THE NYMPH OF THE MAYFLY GENUS TORTOPUS (EPHEMEROPTERA: POLYMITARCIDAE)[1]

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ABSTRACT

Immatures of this genus had not been taken prior to the discovery of large numbers of *T. incertus* nymphs during a biological survey of the Savannah River. The nymphs honeycomb the clay banks of the river with their burrows and follow the river level up or down, as evidenced by abandoned burrows 5 or 6 feet above low-water level. Apparently the insect requires 2 years to develop from egg to adult, and emergence of adults is restricted to the period from late July to early September. The similarity of the distribution of hairs on the legs, and the type of burrows occupied by the nymphs, suggest that the insect strains its food much as does its African relative *Povilla*. The nymph of *T. incertus* is described and figured.

The U. S. Public Health Service conducted extensive physical, chemical, and biological surveys of the Savannah River from July 1951 through July 1952. The results were summarized in an interim report (Gold et al. 1954). In the course of these studies, nymphs of the burrowing mayfly *Tortopus* were found to be abundant in the banks of the river. Since little was known of this genus of mayflies in North America, a special effort was made to record observations on its ecology and morphology.

The Savannah River is primarily a mountain and piedmont stream; nearly 70 percent of its drainage basin lies in these physiographic provinces, only 30 percent in the coastal plain province. The river retains many of its piedmont characteristics even where it crosses the coastal plain between the cities of Augusta and Savannah, Georgia. It may be distinguished from the streams arising within the coastal plain by the fact that its waters are not colored brown by the lignins so prevalent in coastal plain streams; instead, it possesses a rather high turbidity due largely to suspended silt from the piedmont. In addition, it has a pH near the neutral point, and a very low mineral content. Prior to 1951, when Clarke Hill dam was completed 20 miles upstream from Augusta, the river was subject to rather extreme fluctuations in flow.[5]

Crossing the coastal plain the river follows a meandering channel through a densely wooded flood plain 3 to 5 miles wide. While the river bottom is composed largely of shifting sand, there are a number of places where the river swings to the edge of its flood plain and encounters Cenozoic sedimentary formations, exposing other types of bottom materials such as clay, marl, gravel, sandstone, and limestone. At meanders, where the river is cutting away at its own flood plain, caving, vertical, or undercut clay banks occur on the outer edge of the bend. These banks drop precipitously below the water level to the deepest part of the channel, which is often 10 to 12 feet at low water.

The shifting sand of the river bed has only a depauperate fauna, but the more stable benthic substrates such as fallen trees, brush piles, rock outcroppings, and clay banks are all rather densely populated by macroinvertbrates, particularly in areas of rapid current. The clay banks support a community of organisms dominated by nymphs of the burrowing mayfly, *Tortopus*. Such banks, profusely perforated by burrows of *Tortopus* nymphs, are present at almost every bend of the river (figs. 1 and 2). The clay substrate inhabited by *Tortopus* is always firm, nearly always vertical, and usually exposed to swift water. This habitat is difficult to sample adequately; however, several qualitative collections were made in June and July 1952, from clay banks located near the mouth of Upper Three Runs, Aiken County, South Carolina; near Hancock Landing, Burke County, Georgia; and near the mouth of Steel Creek, Barnwell County, South Carolina (172 to 155 miles from the mouth of the river).

On July 30, 1952, a representative quantitative sample was taken from a clay bank near Ebenezer Landing, 52 miles from the river's mouth. In this instance a block of perforated clay was removed from the bank 2 feet below the water line, and its volume was measured by displacement. It was then broken up and washed through a series of screens. The organisms present were sorted, identified, and counted, and their volume determined by displacement (table 1). *Tortopus* nymphs comprised 54 percent of the number of organisms from this sample and 94 percent of the volume. Many of these nymphs were about to emerge; thus the biomass of the *Tortopus* population was probably at its maximum. The other organisms found do not usually burrow in hard clay, but the burrowing

[1]This investigation was supported in part by a grant from the National Institute of Health, U. S. Public Health Service (No. RG-4058) to Berner. Accepted for publication August 7, 1958.

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[5]High 350,000 cu.ft./sec.; low, 1,040 cu.ft./sec.; average, 10,860 cu.ft./sec. at Augusta, Georgia.

activities of the mayflies provide them with a suitable habitat. This one sample obviously cannot be considered quantitatively representative of all clay bank areas of the river, but it does demonstrate that large populations of organisms are present in the substrate excavated initially by *Tortopus*. This observation was substantiated by the qualitative sampling of other clay banks where large numbers of *Tortopus* were also found.

Table 1.—Quantitative clay bank samples, Savannah River 52 miles from river mouth July 30, 1952.

Organisms	Number	Volume (cc.)
Nematoda: Undetermined	107	0.05
Arthropoda, Insect		
Plecoptera: *Acroneuria* sp.	4	0.05
Ephemeroptera: *Tortopus incertus* last instar	57	4.80
Tortopus incertus other instars	457	22.40
Stenonema sp.	18	0.02
Isonychia sp.	99	0.24
Tricorythodes sp.	4	0.00
Caenis sp.	5	0.01
Baetinae, undetermined	1	0.00
Odonata: Cordulinae, undetermined	1	0.00
Argia sp.	1	0.00
Neuroptera: *Corydalus cornutus*	5	0.80
Trichoptera: *Cheumatopsyche* sp.	5	0.00
Macronemum carolina	15	0.15
Macronemum carolina, pupa	1	0.04
Potamyia flava	1	0.00
Coleoptera: *Stenelmis decorata*, adult	117	0.17
Stenelmis sp., larva	26	0.05
Diptera: *Palpomyia* group	1	0.00
Pentaneura monilis group	4	0.00
Chironomidae, undetermined	2	0.00
Mollusca, Gastropoda *Pleurocera* (?) sp.	15	0.10
Mollusca, Pelecypoda *Sphaerium* sp.	1	0.00
Total	947	28.80

Volume of Clay Substrate—8000 cc.
Area of Exposed Surface—1600 cm²

The *Tortopus* burrows enter the bank at right angles to the exposed surface and form U-shaped tubes with parallel arms. The parallel arms sometimes adjoin each other so closely that the septum between them is broken. Apparently, a burrow is enlarged in length and diameter as the size of its occupant increases. This is accomplished by the nymph digging straight back from the end of the burrow and piling some of the clay in the center of the tunnel to form the septum separating the two arms. This method of construction allows the nymph to keep a current of water flowing through the burrow as it is enlarged. Mayfly burrows of this type were described by Swammerdam (1737) and were figured by Réaumur (1742) from the Marne River. These burrows were attributed to *Polymitarcys virgo* (Oliver)[6] by Wesenberg-Lund (1943) and to *Ephemera* by Verrier (1956). An examination of Swammerdam's plates indicates that he was illustrating the nymph of *Palingenia* while Réaumur's are possibly those of *Ephoron*.

One peculiar feature of this community is its apparently migratory nature. On many banks, abandoned mayfly burrows are found in abundance 5 or 6 feet above low-water levels, while at the same time, both occupied and unoccupied burrows are to be found at least 6 feet below the water surface. Since the uppermost of these burrows could only be occupied for a relatively

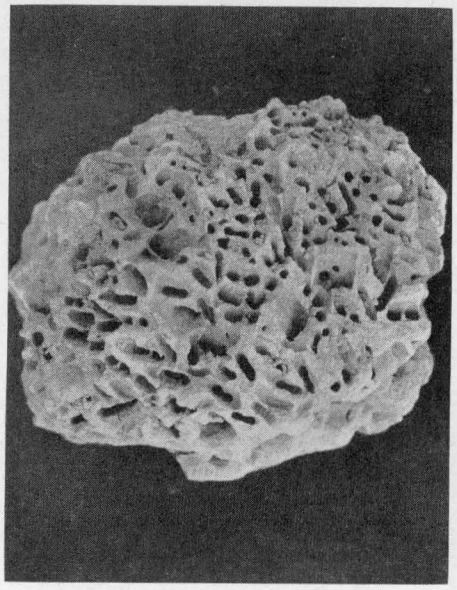


FIG. 1.—A mass of clay from the banks of the Savannah River showing the perforations produced by *Tortopus* nymphs.

short span of the nymphal life of the mayfly, it seems obvious that some individuals must move about in this honeycomb, building new burrows or occupying old ones above the normal levels while the river is high, and retreating to successively lower ones as the river level drops. The location of these burrows at just the points where the river current impinges upon a firm substrate undoubtedly aids the erosive action of the river against banks that would otherwise be very resistant to such attack.

Nymphs of *Tortopus* were sometimes found in bottom samples collected with a Peterson dredge. These nymphs are believed to have been washed from the steep clay banks which had crumbled

[6]The genus *Polymitarcys* was synonymized with *Ephoron* by Edmunds and Traver (1954).

into the river to form a clay bottom. Occasionally *Tortopus* nymphs were found burrowing in rotten wood in these areas. In addition to burrowing in compact gray clay, populations have been observed in sandy clay, peat, and unconsolidated sandstone.

The burrowing habits of *Tortopus* appear to be similar to those of *Povilla*, a genus of mayflies widely distributed in tropical regions. Kimmins (1948) reported that *Povilla* has caused damage to underwater wood by tunneling in it. *Povilla adusta* from Lake Nyasa in Central Africa was observed lining its tunnels with a substance having a thin papery texture. Nymphs of *Povilla* have also been found living in burrows in fresh-water sponges.

Recently Hartland-Rowe, studying *Povilla* in Uganda, has observed the nymph secreting silk from its anus and molding it with its mouthparts, then spreading the silk over the burrow with the fore legs (personal communication). Although silk secretion has not been observed for *Tortopus*, it is possible that it may have this same habit.

The disposition of the long hairs on the legs and on the head indicate that *Tortopus* feeds in very much the same manner as *Povilla*, which catches floating organisms or pieces of debris on its filtering brushes. These bits and pieces are then removed by the palps. Hartland-Rowe (1953) reports that *Povilla* feeds by rhythmically beating its abdominal gills for a few seconds at frequent intervals, thus producing an intermittent current of water from the anterior end of the body. He noted that food was transferred from the brushes to the mouth by two distinct simultaneous widesweeping movements: (1) by the maxillary palpi of one side removing the food from the mandibular brush of that side and (2) by the maxillary and labial palps of the opposite side collecting food from the tibial and femoral brushes. He also noted that this action is accompanied by an inward flick of the leg, bringing the brushes within reach of the palps. The movements are alternately from side to side.

Examination of the contents of the anterior portion of the digestive tract of several specimen of *Tortopus* to determine something of the feeding habits of the nymphs was not productive. The food was so thoroughly macerated into finely divided material that it was not possible to identify any of it. Occasionally small sand grains appeared in the gut contents, apparently ingested accidently during the course of feeding. We are convinced, however, that the food of these nymphs is obtained by filtration of river water and not by ingestion of clay as suggested for *Palingenia* by Schoenemund (1929, 1930) and Unger (1929). Plankton and periphyton were extremely scarce in the Savannah River. The base of the food chain of the *Tortopus* community is probably the organic debris being carried into the burrows by the swift current and the activities of the nymphs.

Attempts to observe *Tortopus* in the laboratory have thus far met with little success, because of the difficulty in keeping specimens alive. In 1954, living nymphs were carried from the Savannah River to Gainesville, Florida, where they were kept for about 3 weeks. However, no untreated flowing water was available in the laboratory at that time, and the nymphs were unable to feed. Very often they left their burrows and swam about, apparently searching for a more suitable site.

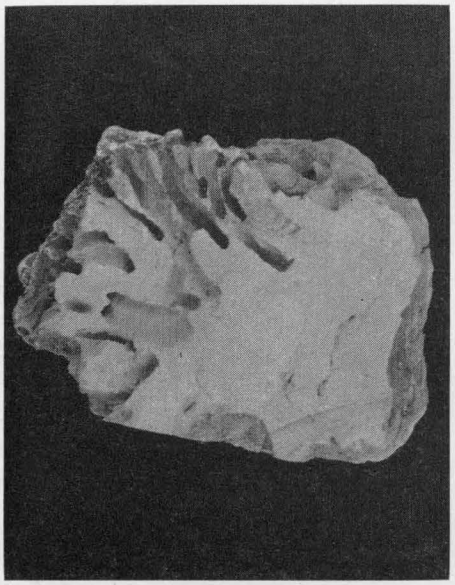


FIG. 2.—A section through the *Tortopus* burrows to show their interior.

Early in October 1956, when the Savannah River was revisited in an attempt to secure additional nymphs, the water was very high and even the burrows highest on the bank were submerged. Collecting was attempted but only empty burrows were found, probably because the river level had risen just a few days earlier and nymphs had not yet moved from the lower to the higher burrows.

Nymphs of *Tortopus* have also been taken from two other streams in Georgia. One of these collections was from the Canoochee River, 5 miles east of Claxton and ½ mile downstream from the bridge on U. S. Highway 280 at the Bryan-Evans County line, on August 6, 1958; the other was from the Choopee River in Tattnall County, 3 miles west of Reidsville and ¼ mile upstream from the bridge on U. S. Highway 380, on August 7, 1958. In addition, burrows believed to be those of *Tortopus* have been seen in Georgia on the Altamaha River at the Long-Wayne County line, just upstream from the bridge on U. S. Highway 301, and the Alapha River, 4 miles northeast of Naylor, at the Lowndes-Clinch County line.

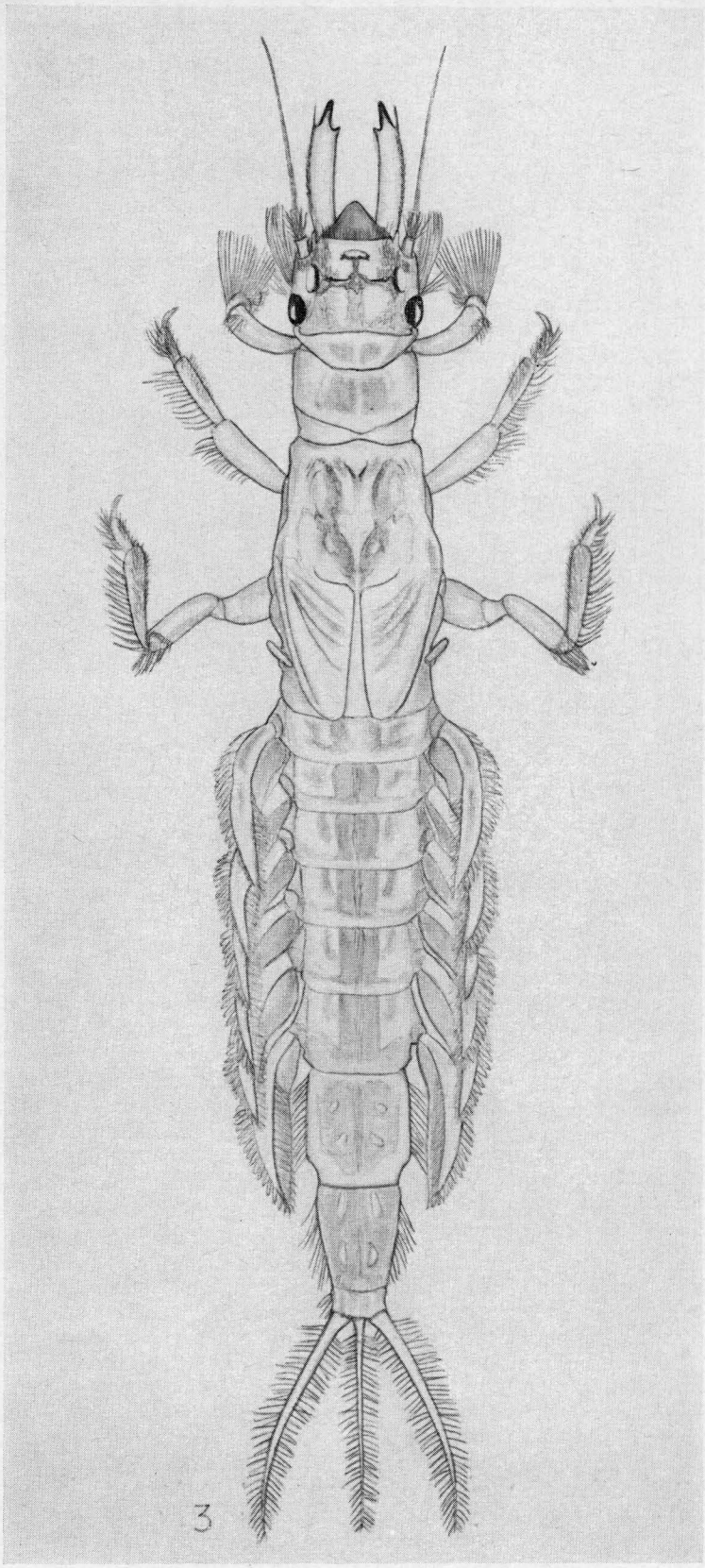
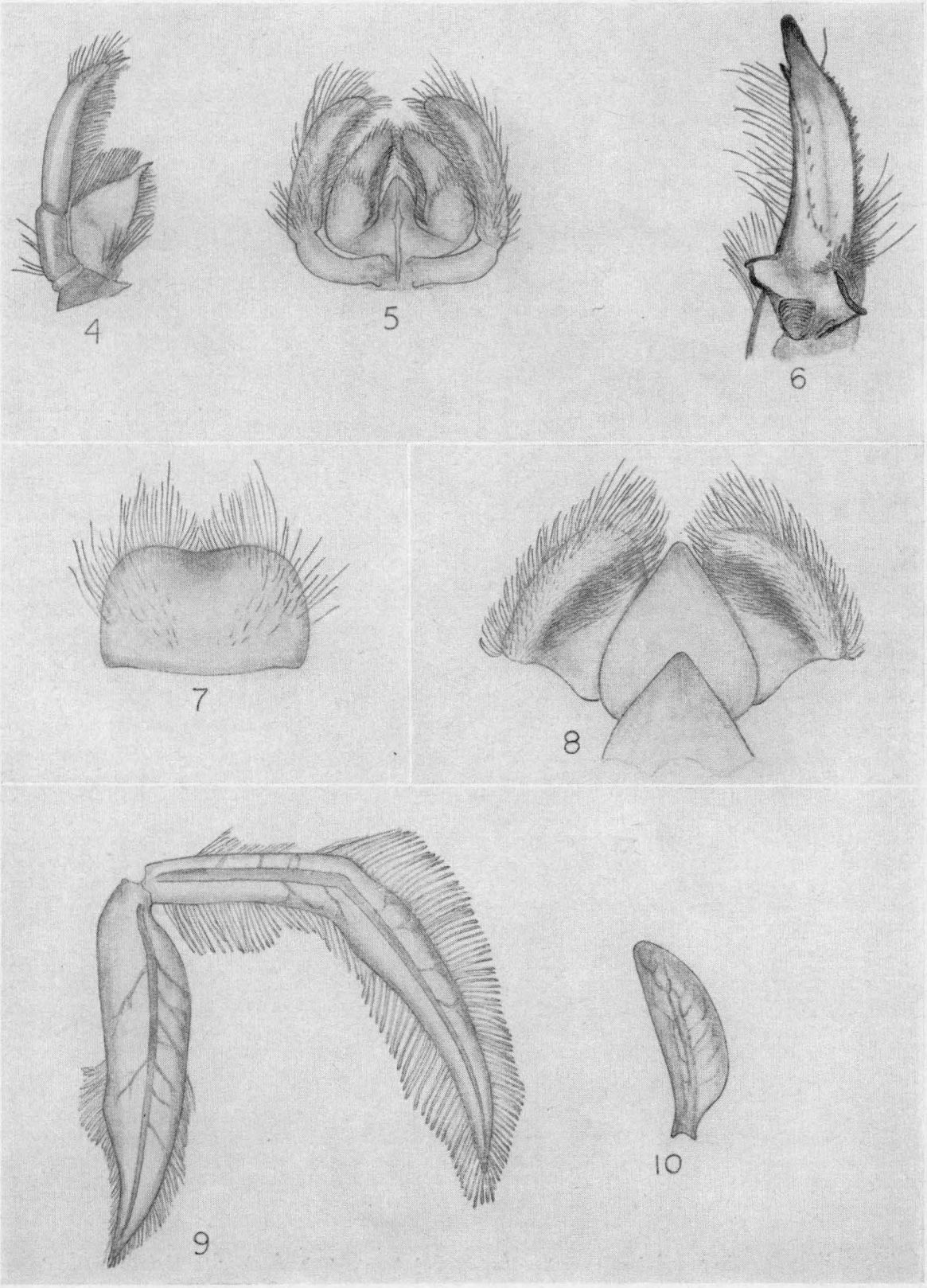


FIG. 3.—A mature female nymph of *Tortopus incertus*.



FIGS. 4–8.—Mouthparts of *Tortopus incertus*. 4. Left maxilla, 5. labium, palps displaced laterally, 6. right mandible, 7. labrum, 8. hypopharynx.
FIGS. 9–10.—Gills of *Tortopus incertus*. 9. 4th gill, right side, 10. 1st gill, right side.

LIFE HISTORY

Approximately 500 nymphs collected July 30, 1952, and 100 nymphs collected July 10, 1954, were examined to learn something of the life history of *Tortopus incertus*. Among the nymphs there are three size groups—those about to emerge as adults; those which probably would have emerged within 4 to 6 weeks; and those which were quite small, half or less than half as large as the mature nymphs. Sex of the small forms was not determinable, but if they were females they were only approximately one-third the size of the mature female nymph. It appears that the species emerges in two broods, one in late July or early August and the other in late August or early September. The appearance of the smaller nymphs indicates that the species requires 2 years to develop to maturity. These young specimens were developed from eggs laid the year before collection, and were destined to mature the year following collection.

The restricted period of emergence of the Savannah River form coincides with the records by Needham et al. (1935) for adults of *T. incertus* from Spring Creek, Georgia, in August; from Eufalfa, Alabama (Chattahoochee River), September 4; and from Macon, Georgia, in August. These conclusions regarding periods of emergence are also supported by the collection of this species from the Apalachicola River, Florida, on July 29 (Berner 1950), as well as by the following records.

Louisiana.—Natchitoches, Natchiotoches Parish, July 2, 1956 (J. E. Sublette).

Mississippi.—Tombigbee River, Munroe County, July 24, 1954; Bull Mountain Creek at Highway 25, Itawamba County, July 25–26, 1954; Leaf River, Smith County, August 15, 1954; Pearly River at Highway 84, Lawrence County, August 16–17, 1954; and Bayou Chitto at Highway 24, Pike County, August 18–19, 1954 (all collected by C. D. Hynes).

South Carolina.—Beulah Pond, Aiken County, July 22, July 29, and August 8, 1952 (William Cross).

Tortopus NEEDHAM AND MURPHY

Traver (1950) has discussed the genus *Tortopus* at some length, indicating the characteristics which differentiate the adults from those of the closely related *Campsurus* Eaton. The discussion enlarges on that of Ulmer (1942) and indicates those species which should be transferred from *Campsurus* to *Tortopus*. Although Traver's paper deals primarily with Neotropical mayflies, the discussion includes the nearctic representatives of *Tortopus* as well. The northern species include the following: *primus* (McD.), known from Illinois and Nebraska; *incertus* (Traver), from Georgia, Alabama, and Florida; *manitobensis* (Ide) from Manitoba; and *circumflus* (Ulmer), from Texas.

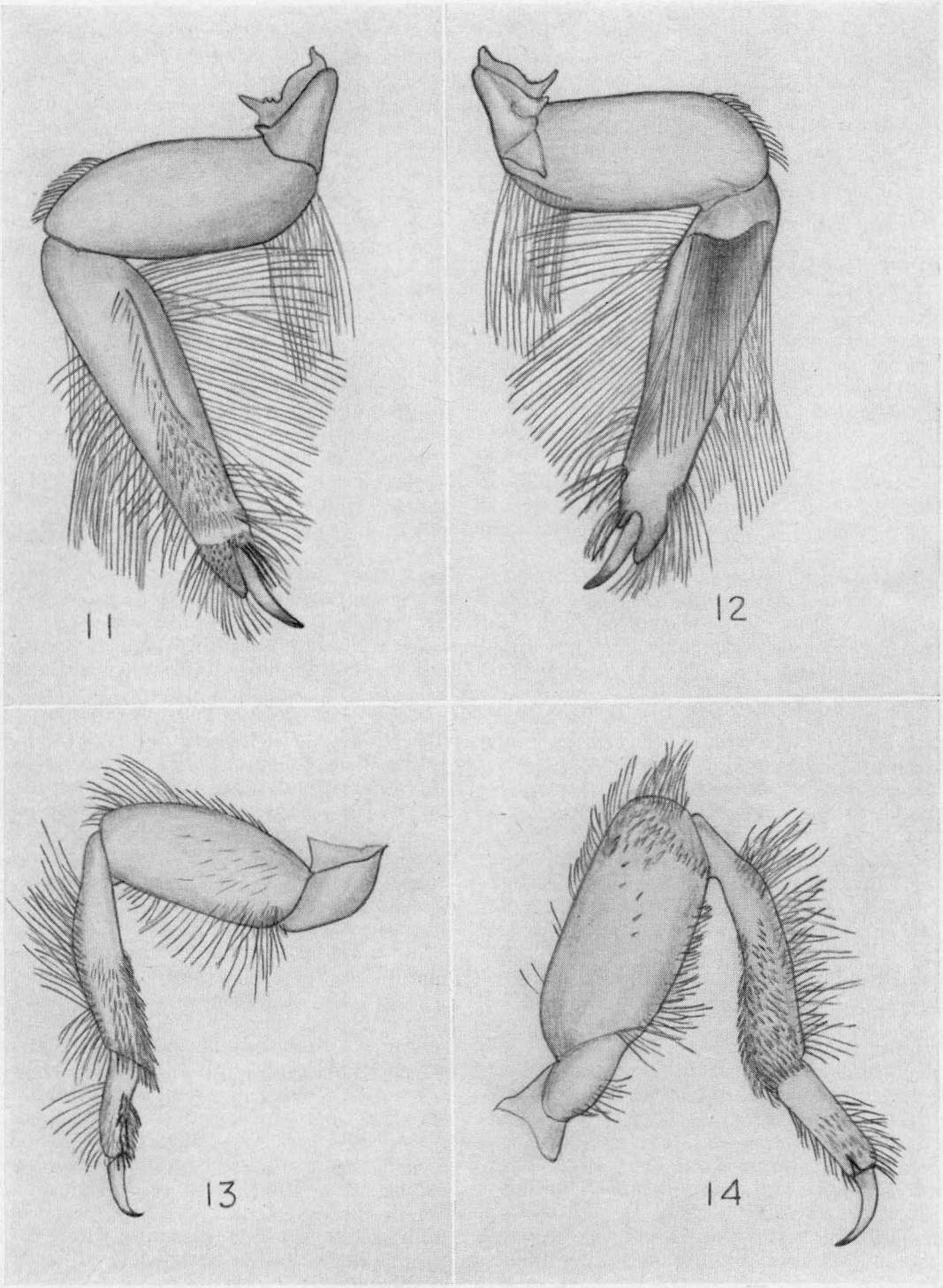
In his discussion of the mayflies of Illinois, Burks (1953) synonymized *primus*, *incertus*, and *manitobensis*, and mentioned the possibility that all of these might be synonyms of *puella*. It is our opinion that it is better to leave these species under the original names until a comprehensive study of the entire genus is undertaken.

At the time of publication of Traver's 1950 paper, the nymph of *Tortopus* was unknown, and *Campsurus* was described in the nymphal stage from two specimens, one illustrated by Needham and Murphy (1924) and one described and illustrated by Ulmer (1920). Both of these descriptions were of South American species, and the nymphs of *Campsurus* still remain relatively unknown.

Although no male adults of *Tortopus* were collected at the Savannah River, the specimens are assigned to the species *Tortopus incertus*. During the examination of nymphs in the last instar several males were found that were at the point of emerging, and in these the genitalia were fully developed. It was possible to dissect out the genitalia for study, and they conclusively proved the species to be *incertus*. In spite of the fact that these were subimaginal structures, there was little difference between them and those of the adult. As the subimaginal stage is of such brief duration, there is probably no opportunity for structural changes to develop in the genitalia.

DESCRIPTION OF THE NYMPH OF *Tortopus incertus* (TRAVER)

There are several characteristics distinguishing the nymph of *Tortopus* from that of *Campsurus* as described by Ulmer (1920) and illustrated by Needham and Murphy (1924). *Campsurus* has a row of spines on the outer edge of the mandibular tusk and about eight or nine saw-like teeth on the inner edge with the proximal tooth being the largest (Ulmer, 1920). In *Tortopus* the mandibular tusks have heavy spines on the outer margin, while the inner margin bears only weak spines which are so small as to be difficult to see in profile. *Tortopus* also has a large, thumb-like spine proximal to the tip on the medial side; *Campsurus* nymphs do not seem to have this spine. The clusters of hairs on the head of *Tortopus* are differently arranged than those of *Campsurus* as illustrated by Needham and Murphy, and the first gill of *Tortopus* has a single lobe while that of *Campsurus* is bilobed. Ulmer describes the median caudal filament of *Campsurus* as being about 1⅓ times as long as the laterals, but in *Tortopus* the median filament is shorter and thinner than the laterals in male nymphs and approximately the same length, but thinner, in females. Whether these characteristics are of generic value is not determinable at present, as there is insufficient comparative material available for study; however, arrange-



FIGS. 11–14.—Legs of *Tortopus incertus* nymph. 11. Fore leg, outer surface, 12. fore leg, inner surface, 13. middle leg, outer surface, 14 hind leg, outer surface.

ment of the mandibular spines, especially the subterminal one of *Tortopus*, the difference in the first gills, and the difference in length of the median caudal filament probably hold throughout the two genera.

Measurements.—Body length of mature female nymphs varies from 19.3 to 23.2 mm., average about 22 mm.; caudal filaments 5.5–6 mm. Body length of male nymphs averages about 15.5 mm.; lateral caudal filaments 12–14 mm., median filament 5–6 mm. Body measurement does not include mandibular tusks.

Head.—Wider than long with ratio of width (across eyes) to length (frontal ridge to occiput) averaging 0.69; eyes small, located very close to the posterior margin of the head. Ocelli large. Antennal bases prominent; just medial to each base there is a prominent spine projecting forward. Frontal shelf a strongly chitinized, slightly emarginate ridge; frons descends ventrally between the antennal bases as a snout-like projection.

Epicranial suture outlined with black; blackened margin of lateral ocelli continues inward to meet at mid-line; anterior to point of juncture there is a large wedge-shaped black marking which runs anteriorly to fuse with the black base of the median ocellus. Just medial to each compound eye there is a cluster of fine hairs; anterior to each eye there is another such cluster. Emerging from the epicranial suture there is a dense row of long hairs that runs laterally and forward along the outside of the lateral ocelli, proceeds forward to overlap the finger-like spine, and then runs laterally across the antennal base. Frontal shelf margined with long hairs which become even longer laterally. Basal segment of antenna with a few hairs close to the point of attachment; second segment with a dense cluster of long hairs just distal to the point of attachment to the basal antennal segment; flagellum free of hairs. In dorsal view, mandibles project forward about as far in front of the head as the length of the head posterior to the frontal ridge. From above mandibular tusks are somewhat triangularly shaped and end in a long, finger-like point; near the base of the terminal spine, there is a thumb-like spine on the inner side. The inner margin of the mandible carries long hairs which are sparsely distributed along this surface up to the subterminal spine. Outer edge slightly curved and bearing a series of long, coarse spines along the margin; inner edge straighter and with small thin spines which are not at the edge but close to it. At least two of the distal spines on both the inner and outer margins of the mandible are long and thin. Across the proximal end of the dorsal surface of the mandible there is an irregular row of spines which becomes broader toward the outer margin. A band of long hairs at the base of the mandible is quite conspicuous on the outer side, appearing to project sidewise from the mouth. The tips of the mandibles vary in degree of wear depending on the age of the nymphs; in those which have recently molted, the points are sharp while in those nymphs which have been in a particular instar for some time the tusks are well worn, sometimes the points being almost completely obliterated. The muscles of the head are extremely heavy so that it is difficult to remove mouthparts without tearing the chitin of the head. This is particularly true of the mandibles which have massive muscles attaching them. Mouthparts as shown in the illustrations (figures 4–8); labial palps have been displaced laterally. Normally the labial palps are held together beneath the labium and fit between the paraglossae with their tips slightly divergent so that in ventral view they appear to be held in a V-shaped manner.

Thorax.—Pronotum wider than long; anterior to midline there is a sulcus which runs medially from the anterolateral corner to the anterior third of the midline as shown in figure. At the anterolateral corner there is a small spinelike process which runs around and under the head; a few long hairs are attached to this process. Anterior margin of pronotum relatively straight; posterior margin arched posteriorly. The sulcus is deep at the anterolateral corners of the pronotum, but becomes shallow towards the midline. That part of pronotum anterior to sulcus marked with blackish stippling as shown in drawing. Behind the sulcus there is a large, rectangular, stippled, black area on either side of the midline. Mesonotum with a prominent, shield-shaped, black marking that extends from the anterior border to about the level of the base of the wing pads; broad part of the mark is at the anterior margin. Median line with a V-shaped black mark at the anterior margin; continues posteriorly the length of the mesonotum as a geminate mark. Other small black shadings over the mesonotum as shown in the illustration. Wing pads of mature nymphs have major veins outlined in purplish black, with the costal border heavily colored. Sternum unmarked. Anterior pair of legs so closely set together that the coxae are almost in contact; coxae of middle legs more widely separated; coxae of hind legs widely separated. Forelegs short and strong, heavily set with long hairs as shown in figures 11 and 12; claws larger and longer than those of *Campsurus*. There does not appear to be a clear separation of the tarsus and tibia although there is a line across the distal part of the tibiotarsus which indicates that this may be the area of fusion. The distal end of the tibiotarsus of the foreleg is covered on the outer surface by long, coarse spines as well as long coarse hairs; inner surface also with long spines and hairs; hairs begin in a transverse bar near the basal part of the tarsus, run laterally across to the front margin and continue distally to the very edge of this segment of

the leg; a row of hairs on the posterior margin of tibiotarsus, independent of the transverse bar, begins near the proximal end of the segment and continues to the distal end where there is a row of very long sharp spines. Middle and hind legs also hairy and spiny as shown in figures 13 and 14.

Abdomen.—Seven pairs of gills; first pair very small, single, and recurved over the abdomen. Gills 2 through 7 similar, coarse, large and heavily chitinized; composed of two lobes, the outer elbowed about midway its length so that it is bent back over the abdomen; outer lobe excavated on underside to receive the lower blade; two blades interlocked when at rest. Both lobes with a very heavy central trachea, lateral branches much less conspicuous; gills margined with coarse hair-like processes into which small tracheae can be seen to run. Hair-like processes, similar to those shown in Needham and Murphy's (1924) drawing of *Campsurus*, give the gills a feathery appearance. The gills are strongly attached to lateral abdominal protuberances and are difficult to detach without tearing the abdomen. Segments eight and nine somewhat longer than the preceding segments; segment ten relatively short. Color pattern of the tergites approximately as shown in figure 3; however, there is some variability. There is a mid-dorsal pale stripe running the length of tergites 2 to 8; on tergite one, the stripe is wide but becomes narrow on the other segments; stripe is obsolescent on tergite nine, and only faintly indicated on ten. The stripe is clearly outlined with a fine, dense growth of hairs that emerge along its entire length. Lateral to the midline there is a submedian, purplish-brown line running the length of each of tergites 2 to 7; the lateral margins of these wide, sub-median lines are strongly outlined in dark purple. At the posterior margin of tergites 1 to 7 the submedian lines extend laterally out to the gill base; lateral to the submedian lines there may be purplish-brown blotches which are somewhat variable in shape but they are approximately as shown in figure 3. Tergites 8 and 9 almost completely covered by purplish-brown stippling, except for minute pale areas as shown in figure 3. Median portion of tergite 10 is purplish brown; this median area is bordered by a pair of pale stripes and lateral to these there is another purplish-brown blotch. Lateral portions of tergite 9 covered with a fine, long pubescence which becomes rather heavy at the posterior margin of the area of pigmentation; pubescence also heavy along lateral margins of tergite nine. Tergite 10 has much more limited pubescence, the fine hairs being confined to the posterior margin just lateral to the pigmented areas and extending along the length of the lateral margins. Ventrally, abdomen white without color pattern; lateral margins of segments 2 to 8 also covered with fine, long hairs which cannot be seen in dorsal view because of gills. Ventrally, the very heavy musculature of the gills can be clearly seen through the sternites, running obliquely from the anterior margin to the posterolateral corner; in this ventral view, abdominal segments 2 to 7 are triangularly shaped with the apex of the triangle cut off by the posterior margin of the segment ahead. Caudal filaments as shown in the drawing; all of them covered with long, fine hairs. Median filament of females smaller in diameter than laterals and about the same length; in males, lateral filaments much longer than those of females and more than twice the length.

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