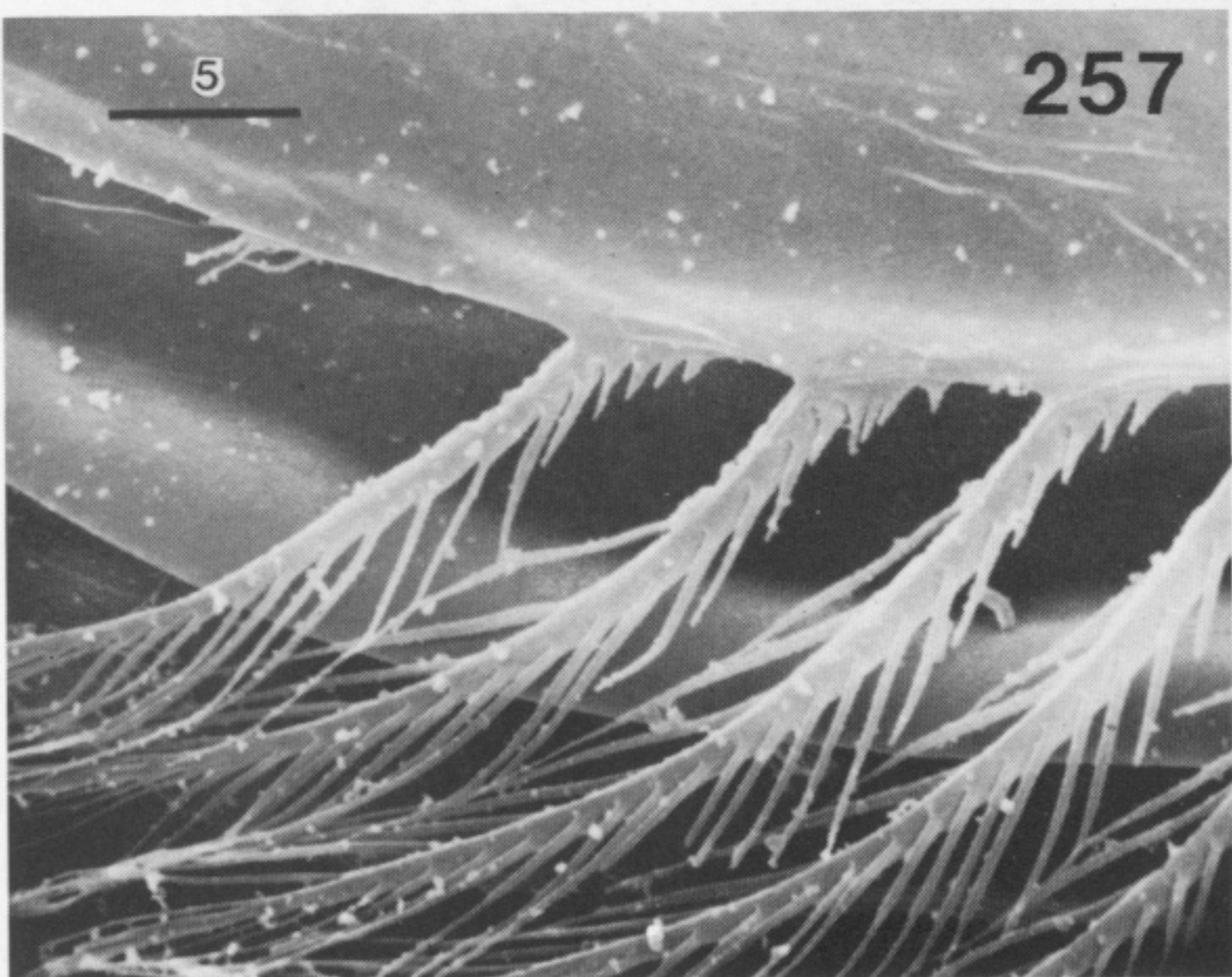
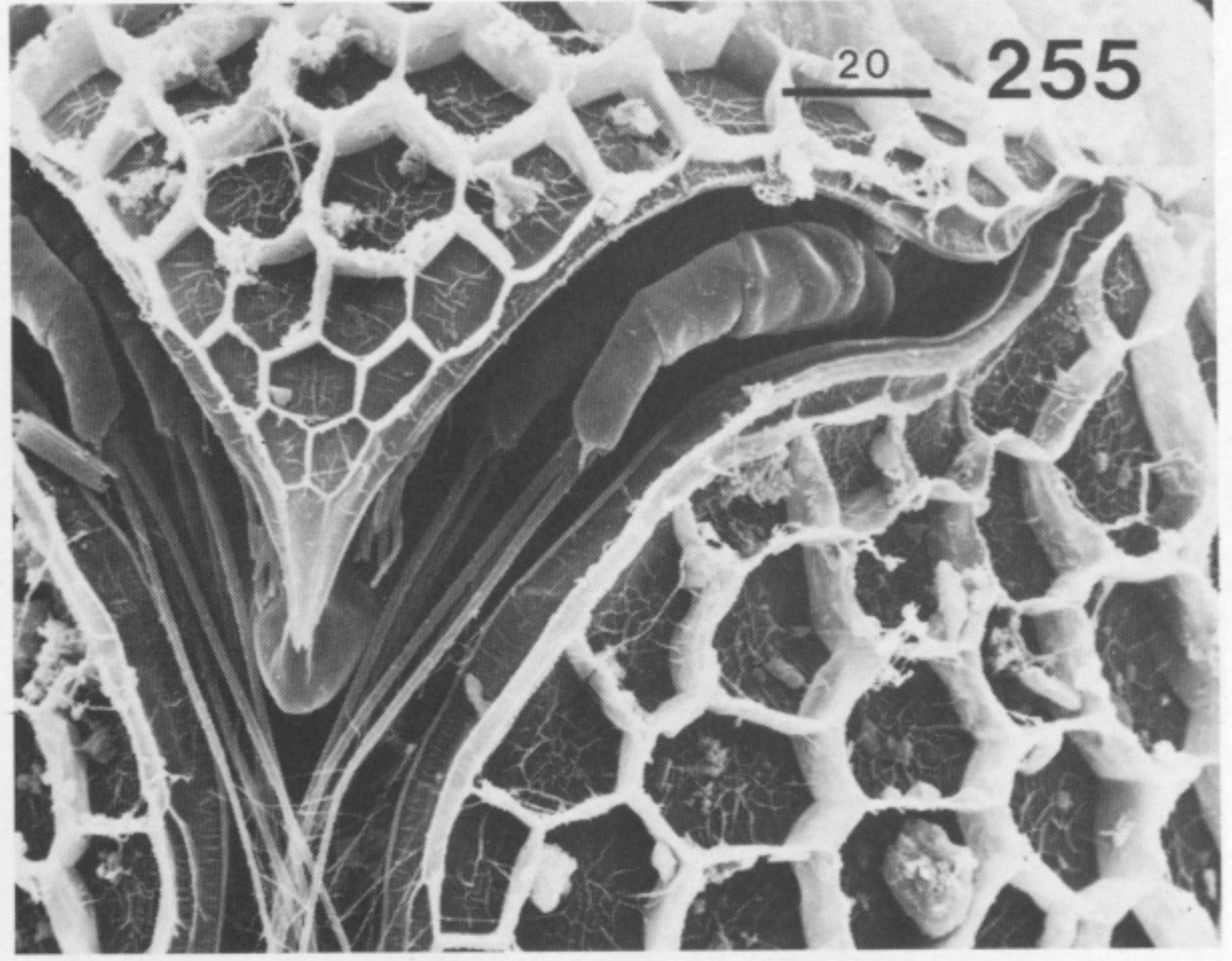
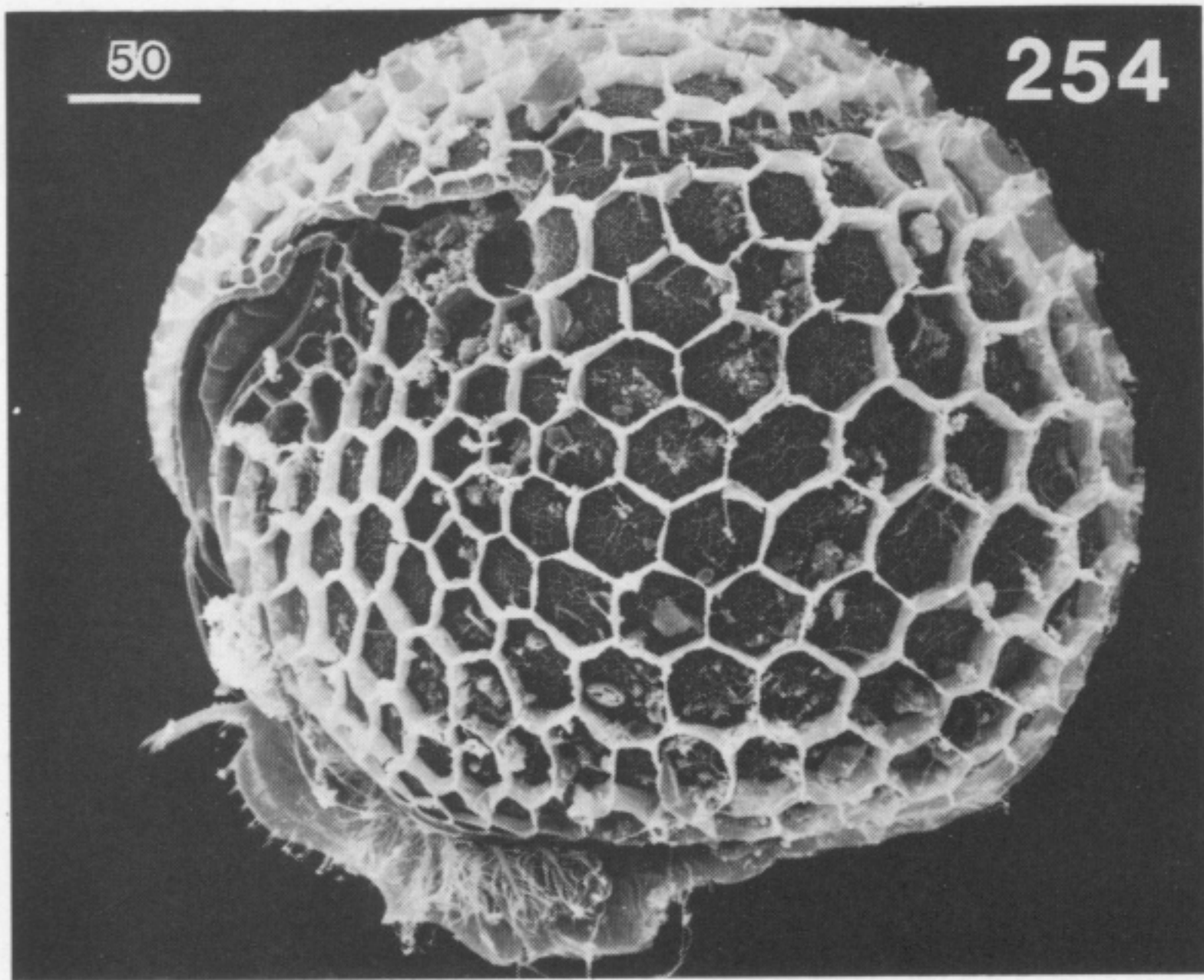
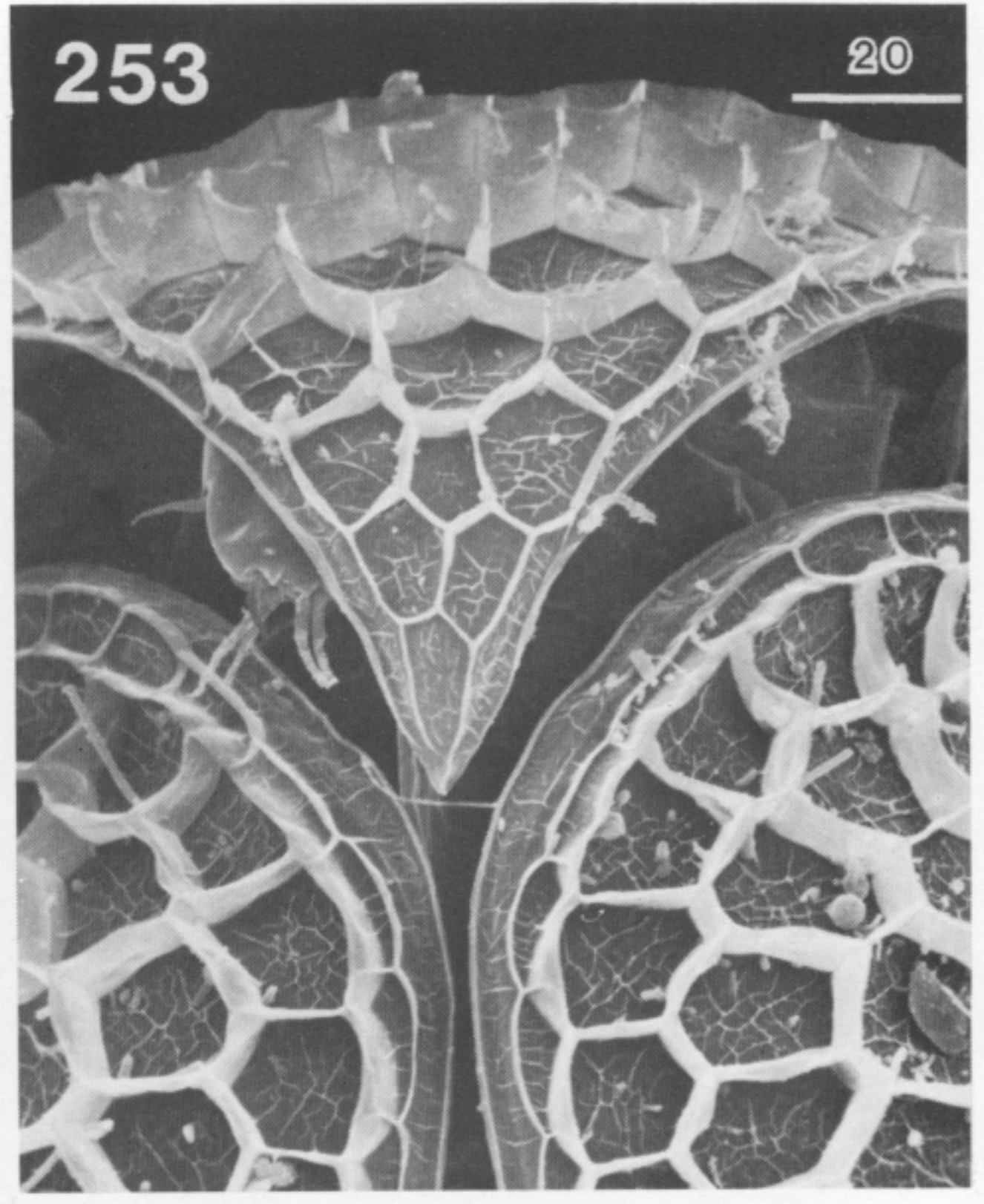
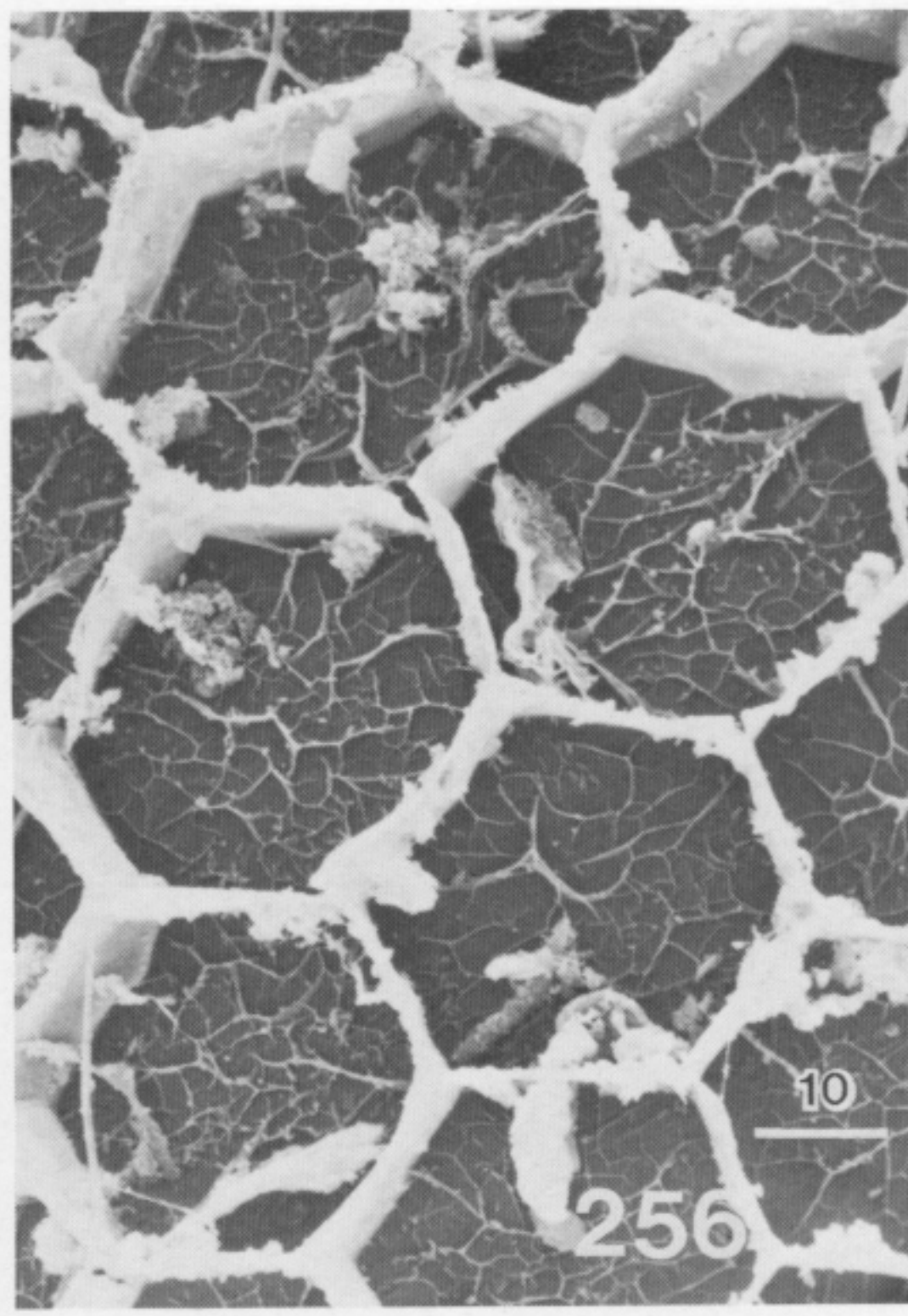
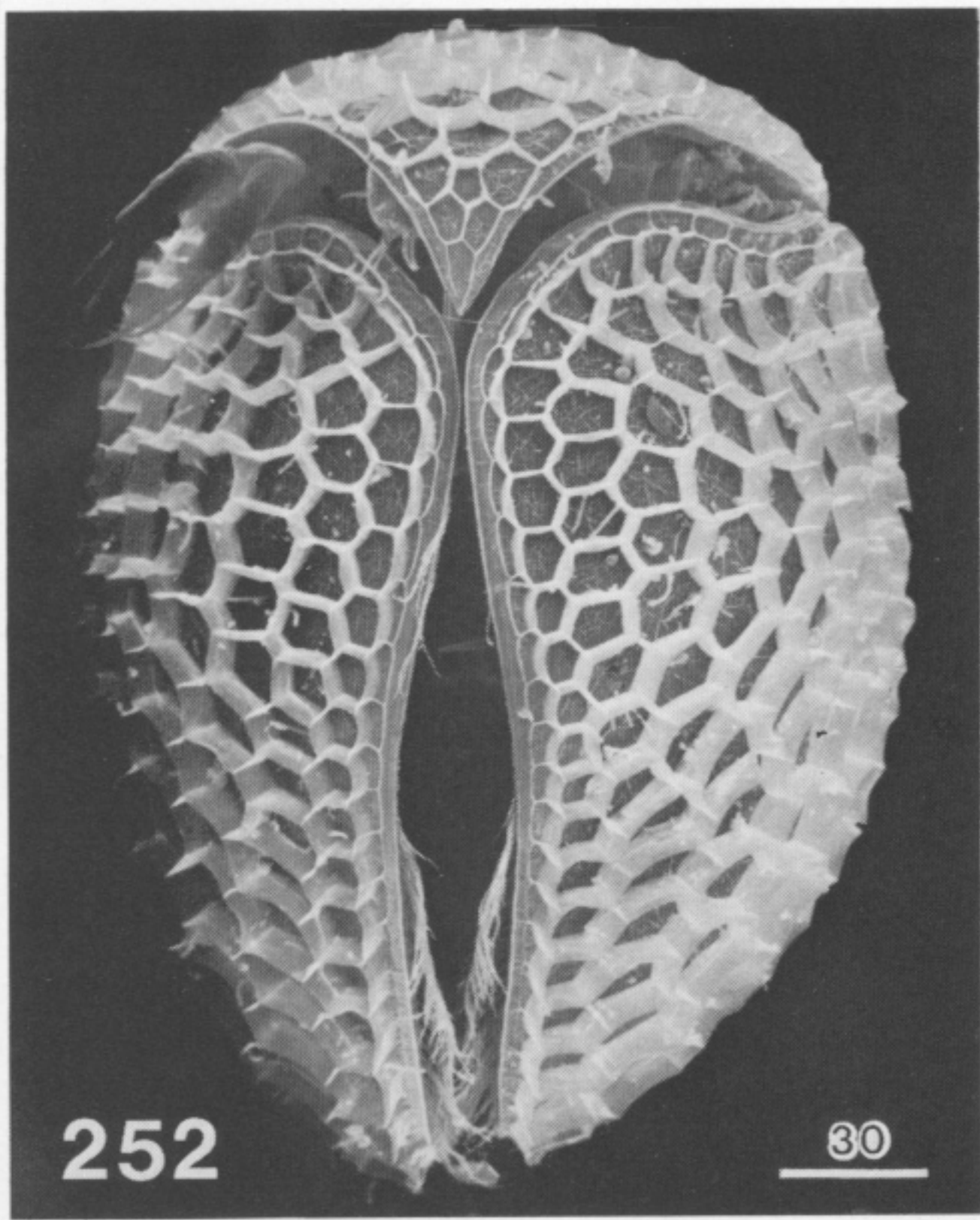
FIGURES 182-188. For description see p. 376.



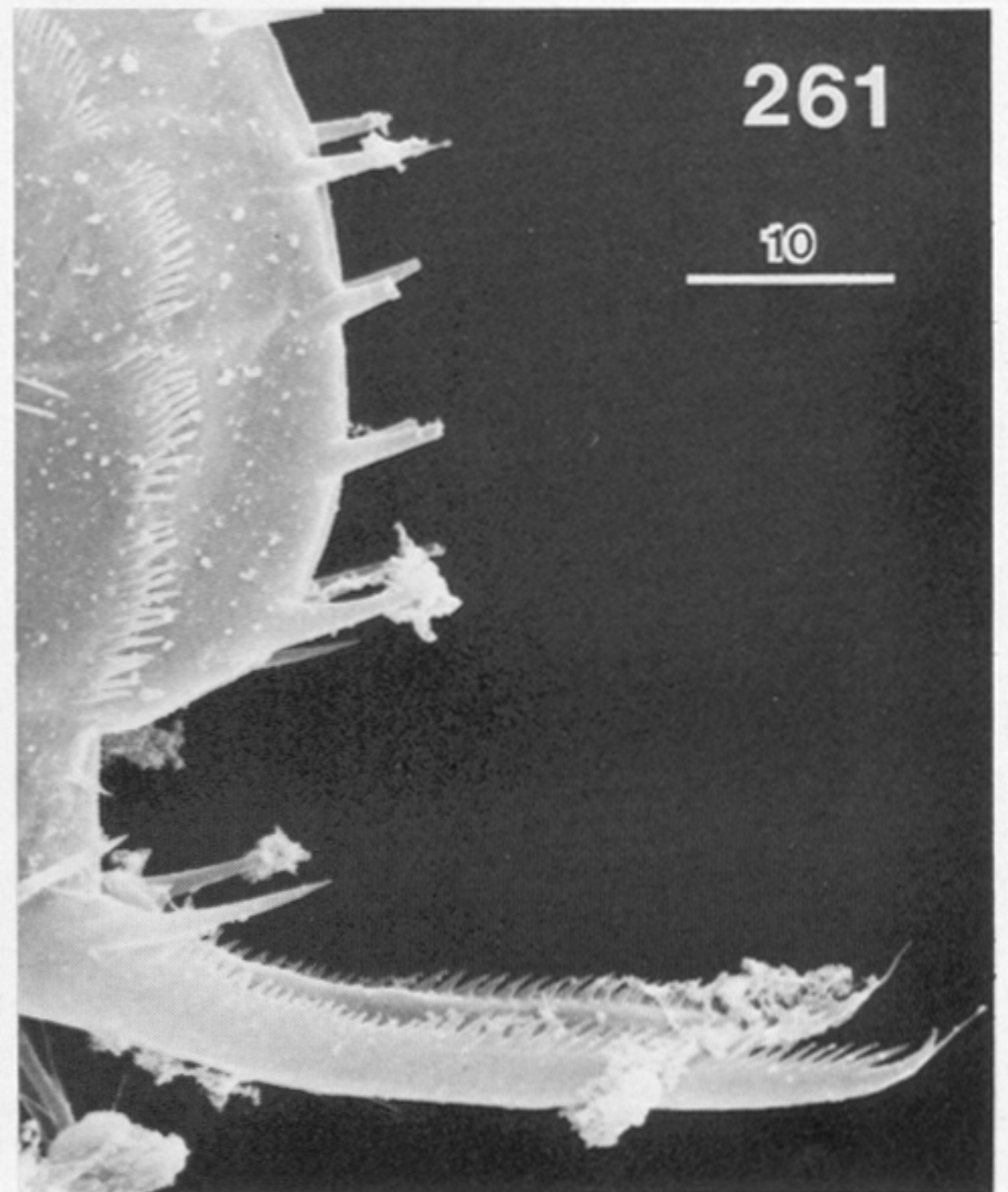
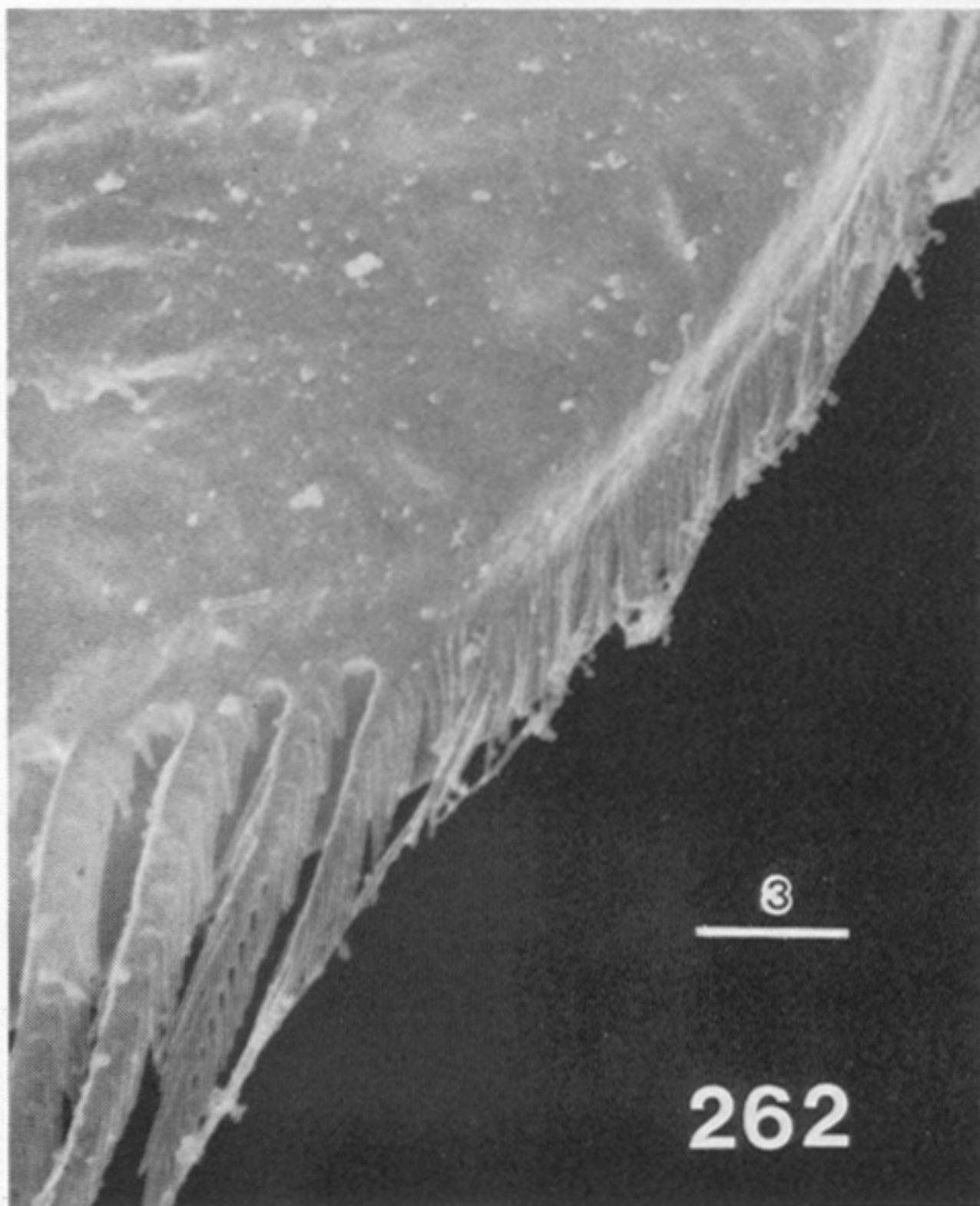
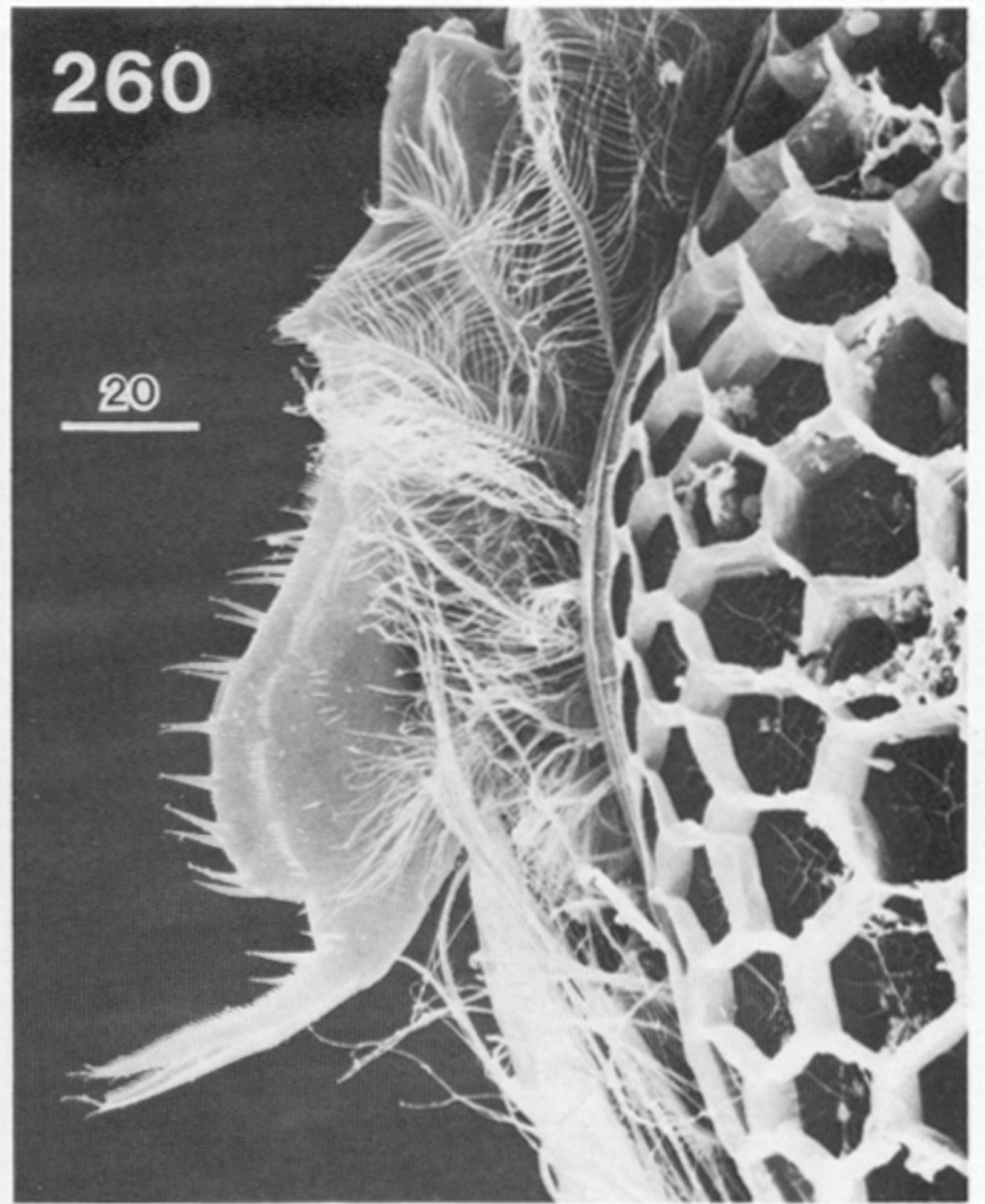
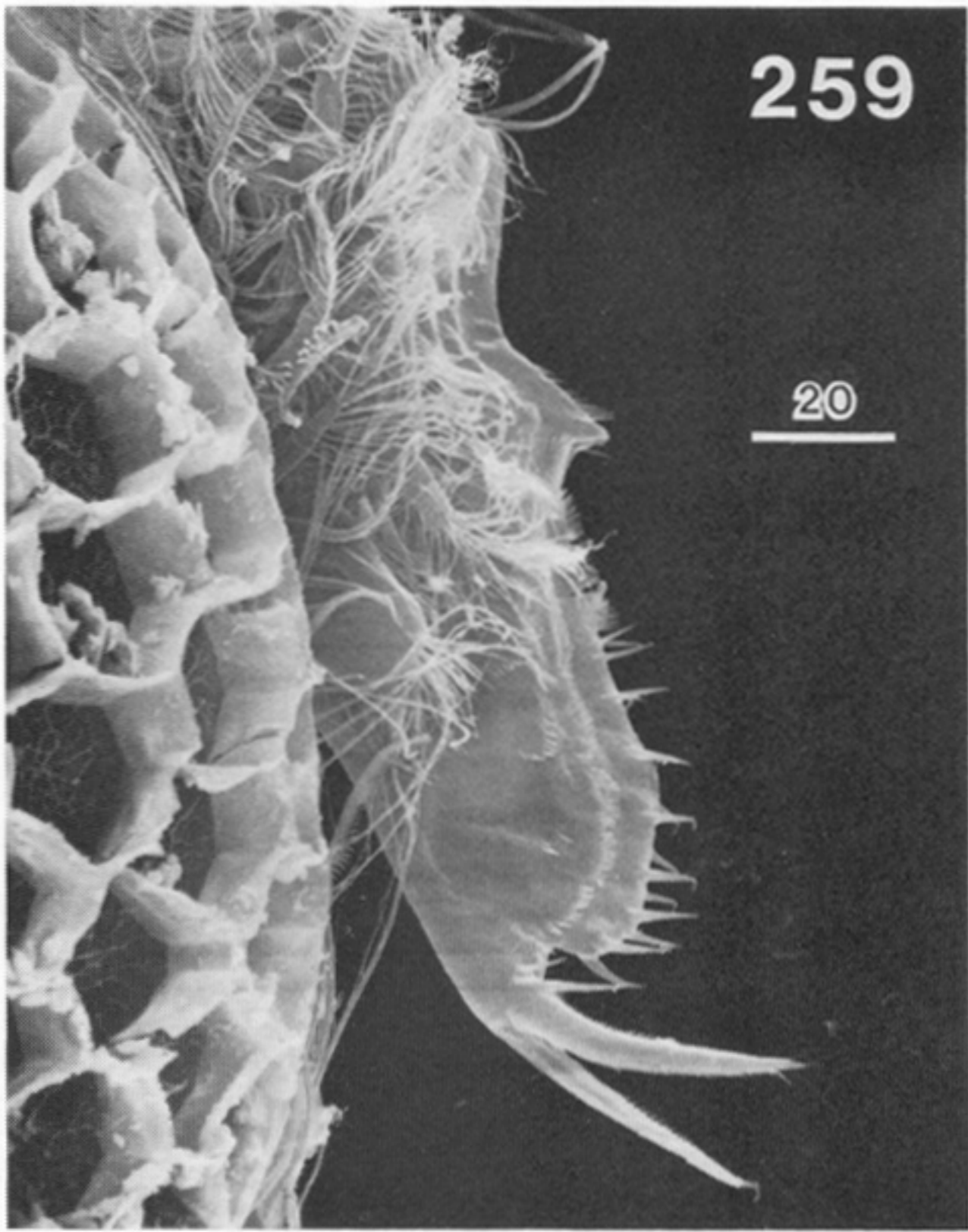
FIGURES 224-229. For description see p. 377.



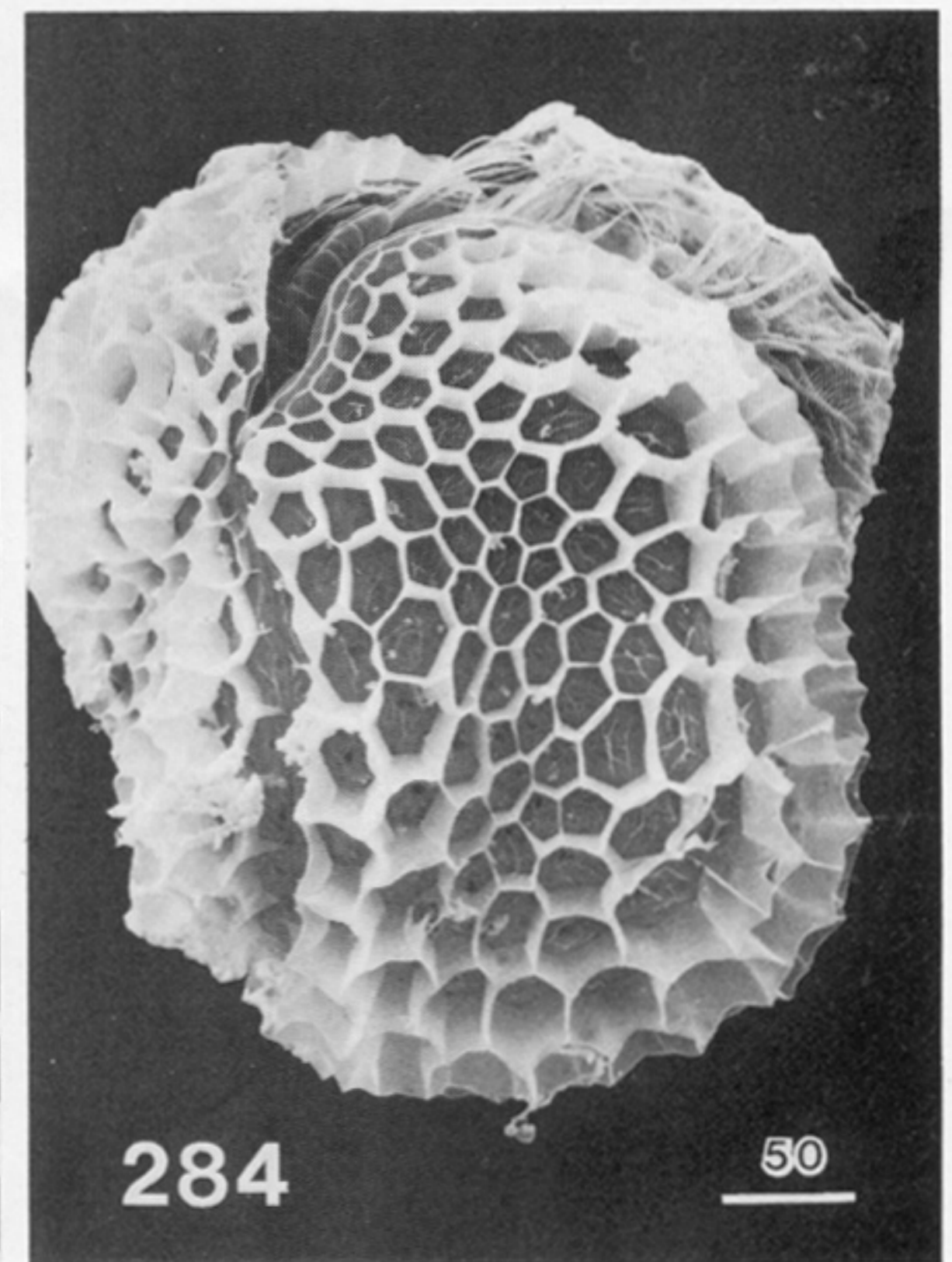
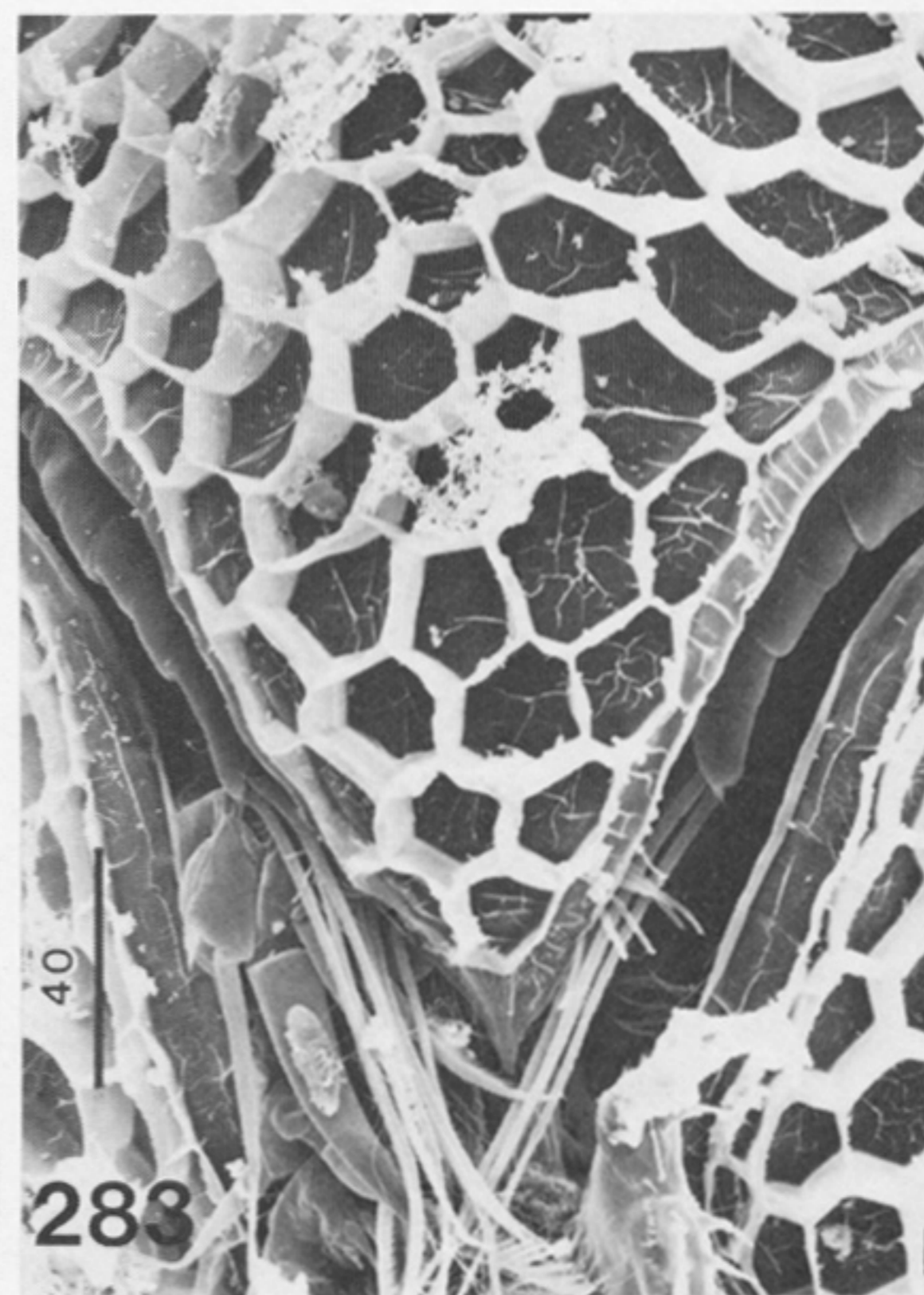
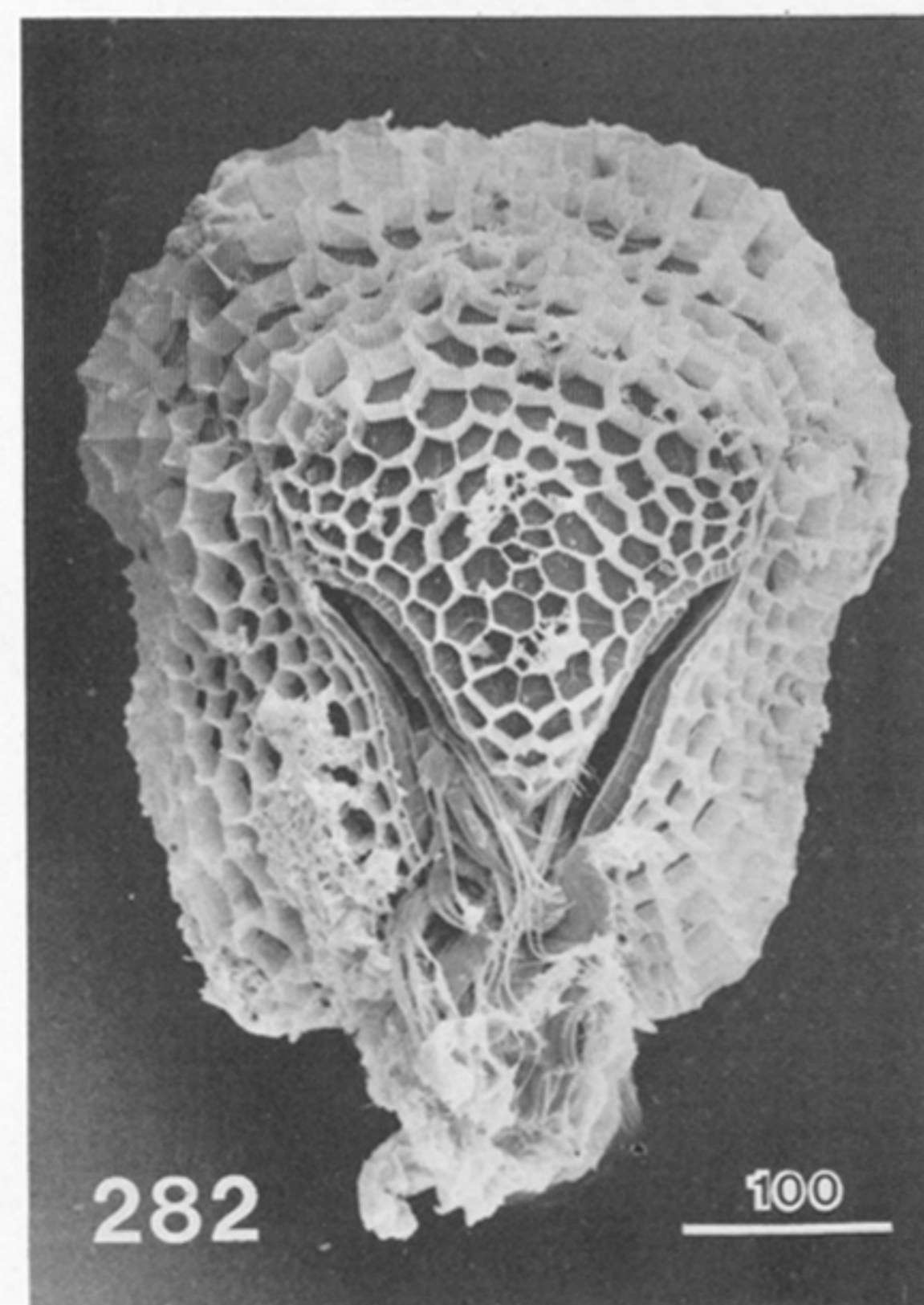
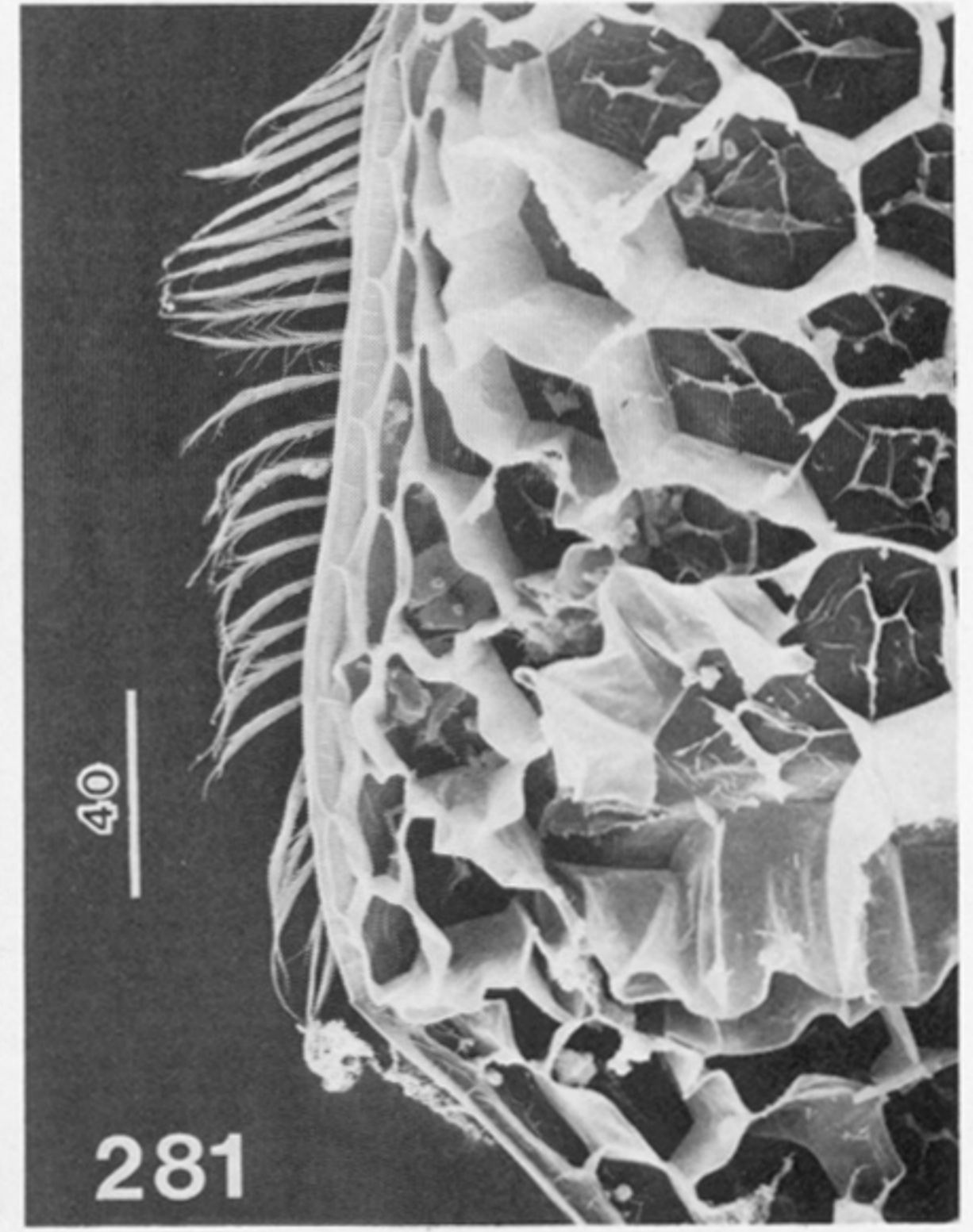
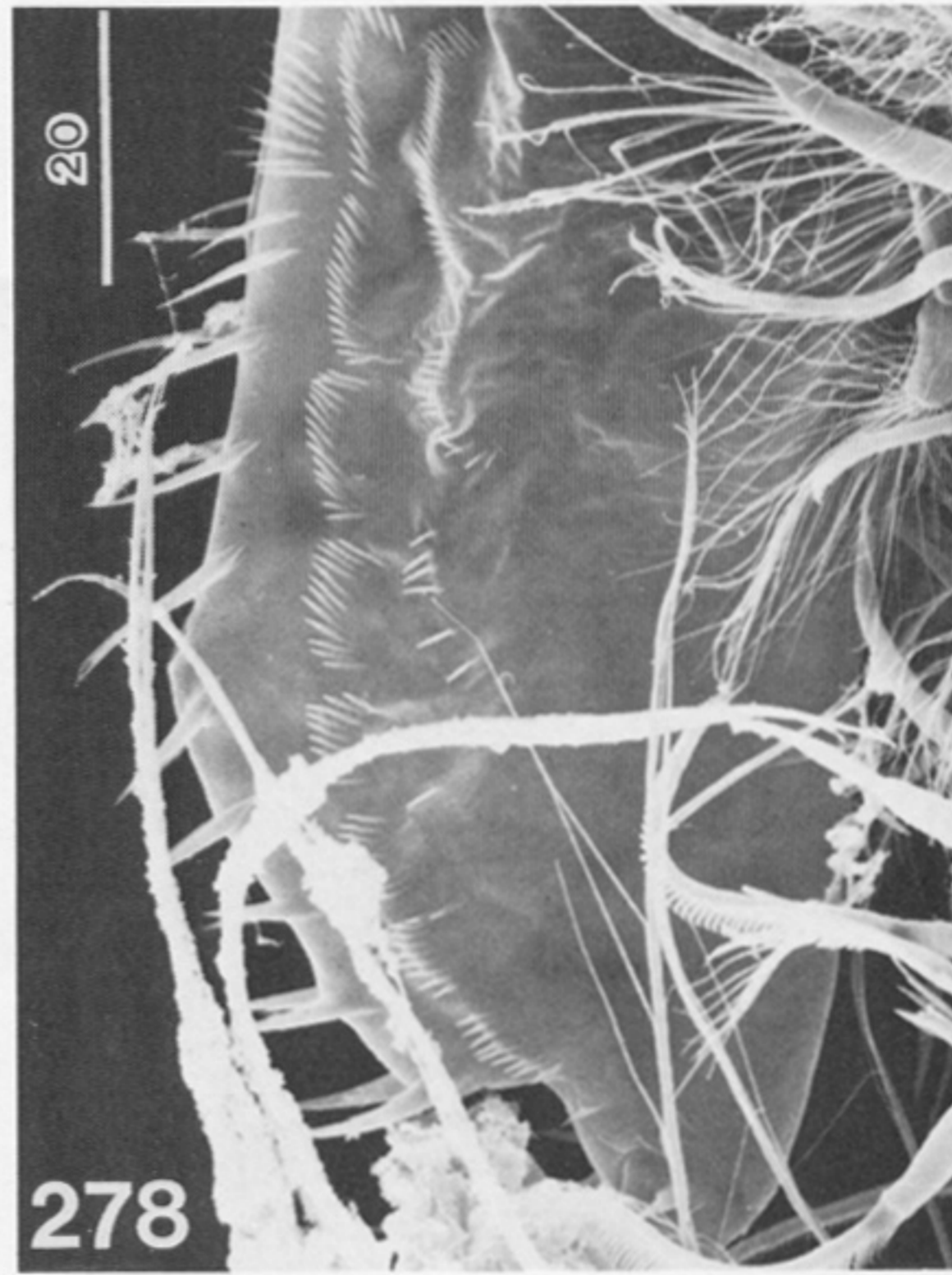
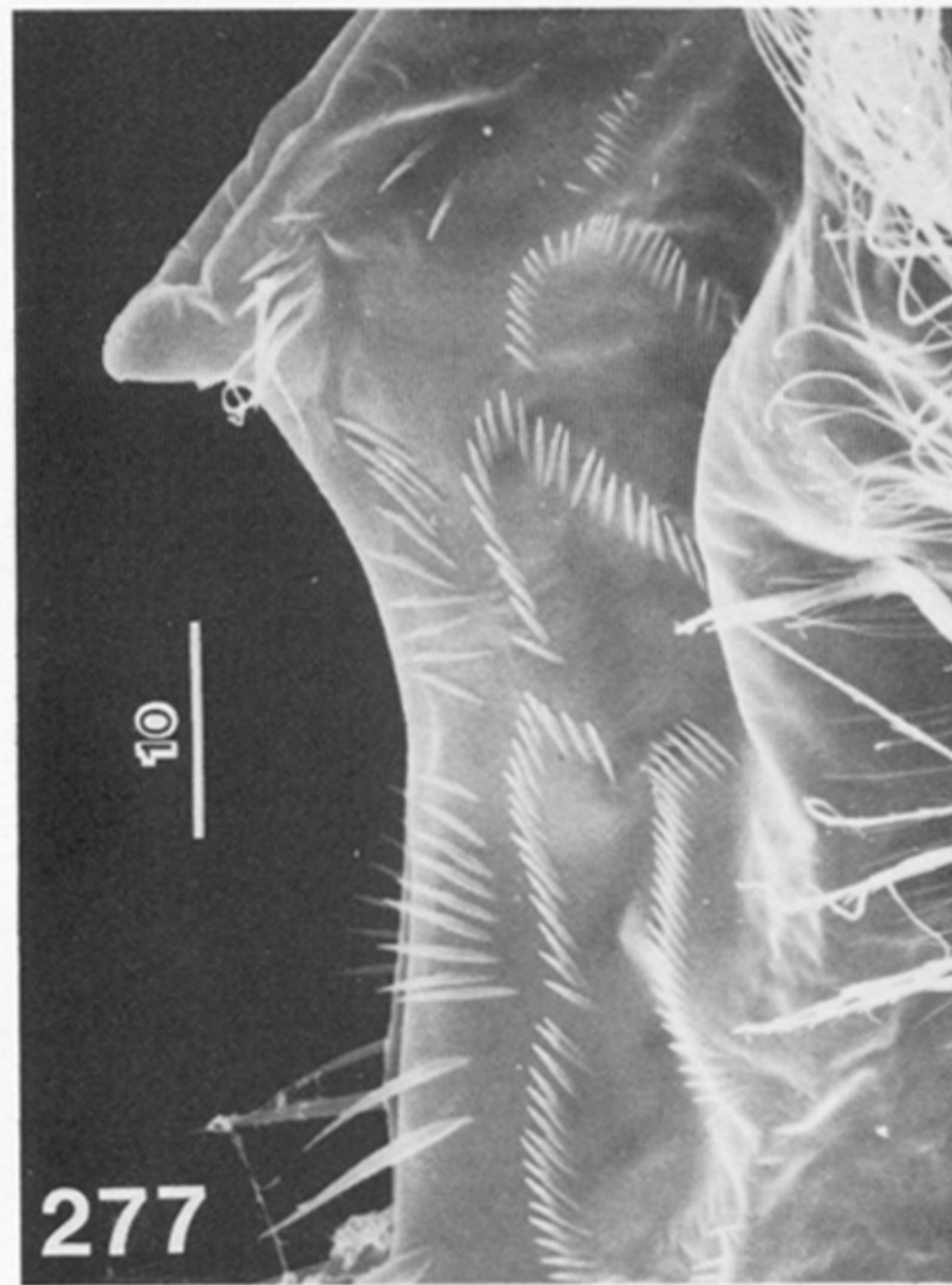
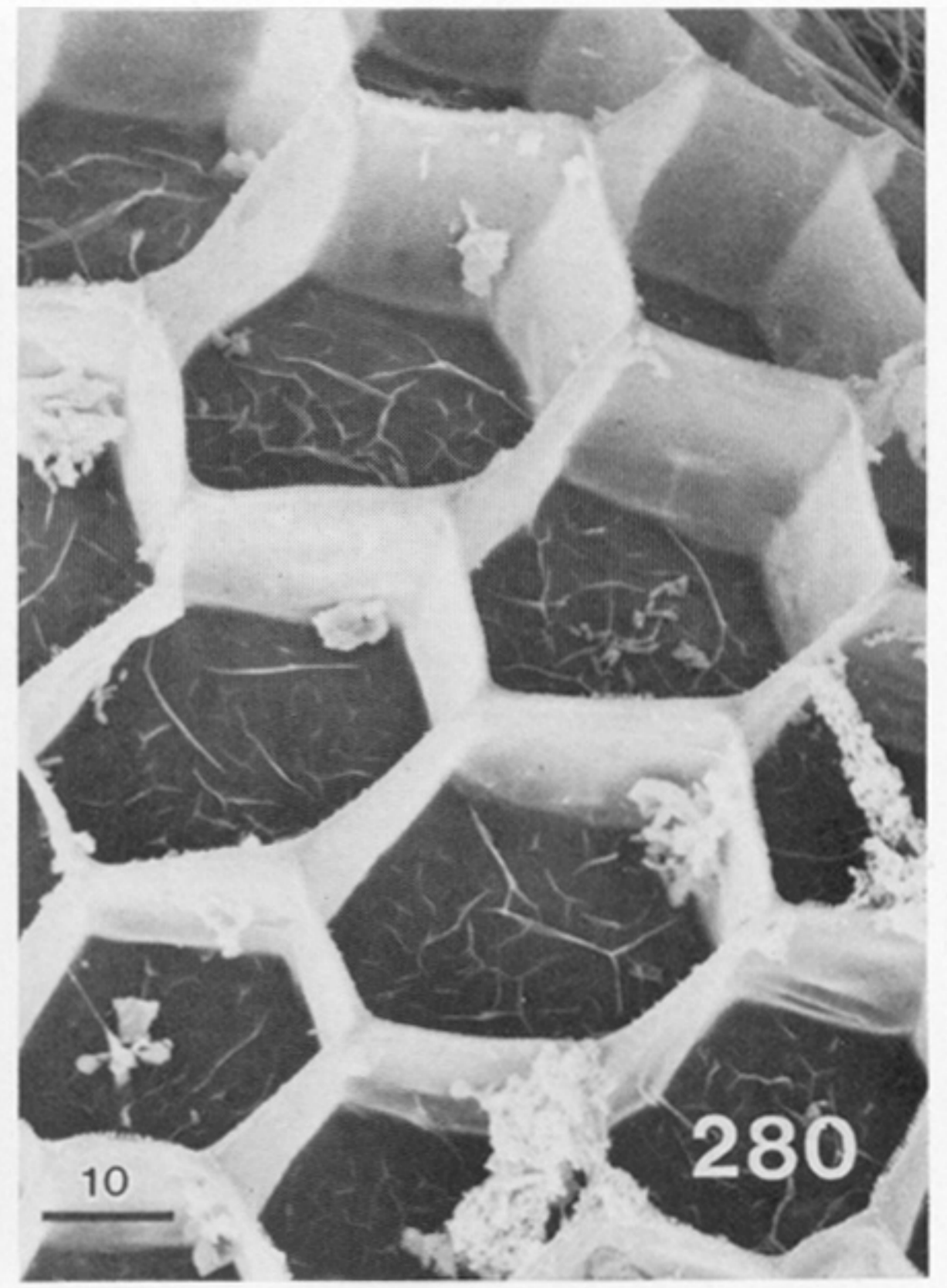
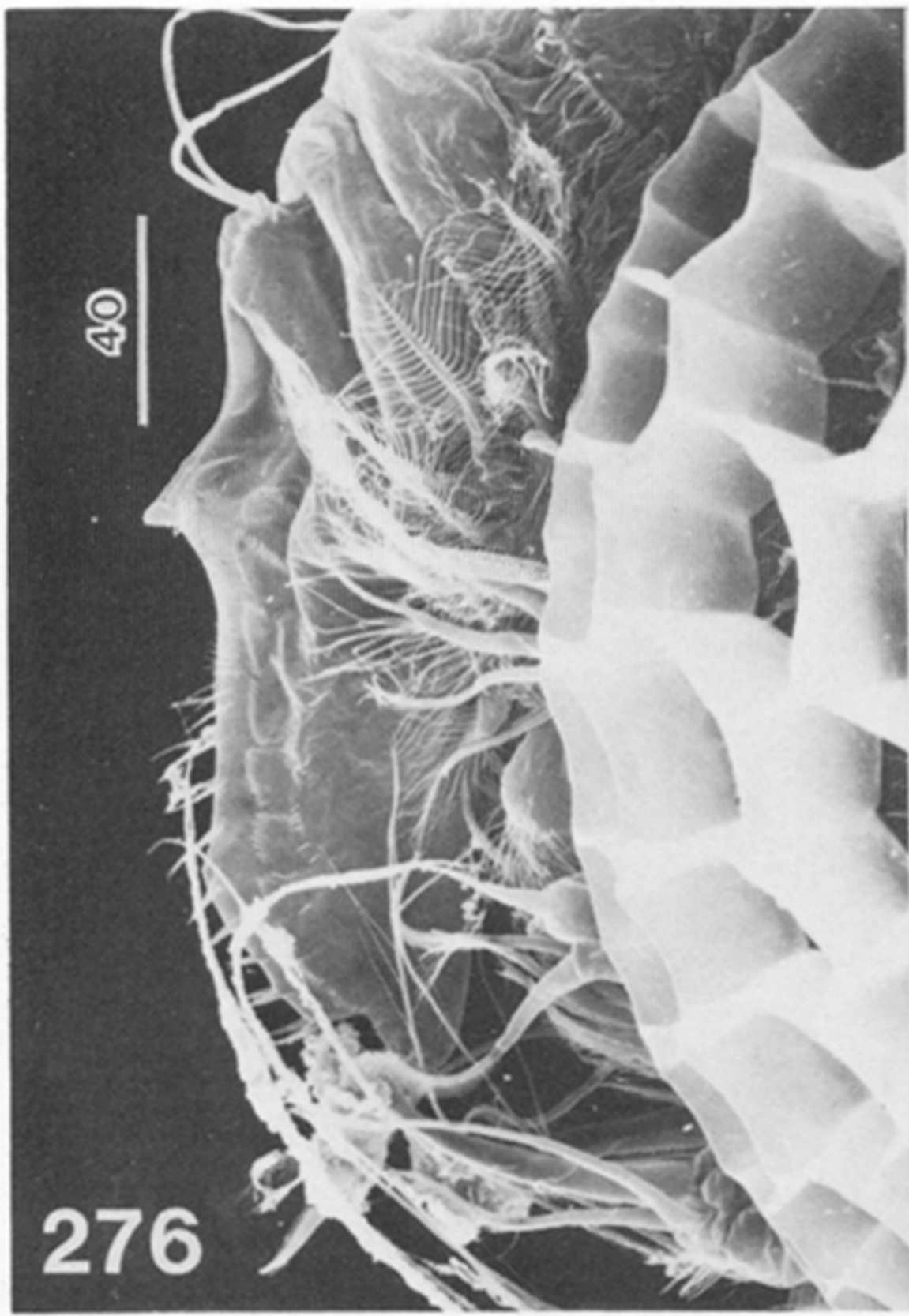
FIGURES 230-235. For description see p. 377.



FIGURES 252-258. For description see p. 377.



FIGURES 259–262. For description see opposite.



FIGURES 276-284. For description see opposite.