Assumed Amphi-Atlantic distribution of *Oxyurella tenuicaudis* (Cladocera, Chydoridae) denied by a new species from North America

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Abstract

Up to now the taxon *Oxyurella tenuicaudis*, described from Norway, has been claimed to occur in North America as well. However, our close study and comparison of populations from the two continents show them to be different in many major morphological details, involving principally the female and male postabdomens, labrum, headpore configuration, and the external sculpturing of the shell. The new species *O. brevicaudis* occurs from the Maritimes to Manitoba in southern Canada, southward throughout the region east of the Plains to Guatemala and possibly Panama. Two enigmatic outlier populations are known from the Northwest Territories and the State of Washington. A greater frequency of occurrence in the southeastern states compared with southern Canada, together with its extension of range into the Tropics, suggests that this taxon prefers the lower north temperate latitudes. Although widely distributed, its frequency of occurrence is very low.

Just as interesting as the characters that separate these two species are those that unite them into the cohesive genus *Oxyurella*. Although the few other species in the genus have not been studied in sufficient detail, fragmentary information suggests that they also conform to the pattern of commonality emerging from this study. These potential generic characters include: 1) only one seta on the outer distal lobe of trunklimb I and two on the inner distal lobe; 2) 4 median headpores not connected to one another by any channel or raised chitinous ridge, although the light microscope shows irregular dark thickenings around each pore and occasional connections between the three anterior pores; 3) antennules of the male being very similar to those of the female except for the 2-segmented male seta and the addition of one more aesthetascs at the tip, for a total of 10 compared with the typical number of 12 in chydorid males; 4) a significant reduction in size of the seta arising from the middle endopodite segment of the male antenna as compared with the female; 5) use of the entire shell as an ephippium, without any external modification but with an internal foam-like mass secreted (?) into the brood pouch around the egg.

Other populations outside western Europe claimed to be *O. tenuicaudis* need to be studied closely to evaluate their presumed conspecificity. Very likely at least some will be found to be different. As aids in this process of evaluation, besides specimens from Gjennestadvannet placed in various museums, including the Zoological Museum in Oslo, a lectotype has been selected and designated herein from among the few specimens mounted and studied by G. O. Sars.

Introduction

In some comments accompanying his brief published description of *Alona* (now *Oxyurella*) *tenuicaudis* in 1862, G. O. Sars stated that the structure of the postabdomen of this species, particularly the marginal denticles, is so characteristic that no other species could possibly be confused with it. At this

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beginning point in his career, Sars was concerned only with the Cladocera of western Europe, and even more narrowly with those occurring in the vicinity of Oslo (Frey 1982e). He could not know what other related species might occur elsewhere in the world, and hence he had no basis for judging the value of various characters in discriminating among them.

The taxon *Oxyurella tenuicaudis,* chiefly on the basis of these distinctive postabdominal features, has now been reported not only from throughout western Europe but also from various localities in Asia and other continents, including North America (see Smirnov 1971, for world distribution). However, our close study of populations on the two sides of the Atlantic Ocean demonstrate they are not the same. Accordingly, the taxon in North America is described herein as a new species, and the description of the taxon in Scandinavia is expanded to facilitate the comparisons that eventually will have to be made between it and populations of presumably the same species from other regions and continents. Through the use chiefly of gross characteristics, such as the postabdomen of *O. tenuicaudis,* in defining species, the concept has gradually evolved, but without any rigorous formulation of it, that many species of Cladocera are virtually cosmopolitan in distribution. However, nearly all the instances of claimed cosmopolitanism in the chydorids we have investigated to date are turning out to be instances of inadequate taxonomic resolution instead (Frey 1982c).

The present paper is part of a continuing program to ascertain what species of chydorid Cladocera occur in North America. For those taxa having names originating elsewhere, careful comparisons, as in the present study, must be made between North American populations and those from the regions of original description.

Materials and methods

For making comparisons of this kind one seeks large samples from single points in time and space containing all growth and reproductive stages. For *O. tenuicaudis* and its cognate taxon from North America, this objective was difficult to achieve, first because the taxa although widespread are infrequent in their occurrence, and second because the number of specimens in any sample tends to be very low.

For Scandinavia, many lakes in the vicinity of Oslo, including all those specifically mentioned by Sars (1862a, 1862b) were sampled by DGF in August 1965, and many lakes in Denmark were sampled over a 10-month period in 1971–1972. For North America extensive suites of samples are available in our collection from New York and New England, the southeastern States, particularly Florida, the lake districts of the northern tier of States in the Midwest, and one small lake near Bloomington. Canadian specimens derive from the many samples collected by R. Chengalath and B. J. Hann in the Canadian national parks. All samples were collected with a 15-cm wide conical net of 110 or 150 μm Nitex webbing protected by a hinged screen of brass hardware cloth to keep out large items of debris. By means of a 3-m sectional pole the net was worked vigorously in beds of aquatic macrophytes and over other kinds of substrate in the littoral zone. The samples were preserved in the field with concentrated formalin in a rough ratio of 1:15.

In the laboratory the samples were inventoried to determine the species present, their general abundance, and reproductive state. Samples positive for *Oxyurella* were subsequently examined systematically in a scored petri dish. All specimens and exuviae as encountered were removed to a mixture of glycerol and water in a depression slide for convenience of storage and subsequent study. Temporary mounts of whole specimens in glycerol were used for length measurements and for drawings of intact animals and some of their parts. Where available, exuviae were dissected with tungsten needles for trunk limbs, postabdomens and claws, antennules, antennae, headshields, and other components. Where no exuviae were available, whole specimens were dissected, usually with less satisfactory results.

All camera lucida drawings were made with a Wild M20 compound microscope provided with phase-contrast optics. The scanning electron micrographs were made with an ETEC Autoscan at 20 kv accelerating voltage. The specimens were dehydrated in alcohol, then critically dried, and sputter coated with gold-palladium.

***Oxyurella tenuicaudis* (G. O. Sars, 1862)**

Brief annotated synonymy

Camptocerus alonoides Schoedler, 1858: 27. Name only mentioned, unaccompanied by any illustrations or description; hence a *nomen nudum.*

Alona tenuirostris G. O. Sars, 1862: 285–286, no Figs. Sars presented this paper before the Science Society of Christiania on 29 November 1861. The Proceedings of the Society for 1861 were published early in 1862 (see Frey 1982e).

Alona camptocercoides Schoedler, 1862: 24, Pl. 1, Figs. 8–10. Contains only figures. Lists *Camptocercus alonoides* as a synonym. This paper was published for a public examination of Schoedler on 23 September 1862, and hence considerably later than Sars' description of *tenuicaudis,* which therefore has priority.

Alona camptocercoides Schoedler, 1863: 24–25, Pl. 1, Figs. 8–10. Contains the same illustrations as in the previous paper but in addition now has a written description.

Oxyurella tenuicaudis (Sars): Dybowski and Grochowski 1894: 381. In a key to the genera of Cladocera in the vicinity of Lemberg (Lwów), then in Poland, the authors erected this genus specifically for the *Alona tenuicaudis* of Sars. They give no formal description of the genus beyond the few characters used in the key, chief of which is the narrowing of the postabdomen toward the base of the claws.

Euryalona tenuicaudis (Sars): Daday 1905: 178–179, Pl. 11, Figs. 12 & 13. Unaware of the paper by Dybowski and Grochowski, Daday transferred this taxon to Sars' (1901) genus *Euryalona.* However, Daday's paper really should not be included in the synonymy of *tenuicaudis,* as the taxon from Paraguay he listed under this name was subsequently described by Birge (1910) as *Odontalona longicaudis.*

Odontalona tenuicaudis (Sars): Birge 1910: 1045–1048, Pl. 71, Figs. 5 & 6. Likewise unaware of the paper by Dybowski and Grochowski, Birge erected the genus *Odontalona* for the *tenuicaudis* of Sars and his new species *longicaudis.*

A full synonymy, including references to *O. tenuicaudis* in other parts of the world, is not presented here because of questions concerning conspecificity, although it seems reasonable that what is called *O. tenuicaudis* in western Europe is a single taxon. Anyone interested in a more detailed synonymy should consult Smirnov (1971) and Flössner (1972).

Material available

The problem with *O. tenuicaudis,* as likewise with all but one of the other 51 taxa of Cladocera G. O. Sars described from Norway (Frey 1982e), is that the brief Latin description he published is unaccompanied by any illustrations, and Sars himself did not designate any type specimen. The only supplementary materials available are the following:

a) In the Zoological Museum of the University of Oslo:

1. Slide F9037: 2 specimens in balsam. No locality or date.

Lectotype: One of these specimens was tentatively selected by DGF as a lectotype in 1965 and is herewith officially designated as the lectotype. It is the larger specimen, toward the upper right corner – a parthenogenetic female .56 mm long, which shows many of the essential details of morphology quite clearly. For the 52 species of Cladocera Sars described from Norway, there are few specimens in the Zoological Museum in Oslo that can be ascribed positively to the collections or specimens he used in preparing the descriptions (Frey 1982e). Sars preferred to work with live specimens, from which he prepared detailed camera lucida drawings and then painted them to approximate their appearance in life. He seldom saved and curated these specimens. But as he collected mainly in the close vicinity of Oslo, as revealed by his diary, any specimens extant are likely from this general region and hence likely candidates for designation as lectotypes. In his description of *Alona tenuicaudis,* Sars merely states that he collected this species in two small ponds near Oslo, without actually specifying which particular ones.

2. Slide F9038: 12 specimens, including 2 males, in glycerine jelly. Dried out. No locality or date.

3. Liquid sample F12420, labelled '*Alona tenuicaudis* G. O. Sars,' in a bottle labelled 'Crustacea Norv./Cladocera/5324.09/det. G.O.S.' This tube originally contained 55 specimens, including 13 males, of which 2 females and 2 males were transferred to the collection in Bloomington some years ago.

b) In the Sars Archive, Department of Manuscripts

in the University of Oslo Library:
1. Cat. Entry No. 613 is a prize-winning unpublished manuscript (see Sars 1861 in bibliography for a complete citation), which contains an expanded description of *tenuicaudis* and 5 illustrations.
2. Cat. Entry No. 152 is a series of colored portraits of Cladocera, including a female and a male of *tenuicaudis* from Moss (not dated), and a female from 'Dam ved Lille Frøn' collected 7 July 1883.
3. Cat. Entry No. 468 is a series of notebooks, and compilations, two of which contain records of *tenuicaudis* collected near Oslo. Item 5 has the entry 'Frognerdammen (nedre) Juni 89', and Item 58 'Skaerhalden (Hvalöerne)--i sumpige Damme v. af Praestegaarden,' male and female, dated 1883.

Of our 91 samples from southern Norway, the following yielded specimens of *O. tenuicaudis* (for each locality, the numbers in parentheses are the accession numbers of the samples in our collection in Bloomington): Holmendammen, 4 Aug. (1605–06); Bogstadvannet, 7 Aug. (1619–20); Östensjövannet, 8 Aug. (1644); Vannsjö at Dillingöya, 12 Aug. (1660); Ulvenvannet at Engelsrud, 15 Aug. (1675); roadside channel near Horten, 15 Aug. (1678); Gjennestadvannet, 15 Aug. (1682); Goksö, 15 Aug. (1684). As none of these samples contained any mature ephippial females, two samples from Denmark were used for this reproductive stage: Teglgårsø in Hillerød, 19 Oct. 1971 (2993); Store Følstrup Dam near Hillerød, 20 Oct. 1971 (2997).

Sars' description of the species

The brief Latin description by Sars (1862b) is based on that given in his unpublished manuscript of 1861 and differs from it only in some minor details. Hence, a free translation of the published description is given below:

> Somewhat resembles *Alona quadrangularis*, but the rostrum is shorter, blunter, and less erect. Shell with indistinct longitudinal striae; subquadrangular in lateral view; dorsal margin weakly arched, posterior margin truncate, ventral margin almost straight. Antennules short and stout. Lower branch of antennae with 5 [swimming] setae. Postabdomen long and narrow, the posterior [dorsal] margin almost straight, armed on both sides with 18–20 denticles, of which those attached to the distal end are distinguished by their unusual length. Postabdominal claws slender, provided with a long basal spine. Ocellus smaller than the eye, located about midway between it and the tip of the rostrum. Color somewhat tawny [yellowish hyaline]. Length about 0.5 mm.

Sars' expanded description in Norwegian in his unpublished manuscript gives a number of additional points:

1. The dorsal margin of the animal from the tip of the rostrum backward is evenly curved and slopes down only slightly posteriorly, whereby the body height is greatest behind the middle. [This is one of the chief resemblances to *Alona quadrangularis*.]
2. The lower margin of the shell is almost straight, or at best weakly convex in front of the middle. It and the anterior margin are provided along their entire length with short setae.
3. The indistinct longitudinal striae are visible almost exclusively toward the posterior portion of the shell.
4. The tips of the antennules barely reach half way toward the tip of the rostrum [from the ocellus].
5. Both branches of the antennae are about the same length, and in both the basal segment is about as long as the other two segments combined.
6. Of the five swimming setae on the lower branch [endopodite] of the antenna, the one arising from the basal segment is much shorter than the others.
7. The ventral margin of the labral keel is strongly curved, and passes into the posterior margin with scarcely a change in curvature.
8. The basal spine on the postabdominal claw is about half as long as the claw.

A description combining the published and unpublished statement is reasonable as far as it goes, except for two features – the claimed resemblance in shape to *Alona quadrangularis*, and the number of marginal denticles on the postabdomen.

The claimed resemblance to *A. quadrangularis* is not supported by the specimens in the Sars collection nor by his several paintings subsequent to the original manuscript. The colored drawing on Plate 98 of the unpublished manuscript does indeed show the dorsal margin sloping downward only slightly posteriorly and the posterior–ventral angle rather narrowly rounded. But his later painting of *tenuicaudis* from the pond near Lille Frøn has a more evenly arched dorsal margin, with the maximum body height about in the middle, and the posterior-ventral angle is more broadly rounded. Immediately to the left on this plate is a painting of *Alona quadrangularis* from Östensjövannet, which is not at all similar in shape to the adjacent *tenuicaudis*. Sars' paintings of the male and female *tenuicaudis* from Moss likewise have a more evenly curved dorsal margin, quite unlike that of *A. quadrangularis*. Also, none of the major works on European Cladocera with original drawings (e.g. Hellich 1877; Lilljeborg 1901; Šrámek-Hušek *et al.* 1962; Smirnov 1971; Flössner 1972) show this shape. However, among the 70-odd specimens in our sample from Östensjövannet (1644), the largest reproductive females approach the shape described by Sars and illustrated in his unpublished manuscript as to the curvature of the dorsal margin and the relatively sharp posterior-ventral angle. Smaller reproductive females in the same sample, on the other hand, tend to have the dorsal margin more evenly rounded and bending downward posteriorly (as in Sars' other paintings), and the posterior-ventral angle more broadly rounded. Thus, this character, like so many others in the chydorids, can change progressively and appreciably with size of individuals, and hence any critical description must take cognizance of these changes.

Regarding the number of marginal denticles Sars claimed to be present on the postabdomen, P. E. Müller (1867) was concerned, because his specimens never had more than 14. As explained later in this paper, there are 13–15, occasionally 16, postanal denticles, of which those in positions 11–14 counting from the distal end are occasionally double. In addition, the anal groove is bordered by a few (generally 1–3) very small denticles on either side. Even counting all these entities separately yields totals only of 14–18. Lilljeborg (1901) gives a more acceptable range of 10–20 denticles, although 20 still seems unrealistically large and 10 too small. Subsequent authors mostly have quoted the range given by Lilljeborg.

Lilljeborg's description of the species

Of the various taxonomic treatments of Cladocera in western Europe, Lilljeborg's (1901) has the most detailed description of *tenuicaudis*, including the first description of the mature male. Subsequent authors have tended to rely heavily on Lilljeborg, even to the extent of copying his illustrations. Hence, a summary of Lilljeborg's expanded diagnosis is given below as a guide for preparing a more definitive description.

Female. Length about 0.6 mm. Almost oval in lateral view, not appreciably lower toward the front, both posterior angles rounded. Ventral margin of shell most commonly weakly concave in middle and a little convex anteriorly; at times almost straight. Posterior margin more or less convex, provided with a submarginal row of fine, short setules. Posterior–ventral angle without any trace of a tooth or spine but provided instead with relatively long setae closely spaced. Seen from above, the body is strongly compressed from side to side and narrows posteriorly; it completely lacks a keel on the shell and head. Shell sculpturing variable, most commonly with weak longitudinal striae, at least in the posterior portion, and occasionally with some cross striae; sometimes without any distinguishable pattern. Head relatively large, strongly bent downward; the relatively long and moderately pointed rostrum is vertical. Eye small and only a little larger than ocellus, which is located about halfway between eye and tip of rostrum. Labral keel large, almost rhomboidal or hatchet-shaped, with rounded or very blunt angles. Antennule short, stout, somewhat crooked; on posterior side somewhat distad from middle is the [typical] antennular seta plus one subapical aesthetasc[1]; two of the terminal aesthetascs are longer than the others. Antennae short, with 8 swimming setae, of which the one arising from the basal segment of the inner branch [endopodite] is the smallest, although it still projects beyond the tip of the branch. Postabdomen elongate, somewhat tapered distally, with a sharply projecting pre-anal angle; postanal margin straight or weakly concave, provided with two rows of 10–20 marginal denticles, mostly delicate, but with the distalmost 3–5 pairs strongly increasing in size distad and much larger than the others; distad from these large denticles is a much smaller one. Color more or less bright brownish yellow.

Male. Length 0.42–0.44 mm. In lateral view differs from female as follows: posterior margin is transversely rounded behind; anterior ascending part of ventral margin is strongly concave; rostrum is shorter and blunter; eye is relatively larger than in the female and considerably larger than ocellus;

antennules stouter, but as in female they do not reach tip of rostrum. Antennules have a segmented seta arising from anterior edge distad from middle, and posteriorly an aesthetasc, likewise distad from middle. Postabdomen lacks marginal denticles, but has at distal end on each side two tubercles or knobs provided with delicate setules, as well as on each side a submarginal row of rudimentary fascicles of very fine setules; narrowed distal tip that bears the claw and is set off from rest of postabdomen has a single relatively long and slender spine distad from the two tubercles, and has the genital pores located ventrally near or just anterior to the base of this distal portion. Postabdominal claw similar to female, but smaller. Color generally darker than in female.

Lilljeborg found this species in several, mostly small, waterbodies. Usually only scattered specimens were recovered, although in one small marsh near Malma the species was at times abundant. Lilljeborg also noted a number of instances where *tenuicaudis* had been collected in brackish water. He found males occasionally in the vicinity of Uppsala from the end of August into September and October.

Expanded description

This expanded description is based chiefly on the large series of specimens, including males, from Gjennestadvannet (sample 1682), which is located near Tönsberg on the west side of Oslofjord. Close comparison of this population with other nearby populations, such as those from Östensjövannet (1644) and Holmendammen (1605–06), revealed no significant differences, suggesting thereby that the various populations in the Oslofjord region constitute a single taxonomic entity.

a) Parthenogenetic female

General shape (Plate 1.1). Length about 1.6 times maximum height. Dorsal margin quite uniformly curved from posterior–dorsal angle to compound eye, more sharply curved from there to tip of rostrum; downward curvature of dorsum less in posterior half because of high posterior-dorsal angle; very large specimens can resemble *Alona quadrangularis* in shape by having maximum height behind the middle (Plate 1:2). Posterior margin rather weakly and evenly convex; posterior–dorsal angle only a little farther forward than posterior–ventral angle, giving the animal a somewhat truncated appearance, especially in very large specimens; posterior-dorsal and posterior–ventral angles quite broadly rounded; posterior–ventral angle sometimes more narrowly curved in large specimens. Ventral margin almost straight, or slightly convex in front of ventral bulge. Body markedly flattened from side to side (Plate 2:2 & 3); entire dorsum transversely rounded, with no hint of a keel on head

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[1] Lack of agreement in naming these structures has created confusion in the literature on Cladocera. One of us (DGF) has consistently used the term olfactory setae, but this is inappropriate for two reasons: 1) the sensory function of these structures has been claimed variously to be chemoreception, touch, and even audition, but as no unequivocal demonstration of function has been made, calling them olfactory prejudges the outcome and even then may be only partially correct; 2) they are scarcely setae in the usual sense, but rather thin-walled, soft, bladder-like structures, having a dark granule (or annulus) at or near the tip (which enables certain identification of these structures) and a refractile body at the base embedded in the antennule, each such body being innervated to a ganglion in the antennule (Scourfield 1896). At least since the beginning of this century these structures have most commonly been named olfactory setae in English-language publications. Birge (1918) and Brooks (1959) used this term, with Birge using also the not inappropriate synonym sense-rods and Brooks sense-hairs. Complicating the issue is the use of the term Tastborste for the lateral seta of different morphology (called antennular seta in the present paper) by Herbst (1962), Flössner (1972), and others. Lilljeborg (1901) himself used the expression cylindrical papillae or sensory papillae for the terminal structures, and the latter term is now rather common in the Continental literature (e.g. Sinnespapillen in Flössner 1972, and chuvstvitel'nyye papilly in Smirnov 1971). But papilla in the English language refers most commonly to a small nipple-like projection, not to the more analogous elongate nipples or teats of a cow's udder, and hence is not too appropriate.

The term aesthetasc (of Greek origin, literally meaning a sensitive, or sensory, bag) has been in the literature for some time as a designation for the various thin-walled presumably chemoreceptors occurring mostly on the antennules and antennae in various groups of Crustacea (Barber 1961). Herbst (1962) quite certainly prefers this term over Riechstäbchen (still another synonym), and so do we. In his book on the Chydoridae of the World, Smirnov (1971) is inconsistent, using aesthetascs and the Russian equivalent of sensory papillae quite interchangeably. The term should not be shortened to aesthete, as Wilson (1959) has done for the copepods, as this term has been used for quite different sensory structures in the Amphineura.

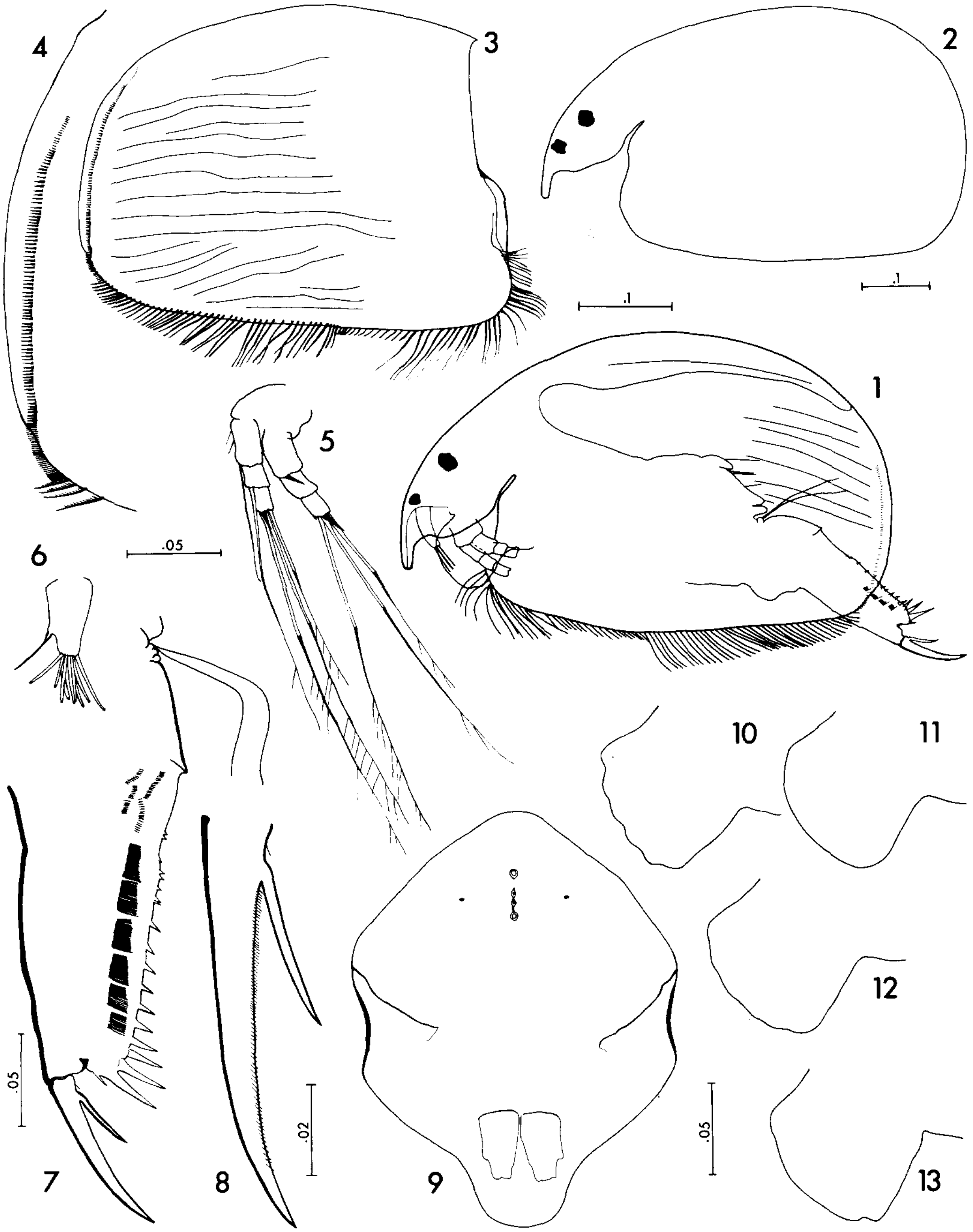

Plate 1. Oxyurella tenuicaudis (G. O. Sars, 1862), parthenogenetic females. Figure 2 is from Östensjövannet, Norway (F1644). All other figures are from Gjennestadvannet, Norway (F1682): *1.* whole view; *2.* outline of largest reproductive female in sample; *3.* shell; *4.* details of setation at posterior-ventral angle and along posterior margin; *5.* antenna; *6.* antennule; *7.* postabdomen and postabdominal claw; *8.* postabdominal claw; *9.* head shield; *10–13.* labra, showing the four major variations in shape of the keel.

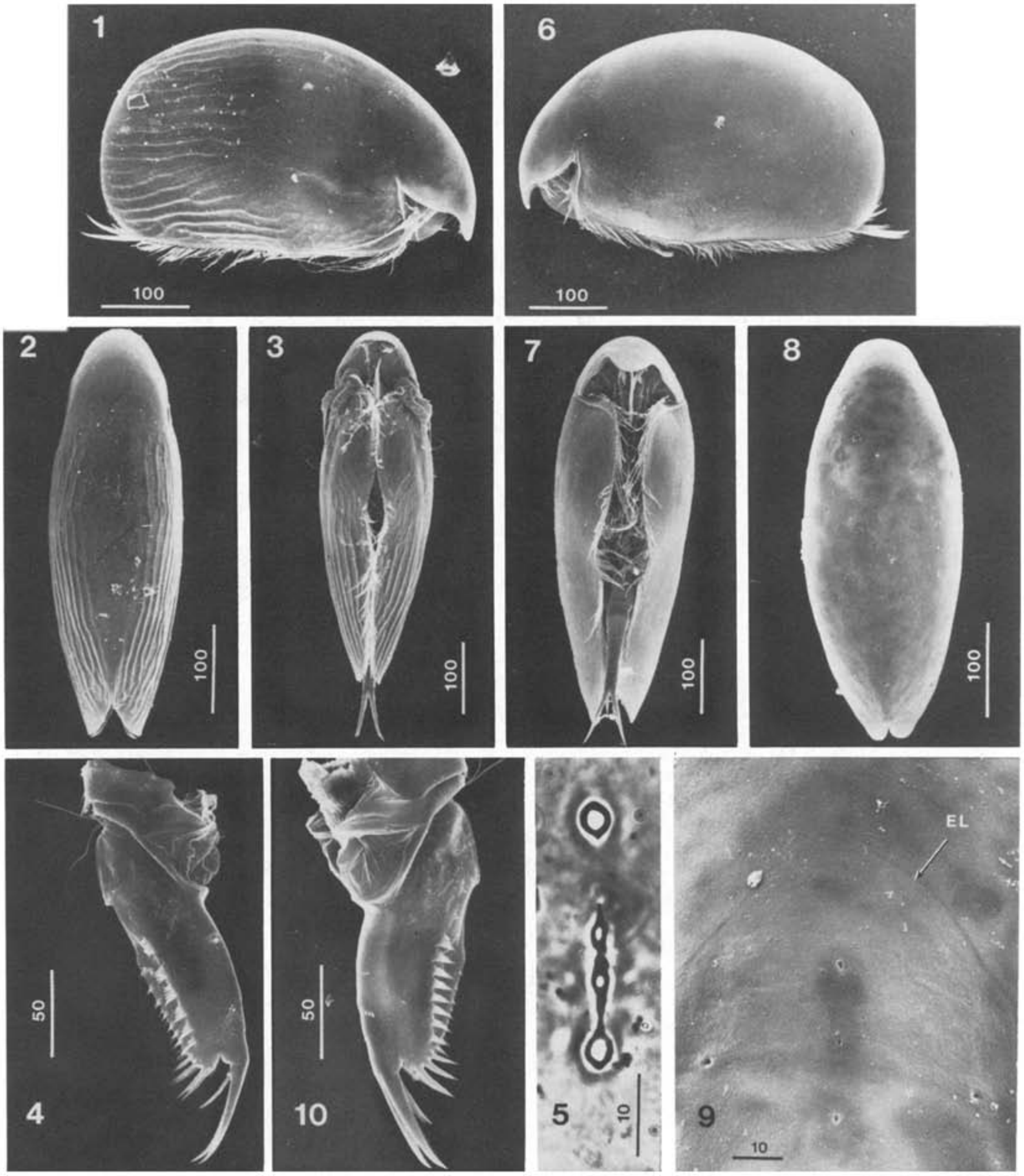

Plate 2. Figures 1–5: *Oxyurella tenuicaudis* (G. O. Sars, 1862). Parthenogenetic females from Gjennestadvannet, Norway (F1682): *1*. side view; *2*. dorsal view; *3*. ventral view; *4*. postabdomen and postabdominal claws; *5*. arrangement of median headpores as seen with transmitted light. Figures 6–10: *Oxyurella brevicaudis* sp. nov. Parthenogenetic females from Clearwater Lake, Fla. (F5019): *6*. side view; *7*. ventral view; *8*. dorsal view; *9*. configuration of headpores (EL = ecdysial line); *10*. postabdomen and postabdominal claws.

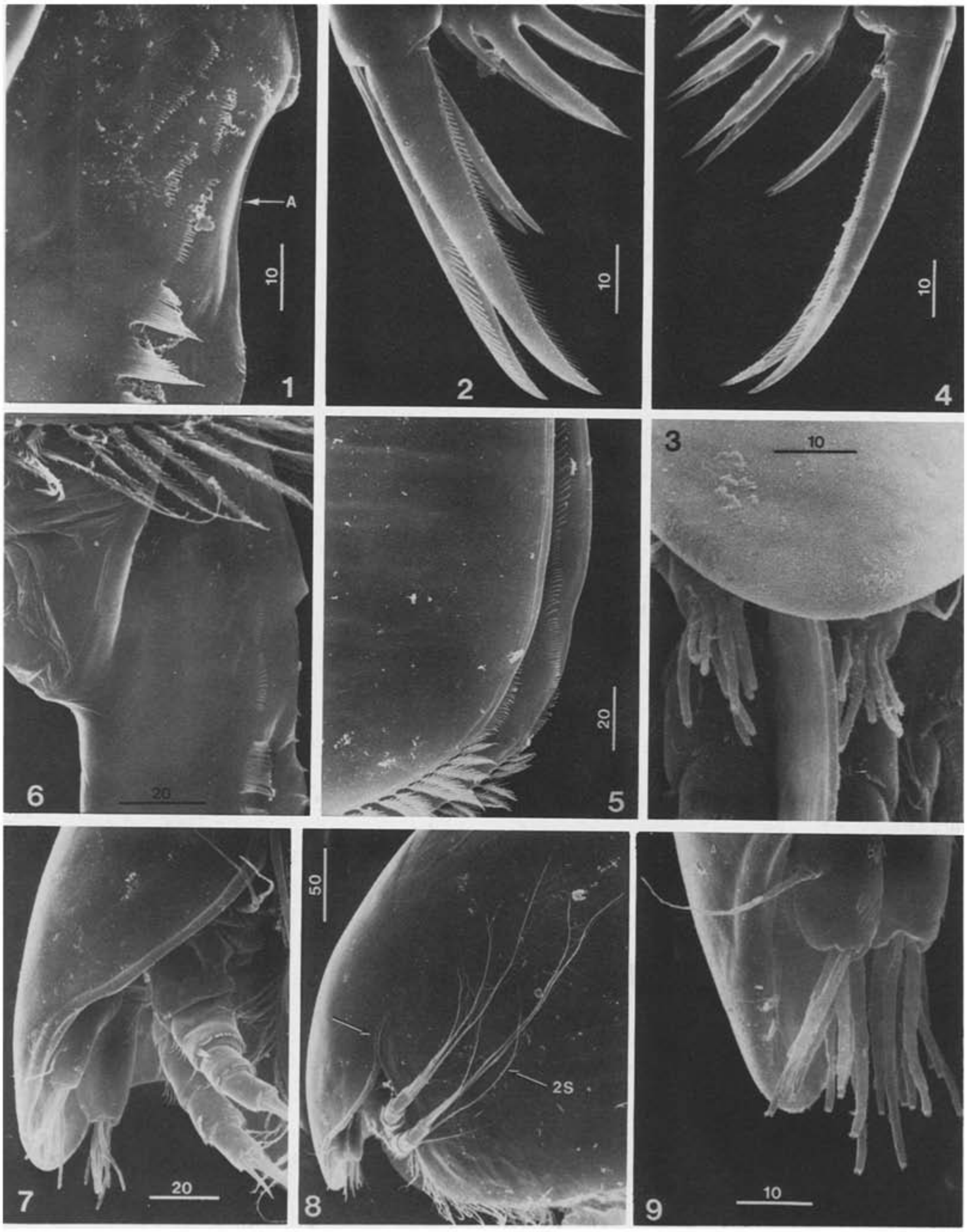

Plate 3. Figures 1–3: *Oxyurella brevicaudis* sp. nov. Parthenogenetic females from Clearwater Lake, Fla. (F5019): *1.* anal groove (= A), completely unarmed; *2.* postabdominal claw, showing the fine setules on anterior surface of basal spine; *3.* rostral margin and tips of antennules, separated by the rostral plate. Figures 4–9: *Oxyurella tenuicaudis* (G. O. Sars, 1862). Parthenogenetic females from Gjennestadvannet, Norway (F1682): *4.* postabdominal claw, showing lack of setules on basal spine; *5.* posterior–ventral angle of shell, showing the configuration of the ascending row of setules beyond the ventral setae; *6.* anal groove, showing fine denticles along distal half; *7.* rostrum, showing the 'rolled' margin; *8.* lateral view of head and left antenna, showing the shell slightly overlapping the head (= arrow) and the relatively long seta (= 2S) arising from the second endopod segment; *9.* antennules, showing the 9 terminal sensory setae and the antennular seta arising from a distinct tubercle.

or shell. Color yellowish hyaline, sometimes dull.

Shell. Subparallel but irregular longitudinal ridges on shell (Plates 1:1 & 3; 2:1–3), especially in posterior portion, showing up as vague striae with phase optics, tending to fade out anteriorly, sometimes branching or even mildly reticulate ventrally and toward anterior–ventral margin; head completely smooth. Both shell and head of intact specimens are covered with shining dark dots or punctae visible under phase, but as these are completely absent from isolated headshields and shells they apparently are associated with the soft tissue; scanning EM shows the surface to be irregularly pitted (see especially Plate 7:4). Entire ventral margin from shell flap at anterior end to posterior–ventral angle provided with marginal setae (Plate 1:1 & 3), those at ventral bulge being abruptly shorter than the adjacent ones; anteriormost setae very delicate, followed by much longer and stouter ones; setae behind ventral bulge long, distinctly plumose, decreasing in length gradually toward posterior–ventral angle, where they end abruptly. Following them is a marginal row of delicate, closely-spaced setules around the posterior–ventral angle (Plates 1:4; 3:5), about half as long as the most posterior ventral setae; these turn inward about midway through the angle, usually suddenly and often accompanied by a weak notch in the posterior margin, then continue dorsad in submarginal position, where they are stouter and more widely spaced ventrally and gradually become more delicate and shorter dorsally. Shell narrowly overlaps part of free margin of headshield (best shown in Plate 3:8); in the light microscope this configuration gives the impression of a curved, elongate, channel ending at the mandibular articulation where the head and shell come together (Plate 1:1 & 2).

Head. In lateral view, rostrum moderately long, slender, finely rounded at tip, not reaching level of ventral margin of animal (Plate 1:1). Ocellus distinctly but variably smaller than eye, usually slightly closer to eye than to tip of rostrum. In plane view (Plate 1:9), headshield longer than broad; rostrum narrow, rather sharply set off from rest of headshield; posterior portion tapered, subtriangular, rather narrowly rounded at posterior tip; pronounced lateral expansion anterior to mandibular articulation with chitinous thickening between, resulting in a characteristic (for *Oxyurella*) elongate channel between headshield and shell in lateral view in the light microscope (Plate 1:1 & 2). Four median pores, of which the anterior and posterior pores are considerably larger than the two middle pores; unconnected to one another by any channel; posterior minor pore about midway between two major pores; usually the three anteriormost median pores present a beaded appearance, in the light microscope (Plate 2:5), as in *Alona setulosa,* resulting from a dark, warty chitinous thickening not visible at the surface connecting the two minor pores with the anterior major pore; sometimes only the two minor pores are so connected; posterior major pore never involved in this beaded pattern. Interpore (IP) distance (24–27 μm in mature specimens) subequal to postpore (PP) distance in immature specimens, markedly less than PP distance in large specimens. Lateral pores located generally somewhat greater than IP distance to either side of anterior minor pore.

Antennule (Plate 1:6). Rather elongate and slender in lateral view; in frontal view chunkier, much broader at base than apex, and with somewhat irregular margins. Nine aesthetascs at tip, all apical, mildly unequal in length, with the medialmost aesthetasc being distinctly the longest and one lateral aesthetasc being almost as long. Antennular seta arises from a distinct tubercle located about 2/3 distance toward apex; more than half as long as antennule, slender, tapered, and finely pointed. Tip of antennule extends somewhat more than half way from ocellus to tip of rostrum (Plate 1:1); apical aesthetascs slightly surpass tip of rostrum. Lilljeborg (1901) states that one of the aesthetascs is subapical, and his Figure 3 on Plate 68 shows it arising near the antennular seta. Flössner (1972) repeats this description almost verbatim. However, our careful study of specimens both with light and electron microscopes, showed unequivocally that all 9 aesthetascs are strictly terminal (Plate 3:7 & 9). Smirnov (1971) shows these relationships correctly in his Figure 622.

Antenna. Antennal formula $\frac{0(1)\text{–}0\text{–}3(1)}{1\quad\text{–}1\text{–}3(1)}$. Seta arising from basal segment of ventral branch (endopodite) very slender and delicate, somewhat longer than ventral branch (Plates 1:5; 3:8). Seta arising from middle segment much longer but distinctly shorter than the two longest terminal setae of this branch. Each branch has three terminal swimming setae, one of which is 2/3 or less as long

Plate 4. Oxyurella tenuicaudis (G. O. Sars, 1862). Figures 1 and 2 are of ephippial females, Figure 3 of an incipient ephippial female, all the rest of parthenogenetic females. Figures 1 and 2 are from Teglgårsø, Denmark (F2993). All other figures are from Gjennestadvannet, Norway (F1682): *1.* ephippium formed from entire shell, showing the foam-like material surrounding the egg; *2.* ephippial female, showing the same; *3.* incipient ephippial female, showing the typical J-shaped ovary: *4.* trunklimb I (ODL = outer distal lobe; IDL = inner distal lobe; AS = accessory seta; C = corm; EH = ejector hooks); *5.* trunklimb II (G = gnathobase); *6.* trunklimb III, showing one of the soft seta unusually long; *7.* trunklimb IV; *8.* trunklimb V.

as the other two. Each branch has a stout terminal spine, somewhat shorter than the terminal segments from which they arise. Dorsal branch (exopodite) in addition has a smaller spine on the basal segment. Additional setules and rows of fine spinules occur (Plate 3:7 & 8), which are not visible with the light microscope or only barely.

Labrum (Plate 1:10–13). Variably hatchet-shaped; anterior–ventral and posterior–ventral angles usually narrowly rounded, distinct; anterior and posterior margins sub-parallel, at times converging somewhat basally; anterior margin distinctly shorter than posterior; ventral margin (the 'blade' of the hatchet) shallowly convex, at times smooth (Plate 1:11), at other times wavy (Plate 1:12), sinuate (Plate 1:10), or notched near the posterior–ventral angle (Plate 1:13); angle behind 'blade' rather sharp and usually distinctly obtuse. Among more than 200 specimens scored, 14% had a smooth margin, 38% slightly wavy, 29% sinuate, and 19% notched.

Trunk limb I (Plate 4:4). ODL (outer distal lobe) with only 1 seta, IDL (inner) with only 2, all subequal in length. Corm with the typical 3 groups of setae distally; ventral group with 3 setae subequal in length and accessory seta well developed; middle group with middle seta the longest, accessory seta rudimentary and sometimes not resolvable at all with 100 × phase objective; dorsal group with only 2 setae plus a slender but well developed accessory seta plus a very short seta proximad on dorsal margin. Two typical ejector hooks at base.

Trunk limb II (Plate 4:5). Gnathobase with 4 stout setae, the longest with several long, slender setules arising at an angle from apex; 7 setae in gnathobase filter comb. Eight scraping spines, increasing in length gradually away from the gnathobase; no denticles or setules visible on any of the scraping spines at 40 × phase, but at 100 × extremely fine setules are visible on all the spines, most clearly on the first six.

Trunk limbs III–V (Plate 4:6–8). Limbs III, IV, and V have 7, 6, and 4 'soft' (filtering) setae, respectively, on the exopodite and 7, 5, and 0 setae, respectively, in the gnathobasic filter, not all of which could be resolved in the specimens drawn. Noteworthy is the extremely long soft seta on limb III.

Postabdomen. About 3 times as long as broad, somewhat tapering distally (Plates 1:7; 2:4). Ventral margin unevenly convex; two slight notches in contour in distalmost third and an even less distinct one about in middle; proximal and middle notches associated with a median and two lateral transverse crescents of fine setules, distal notch only with a median crescent (crescents visible with oil immersion phase and SEM). Dorsal margin with a sharpish and rather prominent pre-anal angle and a much more subdued, often barely visible, postanal angle; anal groove about as long as pre-anal portion, which is keeled; postanal portion straight or weakly concave, roughly half the length of the postabdomen; distal tip strongly incised, forming a distinct peduncle for the claws. Postanal margin provided with 13–15, occasionally 16, marginal denticles on each side, of which those in positions 11–14 counting from the distal end exhibit a weak tendency toward doubling (⩽20%); proximalmost 8–12 denticles are small and increase in length slightly and very gradually distally; these are followed by 3–4 denticles that increase in size rapidly to form the distal cluster Sars considered typical of *tenuicaudis* but which instead is now known to be characteristic of the entire genus; distal cluster followed by a single, much smaller denticle attached near the claw peduncle; distal half of anal margin provided in addition with several (most commonly 1–3) minute denticles on either side, the proximal half of the groove being unarmed (Plate 3:6); total numbers of denticles, including all anal denticles and members of double denticles counted separately are 14–18. lateral surface provided with 6, sometimes only 5, low fascicles arranged in a row roughly parallel to dorsal margin; individual setae of each fascicle increase somewhat in length and stoutness distally, but even those of distalmost fascicles do not project beyond margin of postabdomen. Along proximal half of anal groove at some distance from margin is a row of two crescents of very fine setules, the proximal crescent overlapping the pre-anal angle, and still farther removed from the margin a row of 3 similar crescents of even smaller setules (Plates 1:7; 2:4; 3:6). Anterior margin, which articulates with the abdomen, distinguished by a characteristic fold along its length, which shows up as a rolled chitinous thickening in whole specimens. Abdominal setae short, only about 1/3–1/2 longer than length of pre-anal margin.

Postabdominal claw (Plates 1:8; 3:4). Long, slender, tapered to a fine point; curvature of convex margin greatest in distal third. Concave surface of claw finely setulated along almost its entire length and with 1 or 2 short and delicate spinules proximad from base of spine. Basal spine slender, up to almost half as long as claw, faintly sigmoid at base and with tip curving away from claw; no fine setules on concave surface.

Size. Overall range in length of Gjennestadvannet population (n = 226) was 0.30–0.57 mm. Analysis of this population (Fig. 1) revealed the expected two prereproductive instars with discrete frequency spikes, instar I at 0.30–0.33 mm and instar II at 0.36–0.40 mm. The smallest females carrying eggs measured 0.43 mm. The largest specimens in the sample from Östensjövannet measured 0.63 mm.

b) Ephippial female

Except for being somewhat higher relative to length and in having the dorsal portion of the shell pinched together into a sort of rounded keel, the ephippial female is indistinguishable from the parthenogenetic female (Plate 4:2). The shell does not bulge outward (Plate 7:1) as a locule to receive the resting egg, and as the entire shell functions as the ephippium (Plate 4:1), there are no lines of structural weakness demarcating any part of the shell that will separate from the ephippium on molting.

The light microscope shows the resting egg to be surrounded by a foamy mass, which conforms anteriorly and dorsally to the general shape of the broodpouch (Plate 4:1 & 2), suggesting thereby that the material is secreted into the broodpouch to help retain the egg in this primitive ephippium and to protect it in much the same manner as do the structural modifications of the shell and pigmentation in more advanced kinds of ephippia. Scanning electron micrographs (Plate 7:2 & 3) of the single ephippium recovered from which the left shell had been dissected away revealed the peculiar configuration and texture of this foamy mass but did little to clarify its relationship to the brood pouch. As in *Pleuroxus denticulatus* (Shan 1969), both ovaries participate in the production of the single ephippial egg via an anterior transverse connection between the half right ovary and the full left ovary, which results in a J-shaped ovarian mass (Plate 4:3).

The 5 ephippial females from Teglgårsø and Store Følstrup Dam measured 0.46–0.50 mm.

c) Males

The major morphological differences between mature males and females of chydorids concern the general body shape, rostrum, antennules, trunk limb I, postabdomen, postabdominal claw, and sometimes also the number and length of swimming setae on the antenna and the length of the ventral setae on the shell. Usually, also, there are stepwise changes in these structures from one instar to the next, enabling the instar of any individual to be determined easily.

Shape. Instars I and II (Plate 5:3 & 2, respectively) are quite similar in shape to the corresponding female instars. The mature male is somewhat flatter dorsally and more elongate (Plates 5:1; 6:1); the major difference is the anterior–ventral margin, which bends sharply upward in region of ventral embayment, is markedly concave, and forms a narrowly curved, almost right-angled anterior–ventral angle; marginal setae at ventral embayment considerably longer than in female, those anterior to embayment being long, delicate, profusely branched (Plate 6:1), giving a much different appearance from female; shell markings same as in female.

Head and rostrum. Essentially undifferentiated from female, or at best with rostrum only very slightly shorter and less sharply set off from headshield.

Antennule (Plate 5:4). That of mature male very similar in morphology and size to female; 10 terminal aesthetascs (instead of the expected 9 or 12, according to Scourfield 1896), of which 9 correspond to those of female in length and placement; the 10th is very slender and less than half as long as any of the others, located toward the lateral margin near the insertion of the male seta; tips of aesthetascs barely exceed tip of rostrum. Antennular seta arising from a distinct tubercle distad from the middle, about half as long as antennule. Male seta arises from middle of anterior surface close to apex; distinctly longer than longest aesthetascs and evenly tapering to a sharp point; basal half more heavily chitinized. Close study revealed no additional aesthetascs, contrary to Lilljeborg's description and illustration.

Antenna (Plate 5:5). Formula $\frac{0(1)\text{-}0\text{-}3(1)}{1\ \ \text{-}1\text{-}3(1)}$ as in the female. However, the seta arising from the middle segment of the endopodite is much shorter than

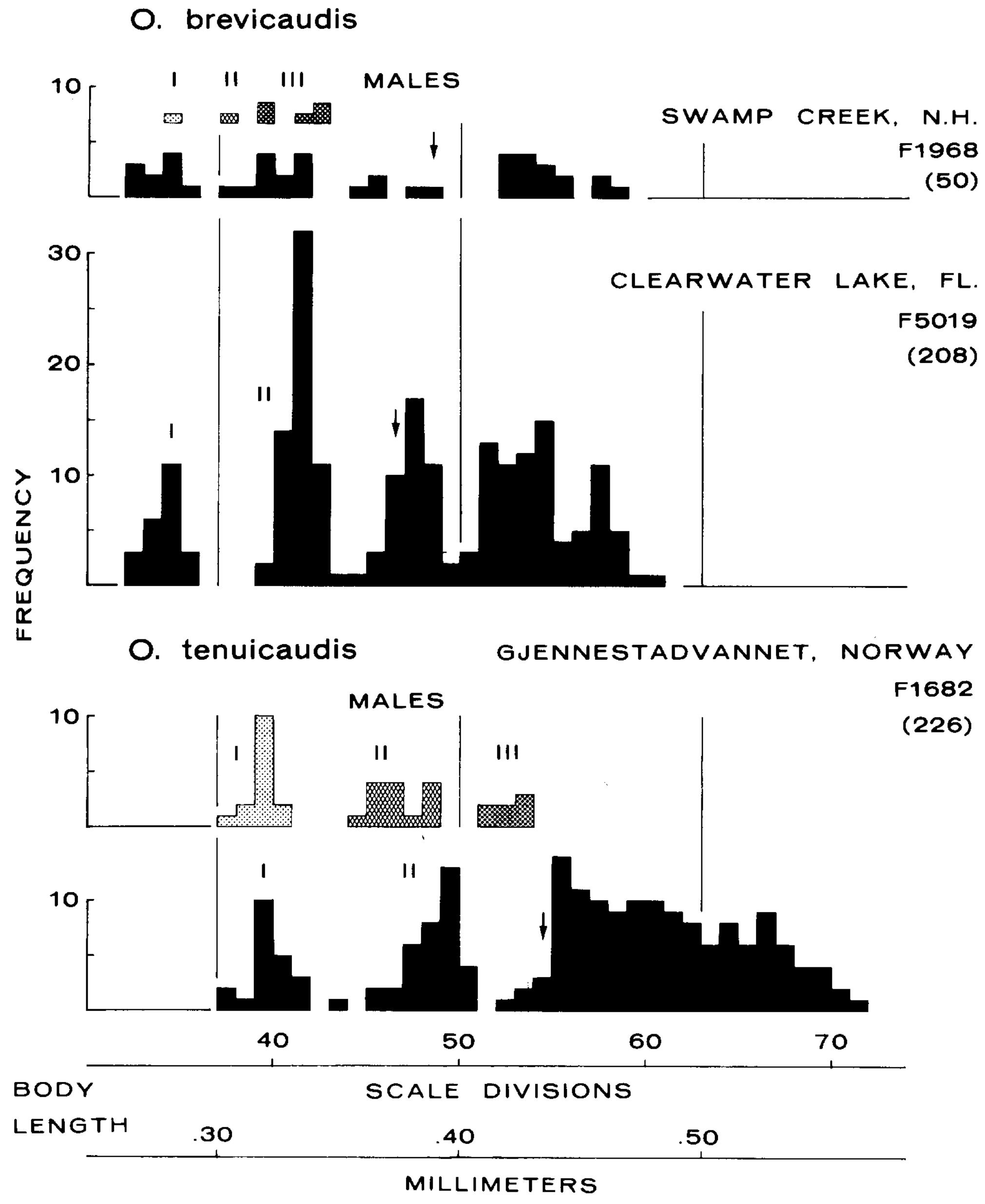

Fig. 1. Size-frequency analysis of a population of *O. tenuicaudis* from Gjennestadvannet, Norway, of the type population of *O. brevicaudis* from Clearwater Lake, Fla., and of a gamogenetic population of this taxon from Swamp Creek, N.H. The three male instars can be identified by specific morphological features discussed in the text. The two prereproductive instars of females of both species sort out as discrete frequency spikes in the three populations. Instar by instar and stage by stage, *O. tenuicaudis* is significantly larger than *O. brevicaudis*.

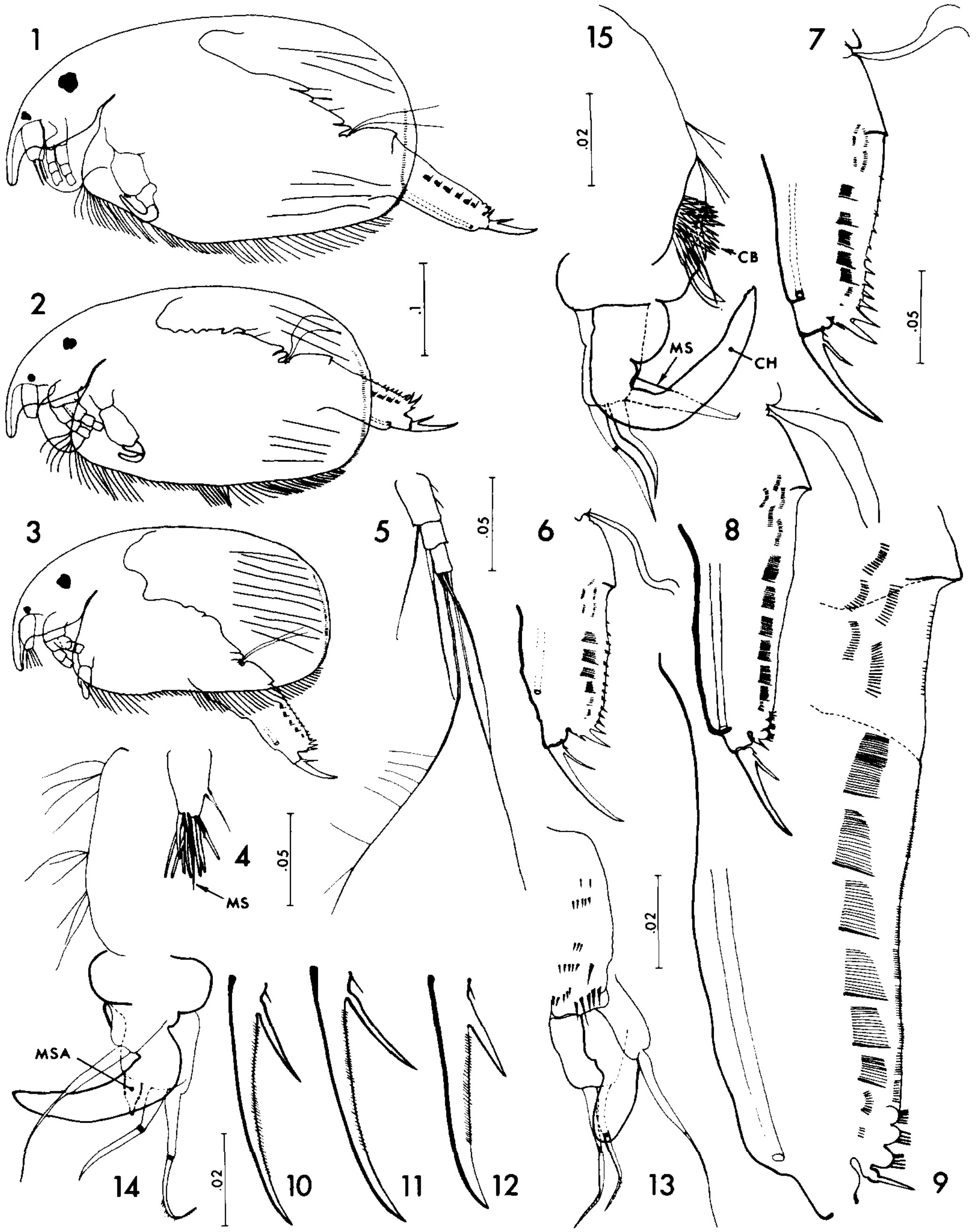

Plate 5. Oxyurella tenuicaudis (G. O. Sars, 1862). Males from Gjennestadvannet, Norway (F1682): *1.* mature male; *2.* instar-II male; *3.* instar-I male; *4.* antennule, mature male (MS = 2-segmented male seta); *5.* endopodite of antenna, mature male, showing the markedly smaller seta arising from the middle endopodite segment than in the female; *6–8.* postabdomens and postabdominal claws of instars I and II and of mature males, respectively; *9.* postabdomen, mature male; *10–12.* postabdominal claws of instar-I, instar-II, and mature males, respectively; *13.* part of trunklimb I, instar-I male; *14.* part of trunklimb I, instar-II male (MSA = male seta anlage); *15.* part of trunklimb I, mature male (MS = male seta; CH = copulatory hook; CB = copulatory brush).

in the female, the basal segment barely exceeding the tip of the ramus.

Trunk limb I. The three ODL and IDL setae are relatively shorter than in the female, and the ODL seta becomes progressively shorter from instar I to III. The accessory male seta of the IDL is first visible in instar II (Plate 5:14) as an anlage with a short, stout base and almost invisible apical portion; in instar III (Plate 5:15) this is well developed, somewhat hooked at the apex, considerably broader at the base than the other two IDL setae and about as long as them; basal half well chitinized,

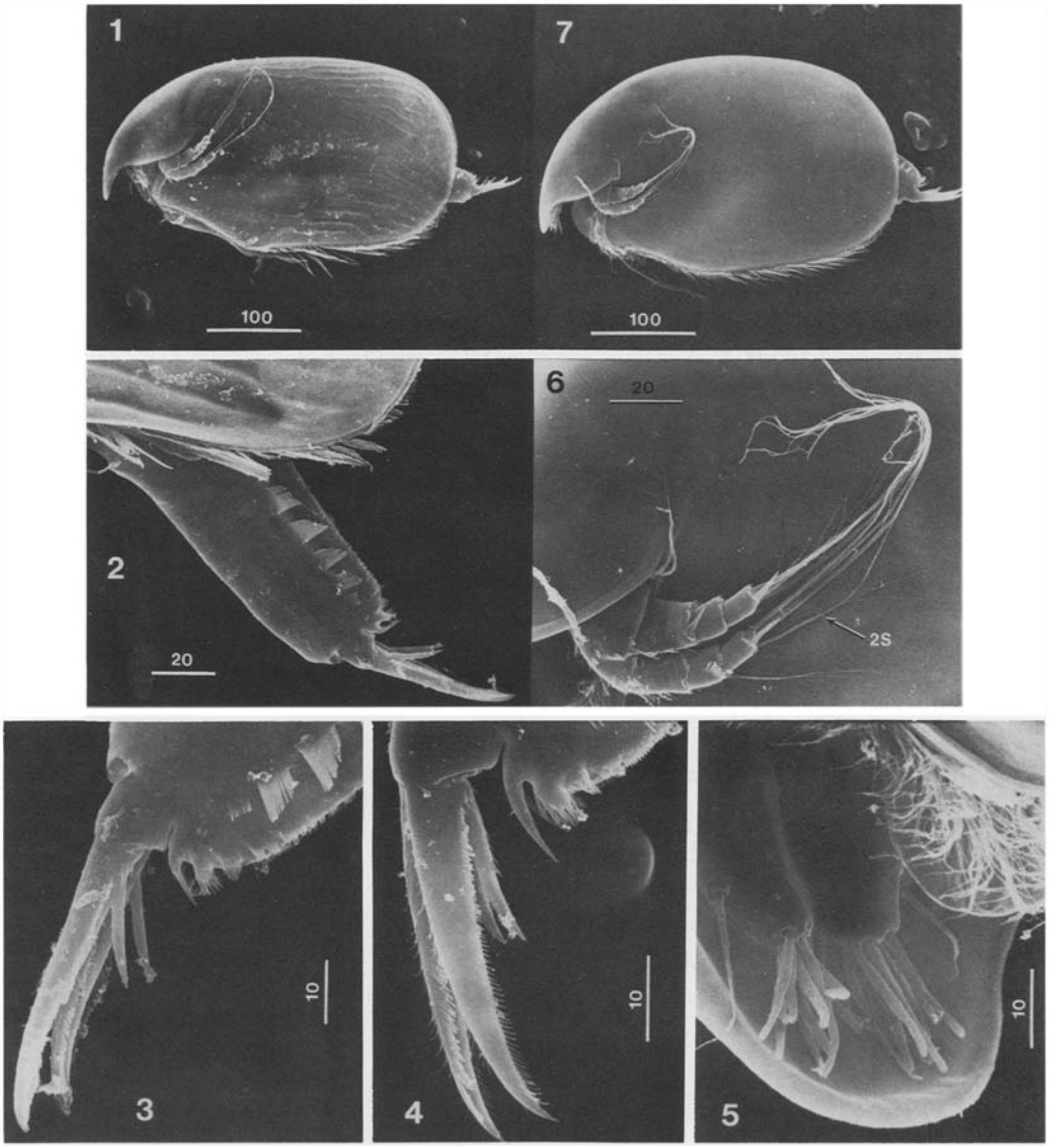

Plate 6. Figures 1–3: *Oxyurella tenuicaudis* (G. O. Sars, 1862). Mature males from Gjennestadvannet, Norway (F1682): *1.* side view showing concave ventral margin anteriorly; *2.* postabdomen and postabdominal claw; *3.* tip of postabdomen and postabdominal claw. Figures 4–7: *Oxyurella brevicaudis* sp. nov. Mature males from Old Lake, Ind. (F6055): *4.* tip of postabdomen and postabdominal claws; *5.* ventral view of rostrum with antennules and their setae and also showing the slender profusely branched setae along ventral margin of shell anteriorly; *6.* antenna, showing the shortened seta arising from the middle endopod segment (= 2S); *7.* side view.

distal half very thin and translucent. Copulatory hook is short, stout, slightly curved, and peg-like in instar I, extending posteriorly along axis of limb (Plate 5:13); in instar II (Plate 5:14) it is much larger, J-shaped, tapered to a blunt point, extending ventrally at right angles to limb axis, and heavily chitinized; in instar III (Plate 5:15) it is U-shaped, with the free arm longer and more strongly tapered

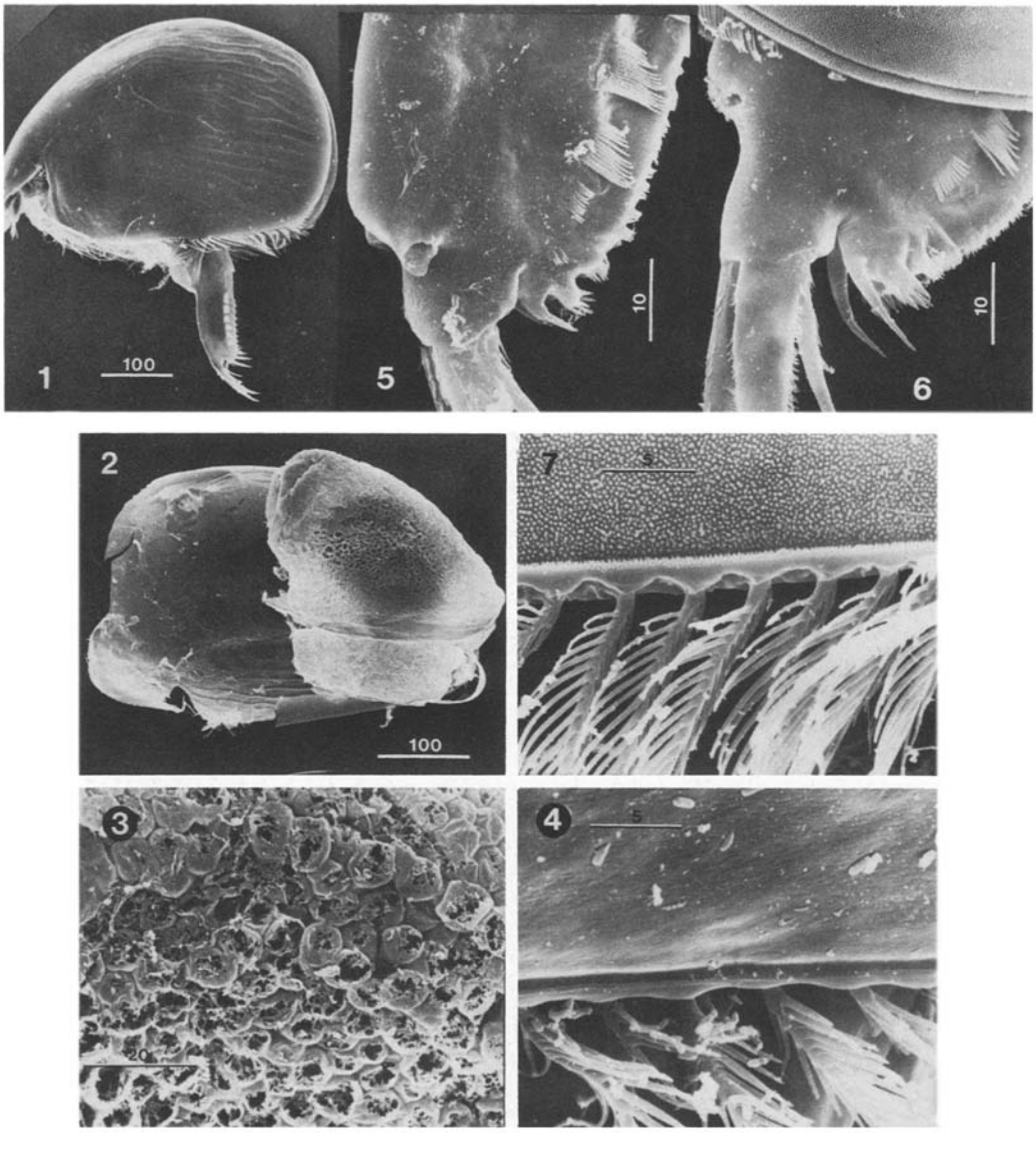

Plate 7. Figures 1–5: *Oxyurella tenuicaudis* (G. O. Sars, 1862). 1–3 are ephippial females or ephippia from Teglgårsø, Denmark (F2993), and 4–5 are from Gjennestadvannet, Norway (F1682): *1.* side view of ephippial female, showing pinching of dorsal margin and greater height as compared with parthenogenetic female; *2.* ephippium, with most of left valve dissected away to expose the foamy mass surrounding the egg; *3.* enlargement of foamy mass; *4.* ventral margin of shell of parthenogenetic female, showing the plumose setae and the irregular pitting of the shell surface; *5.* distal end of male postabdomen, showing the genital pores with their lip-like expansion. Figures 6–7: *Oxyurella brevicaudis* sp. nov.: *6.* distal end of postabdomen of male, showing the genital pores flush with the surface – specimen from Old Lake, Ind. (F6055); *7.* ventral margin of shell, showing the plumose setae and the wart-like texture of the shell – parthenogenetic female from Clearwater Lake, Fla. (F5019).

toward the tip, which is directed forward and has two transverse crescentic ridges. Copulatory brush in instar III consists of a dense patch of rather short, stout setules, and a few much longer setae distally. Copulatory brush seta delicate, difficult to resolve.

Postabdomen. The structure of the postabdomen in instars I and II resembles closely that of the corresponding female instars except for being somewhat broader and having genital pores. In Instar III all the marginal denticles have been lost, and the distal end is completely restructured. The three instars exhibit a progressive displacement distad of the genital pores to their definitive location in instar III (Plates 5:6–8; 6:2 & 3; 7:5). In all three instars the middle fascicles tend to be best developed, the distalmost ones least developed. Ventral margin of instar I conspicuously irregular, that of instar II much more regular but with beginning formation distally of a distinct peduncle for the claw; in both instars the postabdomen is relatively broader than in the female, providing thereby a good recognition character. Mature male lacks marginal denticles of female but has instead a single, long, slender denticle distally near the base of the claw peduncle, followed proximally by 2 or 3 rounded knobs or tubercles that decrease in size proximad, each provided with 4–6 bluntish setae (Plates 5:8 & 9; 6:2 & 3; 7:5); between these and anal groove are about 9 weakly crescentic groups of very fine setules, located slightly submarginally, and at least 2 rows in series of very fine setules along the anal groove; lateral fascicles as in female, except for greater development of middle ones and presence distally of 1 or 2 additional groups of fascicle-like setules, much shorter and less well developed than the definitive fascicles; sperm ducts open on distal side of knob-like constriction that delimits the heavily-chitinized claw peduncle. Genital pores not flush with the surface, but instead project distally as thin, scoop-like lips (Plate 6:3; 7:5).

Postabdominal claw. Essentially same as in female in instars I and II, except for basal spine possibly being a little shorter relatively (Plate 5:10 & 11, respectively). Claw of mature male (Plate 5:12; 6:2 & 3) also resembles that of female but is relatively shorter and stouter, has the ventral margin weakly concave instead of weakly convex, and has the basal spine shorter, stouter, and straight instead of basally sigmoid with tip curving outward.

Size. In the Gjennestadvannet population (Fig. 1), instar-I males (15) measured 0.30–0.32 mm, instar-II (14) 0.35–0.38 mm, and mature males (7) 0.41–0.42 mm. The instar-I males have the same modal length as instar-I females but a smaller mean size, instar-II males are distinctly smaller than instar-II females, and mature males are smaller than the smallest reproductive females, demonstrating once again for chydorids the reduced rate of growth of males compared with females and the great curtailment of size increase accompanying molting to maturity in instar III.

Disposition of specimens. Because of the importance of the Gjennestadvannet population (Sample F1682) in defining the morphology of *O. tenuicaudis* more precisely, suites of specimens consisting of 2 parthenogenetic females mounted on a slide in glycerine jelly and 3 parthenogenetic females in 50% (v/v) ethanol/glycerol have been deposited in each of the museums listed below. In addition, a mature male from this population mounted on a slide in glycerine jelly has been deposited in the Zoological Museum in Oslo.

1. U.S. National Museum of Natural History. Catalogue numbers: slide of females 190886; liquid sample 190887.
2. Canadian National Museum of Natural Sciences. Catalogue number NMC-C-1982-58 for both the slide and liquid sample.
3. British Museum (Nat. Hist.). Accession numbers: slide of females 1982.141; liquid sample 1982.142-151.
4. Zoological Museum, University of Oslo. Catalogue numbers: slide of females F19184a; liquid sample of females F19184b; slide of mature male F19184c.

All the remaining specimens from this sample are in the Frey collection in Bloomington.

Oxyurella brevicaudis **sp. nov.**

Synonymy

Odontalona tenuicaudis (Sars): Birge 1910: 1045–48, Pl. 71, Figs. 5 & 6.

Oxyurella tenuicaudis (Sars): Birge 1918: 720, Figs. 1125 & 1129b; Pennak 1953: 375, Fig. 236D; Brooks 1959: 640, Figs. 27.84 & 27.88b; Frey 1960: 695, Pl. 1, Figs. 10 & 11; Goulden 1966b: 93, Pl. 1, Fig. 11; Smirnov 1971: Fig. 5C; Pennak 1978: 379, Fig. 266D.

Etymology. From *L. breve,* short, and *cauda,* tail, referring to the relatively shorter length of the postabdomen as compared with *O. tenuicaudis* from Scandinavia.

Type locality. Clearwater Lake, Putnam Co., Florida. Geographic coordinates 29°40.0′N and 81°52.9′W.

Type series. All the specimens and exuviae in sample F5019, collected 3 March 1979.

Holotype. A mature parthenogenetic female 0.46 mm long mounted on a slide in glycerine jelly has been deposited in the U.S. National Museum of Natural History (Catalogue number 190888).

Paratypes. Suites of specimens consisting of two mature females mounted in glycerine jelly, a mature female in polyvinyl lactophenol, and 3 mature females in alcohol and glycerol have been deposited in the following museums:

1. U.S. National Museum of Natural History. Catalogue numbers: slide of females in glycerine jelly 190889; slide of female in polyvinyl lactophenol 190890; specimens in liquid 190891.
2. Canadian National Museum of Natural Sciences. Catalogue number NMC-C-1982-59 for slides of females in glycerine jelly and in polyvinyl lactophenol, and for specimens in liquid.
3. British Museum (Nat. Hist.). Accession numbers: slide of females in glycerine jelly 1982.152; slide of female in polyvinyl lactophenol 1982.153; specimens in liquid 1982.154–163.
4. Zoological Museum, University of Oslo. Catalogue numbers: slide of females in glycerine jelly F19185a; slide of female in polyvinyl lactophenol F19185b; specimens in liquid F19185c.

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

Additional specimens. A slide of a mature male in glycerine jelly has been deposited each in the U.S. National Museum of Natural History (Catalogue number 190892), the British Museum (Nat. Hist.) (Accession number 1982.164), the Canadian National Museum of Natural Sciences (Catalogue number NMC-C-1982-60), and the Zoological Museum, University of Oslo (Catalogue number F19186). The first three of these specimens are from sample F1968, collected on 24 August 1966 in Swamp Creek, Sullivan Co., N.H., and the fourth from sample F6055, collected 24 October 1981 in Old Lake, Whitley Co., Ind.

Short diagnosis

Broadly elliptical, with dorsal and posterior margins rather strongly arched, and posterior–dorsal and posterior–ventral angles broadly rounded. Shell without any longitudinal striae or ridges, occasionally with vague polygons posteriorly; shell and head completely covered with small wart-like tubercles, visible with SEM; submarginal setules along posterior margin decrease in size abruptly about half-way upward. Antennule with 9 aesthetascs all apical, of which medialmost is somewhat longer than the others; antennular seta arising laterally from distinct tubercle about 1/3 from tip. Antennal formula $\frac{0(1)\text{-}0\text{-}3(1)}{1\quad\text{-}1\text{-}3(1)}$; relative development of setae and spines much as in *O. tenuicaudis.* Labral keel expanded ventrally; shape variable, but anterior margin generally broadly confluent with ventral margin, less distinctly hatchet-shaped than in *O. tenuicaudis,* angle behind keel most commonly somewhat acute. Four isolated median pores on head, the two middle ones surrounded and occasionally connected to each other by a warty or beaded sub-surface chitinous thickening but never so connected to anterior pore; PP distance much less than IP distance in immature specimens, approaching PP distance but still usually less in large specimens; lateral pores widely spaced, but with LP distance markedly less than twice the IP distance. Postabdomen relatively short; postanal portion markedly tapered distally; anal groove completely unarmed; postanal margin provided on each side with 10–14 denticles, of which proximalmost 6–10 are very short, slender, and exhibit a strong tendency toward doubling; cluster of denticles (typically 4) at distal angle much larger than the rest, provided with very fine setules; single much smaller denticle distal to these; typically 7 high fascicles in a row that is angled to the ventral margin, resulting in the longest member of the distalmost several fascicles projecting beyond margin of postabdomen; 5 rows of crescents of fine setules in region of anal groove, 2 closer to margin, the other 3 farther removed. Postabdominal claw long, relatively stout, virtually straight except for mild curvature in distalmost quarter; provided with a continuous row of fine setules along concave margin and 1 or 2 slender spinules proximal to basal spine; basal spine about half length of claw, only slightly curved, provided

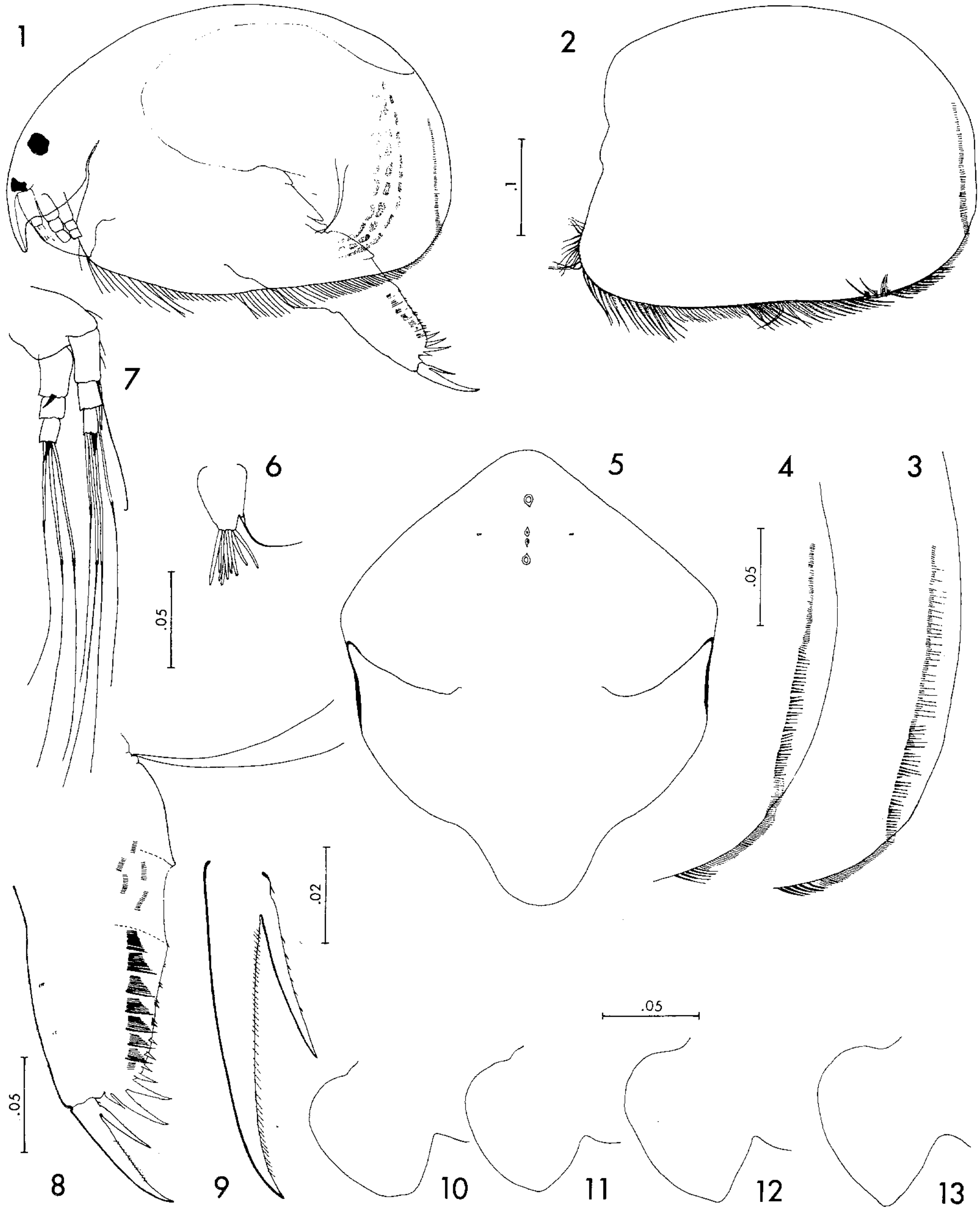

Plate 8. Oxyurella brevicaudis sp. nov. Figure 5 is from Skater's Pond, Ind. (F4075), all the rest from Clearwater Lake, Fla. (F5019). All figures are of mature parthenogenetic females: *1.* whole view; *2.* shell; *3–4.* details of setation at posterior–ventral angle, showing variations in configuration of setules along posterior margin; *5.* headshield; *6.* antennule; *7.* antenna, showing the considerably longer seta on the middle endopodite segment than in the male; *8.* postabdomen; *9.* postabdominal claw; *10–13.* labra, showing intrapopulational variation in shape of keel.

with widely spaced, fine spinules on anterior surface. Dorsal margin of ephippial female higher and pinched together into a rounded keel, otherwise undifferentiated from parthenogenetic female; entire shell functions as ephippium without any surface modifications; egg surrounded by a secreted foam-like material. Adult males more elongate than females, and their dorsal margin is less highly arched; the chief differences from *tenuicaudis* are in characters that separate the females of the two taxa – lack of longitudinal striae on the shell; presence of fine wart-like tubercles on shell and head; shorter and broader postabdomen; fine spinules along anterior margin of basal spine; but in addition the genital pores are somewhat farther removed from distal end, they are flush with the surface, not projecting lip-like, and the anterior edge of the basal spine is distinctly curved outward, even somewhat sigmoid.

a) Parthenogenetic female

Expanded description.

Shape (Plates 2:6; 8:1). Outline broadly elliptical, flattened on bottom; dorsal margin rather highly arched, evenly curved anteriorly to level of compound eye, then more strongly curved to tip of rostrum; posterior margin strongly convex, with both dorsal and ventral angles evenly rounded, broadly confluent with dorsal and ventral margins; ventral margin more or less straight, or with a slight convexity at ventral embayment. Body considerably flattened from side to side, widest near or in front of middle (Plate 2:7 & 8).

Shell. Without any longitudinal striae or ridges (Plates 2:6–8; 8:1–2). Under phase, both shell and head of intact specimens are covered with punctae as also seen in the European taxon. However, these punctae are totally absent in isolated headshields and shells, thereby indicating their association with the underlying soft tissues. There is occasionally a very weak and faint subsurface pattern of irregular polygons in the posterior half. Sometimes clusters of punctae alternating with non-punctate areas are seen in rows parallel to the posterior margin (Plate 8:1). SEM reveals that the surface instead of being smooth or pitted is densely covered with minute wart-like tubercles (best shown in Plate 7:7). Continuous row of marginal setae (Plate 8:1 & 2) from shell flap to midway through posterior–ventral angle; those in region of ventral embayment abruptly shorter; setae posterior to these are conspicuously plumose (Plate 7:7) and gradually decrease in length posteriorly. Posterior to ventral setae is a row of fine, closely spaced, marginal setules about 2/3 as long as the posteriormost setae (Plate 8:4); after a distance equal to several lengths of the posteriormost ventral setae they turn inward abruptly, sometimes sigmoidally but usually unaccompanied by a notch in margin, then continue in a straight line toward the posterior–dorsal angle, cutting secant-like across the posterior curvature; submarginal setules coarser and more widely spaced than marginal setules, tending to be arranged in a number of poorly defined groups ventrally; they then decrease abruptly in length and stoutness about midway along posterior margin, sometimes with individual setules much longer than the others at irregular intervals (Plate 8:3).

Head (Plate 8:5). Plane view much the same as in *tenuicaudis:* somewhat longer than broad; posterior portion tapering, subtriangular, rather narrowly rounded at posterior tip; rostrum narrow, evenly rounded, set off quite sharply from rest of head; pronounced lateral expansion anterior to mandibular articulation, as in *tenuicaudis.* Four median pores on head, completely separated from one another by any channel or raised chitinous thickening; anterior and posterior pores largest, each surrounded by a weak annular thickening visible in the light microscope; two middle pores close to each other, each surrounded by a beaded chitinous thickening, usually unconnected but occasionally connected by a beaded line, never so connected to anterior pore. Lateral pores less than an IP distance on either side of minor pores, each located in a distinct pit (Plate 2:9). IP distance roughly 20–33 μm in mature specimens; always greater than PP distance in mature specimens. Ocellus variably smaller than compound eye, located somewhat closer to eye than to tip of rostrum.

Antennule (Plates 3:3; 8:6). In frontal view rather chunky and markedly conical; about twice as wide at base as apex; straight-sided or nearly so. Antennular seta approaches length of antennule, slender, tapered to a fine point, arising from a distinct tubercle about 1/3 distance from tip. Nine aesthetascs all arising from apex; medialmost aesthetasc somewhat longer than the rest; tips of aesthetascs barely reach tip of rostrum.

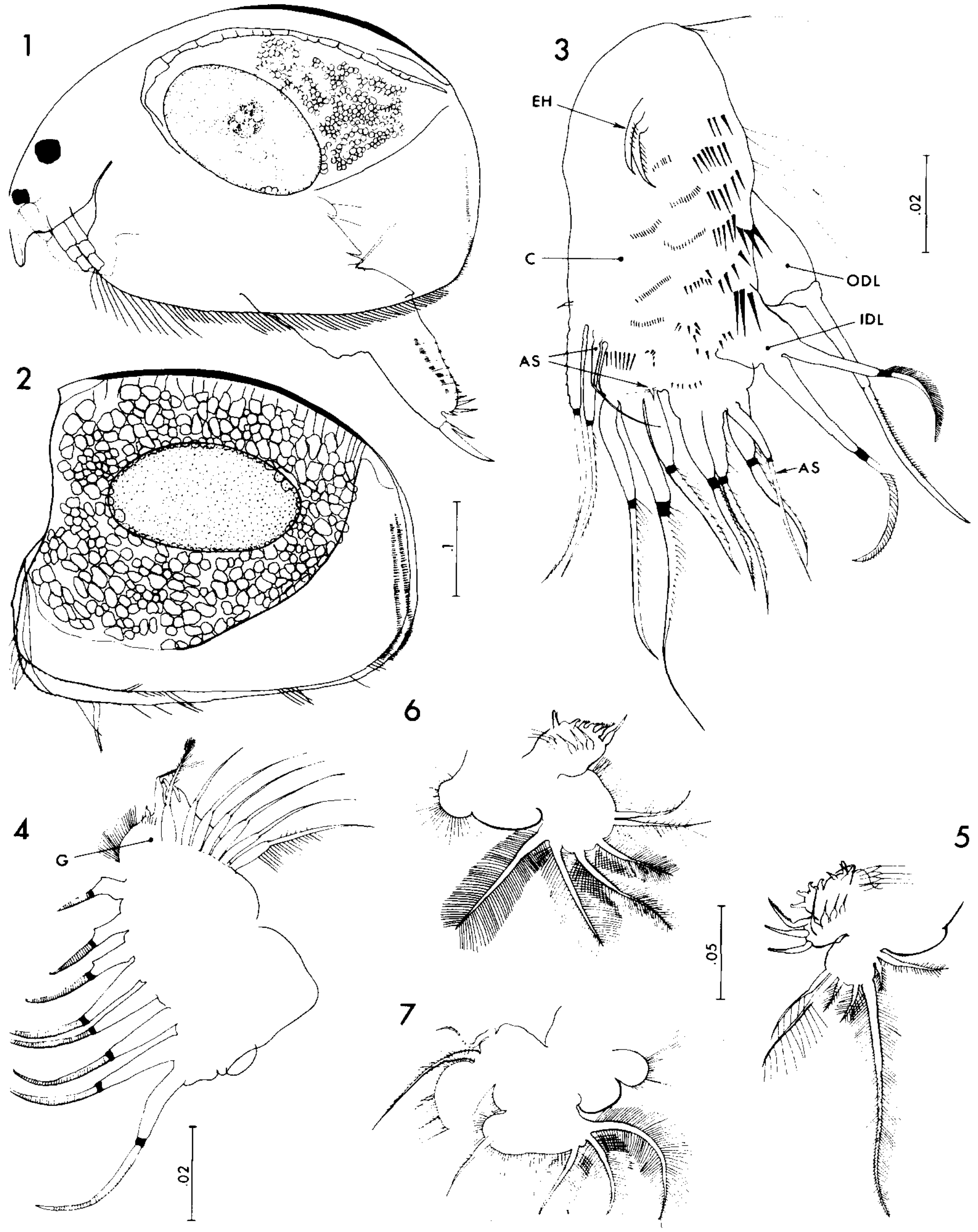

Plate 9. Oxyurella brevicaudis sp. nov. Figure 1 is from Old Lake, Ind. (F6055), Figure 2 from Skater's Pond, Ind. (F4075), and all the rest from Clearwater Lake, Fla. (F5019), the type locality. All trunklimbs are from mature parthenogenetic females: *1.* ephippial female; *2.* ephippium, showing the different distribution of the foam-like material than in *O. tenuicaudis; 3.* trunklimb I (ODL = outer distal lobe; IDL = inner distal lobe; C = corm; EH = ejector hooks; AS = accessory setae); *4.* trunklimb II (G = gnathobase); *5.* trunklimb III, showing the very long seta, as in *O. tenuicaudis; 6.* trunklimb IV; *7.* trunklimb V.

Antenna (Plate 8:7). Formula $\frac{0(1)\text{-}0\text{-}3(1)}{1\quad\text{-}1\text{-}3(1)}$. One terminal seta on each branch about 3/4 as long as other two. Seta arising from basal segment of endopodite very slender, about as long as endopodite. Terminal spines stout, almost as long as terminal segments; spine on basal segment of exopodite somewhat smaller.

Labrum (Plate 8:10–13). Keel expanded ventrally, flattened, blade-like; shape variable, but anterior margin rounded and usually broadly confluent with ventral margin; less distinctly hatchet-shaped than in *tenuicaudis;* posterior–ventral angle variable, but often acute and narrowly rounded; angle behind keel most commonly weakly acute.

Trunk limb I (Plate 9:3). Not appreciably different from *tenuicaudis.* One seta on ODL, 2 on IDL; ODL seta somewhat longer than other 2. Setae of ventral group on corm subequal in length, and accessory seta almost as long. In middle group, middle seta the longest, next the dorsal seta of this group; accessory seta very short, easily overlooked. Dorsal group consists of only 2 slender setae, plus a small seta just proximad on dorsal margin; accessory seta well developed. Ejector hooks at base rather smallish.

Trunk limb II (Plate 9:4). Gnathobase with 4 setae, the longest with long straight setules angled from the tip; 7 setae in gnathobasic filter comb. Eight scraping spines, increasing in length away from gnathobase except that number 5 seems short relative to number 4 in both species; all have delicate setules visible with oil immersion phase, although those of last two are very indistinct.

Trunk limbs III–V (Plate 9:5–7, respectively). Indistinguishable from *tenuicaudis.* Limbs III, IV, and V have 7, 6, and 4 'soft' (filtering) setae, respectively, on the exopodite, and 7, 5, and 0 setae, respectively, in the gnathobasic filter; because of the complex 3-dimensional configuration of the gnathobasic region of Limbs III and IV, the gnathobasic filter setae could not be seen clearly in the orientation of the limbs suitable for showing the 'soft' setae. Limb III has the same very long seta as in *tenuicaudis.*

Postabdomen (Plates 2:10; 8:8). Relatively wider than in *tenuicaudis,* about 2 1/2 times as long as wide. Ventral margin rather strongly convex; 2 distinct notches in distal half and a fainter third notch before the middle, each associated with a short transverse crescent of fine setules, the proximal and middle notches also having a short lateral crescent on either side. Anal groove delimited by distinct angles; length of anal groove somewhat less than pre-anal portion, which is keel-like; postanal portion much shorter than half the length of the postabdomen. Anal groove completely unarmed (Plate 3:1), except for a few small spinules at postanal angle. Postanal portion tapered markedly, provided with a series of 10–13 marginal denticles, of which those in positions 5 through 13 counting from the distal end have a strong doubling tendency, with frequencies ranging from 15% in positions 5 and 6 to 40% in positions 9 and 10; denticles in positions 1–4 are always single; distalmost denticle relatively short and slender; next 2–4 denticles, most commonly 3, very large, curved, decreasing in length and stoutness proximad, forming a distinctive cluster, each denticle provided with several very fine setules mostly attached to concave margin; remaining denticles abruptly much smaller and considerably smaller than the corresponding denticles in *tenuicaudis.* Lateral surface provided with 6–9, most commonly 7, high fascicles in a row converging toward the dorsal margin distally, resulting in longest members of distalmost 3 or 4 fascicles projecting beyond margin; members in each fascicle increase in length distad, with distalmost member being stout and spine-like; occasionally a few very small spinules occur beyond the distalmost fascicles. Proximal to fascicles are 2 crescents or rows of very small setules parallel to anal groove but some distance from its margin, and still farther removed are 3 shorter rows of setules (Plate 3:1), giving essentially the same configuration as in *tenuicaudis.* Abdominal setae short, no more than half again as long as pre-anal margin.

Postabdominal claw (Plates 3:2; 8:9). Long, stout, almost straight except for mild curvature in distalmost quarter; concave margin provided with about 50 fine setules, those in distal half being somewhat longer; row of even longer setules on medial surface, visible with SEM but generally not with the light microscope. Basal spine more than half the length of the claw, only slightly curved, weakly sigmoid at base; concave surface provided with 6–11 very small but distinct spinules, about equal in length, stoutness, and spacing, or with middle ones possibly a little stouter and distal ones perhaps a little longer. Typically 2 small setae at

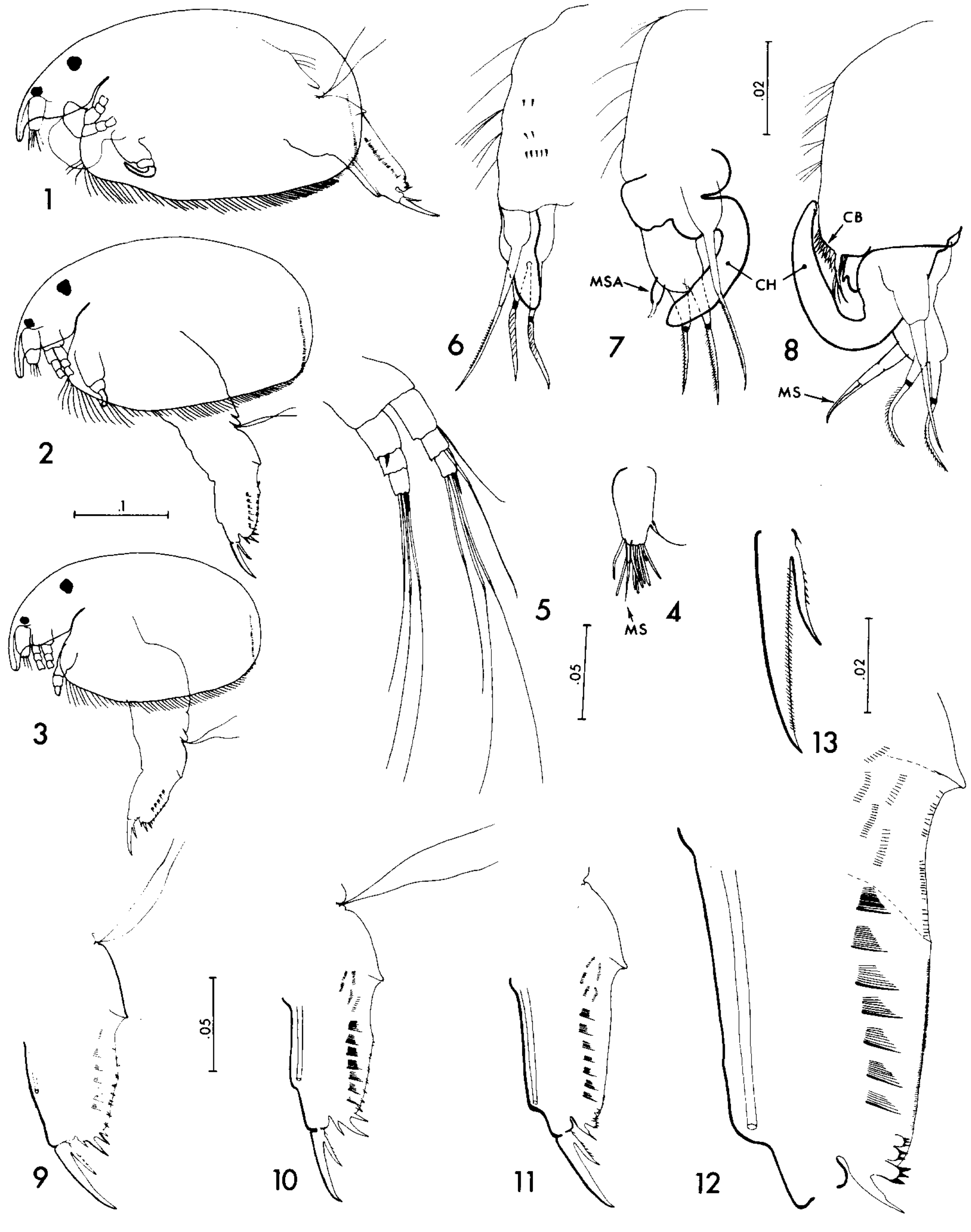

Plate 10. Oxyurella brevicaudis sp. nov. Males from Swamp Creek, N.H. (F1968): *1.* mature male; *2.* instar-II male; *3.* instar-I male; *4.* antennule, mature male, showing the very short 10th aesthetasc attached toward the lateral margin (MS = 2-segmented male seta); *5.* antenna, mature male, showing the reduced development of the seta on the middle endopodite segment; *6-8.* part of trunklimb I of instars I and II and of mature males, respectively, showing the progressive development of the copulatory hook, the accessory male seta on the IDL, and the copulatory brush (CH = copulatory hook; CB = copulatory brush; MSA = male seta anlage; MS = male seta); *9-11.* postabdomens and postabdominal claws of instars I and II and of mature males, respectively; *12.* postabdomen, mature male; *13.* postabdominal claw, mature male.

base of claw near base of spine, sometimes only one.

Length (Fig. 1): The overall length range of the Florida population ($n = 208$) is 0.26–0.48 mm, with instar I measuring 0.26–0.29 mm, instar II 0.31–0.34 mm, and the smallest females carrying eggs 0.37 mm. The size ranges in the population from New Hampshire are almost identical. Thus, this species is distinctly smaller in size, instar by instar and stage by stage, than *O. tenuicaudis* in Scandinavia.

b) Ephippial female

As in *tenuicaudis*, the ephippial female is undifferentiated externally from the parthenogenetic female except in being relatively higher (Plate 9:1) and in having the dorsal margin pinched together into a rounded keel. Likewise as in *tenuicaudis*, the entire shell functions as an ephippium (Plate 9:2), and there is no special egg locule nor any distinctive shell patterning. The egg becomes surrounded by a foam-like material, also as in *tenuicaudis*, although in the cast ephippium the foam extends to the dorsal and anterior margins, seemingly less confined by the inner lining of the brood pouch than in *tenuicaudis;* the dorsalmost cells perpendicular to the hinge have peculiar annular thickenings in their walls, suggesting that they may have a different origin than the foam-like material.

c) Males

Shape (Plates 6:7; 10:1–3). More elongate than parthenogenetic females, and dorsal margin less strongly convex. Ventral margin of mature male strongly concave in front of the ventral bulge; marginal setae along bulge considerably longer than in female, and setae in front of bulge long, very slender, and with long, hair-like lateral branches.

Head and rostrum. Essentially undifferentiated from female.

Antennule (Plates 6:5; 10:4). Almost indistinguishable from female except for presence of an additional short aesthetasc and the special 2-segmented male seta, which arises from anterior surface near tip of antennule; male seta somewhat longer than aesthetascs, basal segment much more heavily chitinized. Ten aesthetascs (instead of 9 or 12, as predicted from Scourfield 1896), of which the 9 that also occur in the female, have about the same relative lengths as in the female; 10th aesthetasc much shorter than the others. Antennular seta slender and sharply pointed, about half as long as antennule, arising from a distinct tubercle about 1/3 distance from tip; possibly somewhat shorter than in *tenuicaudis*.

Antenna (Plates 6:6; 10:5). Formula $\frac{0(1)\text{-}0\text{-}3(1)}{1\quad\text{-}1\text{-}3(1)}$. As in the male of *tenuicaudis*, the seta arising from the middle segment of the exopodite is much shorter than in the female (cf. Plate 8:7).

Trunk limb I. The ontogenetic changes that occur from instar I to maturity (Plate 10:6–8, respectively) are scarcely distinguishable from *tenuicaudis*, including the progressive shortening of the ODL and IDL setae, the general morphology of the anlage of the male IDL seta in instar II and its achieving a size comparable to the other 2 IDL setae in instar III, the progressive development of the copulatory hook, and the general morphology of the copulatory brush and the uncertain presence of a copulatory brush seta in instar III.

Postabdomen. The ontogenetic changes from instar I to maturity (Plate 10:9–12, respectively) parallel those in *tenuicaudis*. The general shape of the postabdomen and its armament in instars I and II are very similar to the corresponding female instars. The chief difference is the presence of genital pores, that of instar II being associated with a distinct notch in the ventral margin about 1/3 the distance from the tip (Plate 10:10); the pores, the broader postabdomen of instar I, and the ventral notch in instar II provide the best first means of recognizing immature males if trunk limb I cannot be seen clearly; in *brevicaudis* the genital pore of instar II is farther from the tip than in *tenuicaudis*. Postabdomen of mature male quite similar to that of *tenuicaudis* in lacking the marginal denticles of the female except for a single enlarged denticle distally, and also in having instead 2 or 3 rounded tubercles distally, each provided with 2–3 short, stout spines (Plates 6:4; 7:6; 10:12). The dorsal margin between the tubercles and the postanal angle is provided on each side with a row of very fine setules, which tend to be organized into about 9 groups. Anal groove likewise bordered by several groups of somewhat larger setules, unlike female, which is completely unarmed. Genital pores flush with the surface, not expanded distally lip-like as in *tenuicaudis* (Plate 6:4; 7:6).

Postabdominal claw. Instars I and II (Plate 10:9 & 10, respectively) much the same as in female.

Claw of mature male (Plates 6:4; 10:13) also resembles that of female, except for being somewhat shorter and stouter and the basal spine being distinctly curved or even sigmoid instead of almost straight.

Size. No males were recovered from Clearwater Lake, Fla., but the few specimens of instars I, II, and III in the sample from Swamp Creek, N.H., measured 0.27 mm (1), 0.30 mm (1), and 0.31–0.34 mm (5), respectively. Figure 1 shows that the mature males are smaller than the smallest mature females in the sample, as seems characteristic of chydorids in general. Additional mature males from Old Lake, Ind. (F6055) and Mann's Creek Lake, Wisc. (F6120), measured 0.36 mm (2) and 0.35–0.36 mm (4), respectively.

Distribution

Oxyurella brevicaudis is widely distributed in North America throughout the region east of the Great Plains from southern Canada into the Gulf States and even further southward at least to Guatemala and possibly Panama. Within this region it tends to be very infrequent in its occurrence. It seems to be less frequent in southern Canada than in the Gulf States, which together with its extension of range into the Tropics suggests that its major distribution is in the lower north temperate latitudes of the Western Hemisphere.

In southern Canada the species has been recovered from less than 1% of many samples examined. Hann (1975), for example, had only 5 positive samples out of 672 collected in Ontario in 1972–73; Chengalath (1980) only 2 positive samples from Nova Scotia (plus a 3rd record, from Québec, discovered subsequently) out of 356 samples collected from coast to coast and from as far north as Wood Buffalo National Park and Hay River in the Northwest Territories; and Brandlova *et al.* (1972) had no recoveries out of 344 samples from 244 different waterbodies collected in Ontario in 1967–70. In the southern states, on the other hand, roughly 5% of the available samples were positive – 4 out of 74 samples from Mississippi, 6 out of 111 from Louisiana, and 15 out of 477 from Florida. The species tends to occur more commonly in small waterbodies – in ponds, roadside ditches, etc. – as does also *O. tenuicaudis* in Europe.

From the rest of the continent there are only two records. Bardach (1954) found the taxon (reported as *O. tenuicaudis*) in one sample from northeast of Great Slave Lake, NWT, and Kiser reported (in correspondence) that among the very numerous collections he has made in the Northwest, he found the taxon only once – in Scott's Lake, Thurston Co., Wash. Attempts to locate Bardach's specimens were unsuccessful, but Kiser's are typical *brevicaudis.* Thus the taxon does extend to the West Coast, but it is extremely infrequent west of the Rockies. Chengalath (1980) had no positive records among a total of 190 samples from Manitoba (39), Saskatchewan (51), Alberta (53), British Columbia (31) including Vancouver Island, and Northwest Territories (16).

The generally very low abundance of *O. brevicaudis* makes it time consuming to examine a large sample carefully, specimen by specimen, on the rare chance of finding that occasional individual of this species. This is one of the reasons that persistence of the species over time at a particular site is difficult to establish. The longest time series of samples available from a particular site is that from Skater's pond near Bloomington. Here, small numbers of specimens were recovered in 4 years from samples collected during the period 1975–81, but only in the months October through April. Such presence only in the cold season is difficult to reconcile with the other evidence that suggests a more southern affinity of the species.

The detailed records of occurrence are the following. The information in parentheses after each record is either documentation from the literature, the accession numbers of the samples in our collection in Bloomington, or the slide numbers in the E. A. Birge collection. Numbers preceded by C are splits of Chengalath's samples.

Nova Scotia: Holdrights Lake (5760 = C253) south of the entrance to Kejimkujik National Park and Grafton Lake (5767 = C260) in the Park (Chengalath 1980).

Québec: Lac Soumire in La Mauricie National Park (5805 = C297).

Ontario: Point Pelee, Silver Lake, Bob's Lake (Lanark Co.), and Green Bay (Hann 1975).

Northwest Territories: Thelon Watershed, District of Mackenzie (Bardach 1954).

Washington: Thurston Co. – Scott's Lake (R. W. Kiser sample 1014).

New England: Listed by Birge (1918), but no localities specified.

New Hampshire: Grafton Co. - Fowler River (1978); Merrimack Co. - Eagle Pond (1973); Sullivan Co. - Otter Pond (1964), Swamp Creek (1968).

New York: Hamilton Co. - Pond at Sabbatis Boy Scout Camp (3372).

Michigan: Barry Co. - Hamilton Lake (1857), Lawrence Lake (Keen 1976); Cheboygan Co. - Twin Lake (283).

Indiana: Kosciusko Co. - Winona Lake and Wyland Lake (Mueller 1964). Lagrange Co. - Atwood Lake (2520), Long Lake (2883), Oliver Lake (3802); Monroe Co. - Skater's Pond (4073, 4075, 4086-87, 4091, 4143, 4148, 4166, 4168, 4173, 4235, 5528, 5969, 6168); Noble Co. - Big Lake (2333), Cree Lake (2508); Whitley Co. - Cedar Lake (6051), Loon Lake (3698, 4471), Old Lake (4848, 6055).

Wisconsin: no localities specified (Birge 1918); Oneida Co. - Hemlock Lake (6109); Vilas Co. - Mann's Creek Lake (6119-20).

Minnesota: Cook Co. - Squint Lake (Synerholm 1974).

Iowa: Dickinson Co. - 'grassy kettle holes' (Stromsten 1920).

Tennessee: Obion Co. - Reelfoot Lake (Hoff 1943), roadside ditch at Reelfoot Lake (4679).

Arkansas: slide in E. A. Birge collection from Hot Springs (C-53-10).

Oklahoma: Pontotoc Co. - Ada Lake (Mackin 1931); Jones (1954) has two records of *Oxyurella* from Pontotoc Co., hence likely from Ada Lake also.

Texas: slides in E. A. Birge collection from San Marcos (A-6-2), Dallas (C-53-7), and Hutchins (C-53-9).

Louisiana: Calcasieu Par. - Lake Charles (Birge 1910; and slides C-53-6 and C-53-8 in E. A. Birge collection); Concordia Par. - swamp pond along Hgy. 84, 1 mi. E of Frogmore (4669); Iberia Par. - Shaw Island Lake (Binford 1975); Iberville Par. - roadside ditch along Hgy. 69 S of White Castle (4622); Lasalle Par. - Old River on Hgy 84 (4664); Natchitoches Par. - lake along Hgy. 1226, 5.2 mi. N of Hgy. 84 (3855); Tensas Par. - Lake St. Joseph (4675).

Mississippi: Bolivar Co. - Lake Bolivar (4578); Lawrence Co. - creek 0.8 mi. S of New Hebron (Chien 1969); Leake Co. - gum swamp just W of Edinburgh (4594); Neshoba Co. - farm pond along Hgy. 16 (4593); Winston Co. - farm pond along Hgy. 15 (4585).

North Carolina: Bladen Co. - Pages Lake (4997); Wake Co. - Panther Lake (4978-79, 4985), Sunset Lake (3785), Yates Pond (4976).

South Carolina: Bamberg Co. - pond at jct. Hgys. 21 and 61 (5002, 5181).

Georgia: Charlton Co. - Billy's Lake in Okefenokee Swamp (198).

Florida: Alachua Co. - pond near jct. Hgys. 325 and 346 (5025, 5223), Santa Fe Lake (5212); Gilchrist Co. - roadside ditch along Hgy. 26 (5228a); Highlands Co. - Lake Annie (2918), Huckleberry Lake (5068), Mirror Lake (141), pond in Highlands Hammock State Park (5043), Wolf Lake (5124); Leon Co. - Cypress Lake (5242), Grassy Lake (5335), Pecks Pond (5369); Putnam Co. - Clearwater Lake (5019, 5209), Goose Lake (5155a).

Cuba: Laguna la Luisa (Kořínek, ms).

Guatemala: slide in E. A. Birge collection from Los Amates (A-3-3); Aguada Terminos (Goulden 1966a); Laguna de Petenxil (Goulden 1966b).

Panama: few specimens from a pond (Dodds 1926). As these specimens are not in the University of Michigan Museum of Zoology, nor in the U.S. National Museum of Natural History, the identification could not be verified.

Discussion

Oxyurella tenuicaudis is one of many species of chydorids claimed to be amphi-Atlantic in distribution, i.e. occurring on both sides of the North Atlantic Ocean. But besides Europe and North America it is also claimed to occur across Asia to China, south to New Guinea, and even into northern Africa and South America (see Smirnov 1971, for details of distribution). Hence, although it is scarcely cosmopolitan, it is still intercontinental and very widespread.

When Birge (1910) established the genus *Odontalona* for Sars' species *tenuicaudis* and his own new species *longicaudis* from the Americas, he noted that the postabdomen of the American *tenuicaudis* was shorter and broader than that of the European taxon. J. Green in a letter to DGF dated 17 January 1961 commented on the same difference as apparent to him from published illustrations, and he inquired whether this difference were real or the result of inaccurate illustrations. Finally, Goul-

Table 1. Morphological differences between *O. tenuicaudis* and *O. brevicaudis.*

Character	*O. tenuicaudis*	*O. brevicaudis*
Mature Females		
Shape	1. relatively elongate; length generally ≥ 1.6 times maximum height	1. more compact; length generally ≤ 1.6 times maximum height
	2. dorsal margin rather weakly arched	2. dorsal margin more strongly arched
Shell	3. posterior margin weakly convex	3. posterior margin strongly convex
	4. longitudinal striae or ridges present	4. no markings except occasional vague polygons posteriorly
	5. surface of shell (and head) with irregular small pits	5. surface of shell (and head) densely covered with minute wart-like tubercles
	6. submarginal setules along posterior margin decrease in size gradually upward	6. submarginal setules decrease in size abruptly about half way upward
Head	7. $IP < PP$ except in some smallest specimens	7. $IP > PP$
	8. $LP > 2\ IP$	8. $LP < 2\ IP$
	9. the 2 minor median pores surrounded and connected to each other by irregular beaded thickening, sometimes also connected to anterior median pore	9. the 2 minor median pores surrounded by irregular beaded thickening, seldom connected to one another and never to anterior median pore
Labrum	10. distinctly hatchet-shaped, with anterior–ventral and posterior–ventral angles relatively sharp	10. shape variable, vaguely hatchet-shaped; anterior margin broadly confluent with ventral margin; posterior–ventral angle at times narrowly acute
	11. angle behind keel distinctly obtuse ($>90°$)	11. angle behind keel weakly acute ($<90°$)
Postabdomen	12. elongate; about 3 × longer than wide; postanal portion about 1/2 length of postabdomen	12. shorter; about 2 1/2 × longer than wide; postanal portion $<1/2$ length of postabdomen
	13. postanal portion tapered slightly	13. postanal portion tapered markedly
	14. proximal marginal denticles longer, with weak tendency toward doubling in positions 11–14	14. proximal marginal denticles very short, with strong tendency toward doubling in positions 5–13
	15. small denticle-like spines along distal half of anal groove	15. anal groove completely unarmed
	16. typically 6 low lateral fascicles in row parallel to dorsal margin; distalmost fascicles do not project beyond margin	16. typically 7 high lateral fascicles in row strongly angled to dorsal margin; distalmost fascicles project beyond margin
Postabdominal claw	17. long, very slender, curved; distal third more strongly curved	17. somewhat shorter and distinctly stouter; proximal 3/4 almost straight; distal 1/4 weakly curved
	18. basal spine slender, curved outward; up to 1/2 length of claw	18. basal spine, only slightly curved; more than 1/2 length of claw
	19. basal spine unarmed	19. basal spine with 6–11 fine spinules on anterior surface
Size	20. distinctly larger, instar by instar; length range .30–.57 mm; smallest mature females .43 mm	20. distinctly smaller, instar by instar; length range .26–.48 mm; smallest mature females .37 mm
Instar-I Males		
Postabdomen	21. genital pore about 1/5 distance from tip	21. genital pore about 1/3 distance from tip
Instar-II Males		
Postabdomen	22. width about 1/5 of length	22. width about 1/3 of length
	23. small clusters of setules distad from fascicles	23. such setules lacking
Mature Males		
Postabdomen	24. genital pores projecting lip-like distally	24. genital pores flush with surface

Note: Other differences between the males and between ephippial females of the two species are essentially the species differences listed under the mature females.

den (1966b) besides illustrating a short postabdomen from a Guatemala specimen suggested that the differences between the European and American forms warranted recognition at the level of subspecies.

The present study has demonstrated not only that these differences in shape and structure of the postabdomen are real and significant, but that they are part of a whole suite of characters that help differentiate the North American from the European taxon (Table 1) and justify establishing the North American taxon as a full species. One would like to know if the cognate populations from elsewhere in the world are conspecific with the *tenuicaudis* from Scandinavia. The eventual answer whether yes or no will be important in helping to interpret the evolution and geographic distribution of this and the other species within the highly distinctive genus *Oxyurella.*

This is still one more example of a taxon formerly considered virtually cosmopolitan, or at least intercontinental, that is now understood to be composed of two or more species, no one of which by itself encompasses the full distribution claimed previously. Examples of such taxa already in the literature are *Alona rustica* (Flössner and Frey 1970), *Eurycercus lamellatus* (Frey 1975), *Alonopsis elongata* (Kubersky 1977), *Chydorus sphaericus* (Frey 1980a), *Ephemeroporus barroisi* (Frey 1982a), and *Chydorus reticulatus* (Frey 1982d). Unfinished studies on a number of other taxa are helping to reinforce the strong impression that many presumed instances of cosmopolitanism arose stealthily from an inadequate taxonomic resolution. The guiding principle of chydorid distribution must be restructured from a tacit acceptance of cosmopolitanism until proved otherwise to a firm denial of cosmopolitanism until demonstrated unequivocally to be so (Frey 1982c).

The characters most useful in separating the two taxa in this paper are numbers 3–5, 7–10, 12, 14–16, 19, and 22 in Table 1, relating primarily to shape and surface markings, various features about the postabdomen, shape of labrum, and morphology and arrangement of the headpores. Brief diagnoses for distinguishing between mature females of these two taxa are the following:

O. tenuicaudis. Shell with vague longitudinal ridges; posterior margin weakly convex. Postabdomen about 3 times longer than wide; row of usually 6 low lateral fascicles parallel to dorsal margin, with none of distalmost fascicles projecting beyond the margin; small marginal denticles along distal half of anal groove. Labrum typically hatchet-shaped; anterior angle narrowly rounded. In light microscope the 2 minor median pores are connected by an irregular beaded thickening and sometimes also to anterior pore; PP distance greater than IP distance, and lateral pores more than an IP distance to either side of minor median pores.

O. brevicaudis. Shell without longitudinal ridges but densely covered with small wart-like tubercles; posterior margin strongly convex. Postabdomen shorter, about 2.5 times longer than wide; row of usually 7 high lateral fascicles distinctly angled to dorsal margin, with the longest setae of some of distalmost fascicles projecting beyond margin; anal groove completley unarmed. Labrum scarcely hatchet-shaped; anterior angle broadly rounded. In light microscope the 2 minor median pores are surrounded but seldom connected to one another by irregular thickenings and never so connected to anterior pore; PP distance always less than IP distance, and lateral pores less than an IP distance to either side of minor median pores.

Of even greater significance than the differences between these two taxa are the shared characters that unite them into a highly distinctive genus. Full evaluation of these characters as plesiomorphic will have to wait until the other species presently in the genus – *singalensis, longicaudis, ciliata,* and *wallaciana* – have been studied in comparable detail.

1. Both species of *Oxyurella* in this paper have just two setae on the IDL, whereas the typical number in chydorids is three, which Smirnov (1971) suggests may be the minimum number required for hanging on to the substrate. The only previous description and illustration of trunk limb I in *tenuicaudis* are by Smirnov (1971), who states that there are three setae here (on what he calls the outer branch of the endite), but, whereas his Fig. 116B of a specimen from Ivan'kovo Reservoir shows three setae, Fig. 623I accompanying the description seems to show only two, although the details of the drawing are not entirely clear. Our careful examination of many specimens of both species has convinced us that only two IDL setae are present, invariably. A prior example of chydorids with only

two IDL setae, which at that time was thought to be unique among the chydorids, is the two species of moss chydorids in the genus *Bryospilus*, which are so completely restricted to scrambling over and through the substrate that they have lost their ability to swim (Frey 1980b). A single seta on the ODL is noteworthy but not unusual. More commonly chydorids have a very small second seta in addition.

2. In species of the subfamily Aloninae the basal tip of the mandible articulates with a socket on the head located precisely where the head and shell join. This is one of the major characters separating the Aloninae from the Chydorinae (Frey 1966). Often the portion of the headshield anterior to this articulation is expanded as a fornix, which covers over the base of the antenna and overlaps the adjacent shell. The antenna and the two sensory setae arising from the basal segment project through this gap between head and shell, the sensory setae typically being positioned close to the mandibular articulation.

The relationships in *Oxyurella* are completely different. Instead of a fornix expansion of the head overlapping the shell, a portion of the shell narrowly overlaps the head, thereby closing off a part of the gap between head and shell and displacing the functional space for the antennae some distance from the mandibular articulation. In transmitted light this configuration resembles a narrow sigmoid channel extending dorsad from what in reflected light (or scanning EM) seems to be the place where the head and shell come together, and hence the presumed location of the mandibular articulation. The functional advantages of this peculiar configuration are unknown.

3. The pattern of pores on the headshield is very useful in interpreting phylogenetic relationships. In the Aloninae the most common pattern is two or three pores on the midline connected by some kind of channel or by a continuous or interrupted chitinous line. Some taxa (e.g. *Monospilus* and *Euryalona*) have only a single median pore. A few have two *(Bryospilus)* or three *(Alona pulchella)* median pores that are not connected to one another in any way. *Oxyurella* is unique among the chydorids, so far as known, in having four median pores, which are not connected by any channel. Each is surrounded by an irregular chitinous thickening. The four pores can be completely separated from one another, as in most specimens of *brevicaudis*, or the middle pores can be connected to each other by a beaded line, and these in turn can be connected to the anterior pore, as in some specimens of *tenuicaudis*. *O. singalensis* also shares this pattern of four separated pores on the midline, suggesting that this pore arrangement may well be characteristic of the genus *Oxyurella*.

4. Descriptions of ephippial females in the literature are about as rare as those of males, and descriptions of the definitive isolated ephippia are even rarer. Typically the portion of the shell in which the egg will become located on molting is bulged out to form a locule, and the shell itself is often pigmented in varying degree and structurally modified with ridges, reticulations, spines, etc. Also, typically, a variable amount of the anterior, or anterior and ventral, or even the entire free margin of the shell is sloughed off along predetermined lines of structural weakness, leaving an abbreviated structure that is most difficult to associate by means of morphological details with the species that produced it. In extreme cases the ephippium consists of little more than an egg locule and a surrounding narrow and wafer-thin margin representing the two valves of the shell closely appressed and trimmed precisely to the minimum needed to protect the egg. The nature of the ephippium is so highly variable within the family that any patterns of similarity must be highly significant phylogenetically. Hence, special effort should be made, as with males, to seek out ephippial females and ephippia, as these together constitute the functional components (as individuals) of the evolutionary mechanism.

In the two species of *Oxyurella* treated in this paper, the entire shell functions as the ephippium, without any special egg locule, modification of the surface pattern, or pigmentation. The chitin of the shell is thickened dorsally, and the dorsum of the animal is pinched together to form a rounded keel, but these features are present in all ephippia and probably are necessary to provide the spring-like closure of the two valves around the resting egg. Not visible externally is the foam-like mass surrounding the egg, which is likely secreted into the brood pouch. This material presumably affords the same protection against egg predators and light intensity that the more highly evolved ephippia of other species achieve by very tight appression of the valves and pigmentation. Intuitively at least this ephippium seems to be very primitive.

5. In chydorid Cladocera males usually are considerably differentiated from females in their morphology. Typically their body is less highly arched, the rostrum shorter, the antennule larger and with more aesthetascs, the first trunk limb modified for copulation, and the postabdomen and claw variably changed from the female configuration to function in sperm transfer. Additional aesthetascs on the antennule and setae on the first trunk limb presumably are involved in various discriminating and coordinating functions in achieving mating between males and females of the same species. As the ephippial female appears to be identical to the parthenogenetic female in details of morphology except in structure of the shell but with no additional sensory structures or modifications of existing ones, the chief responsibility in reproductive discrimination seems to reside in the males. Working broadly among the chydorids we have become accustomed to finding very considerable differences between males and females, and sometimes between males of closely related species in which the females are essentially undifferentiated from one another (e.g. the subspecies of *Alona rustica* in Flössner & Frey 1970).

The situation in these two species of *Oxyurella* is that the male is very little differentiated from the female except in trunk limb I, the postabdomen, and a few minor details. The rostrum is unchanged from the female, and the antennule differs only in having the characteristic 2-segmented male seta and in having one additional, very short aesthetasc, but not also in being larger and in having longer and more numerous aesthetascs, as would normally be expected (Scourfield 1896). In structure of the postabdomen the males of both species differ from the females in a common generic pattern while retaining a variety of details that differentiate the females at the species level. In structure of the first trunk limb, males of the two taxa are not appreciably different from one another.

Thus, here is a pair of species in which the females are quite highly differentiated from one another, but in which the males are not additionally differentiated beyond the pattern of male/female differences that seems characteristic of the genus, particularly in the morphology of the postabdomen. The incomplete sketch by Brehm (1938) of the male postabdomen of *Oxyurella longicaudis* and the no more satisfactory sketches by Daday (1898) of the male and the male postabdomen of *O. singalensis* seem to conform to the pattern of male morphology exhibited by the two species in this paper. This suggests that the general pattern of the male postabdomen preceded in evolution the differentiation of the species, and that differences in structure of the postabdomen from one species to another primarily reflect the species differences exhibited also by the females.

6. A few other characters seem to be general for the genus. The cluster of much longer denticles at the tip of the female postabdomen, which Sars considered highly distinctive of *tenuicaudis*, occurs in all the species. The antennal formula $\frac{0(1)-0-3(1)}{1\ -1-3(1)}$, with a swimming seta arising from the basal segment of the endopodite in all instars both male and female, although not unique to *Oxyurella* is shared by all the species in the genus. Likewise the pre-anal portion of the postabdomen is keel-like in all the species. The species as a group are trim in appearance, robust, heavily chitinized, and have 'rolled' edges along the ventral margin of the shell and headshield. They tend to be bright brownish yellow in color, which makes them easy to recover from a mixed sample.

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