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Cretaceous Dinosaurs of North Carolina

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ABSTRACT. — Isolated bones of Late Cretaceous dinosaurs from the Black Creek Formation (Campanian) of Sampson and Bladen counties, accumulated over the last eleven decades, are described and interpreted in the light of more nearly complete material known from elsewhere. A medium-sized carnivorous dinosaur is comparable to the tyrannosaurids *Dryptosaurus* and *Albertosaurus*. One toe bone represents the ostrich-mimic *Ornithomimus*. The enigmatic *Hypsibema crassicauda*, originally based on a mixture of three suborders, is restricted to tail vertebrae and synonymized with *Parrosaurus*; it is probably a sauropod of huge size but uncertain family. Duckbill dinosaur bones are generically indeterminate but evidently belong to the Hadrosaurinae. *"Hadrosaurus tripos"* is not a Cretaceous dinosaur but a Pliocene whale. Also misidentified as dinosaurian are remains of the gigantic crocodile *Deinosuchus [Phobosuchus] rugosus*, which probably preyed on the amphibious hadrosaurs.

A revised list of the Phoebus Landing local fauna includes the sharklike fishes *Asteracanthus, Scapanorhynchus, Squalicorax, Ischyrhiza*, and *Brachyrhizodus*; the bony fishes *Paralbula* and *Pycnodus*; the turtles *Trionyx* and *Taphrosphys*; the mosasaurid sea-lizards *Tylosaurus* and *Platecarpus*; the crocodiles *Deinosuchus* and *Leidyosuchus*; and four dinosaurian genera. Homonymy of *Coelosaurus* Leidy, 1865, with *Coelosaurus* [Owen] 1854 necessitates the transfer of *C. antiquus* Leidy to *Ornithomimus*.

INTRODUCTION

Our knowledge of the Cretaceous dinosaurs of North Carolina is, unfortunately, derived entirely from isolated and often fragmentary bones that were brought to light during extremely sporadic episodes of collecting activity. In the antebellum period an impressive amount of pioneering work was done by Ebenezer Emmons, state geologist from 1851 to 1863. Although Cretaceous reptile bones (mosasaur, crocodile and turtle) are illustrated in Emmons (1858), he seems not to have discovered any dinosaur material — or if he did, it was lost to science with the wartime destruction of the Survey collections (Stuckey 1965).

Thus the first discovery of dinosaurs within the state must be credited to the versatile and energetic Washington Caruthers Kerr, an alumnus of Chapel Hill who had done postgraduate work under Agassiz and others at Harvard. Beginning his service as state geologist in 1864, in the final desperate months of the war, and persevering through the troubled and impoverished era of reconstruction, Kerr re-established the Survey and directed its activities until his death in 1885. The fossil vertebrates collected by Kerr and his assistants were sent to Philadelphia for description by the leading vertebrate paleontologist of the day, Edward Drinker Cope, and were deposited for permanent safekeeping in the United States National Museum. Cope published the Survey's discoveries as they came to hand, and subsequently (1875) compiled a synopsis of all the fossil vertebrates that had been found in the state.

A hiatus in paleontological work then intervened, ending only in 1905 when a survey of the coastal plain deposits was undertaken as a cooperative project of the United States Geological Survey and the North Carolina Geological and Economic Survey. In the course of this work a number of Cretaceous reptile bones were recovered at Phoebus Landing on the Cape Fear River by Lloyd W. Stephenson and his associate, Edward W. Berry (the elder). This material was to have been described in Part II of the State Survey's Report (Volume V), "The Cretaceous Formations of North Carolina," but unfortunately the series was discontinued after publication of Part I (Stephenson 1923). Aside from the identifications by Charles W. Gilmore published in Stephenson's 1912 report and the subsequent citation by Lull and Wright (1942) of specimens believed to be hadrosaurian, Stephenson's material remained undescribed in the National Museum.

After another lengthy hiatus, in the 1950s geologists from the University of North Carolina at Chapel Hill undertook systematic survey work along the Cape Fear River. Their published reports (e.g. Brett and Wheeler 1961; Heron and Wheeler 1964) added greatly to our understanding of Cretaceous sedimentology and stratigraphy. One dinosaurian byproduct of this research was the hadrosaur humerus (described below) recovered by Everett Brett and Walter H. Wheeler at Milepost 49. Wheeler (1966) reported on a mandible of the mosasaurid lizard *Tylosaurus* that he collected at Phoebus Landing in 1964.

A specific search for vertebrate fossils was begun in 1963 by Halsey W. Miller, Jr., then on the faculty of High Point College. Through his excavations of 1964-1965 at Phoebus Landing the number of known specimens was greatly increased, making it possible to prepare a preliminary faunal list (Miller 1967, 1968). All specimens recovered were presented to the Academy of Natural Sciences of Philadelphia and the Sternberg Museum of Fort Hays Kansas State College.

The purpose of this paper is to gather together the piecemeal finds of dinosaur bones from North Carolina and interpret them in the light of more nearly complete material from elsewhere. As the foregoing historical summary implies, the Tarheel state has Cretaceous vertebrates in store for those who seek them, although hitherto the seekers have been few and long between. We hope our contribution will stimulate further delving into this fallow field.

ABBREVIATIONS

AMNH, American Museum of Natural History.
ANSP, Academy of Natural Sciences of Philadelphia.
PU, Princeton University Museum of Natural History.
SM, Sternberg Museum, Fort Hays Kansas State College.
UNC, University of North Carolina at Chapel Hill.
USNM, National Museum of Natural History, Smithsonian Institution.

LOCALITIES

Figure 1 shows the sites from which dinosaurian (or supposedly dinosaurian) bones have been recovered.

(1) Marl pits of James King, Sampson County. According to Kerr (1875: 198-199) King's farm lay "some 10 miles from the depot [Faison's Depot], southwest . . . . This locality is on the waters of Six Runs Creek." The heterogeneous collection of bones upon which Cope based *Hypsibema crassicauda* was found in the "blue marl," now the Black Creek Formation.

(2) Marl pit of W. J. Thompson, Sampson County, "about ten miles distant from the marl pit in which the Hypsibema was found" (Cope 1875: 40). This appears to be the locality mentioned in passing by Kerr (1875: 198): "[Blue marl sample] No. 35 is from the farm of J. C. Pass, a mile and a half west of Faison's Depot . . . . Another well known outcrop in the same neighborhood is at Dr. Thompson's. . . ."

Stephenson's (1923) map shows an extensive area of Duplin Marl (Miocene or Pliocene) extending southward from Faison. In the same region Stuckey's (1958) map indicates only an insignificant, mile-wide patch of Duplin (Yorktown) lying west of Six Runs Creek. The discrepancy between these maps is probably less a matter of fact than of emphasis, the later cartographer choosing to ignore the patchy, surficial remnants of a once-extensive Cenozoic cover. Under the circumstances it is easy to see why Cope assumed the type specimen of *Hadrosaurus tripos* to be a dinosaur vertebra from the Cretaceous "blue marl," overlooking the possibility (now confirmed) that it is a whale vertebra derived from the Duplin Marl.

(3) Milepost (or Mile Board) 49 near Donahue Landing, south bank of the Cape Fear River about 15 air miles (24 km) southeast of Elizabethtown, Bladen County. A hadrosaurine humerus encrusted with bryozoa and *Exogyra* spat was found at the base of the Peedee Formation, evidently reworked from the underlying Black Creek Formation. Detailed

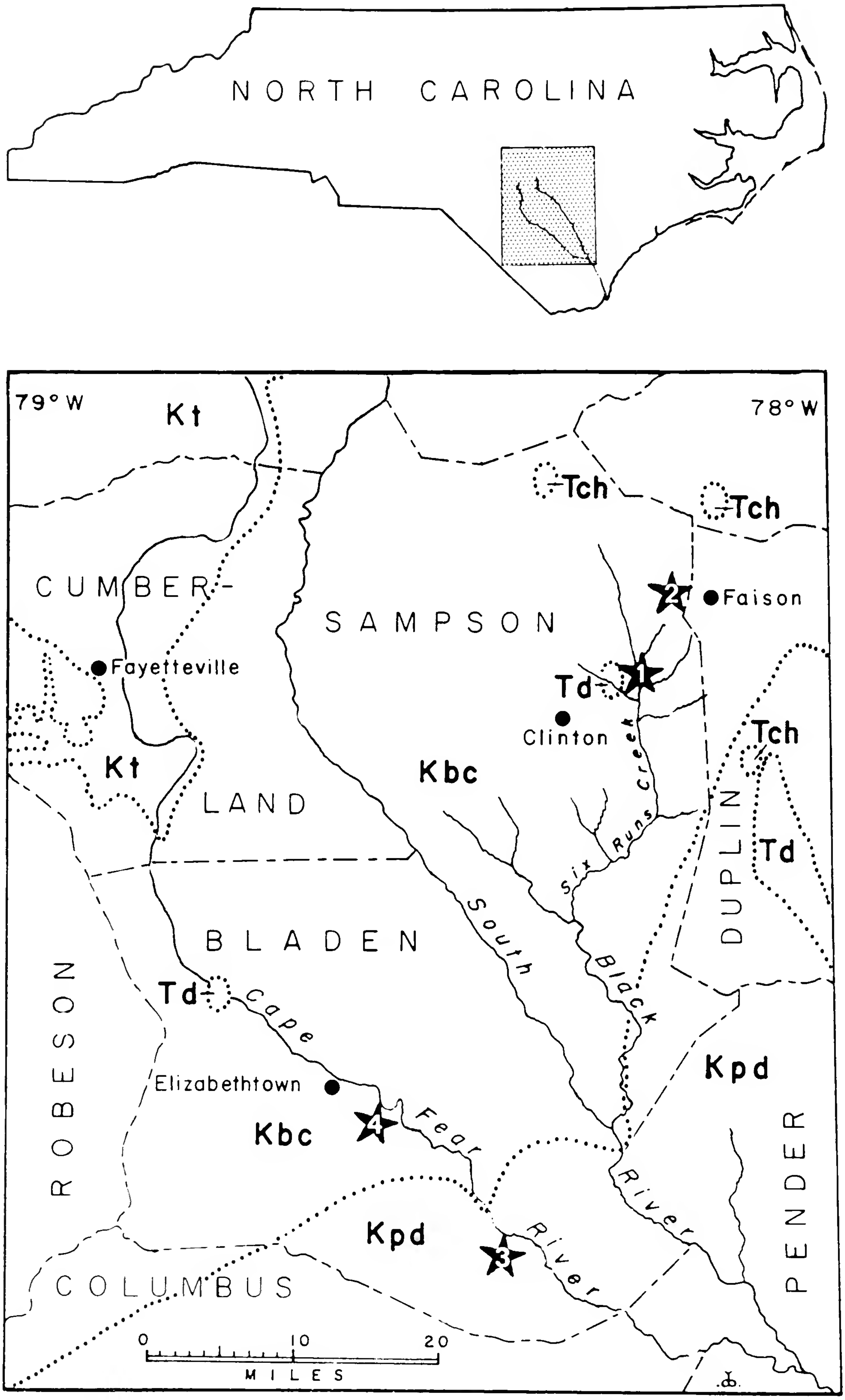

Fig. 1. Index map of Cretaceous dinosaur localities in North Carolina (for descriptions see text). Formation boundaries are dotted. Formations in descending order: **Td**, Duplin (Yorktown); **Tch**, Castle Hayne; **Kpd**, Peedee; **Kbc**, Black Creek; **Kt**, Tuscaloosa. Latitude 35° North passes through Clinton.

analyses of this locality were provided by Brett and Wheeler (1961: 67-69, "Station 2") and Heron and Wheeler (1964: 46, "Locality 12").

(4) Phoebus Landing, south bank of the Cape Fear River below Milepost 68, about 5 air miles (8 km) east-southeast of Elizabethtown, Bladen County. The source of most of the dinosaur bones described in this paper, Phoebus Landing was discussed by Stephenson (1912: 120; 1923: 10), Miller (1967), and Heron and Wheeler (1964: 42, "Locality 8").

THE BLACK CREEK FORMATION

A succinct analysis of this formation was provided by Heron and Wheeler (1964) in their guide to the Cretaceous strata along the Cape Fear River. For the convenience of readers who lack ready access to the guidebook we abstract pertinent passages here.

"The Black Creek Formation consists of poorly indurated, laminated or thin-bedded clayey silts and silty clays, dark clays, and loose, coarse light gray, well sorted sand, as well as thick lenses of this sand. These sands, silts and clays contain substantial quantities of glauconite, lignite, shell material, iron sulphide, and some amounts of phosphate, amber, and marine microfossils. . . . Lignitized wood . . . occurs as logs and large branches which may be partly silicified, or as mats of twigs and other vegetable matter, as scattered fragments, and, rarely, as very thin layers in some sands. Many sands are locally cemented and stained by ferric iron.

"[Donald J. P.] Swift [unpubl. dissert., 1964] has distinguished four types of stratification in the Black Creek: a *fluvial* stratification recognized by nearly perfect separation of sediment into sand and clay, grouping of strata into strata sets, sand beds with imperfectly developed third order stratification of thin beds and laminae of sand separated by very thin laminae of finer sand, and sands with an impoverished transition zone suite of accessory minerals (glauconite and Foraminifera sparse or lacking).

"In *fluviomarine* bedding the sands are finer-grained, darker and more clayey, the grouping of strata into strata sets is not as pronounced, and strata sets are relatively continuous whereas the individual strata tend to lens and bifurcate. The sediments carry a transition zone suite of accessory minerals, including Foraminifera, *Ostrea* fragments and up to 15% of glauconite. Though marine, their stratification is controlled by river flooding.

"A *lagoonal* stratification ranges from a lenticular thinly bedded type to varieties where bedding is obscured by mottling produced by burrowing invertebrates.

"Finally a *littoral* stratification is found only immediately beneath the Peedee Formation. Strata are of pale sand with a median thickness of 2.5 feet, varying from 1 to 22 feet. . . . These beds are actually lenses when seen in large enough outcrops."

Given such varied circumstances of deposition, the ecologically heterogeneous nature of the Black Creek vertebrate fauna is understandable. Thus the thanatocoenosis at Phoebus Landing combines the remains of fully terrestrial dinosaurs (carnosaurs and ornithomimids) with those of amphibious, presumably paludal and lagoonal forms (hadrosaurs, sauropods and giant crocodiles) and these in turn with remains of marine mosasaurs and sharks.

Time relationships of the Black Creek Formation were interpreted by Brett and Wheeler (1961: 102) as follows. "The stratigraphic situation along the Cape Fear River indicates an onlap condition during Upper Cretaceous time with an encroachment of the ocean onto a gently sloping coastal plain. . . . Upstream and updip from Elizabethtown the Black Creek Formation was, without doubt, deposited during Taylor time represented by the *Exogyra ponderosa* zone (or older near the base); downstream and downdip from Milepost 60 to at least Milepost 49, both the Black Creek and Peedee Formations were also deposited during Taylor time." Thus the dinosaurs discussed in this report are Tayloran, i.e. Campanian, late Cretaceous, in age.

SYSTEMATIC DESCRIPTIONS

Order SAURISCHIA
Suborder THEROPODA
Infraorder CARNOSAURIA
Family TYRANNOSAURIDAE
cf. *Dryptosaurus* Marsh, 1877, or *Albertosaurus* Osborn, 1905

Figs. 2A, 3A, 4B-B[1]

Two teeth from Phoebus Landing were assigned the tentative identification of *Gorgosaurus*? by Miller (1967: 233): USNM 7199 (previously cited as *Zatomis*? [sic] by Stephenson 1912: 120) and the fragmentary ANSP "15331" (actually 15332, two teeth, Fig. 2A). Aside from being carnosaurian these teeth show no characteristics that would permit generic identification. They are as similar to *Dryptosaurus aquilunguis* (Cope) as to *Gorgosaurus* (i.e. *Albertosaurus*); and indeed, Stephenson's invocation of the Triassic tooth-genus *Zatomus* is not so far-fetched as it sounds, for all carnosaurian cheek teeth are essentially alike.

A maxilla tentatively attributed to *Gorgosaurus* by Miller (1967) is here reassigned to the crocodilian genus *Deinosuchus* and is discussed below in the section on non-dinosaurian remains.

Three fragmentary femora are demonstrably carnosaurian. Two of these, from the marl pits of James King in Sampson County, formed part of the mixed lot of bones upon which Cope established *Hypsibema crassicauda* (USNM 7189). The now-missing "left tibia" shaft section (Cope 1875, Pl. 6, Figs. 2-2a) appears instead to be part of a carnosaurian left femur. In morphology it corresponds closely to the left femur of *Dryptosaurus aquilunguis* but is slightly larger, about 10 cm rather than 9 cm in maximum diameter. The badly-eroded fragment that Cope (1875, Pl. 6, Figs. 1-1a; our Figs. 4B-B^1) interpreted as the distal extremity of a right humerus proves on comparison to be a left femur. A more informative specimen is ANSP 15330 (Fig. 3A), the distal one-third of a right femur which Miller collected at Phoebus Landing but omitted from his papers. Its distal condyles are much abraded and the anteromedial ridge that bounds the origin of the femorotibialis muscle is broken away. So far as the damaged state of the specimens permits comparison, ANSP 15330 and Cope's "right humerus" are so nearly identical in size and morphological detail that they might have come from the same individual — although of course they were found many miles apart.

These femora are closely comparable to that of *Dryptosaurus aquilunguis*, the type specimen of which (ANSP 9995, Fig. 3B) came from the "chocolate greensand bed" or New Egypt Formation of late Maestrichtian age near Barnsboro, Gloucester County, New Jersey. As the photographs show, on the dorsal (anterior) surface the rugose area of origin of the femorotibialis muscle is bounded proximally by a prominent low welt that arcs across the face of the shaft and continues down its anteromedial edge as a crest to buttress the internal condyle. The break in slope between shaft surface and muscle insertion is conspicuous in lateral

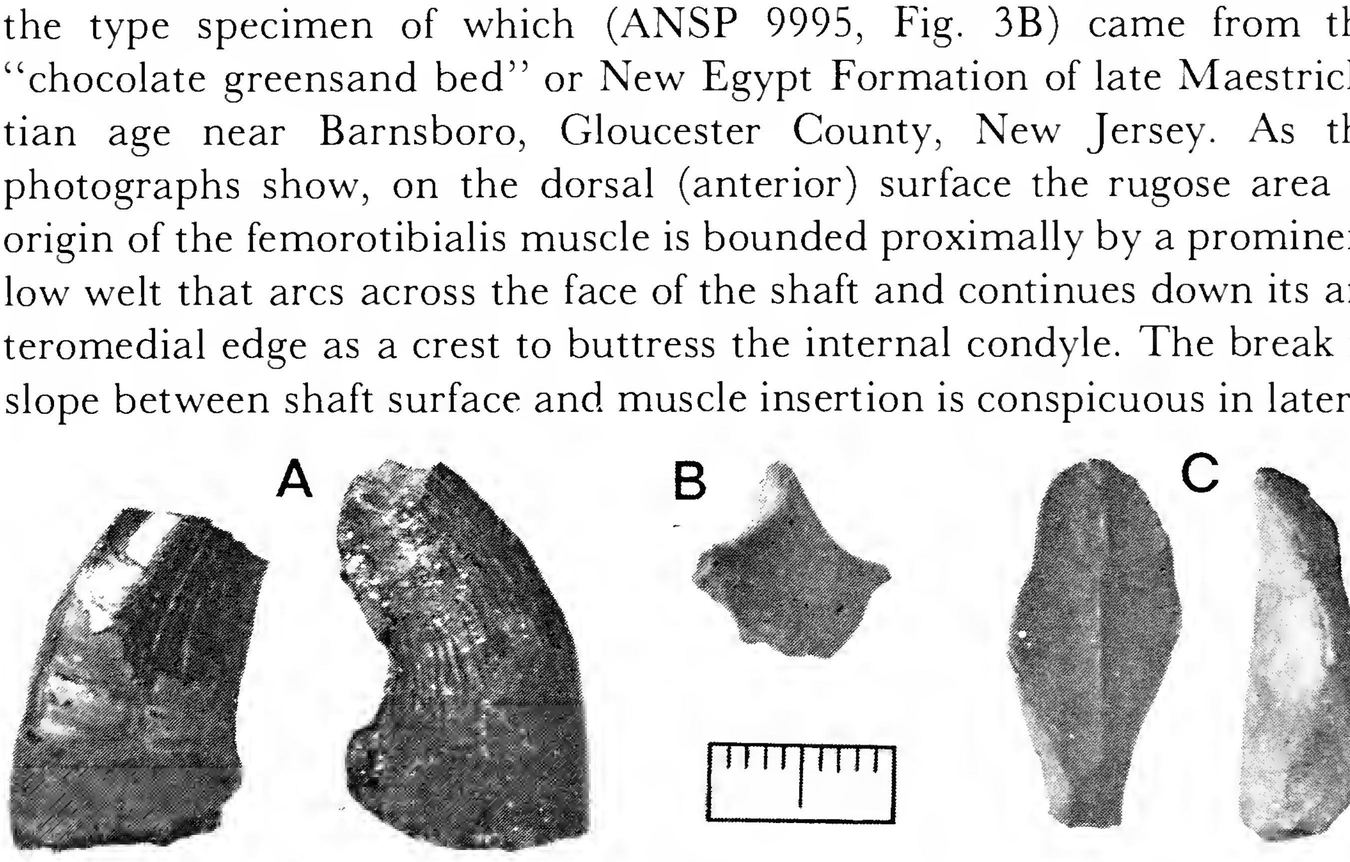

Fig. 2. Dinosaur teeth from Phoebus Landing, Bladen County. **A**, tyrannosaurid carnosaurian cf. *Dryptosaurus* or *Albertosaurus*, ANSP 15332. **B**, hadrosaurine maxillary tooth in occlusal view; **C**, hadrosaurine dentary tooth in lingual and profile views, ANSP 15333. Scale in mm.

Fig. 3. Tyrannosaurid femora (distal ends) in dorsal, medial, ventral and lateral views. **A**, right femur from Phoebus Landing, ANSP 15330. **B**, left femur of *Dryptosaurus aquilunguis*, ANSP 9995 (type), from Barnsboro, New Jersey. Scale in cm.

view. The external condyle is prolonged proximally into a hemi-conical swelling that plunges into the muscle scar.

On the ventral (posterior) surface the intercondylar fossa is relatively broad and nearly flat-bottomed; on its inner side it extends proximally to end in a popliteal pit (which is more prominently marked in the Phoebus Landing femur than in USNM 7189 and the type of *Dryptosaurus*). Above this pit the buttressing ridge from the inner condyle swings diagonally across the shaft to merge with the more prominent ridge from the outer condyle. The condyles themselves are too badly eroded to be informative.

Available femora of *Albertosaurus libratus* (Lambe) from the Oldman Formation (AMNH 5458 and 5664) are either too crushed or too inaccessible (being embedded in panel-mounted skeletons) to be useful for comparison. A right femur of *Albertosaurus sarcophagus* Osborn from the lower Edmonton Formation (AMNH 5218) is closely comparable in both proportions and morphological detail to the Phoebus Landing femur and that of *Dryptosaurus.* The right femur of *Daspletosaurus torosus* Russell (AMNH 5438, paratype) from the Oldman Formation is essentially similar to all the foregoing, differing mainly in that, on the ventral surface, the ridge that runs proximally from the inner condyle crosses the shaft at an angle of 32° to the femoral axis, as compared to 20° in the Phoebus Landing femur and 23° in *Dryptosaurus* and *Albertosaurus* (angles approximate). The lower shaft of the *Daspletosaurus* femur also appears broader in proportion to its depth, although crushing makes this factor uncertain.

The right femur of *Alectrosaurus olseni* Gilmore (AMNH 6554, syntype) from the Iren Dabasu Formation of Mongolia differs conspicuously from all the foregoing in morphology as well as in its slenderer proportions. On the ventral surface it lacks strong ridges extending anteriorly from the condyles, while on the dorsal surface the scar for the origin of the femorotibialis muscle is much less sharply demarcated both proximally and distally, with the result that no pronounced break in slope is evident in lateral view.

In conclusion, so far as its preservation permits comparison *Dryptosaurus* is not distinguishable from *Albertosaurus* on the basis of the distal end of the femur. The femur from Phoebus Landing is extremely similar to both, differing in that its diaphysis is slightly deeper relative to width, so that the lumen is circular rather than oblate in section. It is less similar to *Daspletosaurus* and quite different from *Alectrosaurus.* Having made these comparisons, we do not feel that the material available permits a generic identification for the North Carolina tyrannosaurid.

Infraorder COELUROSAURIA
Family ORNITHOMIMIDAE
cf. *Ornithomimus* Marsh, 1890

A single toe bone of an ostrich-mimic dinosaur from Phoebus Landing (ANSP 15319) was described by Miller (1967: 232, Pl. 3, Fig. 7) who compared it to the first phalanx of the third digit of *Ornithomimus altus* Lambe. This specimen is water-worn, with abraded proximal and distal ends. The bone is symmetrical when viewed from either end. At its proximal end the ventral surface is smooth and flat while the upper profile forms a symmetrical arch. The proximal end bears a pair of shallow concavities for the reception of the distal condyles of a preceding phalanx, whereas if this were the first phalanx it would be singly concave to receive the single condyle of the metatarsal. Thus the Phoebus Landing specimen probably represents the second phalanx of the third digit. It closely resembles phalanx III-2 of all the ornithomimids, including AMNH 2551 from Monmouth County, New Jersey.

The earliest name for an ornithomimid from the Atlantic coastal deposits is *Coelosaurus antiquus* Leidy, 1865, based on a well-preserved tibia (ANSP 9222) from the greensand of Burlington County, New Jersey. However, Leidy's generic name proves to be a junior homonym of *Coelosaurus* [Owen] 1854 (see Appendix). We accordingly transfer the species *antiquus* to the oldest junior subjective synonym of *Coelosaurus* Leidy, which is Marsh's genus *Ornithomimus.* Fragmentary remains indistinguishable from *Ornithomimus* are found from the late Santonian or early Campanian through the late Maestrichtian of New Jersey and Delaware (Baird and Horner 1977). As the Phoebus Landing assemblage is Campanian in age and belongs to the same faunal province as those of New Jersey and Delaware, we concur with Miller's provisional assignment of the North Carolina specimen to *Ornithomimus.*

Suborder SAUROPODOMORPHA

Infraorder SAUROPODA

Family incerta

Hypsibema Cope, 1869

Neosaurus Gilmore *in* Gilmore and Stewart, 1945; *non* Nopcsa, 1923.
Parrosaurus Gilmore, 1945 (replacement name).

Hypsibema crassicauda Cope

Hypsibema crassicauda Cope, 1869: 192; 1870: 122-G — 122-I (*partim*), Pl. 1, Figs. 15-15A-15B; 1871: 211-214 (*partim*); 1875: 36-40 (*partim*), Pl. 5, Figs. 2-2a-2b, Pl. 6, Fig. 3 (only). Type species by monotypy.

Figs. 4A-A^1, 5, 6

Type. — USNM 7189, a syntypic suite of mixed generic origin. We designate as lectotype the caudal vertebra illustrated by Cope (our Figs. 4A-A^1, 5A), collected by W. C. Kerr from James King's marl pits in Sampson County.

Hypodigm. — The lectotype and the following caudal vertebrae from Phoebus Landing, Bladen County: USNM 6136, Berry and Stephenson coll., 1907, cited erroneously as cotype by Lull and Wright (1942: 224)

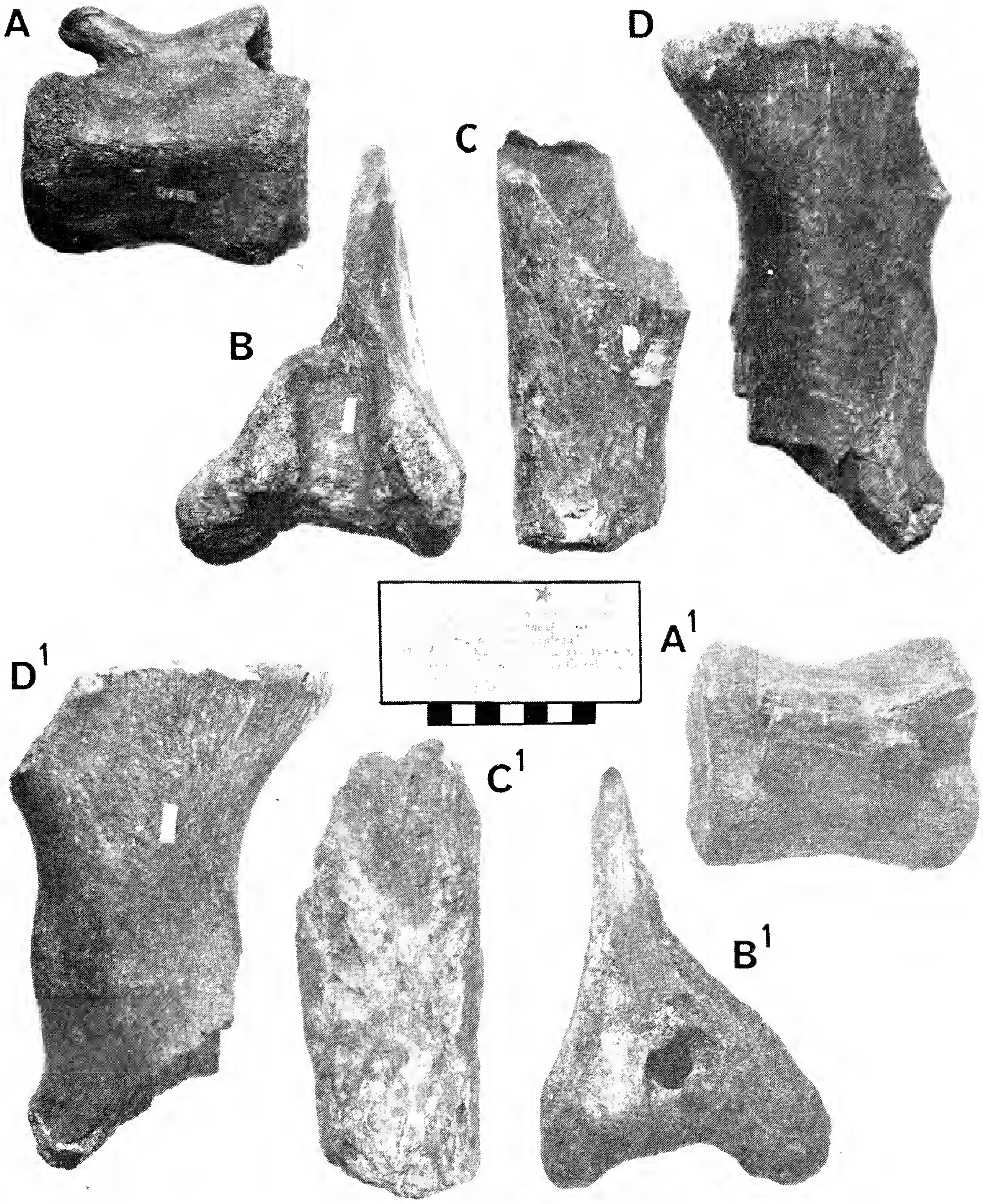

Fig. 4. *Hypsibema crassicauda*, syntypes, USNM 7189. **A-A^1**, lectotype caudal vertebra in left lateral and dorsal views; **B-B^1**, tyrannosaurid left femur (distal end) in ventral and dorsal views; **C-C^1**, hadrosaurian left tibia fragment; **D-D^1**, hadrosaurian right metatarsal II in anterior and posterior views. Scale in cm.

but see Miller (1967: 234); Fig. 5B. USNM 7093, 7094, Berry and Stephenson coll., 1907. ANSP 15307A-C, three vertebrae, Miller coll. (15307B figured by Miller 1967, Pl. 4, Figs. 7-8 as *Hadrosaurus*?); Figs. 6A-A^1, B-B^1, C. ANSP 15338, Miller coll.; Figs. 6D-D^1. USNM 10312, a caudal neural spine, may pertain.

Discussion. — This taxon was born in confusion and has persisted in the same state for more than a century. The bones from James King's marl pits (note the plural) that Kerr submitted to Cope were so obviously water-tumbled and abraded that, even if they had been found in close proximity, their organic association should have been considered unlikely. Whether or not they were found together, the five bones that constituted the original syntypic series can now be shown to represent *three suborders* of dinosaurs. Cope, unfortunately, took their association for granted. In deducing a single species from these disparate elements he inevitably created a monster *incertae sedis* for the confusion of subsequent students.

Of the surviving syntypes illustrated in Fig. 4, A-A^1 is the caudal vertebra which inspired Cope's specific name *crassicauda* ("thick-tailed") and which we designate as lectotype; the other bones are removed from *Hypsibema* and described elsewhere in this paper. The fifth bone (now

Fig. 5. *Hypsibema crassicauda*, caudal vertebrae in posterior and ventral views. **A**, USNM 7189, lectotype from James King's marl pits; **B**, USNM 6136 from Phoebus Landing. Scale in cm.

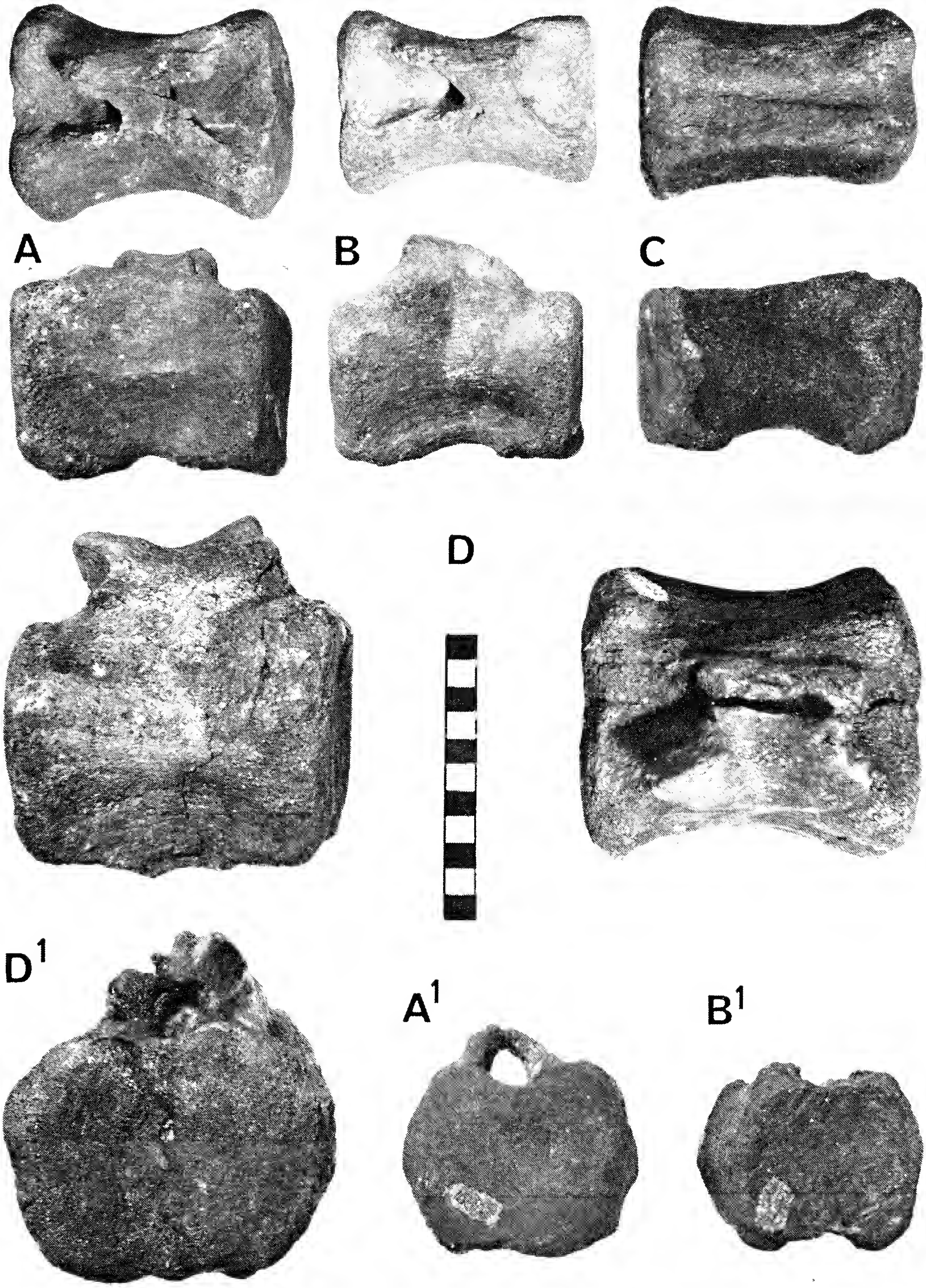

Fig. 6. *Hypsibema crassicauda*, referred caudal vertebrae from Phoebus Landing in dorsal, lateral and anterior views. **A-C**, ANSP 15307A-C; **D**, ANSP 15338. Scale in cm.

missing), which Cope took to be the shaft of the left tibia, appears instead to be part of a carnosaurian left femur.

Material acquired since 1869 adds little to the morphological information provided by the lectotype vertebra. The largest and presumably most anterior vertebra (ANSP 15338) is slightly longer than its centrum height, and the more posterior vertebrae become increasingly elongate, exactly as illustrated by Gilmore in the tail of *Parrosaurus.* The ends of the centra are hexagonal, wider than their height, and slightly amphicoelous (nearly amphiplatyan) with chamfered rims. In well-preserved specimens the upper third of the end surface is rugose, typically showing a semi-sunburst pattern that centers on the neural canal. In lateral view the centra are marked by low, rounded, longitudinal ridges at mid-height; there are no pleurocoeles. Ventrally the centrum is excavated by a broad, moderately deep, boat-shaped sulcus which is bounded laterally by rounded ridges that connect the anterior and posterior facets for the haemal chevrons.

The neural arch is centered at mid-length on the centrum and is completely co-ossified with it, so that only a difference in the orientation of surface striae reveals the position of the neurocentral suture. The anterior zygapophyses are short, terminating well behind the anterior margin of the centrum; their articulating facets are inclined about 30° from the vertical. The neural spine (only the base of which is preserved) arises from the posterior half of the arch at a low angle (22° in the type); its base is broadly ogival in cross-section. An experimental reconstruction in clay shows us that the spine must have projected at least half a centrum length behind its vertebra in order to articulate with the zygapophyses of the next succeeding vertebra. Of course we cannot say whether the spine maintained its initial angle or whether it became more bladelike distally.

The smallest vertebra is a topotypic specimen, now missing, illustrated by Cope (1875, Pl. 5, Figs. 2-2a-2b) as possibly belonging to a young individual of *Hadrosaurus tripos.* (In Cope's plate, oddly, it is shown with the lateral and end views upside down and the dorsal view captioned "below.") Its centrum height is given as 20.5 lines, i.e. 43.4 mm; height at end, 38.1 mm; width of end, 45.1 mm; width of waist, 31.8 mm. In morphology this centrum falls well within the range of variation of the *Hypsibema* caudals from Phoebus Landing. Its small size and lack of co-ossification with the neural arch indicate immaturity. Centrum dimensions of some larger vertebrae are shown in Table 1.

The genus Parrosaurus.—A sequence of 13 caudal centra (USNM 16735) recovered by well-diggers on the Chronister farm near Glen Allen, Bollinger County, Missouri, was described by Gilmore as a new genus and species, *Neosaurus* (later renamed *Parrosaurus*) *missouriensis.* The source

TABLE 1. *Hypsibema crassicauda* and *H. missouriense*, measurements of centra in mm (slightly corrected for abrasion). Data on largest vertebra of *H. missouriense* (USNM 16735) from Gilmore and Stewert (1945).

	ANSP 15338	USNM 7189	ANSP 15308A	USNM 16735
Maximum length	114	113	93	91
Maximum width at posterior end	105	100	79	87
Height at center of posterior end	82	65	56	91

bed was the McNairy Sand Member of the Ripley Formation, considered early Maestrichtian in age. In analyzing these vertebrae Gilmore explicitly noted their similarity to *Hypsibema crassicauda*; but accepting without question the hadrosaurian nature of the latter, he dismissed it from comparison on the grounds that the vertebrae from Missouri could not pertain to a member of the Hadrosauridae. Now that *Hypsibema* has been freed of hadrosaurian encumbrances its generic identity with *Parrosaurus* becomes obvious. Every morphological feature cited for the Missouri vertebrae can be matched in those from North Carolina. Indeed, the possibility of specific identity cannot be dismissed: but until better material is available we prefer to maintain *Hypsibema missouriense* (Gilmore), n. comb., as a separate species.

Affinities of Hypsibema.—A genus known only by its tail bones is necessarily somewhat difficult to characterize and classify. Regrettably, the meager sampling of dinosaur bones from North Carolina affords no additional element that can be attributed to *Hypsibema crassicauda*. Even more regrettably, no attempt has apparently been made to recover the rest of the skeleton of *H. missouriense* which (we suspect) lies buried a few meters underground on the Chronister farm. At present the caudal vertebrae provide the only basis for comparison.

Hypsibema shares with the Hadrosauridae its slightly amphicoelous caudal centra, the amidships position of its neural arch, and the shortness of its anterior zygapophyses. Within that family (as John S. McIntosh has pointed out to us) *Hypsibema* bears some similarity to a series of diminutive caudal vertebrae assigned to *Orthomerus transylvanicus* by Nopcsa (1928, Pl. 6, Fig. 4). But otherwise, as Gilmore justly noted in his analysis of *Parrosaurus*, the caudals are distinctly un-hadrosaurian. Conspicuously lacking, indeed, is the feature that appears to have been a basic adaptation of the hadrosaurs: a laterally-compressed tail heightened by neural and haemal spines to form an effective propulsive organ for swimming. The Ceratopsia and Ankylosauria are excluded from comparison by the relative shortness of their caudal centra, while the other varieties of Late Cretaceous ornithischians are all too small for consideration.

As Gilmore concluded, the sauropod dinosaurs are the only group to which this genus can be plausibly assigned. Judged *ex pede Herculem* by the mass of its tail, *Hypsibema* must have been a dinosaur of brontosaurian size, one worthy of a generic name meaning "high stride." However, the common sauropods of the Cretaceous — the Titanosauridae — are characterized by procoelous caudal vertebrae with forward-set neural arches and prezygapophyses that project beyond the end of the centrum: this condition is exemplified by *Alamosaurus* from the Lower North Horn formation (Maestrichtian) of Utah (Gilmore 1946). *Hypsibema* must therefore belong to some other family, one in which the middle and posterior caudals are amphicoelous to amphiplatyan. Gilmore, after eliminating various possibilities, was unable to place the genus in any family but concluded that it might be assigned tentatively to the Camarasauridae on the basis of the "general make up" of the vertebrae. Neither extensive comparison nor expert advice has enabled us to improve on Gilmore's treatment of the problem, so we must leave the family assignment open until more diagnostic material is found.

Order ORNITHISCHIA
Suborder ORNITHOPODA
Family HADROSAURIDAE
Hadrosaurinae indet.
Figs. 2B-C, 4C-D, 7, 8

As might be expected, bones of duckbill dinosaurs form a large percentage of the total sample. Two mandibular fragments (ANSP 15306 and USNM 7096) from Phoebus Landing were described by Miller (1967: 234). The first of these (Fig. 7) is part of a right lower jaw that includes the basal portion of the coronoid process externally and the posterior end of the grooved dentary (without teeth) internally. Also described by Miller (as an extremely large postzygapophysis) is a right coronoid process (ANSP 15329, Fig. 7) that evidently originated from a jaw comparable in size to ANSP 15306. Although the two specimens cannot be fitted together, their identical coloring and size and the fact that they came from the same locality suggest that they may pertain to the same individual.

Two hadrosaurian teeth (ANSP 15333) from Phoebus Landing are here described for the first time. A shed maxillary tooth (Fig. 2B) is of no descriptive use below the family level. The dentary tooth (Fig. 2C) is un-

Fig. 7. Hadrosaurinae indet., unassociated right dentary fragment and coronoid process from Phoebus Landing, ANSP 15306 and 15329, in lingual and labial views. Scale in cm.

worn and has a complete enameled crown and partial root or fang. The crown is diamond-shaped, 18.0 mm high and 8.7 mm wide, with a labial-lingual diameter of 6.6 mm measured at the base; its superior borders are papillated along a slightly raised edge. The median carina is straight and relatively low and not accompanied by secondary ridges. The angle between crown and root is nearly 140°, in agreement with the hadrosaurine condition as described by Sternberg (1936); on the other hand, the ratio between width of crown and labial-lingual diameter is characteristic of the lambeosaurines. The same discrepancy was pointed out by Langston (1960) in his description of the dentary teeth of *Lophorothon atopus*. Despite this curious point of similarity, however, we feel that a positive assignment of the North Carolina tooth to *Lophorothon* would be unwarranted.

A partial right scapula (ANSP 15322) from Phoebus Landing was described by Miller (1967: 233, Pl. 4, Fig. 6). The fragment preserved appears to come from near the middle of the blade, above the acromial ridge. Its edges are parallel and do not appear to be diverging dorsally. According to Brett-Surman (1976) non-expanding scapular blades of this sort are generally attributable to the Hadrosaurinae.

Two hadrosaurian limb bones, a right second metatarsal lacking its distal end and a fragment of a small left tibia ("fibula" of Cope 1875, Pl. 7, Figs. 1-1a), are here removed from the syntypic series of *Hypsibema crassicauda* (USNM 7189). The tibia fragment (Figs. 4C-C^1) consists of a badly eroded and water worn mid-shaft that is uncharacteristic below the family level. Reconstructed, this tibia would have been about 600 mm long, or about two-thirds the length of the tibia in the type skeleton of *Hadrosaurus foulkii* Leidy (ANSP 10005). The metatarsal (Figs. 4D-D^1) is close in size and morphology to the corresponding element in *Hadrosaurus foulkii.* A right third metatarsal (USNM 5963, Fig. 8B) from Phoebus Landing was listed by Gilmore in Stephenson (1912: 120) as *Trachodon tripos*? (Cope). This bone is 340 mm long and has proportions similar to those of *Kritosaurus.* But since generic differences have not been recognized in the metatarsals of hadrosaurian dinosaurs, no generic identification is possible at this time.

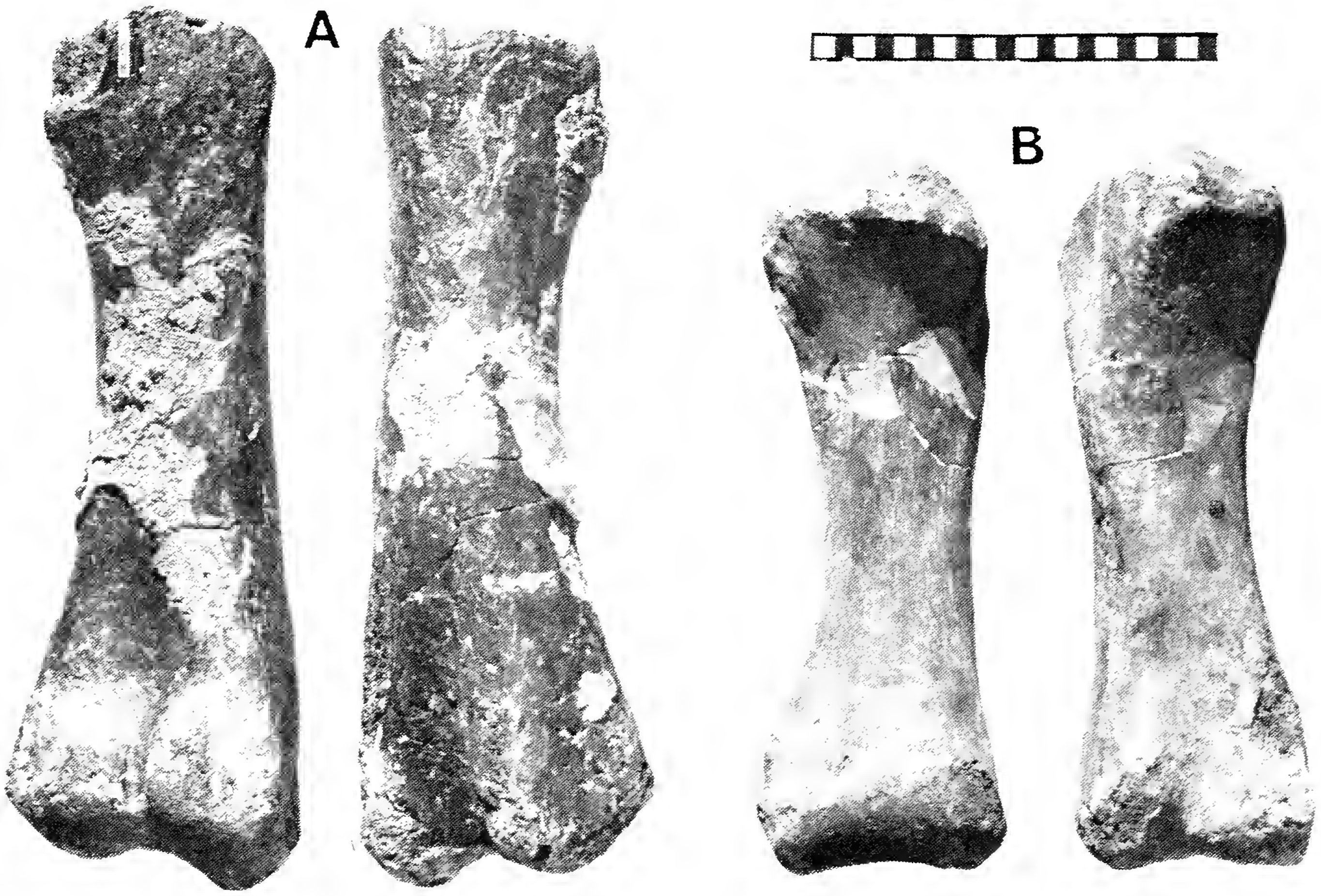

Fig. 8. Hydrosaurinae indet. **A**, distal half of right humerus from Milepost 49, UNC 5735, in anterior and posterior views; **B**, right metarsal III from Phoebus Landing, USNM 5963, in anterior and posterior views. Scale in cm.

Brett and Wheeler (1961: 69) and Heron and Wheeler (1964: 46) mentioned a portion of a dinosaur leg bone collected at Milepost 49 in the base of the Peedee Formation, having evidently been reworked from the underlying Black Creek sediments. This bone (UNC 5735, Fig. 8A) is the distal half of a very large right humerus, measuring fully 415 mm from the condyles to the base of the deltopectoral ridge. The proportions of the shaft are similar to those of *Hadrosaurus foulkii* and *Kritosaurus incurvimanus* Parks (1920: 35, Fig. 9). Reconstructed, the humerus would have been about 830 mm long, exceeded in length only by the lambeosaurine humerus from Baja California described by Morris (1972). From the proportions of other lambeosaurines Morris computed that the Mexican hadrosaur would have been about 16.5 m (54 ft.) long. Although computations of this sort may be possible with lambeosaurines, there is evidence that such is not the case with hadrosaurines: an undescribed hadrosaurine (AMNH 5465) from the lower Two Medicine Formation of Montana has a humerus 765 mm long while its other limb elements are the same length as those in a skeleton of *Kritosaurus notabilis* (AMNH 5350) that has a humerus only 490 mm long. Because of this variability in humerus length within the subfamily Hadrosaurinae, we are not prepared to estimate the North Carolina dinosaur's size, beyond saying that the humerus might have come from an individual exceeding 12 m (40 ft.) in length. The large metatarsal (USNM 5963) described above is about the same size as that in the type skeleton of *Kritosaurus incurvimanus*, which has a total length of about 8.2 m (27 ft.).

In summary, all the hadrosaur material described above appears to pertain to the subfamily Hadrosaurinae but none of the bones can be identified on the generic level.

NON-DINOSAURIAN REMAINS

For the sake of completeness we append here a brief discussion of certain specimens from North Carolina that have been cited erroneously in the literature as dinosaurian.

Class MAMMALIA
Order CETACEA
Suborder MYSTICETI
Family BALAENOPTERIDAE
"Hadrosaurus tripos" Cope, *nomen dubium*

Hadrosaurus tripos Cope, 1869: 192; 1870: 122-I-J; 1875: 40-41, Pl. 5, Figs. 1-1a (only).

Material.—Type, USNM 7190, a large caudal vertebra. Cope's initial publication cited two caudals from the same locality: one "near the thirtieth caudal" with a centrum height of 4.5 in. (USNM 7190) and another, "apparently terminal." Cope's subsequent and more detailed descriptions ignored the second vertebra but added a third from another locality: "A second [sic] and much smaller vertebra from the pit that furnished the remains of Hypsibema crassicauda, belonged to a third individual, and possibly to this species" (Cope 1870). The "terminal" vertebra is now missing and the tentatively referred "second" vertebra, also missing, is attributed by us to a juvenile *Hypsibema crassicauda.* Lull and Wright (1942: 145) cited as cotypes USNM 7190 and 7093, but since the latter specimen is labeled as having been collected by Berry and Stephenson at Phoebus Landing in 1907 it cannot be part of the type material; we take it to be a

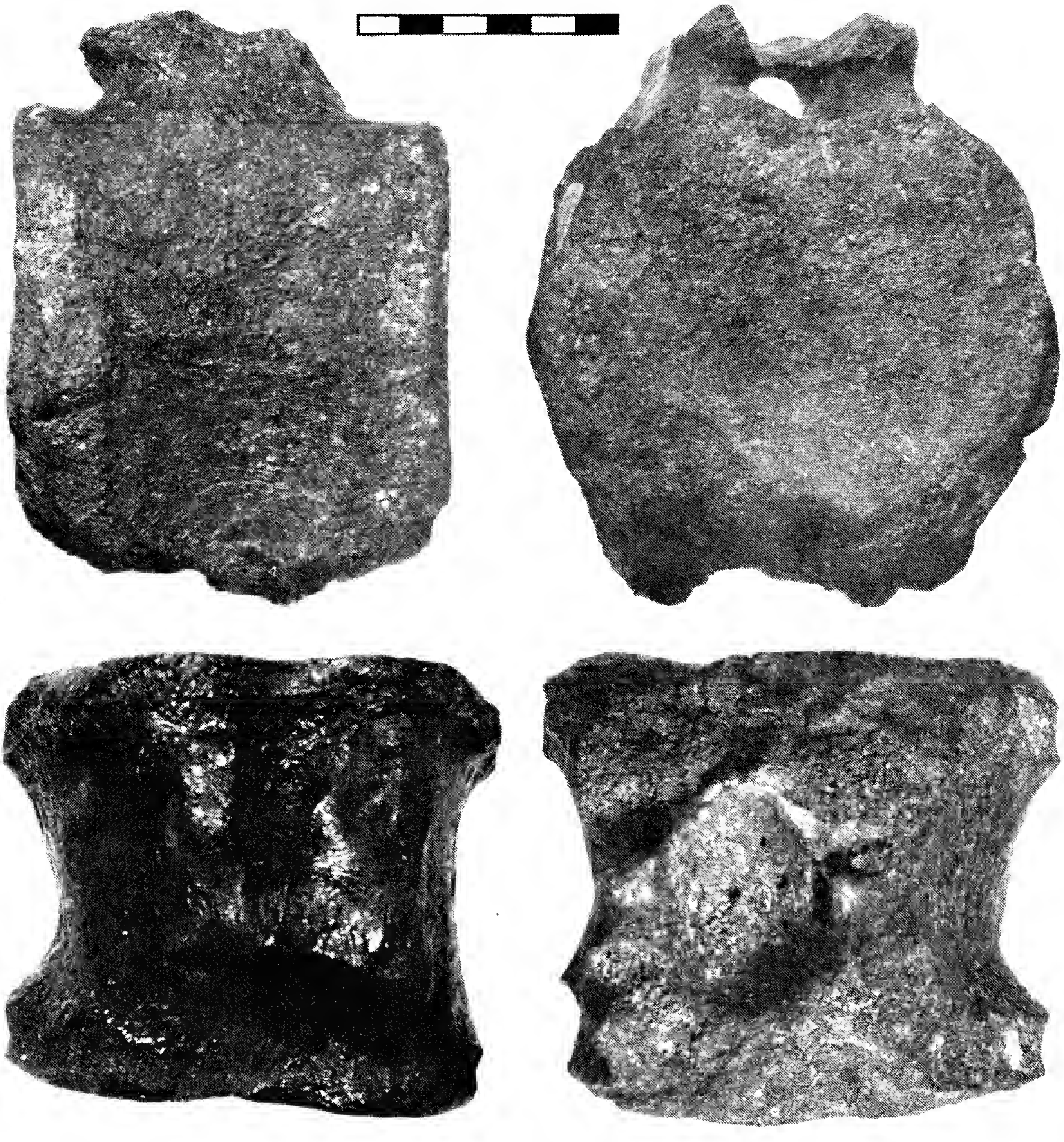

Fig. 9. Balaenopterid whale, caudal vertebra in lateral, anterior, dorsal and ventral views; lectotype specimen of *"Hadrosaurus tripos,"* USNM 7190. From W. J. Thompson's marl pit in Sampson County near Faison, evidently from the Duplin Marl. Scale in cm.

badly damaged vertebra of *Hypsibema.* Two additional caudals from Phoebus Landing, USNM 7094 and 7095, were assigned to *Hadrosaurus tripos* by Lull and Wright; the second is correctly identified (i.e. is cetacean) but USNM 7094 is here transferred to *Hypsibema crassicauda.* Thus USNM 7190, the vertebra upon which Cope's species concept was principally based, remains as the lectotype of *Hadrosaurus tripos.*

Locality and age.—W.J. Thompson's marl pit in Sampson County, about 10 miles (16 km) from James King's marl pit; collected by W. C. Kerr. Cope's original announcement of fossil reptiles from North Carolina began with the curious statement that the remains were "of cretaceous age, which were intrusive in miocene beds." As noted above, the actual stratigraphic relationship is one of residual patches and erosional residue of Tertiary marls overlying a Cretaceous terrane. Its zoological affinities indicate that the type specimen of *H. tripos* (with other misidentified cetacean bones from the "Cretaceous") must have been derived from the Duplin Marl. According to the Geological Society of America's correlation chart (Cooke et al. 1943) the Duplin is a lateral equivalent of the upper part of the Yorktown Formation. Its age is there indicated as latest Miocene, but more recent investigation points to a Pliocene dating (Baum and Wheeler 1977).

Discussion.—As Cope did, we have compared the type specimen of *Hadrosaurus tripos* with the caudal vertebrae of the type species, *H. foulkii* Leidy (type, ANSP 10005) — as well as those of numerous other dinosaurian genera — but we cannot concur with his identification. In its morphology, and particularly in the presence of zones of coalescence between the epiphyses and the body of the centrum, the vertebra is clearly mammalian and evidently cetacean. This reinterpretation was confirmed independently by Clayton E. Ray and Frank C. Whitmore, Jr. (pers. comm., 1977), who identified the specimen as a caudal vertebra of a balaenopterine whale and noted that its size is appropriate to *Megaptera expansa* Cope, 1868. The latter species, however, was rejected by Kellogg (1968: 116-118) on the grounds that Cope's syntypic series is a mixture of generically indeterminate vertebrae of two taxa from three localities in Maryland and Virginia. Surely the nominal species *Hadrosaurus tripos* has no greater claim to taxonomic validity than *Megaptera expansa*; and while it must be removed from the genus *Hadrosaurus*, we feel that there is no genus of whale to which it can be justifiably transferred. We list it therefore as *"Hadrosaurus tripos"* Cope, *nomen dubium.*

The large vertebral centrum (SM 13025) from Phoebus Landing tentatively assigned to *Protamia* by Miller (1968: 470, Pl. 1, Figs. 1, 3) was shown by Boreske (1974: 75, Fig. 26H) to be a cetacean caudal. Like the type specimen of *"Hadrosaurus tripos"* it is evidently an erosional remnant from the Duplin Marl.

Class REPTILIA
Order CROCODILIA
Suborder EUSUCHIA
Family CROCODYLIDAE
Deinosuchus Holland, 1909
Deinosuchus rugosus (Emmons 1858), n. comb.

The anterior portion of a right maxilla identified as *Gorgosaurus*? by Miller (1967: 232-233, Pl. 3, Figs. 8-10; Pl. 4, Fig. 1; ANSP 15303) is demonstrably crocodilian on the basis of its circular alveoli with dished bottoms and the presence of a circular-sectioned, hollow tooth-root in the most anterior alveolus. Brigaded with it under the same catalog number are several unassociated and fragmentary bones (right jugal, left angular, right squamosal?) that appear to represent the same species. The maxilla is exceptionally deep and its dorsal surface slopes down abruptly to the anterior sutural surface with which the premaxilla articulated. Huge size, a deep snout, and a deep dorso-lateral saddle or notch between premaxilla and maxilla are all characteristic of the crocodilian genus *Deinosuchus* Holland, 1909, with which *Phobosuchus* Nopcsa, 1924, is objectively synonymous (see Colbert and Bird 1954). Reassignment of the maxilla from Phoebus Landing to *Deinosuchus* is supported by the evidence of an undescribed partial skeleton from Texas (Wann Langston, Jr., pers. comm., 1978).

The first evidence of this giant crocodile in North Carolina consisted of huge teeth found by Emmons (1858: 219-221, Figs. 38-39) in the "miocene" marl at Elizabethtown, Bladen County. Emmons explicitly recognized the possibility that his specimens might have been reworked from older beds, and subsequent finds make it clear that their source must have been the Cretaceous Black Creek Formation rather than the Cenozoic marl. He assigned the teeth to Owen's genus *Polyptychodon* as a new species, *P. rugosus*. Leidy (1865: 17-18, 116; Pl. 3, Figs. 22-23) recognized the Cretaceous age and illustrated (as "undetermined") two additional teeth. Cope (1871) transferred Emmons' species to *Thecachampsa* and (1875, Pl. 7, Fig. 3) illustrated a characteristic tooth collected by W. C. Kerr. Hay (1902: 513) reassigned the species as *Crocodylus rugosus* (Emmons). Teeth that are virtually indistinguishable from Emmons' type specimens were collected at Phoebus Landing by Miller (1967, Pl. 2, Figs. 5-6; plus specimens not illustrated, ANSP 15308); and a quantity of undescribed material collected by Stephenson and Berry is housed in the National Museum of Natural History.

As the morphology, distribution and taxonomy of *Deinosuchus* are currently being studied by Langston, further analysis would be inappropriate here. The presence of this gigantic crocodilian in the Black Creek fauna of North Carolina is significant to the study of dinosaurs in view of Colbert and Bird's (1954: 21) cogent suggestion that *Deinosuchus* "may very well have hunted and devoured some of the dinosaurs with which it was contemporaneous." As *Deinosuchus* occurs in the hadrosaur-bearing formations of Wyoming, Montana, Texas, North Carolina, Delaware and New Jersey (our observation) — and doubtless elsewhere — we feel justified in proposing that giant crocodiles rather than carnosaurian dinosaurs may have been the major predators upon the amphibious hadrosaurs. In that case the predator/prey ratios computed by Bakker (1972), who assumed that "tyrannosaurs were the only carnivores powerful enough to kill and dismember duck-bills, horned dinosaurs and ankylosaurs," may seriously misrepresent the ecological realities.

Order CHELONIA
Genera indet.

A badly water-worn bone fragment (UNC 3370) from the basal Peedee Formation at Milepost 49 on the Cape Fear River was illustrated by Brett and Wheeler (1961, Pl. 9, Fig. 5a-b) as a "dinosaur tarsal." This bone is the proximal end of the left femur of a large turtle. So far as comparisons can be made it is similar to, but slightly larger than, the femur of *Taphrosphys sulcatus* (Leidy) as illustrated by Gaffney (1975; PU 18707). On the ventral surface of the inner trochanter it bears a transverse, canoe-shaped depression lacking in *Taphrosphys*. A more precise identification of the turtle represented is beyond our competence. The eroded and ablated condition of the bone suggests that it has been reworked from the underlying Black Creek Formation.

A small phalangeal bone (ANSP 15327) from Phoebus Landing that Miller (1967: 232, Pl. 3, Figs. 3-4) thought might belong to a small coelurosaur appears instead to be a proximal pedal phalanx of a turtle, probably *Trionyx*.

THE PHOEBUS LANDING LOCAL FAUNA

Increased knowledge now makes it possible to update the provisional faunal list prepared by Miller (1967, 1968). The tabulation offered here should be considered an interim census, subject to emendation as additional material is recovered and studied. For identification of fish remains we are indebted to Gerard R. Case. A checklist of the dinosaurian specimens is being published elsewhere (Horner 1979).

Class Chondrichthyes

Asteracanthus sp. [including *Edaphodon*? cephalic spine of Miller 1968, Pl. 1, Fig. 10] — hybodont shark.
Scapanorhynchus texanus (Roemer) [*Carcharias*?, *Isurus* of Miller 1967, Pl. 1, Figs. 1-5] — ghost shark.
Squalicorax pristodontus (Agassiz) — galeoid shark.
Ischyrhiza mira Leidy [including *Hypolophus*? rostrum fragments of Miller 1968, Pl. 1, Figs. 5-6] — sawfish.
Brachyrhizodus wichitaensis Romer [*Hypolophus*?, *Protamia*? of Miller 1968, Pl. 1, Figs. 7-9, 13-14; but see Boreske 1974: 74] — rhinopterid ray.

Class Osteichthyes

Paralbula casei Estes [*Egertonia* of Miller 1967, Pl. 1, Fig. 7] — ladyfish.
Pycnodus phaseolus Hay [*Egertonia*? of Miller 1967, Pl. 1, Fig. 8; *Gyrodus*?, *Anomoeodus*, *Bottosaurus*? of Miller 1968, Pl. 1, Figs, 4, 11-12, 15-16] — deep-bodied coral-nibbler.

Class Reptilia

Order Chelonia
- *Trionyx* spp. — soft-shelled turtles.
- *Taphrosphys* sp. — side-necked turtle.

Order Squamata, Family Mosasauridae
- *Tylosaurus* sp. (Wheeler 1966) — shallow water marine lizard.
- *Platecarpus* sp. — deeper water marine lizard.

Order Crocodilia
- *Deinosuchus rugosus* (Emmons) — giant crocodile.
- *Leidyosuchus* cf. *L. formidabilis* Erickson — ordinary sized crocodile.

Order Saurischia, Suborder Theropoda
- cf. *Dryptosaurus* or *Albertosaurus* sp. — medium sized carnivorous dinosaur.
- *Ornithomimus* (?) sp. — ostrich-mimic dinosaur.

Order Saurischia, Suborder Sauropodomorpha
- *Hypsibema crassicauda* Cope — huge herbivorous dinosaur.

Order Ornithischia, Suborder Ornithopoda
- Hadrosaurinae indet. — flat-headed duckbill dinosaurs.

FAUNAL AFFINITIES

In his 1967 analysis of the Phoebus Landing assemblage Miller was impressed by its affinity with those of the Belly River Group (i.e. the Oldman and Judith River Formations) of western Canada and the mountain states. So far as the dinosaurs are concerned, the redeterminations presented in this paper do not controvert that view as a generalization; but we must point out that the material at hand does not permit the identification of Carolinian with Canadian dinosaurs on the generic level. Indeed, the closest affinities of the North Carolina dinosaurs appear to lie elsewhere.

As noted in the preceding pages, the sauropod *Hypsibema* is indistinguishable from *Parrosaurus*, a genus recorded from beds of early Maestrichtian age in Missouri. The carnosaur from Phoebus Landing is as similar to *Dryptosaurus* from the late Maestrichtian (and earlier) of New Jersey as it is to *Albertosaurus*. The single toe bone of an ornithomimid from North Carolina is comparable to ornithomimid bones from the early Campanian to late Maestrichtian of New Jersey and Delaware, as well as to *Ornithomimus* from the Belly River beds. The hadrosaurian dentary tooth from Phoebus Landing has no close counterpart except in *Lophorothon* from the early Campanian of Alabama.

Considering the quality of the evidence available, we suggest that firm conclusions about the affinities of the Black Creek dinosaur assemblage are unwarranted at present. Caution seems particularly appropriate in the light of our observation (Baird and Horner 1977) that the Upper Cretaceous dinosaur faunas of eastern and western North America have more in common with each other than had previously been recognized. And for purposes of biostratigraphic correlation, certainly, the evidence of the invertebrates must greatly outweigh that of the vertebrates.

APPENDIX

Homonymy of *Coelosaurus* [Owen] 1854 and *Coelosaurus* Leidy, 1865

The generic name *Coelosaurus* first appeared on page 15 of a catalogue of the fossil reptiles and fishes in the museum of the Royal College of Surgeons of England, published in 1854. Although no author's name appears on the title page or elsewhere, the catalogue is known to be the work of Richard Owen and is always cited as "Owen (1854)." It is a work of original research and not a mere clerical compilation.

In that publication the name *Coelosaurus* is accompanied by a diagnosis and etymology and is applied explicitly to a single bone, No. 58 in the collection. No species name is associated with the generic name. Under the International Code of Zoological Nomenclature (1961) we must accept the generic name *Coelosaurus* [Owen] 1854 as validly published: it can be invalidated by neither its author's anonymity [Art. 9(7), Recom. 51A] nor its uninominal status [Art. 11(c)(i)]. It is thus a senior homonym of *Coelosaurus* Leidy, 1865. As there is no appeal from the Law of Homonymy, Leidy's name must be rejected.

So far as we can determine the name *Coelosaurus* [Owen] does not appear in the literature either before or after the 1854 publication cited. Its author evidently abandoned it — not surprisingly, as it was based on a mutilated vertebral centrum of indeterminate age that had been redeposited in Pleistocene drift — for he made no allusion to it in his subsequent studies on British fossil reptiles. *Coelosaurus* [Owen] is not listed in the standard nomenclators of Neave, Sherborn, and Schulze-Kukenthal, nor in the indexed bibliographies of vertebrate paleontology compiled by Hay, Camp, and Gregory. We came across it entirely by accident. As a *nomen oblitum* it deserves oblivion in taxonomy although it remains valid for purposes of homonymy.

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Revision of Appalachian *Trechus* (Coleoptera: Carabidae)

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ABSTRACT.—Appalachian *Trechus* are arranged in 2 subgenera, 4 species groups, and 28 species of which 6 species are polytypic. A new key to species and subspecies includes all 40 taxa in the genus known from Georgia, Kentucky, Maryland, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia. Thirteen new taxa are described and illustrated: *T. schwarzi scopulosus*, new subspecies, North Carolina; *T. schwarzi saludae*, new subspecies, North Carolina; *T. vandykei pisgahensis*, new subspecies, North Carolina; *T. haoe*, new species, North Carolina and Tennessee; *T. tusquitee*, new species, North Carolina; *T. valentinei*, new species, North Carolina and Tennessee; *T. stupkai*, new species, Tennessee; *T. luculentus unicoi*, new subspecies, North Carolina and Tennessee; *T. luculentus wayahensis*, new subspecies, North Carolina; *T. nantahalae*, new species, North Carolina; *T. aduncus toxawayi*, new subspecies, North Carolina; *T. aduncus coweensis*, new subspecies, North Carolina, and *T. aduncus howellae*, new subspecies, North Carolina. New locality records are reported for 8 taxa. *Trechus hydropicus* is polytypic, with subspecies *T. h. hydropicus* (Horn), *T. h. beutenmuelleri* Jeannel, *T. h. avus* Barr, and *T. h. canus* Barr.

INTRODUCTION

Species of *Trechus* are numerous and locally abundant in the southern Appalachian mountains (Unaka and Blue Ridge provinces) of western North Carolina, eastern Tennessee, and adjacent portions of Virginia, Georgia, and South Carolina. One species, *T. cumberlandus* Barr, occurs in the Cumberland plateau of Kentucky and Tennessee; *T. tennesseensis* Barr exists in caves in the Appalachian valley of east Tennessee, and *T. hydropicus* (Horn) ranges northward into easternmost Kentucky, western Virginia and Maryland, and eastern West Virginia. Five Appalachian species were recognized by Jeannel (1931) in his revision of North American Trechini, and previously I described an additional 18 species from the area (Barr 1962).

Since 1962 many fresh collections have been made. Study of this material and comparison with my 1960 collections led to the present paper. Thirteen new taxa are described, bringing the total for the region to 40 taxa, which include 28 species, of which 6 are interpreted as polytypic. In contrast, there are only 12 known native species of *Trechus* in

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all the rest of North America. New distributional records are given for 8 taxa, yet no less than 12 taxa are still known from single collections at single sites, suggesting that yet further field investigations and revisions may be necessary before this large and interesting group of small mountain beetles is properly understood from a purely taxonomic point of view.

There seems no special need to divide the Appalachian species of subgenus *Trechus* (males with first two protarsomeres dentate and setose beneath) into two species groups, and I have lumped my "*carolinae* group" (Barr 1962:73) with the *hydropicus* group. The great majority of the species belong to the endemic subgenus *Microtrechus* Jeannel, distinguished by having only the first, instead of the first two protarsomeres dentate and setose beneath in the male. This subgenus occurs in southwestern North Carolina and adjacent parts of Tennessee, Georgia, and South Carolina. Three distinctive species groups recognized by Barr (1962) have been retained in the present revision, although I have shifted one species (*T. verus* Barr) from the *uncifer* group to the *nebulosus* group. In general, the species of *Trechus* reflect the major biogeographic features of carabid distribution in the southern Appalachians as detailed by Barr (1969). Subgenus *Trechus* has most of its species north of Asheville and north of the French Broad River valley, while the species of subgenus *Microtrechus* occur south of the French Broad, although *T. (T.) schwarzi* and *T. (M.) vandykei* each have subspecies in the Black Mountains and on Pisgah Ledge, respectively. Various species and subspecies are endemic to most of the major mountain ranges of the area; lists of endemics by ranges are presented below, and locations of the ranges are shown in figure 46.

The history of *Trechus* speciation in the southern Appalachians has presumably involved vertical expansions and contractions of taxon ranges in response to the colder, wetter climates of Pleistocene glacial maxima alternating with warmer, drier regimes of interglacial periods (Barr 1962, 1969). For cold-limited species, suitable microhabitat areas waxed and waned as did the continental glaciers, with the elevation of the maximum permissible isotherm rising and falling like the level of the sea, from which the cool, wet summits of the mountains emerged like islands or achipelagoes. Because most *Trechus* species are cold-limited, their speciation patterns are essentially insular, and vicar species and subspecies are common.

It is thus not surprising that in the southern Appalachians we encounter arrays of closely similar taxa strung out along the major mountain chains like beads on a string. For some of the altitudinally limited taxa, the choice of assignment to the species or subspecies category is arbitrary: should another glacial maximum ensue, these taxa which are today allopatric could be brought together again (unlike their trechine cousins extrinsically isolated in inescapable cave systems). Applying Emerson's (1945) "practical" definition of a species, one could readily consider the taxa here treated as polytypic *T. schwarzi, T. vandykei, T. tennesseensis*, and *T. aduncus* as 11 or so distinct species because they are probably genetically (extrinsically) isolated from each other at the present time. However, intergradation between *T. hydropicus avus* and *T. h. beutenmuelleri* (Barr 1962:73) provides a morphological yardstick against which these allopatric taxa can be compared. Polytypic *T. luculentus* occurs at such low elevations that existing gaps ought to pose no problems to occasional gene flow between component subspecies. In most instances I have employed a conservative treatment; if I have erred on the conservative side, I will at least have indicated the close relationship of the taxa involved. For example, all of the *aduncus*-group taxa (=polytypic *T. aduncus* in the present paper) have, in my judgment, been derived from a single ancestral form which became isolated relatively recently by the gradual restriction of suitably cool, moist microhabitats to the summits of various mountain ranges in the Great Balsams, Cowees, and Nantahalas. Perhaps *T. aduncus aduncus* and *T. toxawayi* may occasionally interbreed at some intermediate geographic point, but *T. howellae* and *T. coweensis* are probably absolute genetic isolates at the present time. My views on the probable degree of isolation at present are indicated in the taxon accounts, so that the reader may either accept my basically conservative interpretations or superimpose equivocally feasible, more liberal interpretations of his own.

The addition of several new taxa has necessitated rewriting a key to species and subspecies of Appalachian *Trechus*. All known species and subspecies from the states of Georgia, Kentucky, Maryland, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia are included. The present key makes greater use of external morphology than my 1962 key, but determinations should always be checked by examination of an aedeagus where possible (cf. figs. 1-27 in Barr 1962, and figs. 18-43 in the present paper). The range of most species and subspecies is quite limited, and the precise provenance of a specimen, if known, can be used to limit still further the species under consideration.

The accounts of taxa other than those newly described take the form of an annotated checklist; the minimal information given is full taxonomic citation and geographic range. Miscellaneous collecting information and data on syntopic and sympatric relationships with other species of the genus have been added when available.

KEY TO SPECIES AND SUBSPECIES OF SOUTHERN APPALACHIAN *TRECHUS*

1. Males with two segments of protarsus enlarged .... (*Trechus*, sensu stricto) 2

Males with only the first protarsal segment enlarged .... (subgenus *Microtrechus*) 12

2(1). Pronotum about 0.7-0.8 times as long as wide, total length 3.5-5.0 mm. 6

Pronotum (Fig. 1) very transverse, less than 0.7 times as long as wide; length 2.5-3.5 mm .... (*hydropicus*) 3

3(2). Elytra with 5 well-developed striae and trace of sixth stria, inner intervals subconvex; aedeagal apex minutely knobbed (Fig. 18); western Virginia, Maryland, eastern West Virginia .... *hydropicus hydropicus* (Horn)

Elytra with 4 or 5 complete striae, more shallowly impressed 4

4(3). Pronotum with hind angles blunt or sharp, elytra with 4 or 5 striae, at least inner 3 striae moderately impressed; apex of aedeagus knobbed, or thickened and inflected (Figs. 19, 21) 5

Pronotum with hind angles sharp, obtuse; elytral striae very shallow, inner 3 more pronounced than 4th, at best a trace only of 5th stria present; apex of aedeagus unmodified (Fig. 20); Roan and Bald mountains of Tennessee-North Carolina border, southeast to Black and Great Craggy mountains, North Carolina .... *hydropicus beutenmuelleri* Jeannel

5(4). Elytra with 5 striae and trace of 6th (5th and 6th striae may both be very shallow in westernmost part of range); apical recurrent groove long; apex of aedeagus (Fig. 21) thickened and inflected; Grayson County, Virginia, to Harlan County, Kentucky .... *hydropicus canus* Barr

Elytra with 4 striae and trace of 5th; apical recurrent groove short to moderate; aedeagus as in Fig. 19; Blue Ridge in Avery and Ashe counties, North Carolina .... *hydropicus avus* Barr

6(2). Pronotum (Fig. 2) with sides subparallel in basal fourth, hind angles large and nearly right; Roan Mountain, Tennessee, and adjacent North Carolina .... *roanicus* Barr

Pronotum with sides convergent, hind angles small, various (Figs. 3, 4, 5) 7

7(6). Range: mountains of western North Carolina 8

Range: Cumberland plateau from Rockcastle County, Kentucky, to Grundy County, Tennessee .... *cumberlandus* Barr

8(7). Range: Black and Great Craggy mountains and vicinity 9

Range: south and west of Asheville 11

9(8). Smaller, 3.4-4.2 mm, eye diameter equal to or greater than scape length; pronotum sides feebly sinuate before hind angles; elytra with four complete striae and trace of 5th stria; apical groove ending well in advance of anterior apical puncture 10

Larger, 4.4-4.8 mm, eye diameter less than scape length; pronotum sides not sinuate, hind angles obtuse and sharp; elytra with five shallow, complete striae and traces of 6th and 7th striae; apical groove short, ending at level of anterior apical puncture .... *carolinae* Schaeffer

10(9). Pronotum (Fig. 4) sides feebly sinuate before obtuse hind angles; aedeagus apex slender, attenuate, tipped with more or less rounded knob .... *schwarzi scopulosus*, new subspecies

Pronotum sides very briefly but distinctly sinuate before very small, right hind angles; aedeagus apex not attenuate, tipped with knob bearing sharp ventral cusp .... *mitchellensis* Barr

11(8). Larger, 3.8-4.4 mm; pronotum (Fig. 3) a little less transverse, sides shallowly sinuate before hind angles; aedeagus (Fig. 23) 1.31-1.39 mm long; Mt. Pisgah area, Buncombe, Haywood, and Transylvania counties, North Carolina .... *schwarzi schwarzi* Jeannel

Smaller, 3.4-3.6 mm; pronotum (Fig. 5) more transverse, sides more deeply sinuate before hind angles; aedeagus (Fig. 24) 1.08-1.16 mm long; gorge of North Pacolet River, Polk County, North Carolina .... *schwarzi saludae*, new subspecies

12(1). Aedeagus with apex rounded, slightly knobbed, or briefly reflexed; AND/OR internal sac without large, sharp scales which obscure transfer apparatus 13

Aedeagus (Figs. 32-35) with apex conspicuously reflexed and hooked; internal sac armed with many large, sharp scales which obscure transfer apparatus; smaller species, 2.7-3.9 mm .... (*uncifer* group) 15

13(12). Aedeagus (Figs. 25-31) with apex gradually attenuate, rounded or slightly knobbed at tip; transfer apparatus not obscured by scales, consisting of two lamellar copulatory sclerites, left small and triangular, right larger and apically rounded; smaller species 2.4-3.3 mm long, aedeagus 0.43-0.92 mm .... (*vandykei* group) 20

Aedeagus (Figs. 36-43) with apex broad, very briefly narrowed and slightly reflexed at tip; transfer apparatus of heavily sclerotized copulatory pieces, variable in structure but usually not as described above; medium to large species, 3.3-5.5 mm long, aedeagus 0.63-1.27 mm long .... (*nebulosus* group) 27

14(12). Pronotum with sides not sinuate before hind angles, which are always obtuse 15

Pronotum with sides at least feebly sinuate in basal tenth, hind angles obtuse or less than obtuse; aedeagus as in Figs. 32-35 .... *(aduncus)* 17

15(14). Elytra with 3 inner longitudinal striae clearly impressed; aedeagus about 0.9-1.5 mm long, apex greatly produced and slender 16

Elytra with at least 5 clearly impressed striae, disc rather depressed; aedeagus about 0.7 mm long, apex briefly attenuate and produced; Unicoi Mountains, North Carolina-Tennessee .... *talequah* Barr

16(15). Length 2.7-3.2 mm; aedeagus arcuate, apex abruptly narrowed and produced, 0.88-1.03 mm long; Great Smoky and Plott Balsam mountains, North Carolina-Tennessee .... *uncifer* Barr

Length 3.2-3.5 mm; aedeagus very long (1.47-1.49 mm) and straight, apex greatly produced and not deflexed; Great Balsam Mountains, North Carolina .... *satanicus* Barr

17(14). Elytra with two clearly impressed inner striae, 3rd and 4th striae (if present) very shallow; Great Balsam Mountains and associated spurs, North Carolina 18

Elytra with 5, rarely 4 or 6 striae; Cowee and Nantahala mountains, North Carolina 19

18(17). Aedeagus (Fig. 32) thicker, apex briefly produced; Great Balsam mountain crest, also Pisgah Ledge .... *aduncus aduncus* Barr

Aedeagus (Fig. 33) more slender, apex produced and slightly swollen before terminal hook; Toxaway Mountain .... *aduncus toxawayi*, new subspecies

19(17). Aedeagus (Fig. 35) with median lobe strongly arcuate at middle, basal bulb and anterior portion bent at right angles to apical portion; apex with reflexed hook; Nantahala Mountains, North Carolina .... *aduncus howellae*, new subspecies

Aedeagus (Fig. 34) with straight middle portion of median lobe, only basal bulb bent at right angle; apex produced and knobbed; Cowee Mountains, North Carolina .... *aduncus coweensis*, new subspecies

20(13). Length 2.6-3.2 mm, elytra narrower and with 2 to 4 clearly defined striae; aedeagus smaller, 0.45-0.82 mm long 21

Length 3.1-3.3 mm, elytra broadly oval, with at least 5 well-defined striae; aedeagus 0.85-0.92 mm long; eastern Great Smoky and Plott Balsam mountains, North Carolina-Tennessee .... *subtilis* Barr

21(20). Larger, length 2.8-3.2, mean 3.0 mm; aedeagus 0.64-0.82 mm long (Figs. 30, 31); elytra usually with 3 inner striae clearly defined 22

Smaller, length 2.5-2.9, mean 2.7 mm; aedeagus length 0.45-0.72 mm (Figs. 25-29); elytra usually with either 2 or 4 inner striae clearly defined 23

22(21). Aedeagus (Fig. 30) more slender, apex gradually attenuate, slightly knobbed and feebly reflexed; widely distributed in southwestern North Carolina, northeast Georgia, southeast Tennessee .... *barberi* (Jeannel)

Aedeagus (Fig. 31) thicker, apex broader and reflexed, apical knob a little larger; known only from western Great Smoky Mountains, North Carolina-Tennessee .... *tonitru* Barr

23(21). Pronotum with hind angles obtuse, sides not sinuate before base (Figs. 9, 10) 24

Pronotum with hind angles right or slightly more than right, sides briefly but distinctly sinuate before base (Figs. 6, 7, 8) 25

24(23). Hind angles of pronotum rounded (Fig. 10); aedeagus (Fig. 29) 0.58-0.72 mm long, apex gradually attenuate and terminating in small, reflexed knob; Great Smoky Mountains, North Carolina-Tennessee .... *bowlingi* Barr

Hind angles not rounded (Fig. 9); aedeagus (Fig. 28) 0.49-0.58 mm long, apex produced and bluntly truncate; Tusquitee, Snowbird, and Cheoah mountains, North Carolina .... *tusquitee*, new species

25(23). Elytra with only the inner 2 striae clearly defined, but with traces of 3rd and 4th striae; pronotum shallowly sinuate before hind angles; parameres usually with 5 apical setae .... *(vandykei)* 26

Elytra with inner 4 striae more or less equally impressed; sides of pronotum briefly but distinctly sinuate before small, more or less right hind angles; parameres with 4 apical setae; Unicoi Mountains, North Carolina-Tennessee .... *haoe*, new species

26(25). Pronotum sides more strongly rounded, hind angles nearly right (Fig. 6); aedeagus (Fig. 25) a little larger, 0.46-0.51 mm, less arcuate; Black and Great Craggy mountains north to Bald Mountains, North Carolina-

Tennessee .... *vandykei vandykei* (Jeannel)

Pronotum sides more oblique, hind angles a little obtuse (Fig. 7); aedeagus (Fig. 26) slightly smaller, 0.45-0.49 mm, more arcuate; Great Balsams, Pisgah Ledge, and Cowee Mountains, North Carolina .... *vandykei pisgahensis*, new subspecies

27(13). Eyes small and subconvex to flat, their short diameter 2/3 to 3/4 length of scape 28

Eyes large and convex, their short diameter subequal to scape length, or greater than scape length 35

28(27). Sides of pronotum distinctly sinuate before hind angles 29

Sides of pronotum not sinuate, or very briefly and almost imperceptibly sinuate 31

29(28). Hind angles more or less right, apical recurrent groove long, joining or directed toward 5th stria far in advance of anterior apical puncture ... . (*tennesseensis*) 30

Hind angles obtuse (Figs. 17, 45); apical recurrent groove joining 5th stria a short distance in advance of anterior apical puncture; Nantahala Mountains, North Carolina .... *nantahalae*, new species

30(29). Clypeus with pair of oblique striae internal to clypeofrontal grooves; caves in Roane County, Tennessee .... *tennesseensis tennesseensis* Barr

Clypeus without oblique striae internal to clypeofrontal grooves; caves and lowland forests in Great Smoky Mountains, Tennessee .... *tennesseensis tauricus* Barr

31(28). Apical recurrent groove short, joining 5th stria at level of anterior apical puncture; pronotum sides very feebly sinuate or not sinuate before hind angles; hind angles small; elytra with 3 to 5 striae 32

Apical recurrent groove long, joining 5th stria well in advance of anterior apical puncture; pronotum sides not sinuate, hind angles large, blunt, obtuse (Fig. 44); elytra usually with 5 striae; spruce-fir forests in central Great Smoky Mountains, North Carolina-Tennessee . *novaculosus* Barr

32(31). Elytra with 3 to 6 striae, but at most only 4 striae well impressed; pronotum as in Figs. 11, 12; apex of aedeagus produced, knobbed, or hooked; spruce-fir forest in Great Smoky Mountains 33

Elytra with at least 5 well impressed striae; pronotum as in Fig. 16; apex of aedeagus broad, finely reflexed only at tip; caves in Tuckaleechee Cove, Blount County, Tennessee .... *tuckaleechee* Barr

33(32). Pronotum (Fig. 11) sides scarcely or not sinuate; usually at least 5 or 6 striae visible, though only inner 2 to 4 are well impressed; aedeagus 0.92-1.02 mm long 34

Pronotum (Fig. 12) sides finely sinuate immediately before the small, right, hind angles; inner 2 elytral striae complete but lightly impressed, 3rd stria shallower, 4th evanescent; aedeagus (Fig. 38) 0.77 mm long (unique holotype), apex produced and reflexed at tip; known only from Ramsay Cascades area, Great Smoky Mountains, Tennessee .... *stupkai*, new species

34(33). Elytra usually with only inner 2 striae well impressed, although striae 3 through 5 usually discernible as progressively obsolescent traces; aedeagus (Fig. 37) slender and elongate, apex gradually attenuate and hooked at tip, parameres slender, with 4 apical setae; eastern Great Smoky Mountains .... *verus* Barr

Elytra usually with 4 well impressed striae, stria (4 and) 5 obsolescent trace; aedeagus (Fig. 36) much thicker, apex briefly produced, twisted to left, deflexed, feebly knobbed; parameres shorter, broader, non-styliform; with oblique apexes bearing 3-4 setae; central Great Smoky Mountains, North Carolina-Tennessee .. *valentinei*, new species

35(27). Sides of pronotum distinctly sinuate before right or acute hind angles (Figs. 13, 14, 15) .... (*luculentus*) 36

Sides of pronotum very feebly and briefly sinuate before obtuse hind angles 38

36(35). Apical recurrent groove long, joining 5th stria well in advance of anterior apical puncture; pronotum as in Figs. 14, 15; elytra with inner 3 striae deeply impressed, inner 3 intervals convex 37

Apical recurrent groove short, joining 5th stria at level of anterior apical puncture; pronotum as in Fig. 13; elytra with 4 inner striae moderately impressed, 4 intervals subconvex; central Great Smoky Mountains, North Carolina-Tennessee .... *luculentus luculentus* Barr

37(36). Aedeagus 0.95-1.04 mm long; outer striae feeble but discernible; Unicoi Mountains, North Carolina-Tennessee . *luculentus unicoi*, new subspecies

Aedeagus 0.84-0.92 mm long; outer striae obsolete; Wayah Bald area in Nantahala Mountains, North Carolina .... *luculentus wayahensis*, new subspecies

38(35). Elytra with 3 to 5 moderately impressed striae 39

Elytra with all striae very feebly impressed, inner 2 or 3 striae barely discernible; Plott Balsam Mountains, North Carolina . *balsamensis* Barr

39(38). Length 4.5-5.0 mm; elytra with 4 or 5 striae; Plott Balsams and western Great Balsam Mountains, North Carolina .... *rosenbergi* Barr

Length 3.3-4.0 mm; elytra with 3 to 4 striae; central Great Smoky Mountains, North Carolina-Tennessee .... *nebulosus* Barr

CLASSIFICATION OF APPALACHIAN *TRECHUS*

Trechus, sensu stricto

hydropicus group

hydropicus hydropicus (Horn) — western Maryland and Virginia, eastern West Virginia (widespread taxon)

hydropicus avus Barr — Ashe and Avery counties, North Carolina

hydropicus beutenmuelleri Jeannel — Black, Great Craggy, Bald, and Roan mountains, North Carolina and Tennessee (widespread taxon)

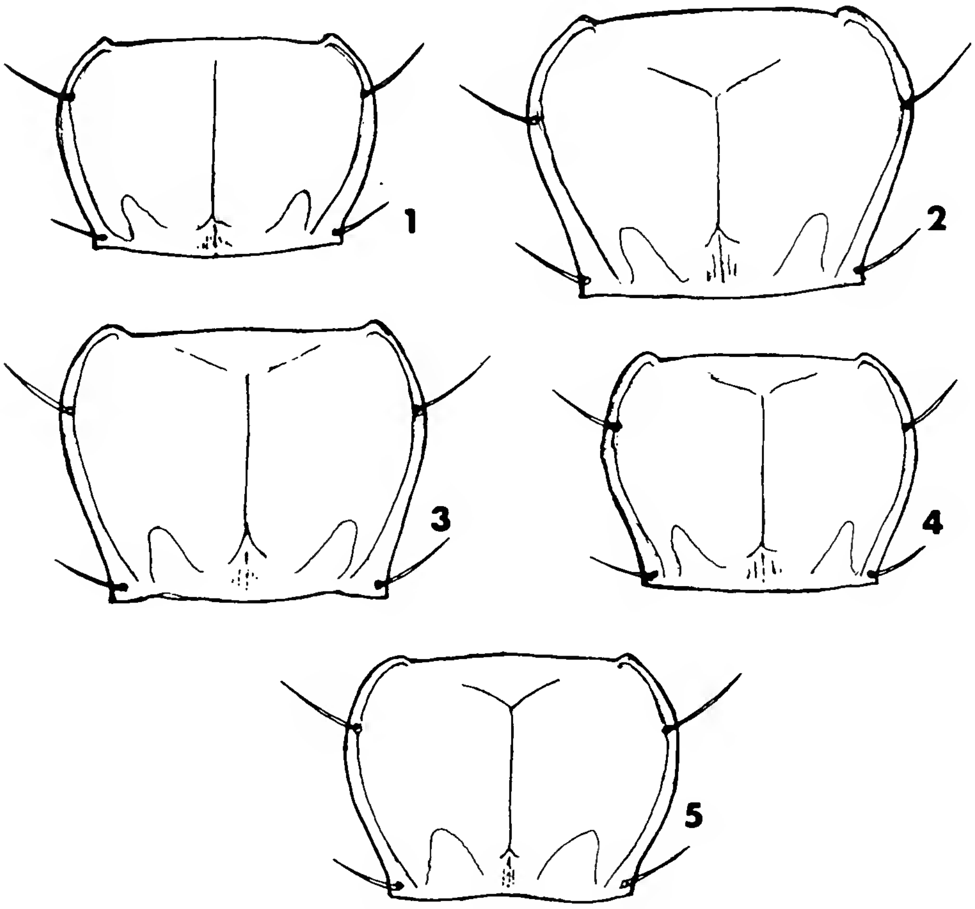
hydropicus canus Barr — Grayson, Washington, and Lee counties, Virginia, to Harlan and Letcher counties, Kentucky

schwarzi schwarzi Jeannel — Pisgah Ledge, Haywood-Buncombe-Transylvania counties, North Carolina

schwarzi scopulosus, new subspecies — Black and Great Craggy mountains, Yancey-Buncombe-McDowell counties, North Carolina

schwarzi saludae, new subspecies — North Pacolet River gorge, Polk County, North Carolina

cumberlandus Barr — Cumberland plateau from Rockcastle County, Kentucky, southwest to Grundy County, Tennessee (widespread taxon)
mitchellensis Barr — Black Mountains, Yancey, Buncombe, and McDowell counties, North Carolina
carolinae Schaeffer — Black Mountains, Yancey County, North Carolina
roanicus Barr — Roan Mountain, Carter County, Tennessee, and Mitchell County, North Carolina.



Figs. 1-5. Pronota of *Trechus* species, *hydropicus* group: 1. *T. hydropicus hydropicus* (Horn), Mountain Lake, Virginia. 2. *T. roanicus* Barr, Roan Mountain, Tennessee. 3. *T. schwarzi schwarzi* Jeannel, Mt. Pisgah, North Carolina. 4. *T. schwarzi scopulosus*, new subspecies, Craggy Dome, North Carolina. 5. *T. schwarzi saludae*, new subspecies, Melrose, North Carolina.

Subgenus *Microtrechus* Jeannel

vandykei group

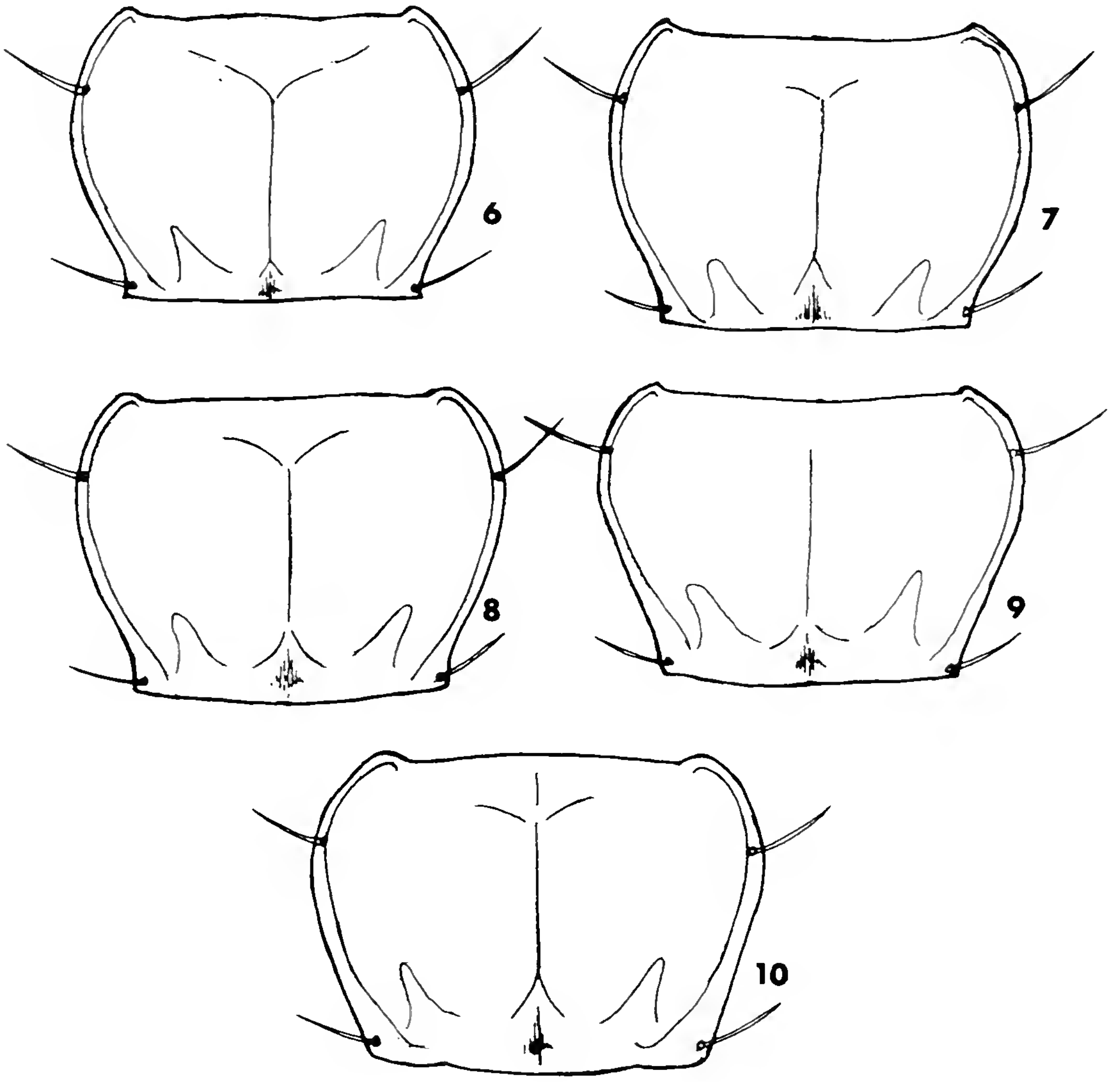
vandykei vandykei (Jeannel) — Black, Great Craggy, and Bald mountains, North Carolina and Tennessee (widespread taxon)
vandykei pisgahensis, new subspecies — Great Balsam and Cowee mountains, Buncombe, Haywood, Jackson, and Transylvania counties, North Carolina
haoe, new species — Unicoi Mountains, Graham County, North Carolina
tusquitee, new species — Tusquitee/Valley River, Snowbird, and Cheoah mountains, Cherokee, Clay, Graham, Macon, and Swain counties, North Carolina

bowlingi Barr — Great Smoky Mountains, North Carolina and Tennessee (abundant and widespread in the Smokies)

barberi (Jeannel) — Unaka mountain and Blue Ridge provinces south and west of Asheville in Georgia, North Carolina, South Carolina, and Tennessee (widespread taxon)

tonitru Barr — Thunderhead Mountain, Blount County, Great Smoky Mountains, Tennessee

subtilis Barr — eastern Great Smoky and Plott Balsam mountains, Haywood and Jackson counties, North Carolina.



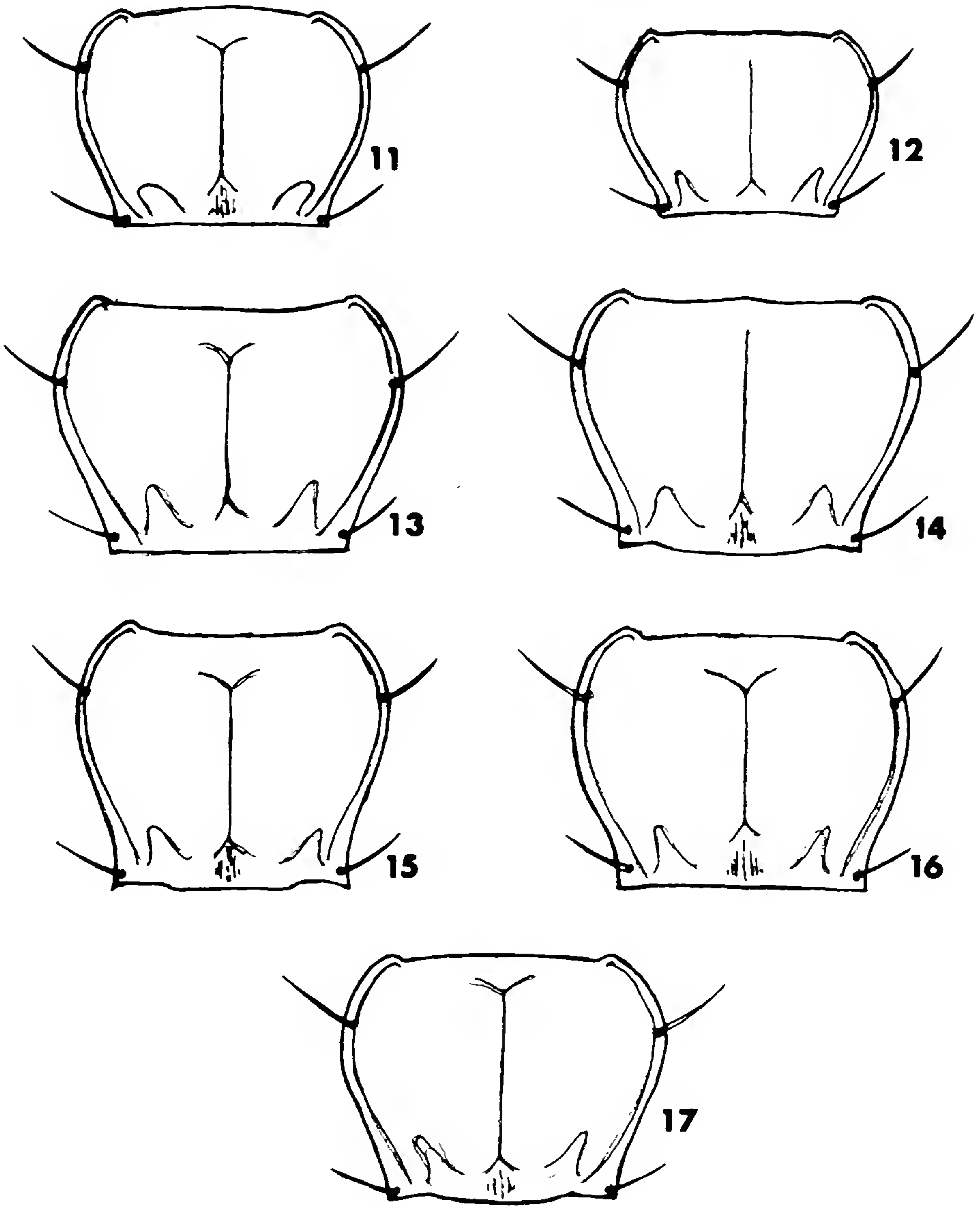
Figs. 6-10. Pronota of *Trechus* species, *vandykei* group: 6. *T. vandykei vandykei* (Jeannel), Balsam Gap, North Carolina. 7. *T. vandykei pisgahensis*, new subspecies, Mt. Pisgah, North Carolina. 8. *T. haoe*, new species, Haoe Lead, North Carolina. 9. *T. tusquitee*, new species, Tusquitee Bald, North Carolina. 10. *T. bowlingi* Barr, Mt. Sterling, North Carolina.

uncifer group

uncifer Barr — central Great Smoky Mountains east to Plott Balsam Mountains, Sevier and Cocke counties, Tennessee, and Haywood and Jackson counties, North Carolina

satanicus Barr — Great Balsam Mountains, Haywood County, North Carolina

aduncus aduncus Barr — Great Balsam Mountains, Haywood, Buncombe, Jackson, and Transylvania counties, North Carolina
aduncus toxawayi, new subspecies — Toxaway Mountain, Jackson County, North Carolina
aduncus coweensis, new subspecies — Cowee Mountains, Macon County, North Carolina



Figs. 11-17. Pronota of *Trechus* species, *nebulosus* group: 11. *T. valentinei*, new species, Mt. Kephart, North Carolina-Tennessee. 12. *T. stupkai*, new species, Ramsay Prong, Tennessee. 13. *T. luculentus luculentus* Barr, Clingmans Dome, North Carolina-Tennessee. 14. *T. luculentus unicoi*, new subspecies, Haw Knob, Tennessee. 15. *T. luculentus wayahensis*, new subspecies, Dirty John Creek, North Carolina. 16. *T. tuckaleechee* Barr, Tuckaleechee Caverns, Tennessee. 17. *T. nantahalae*, new species, Burningtown Bald, North Carolina.

aduncus howellae, new subspecies — Nantahala Mountains, Macon County, North Carolina
talequah Barr — Unicoi Mountains, Graham County, North Carolina, and Monroe County, Tennessee

nebulosus group

nebulosus Barr — central and eastern Great Smoky Mountains, North Carolina and Tennessee
balsamensis Barr — Plott Balsam Mountains, Haywood and Jackson counties, North Carolina
valentinei, new species — central Great Smoky Mountains, North Carolina and Tennessee
verus Barr — eastern Great Smoky Mountains, North Carolina and Tennessee
stupkai, new species — Ramsay Prong, Sevier County, Tennessee, in Great Smoky Mountains
novaculosus Barr — central Great Smoky Mountains, North Carolina and Tennessee
luculentus luculentus Barr — Great Smoky Mountains, North Carolina and Tennessee (widespread in the Smokies)
luculentus unicoi, new subspecies — Unicoi Mountains, Graham County, North Carolina, and Monroe County, Tennessee
luculentus wayahensis, new subspecies — Nantahala and Tusquitee/Valley River mountains, Clay and Macon counties, North Carolina
rosenbergi Barr — Plott Balsam and western Great Balsam mountains, Haywood and Jackson counties, North Carolina
tuckaleechee Barr — Tuckaleechee Caverns, Great Smoky Mountains, Blount County, Tennessee
tennesseensis tennesseensis Barr — Berry Cave, Roane County, Tennessee
tennesseensis tauricus Barr — Bull Cave and vicinity, Great Smoky Montains, Blount County, Tennessee
nantahalae, new species — Burningtown Bald, Nantahala Mountains, Macon County, North Carolina

LOCAL MOUNTAIN FAUNAS OF *TRECHUS* SPECIES

These lists of guilds of associated species reflect changes in the names of some of the species, as well as additions to the known fauna since publication of my 1962 paper on Appalachian *Trechus*. The Cowee and Nantahala mountains must be added to the list of mountain ranges with endemic species or subspecies. Toxaway Mountain, North Carolina, harbors one endemic subspecies, *T. aduncus toxawayi*, along with the common

T. barberi. An asterisk (*) indicates strict endemism; a dagger (†) indicates the taxon is endemic to two adjacent ranges.

A) Roan Mountain, North Carolina-Tennessee
hydropicus beutenmuelleri
*_roanicus_
B) Black and Great Craggy mountains, North Carolina
hydropicus beutenmuelleri
*_schwarzi scopulosus_
*_mitchellensis_
*_carolinae_
vandykei vandykei
C) Great Balsam Mountains and Pisgah Ledge, North Carolina
schwarzi schwarzi
†_vandykei pisgahensis_
barberi
*_aduncus aduncus_
*_satanicus_
†_rosenbergi_
D) Cowee Mountains, North Carolina
†_vandykei pisgahensis_
barberi
*_aduncus coweensis_
E) Plott Balsam Mountains, North Carolina
barberi
†_subtilis_
†_uncifer_
*_balsamensis_
†_rosenbergi_
F) Great Smoky Mountains, North Carolina and Tennessee
*_bowlingi_
barberi
*_tonitru_
†_subtilis_
†_uncifer_
*_nebulosus_
*_valentinei_
*_verus_
*_stupkai_
*_novaculosus_
*_luculentus luculentus_
*_tuckaleechee_ (in cave)
*_tennesseensis tauricus_ (in cave entrance)
G) Nantahala and adjacent mountains, North Carolina
*_tusquitee_
barberi
*_aduncus howellae_
*_luculentus wayahensis_
*_nantahalae_
H) Unicoi Mountains, North Carolina and Tennessee
*_haoe_
barberi
*_talequah_
*_luculentus unicoi_

SYSTEMATIC ACCOUNTS

Trechus Clairville

Subgenus *Trechus*, sensu stricto

hydropicus group

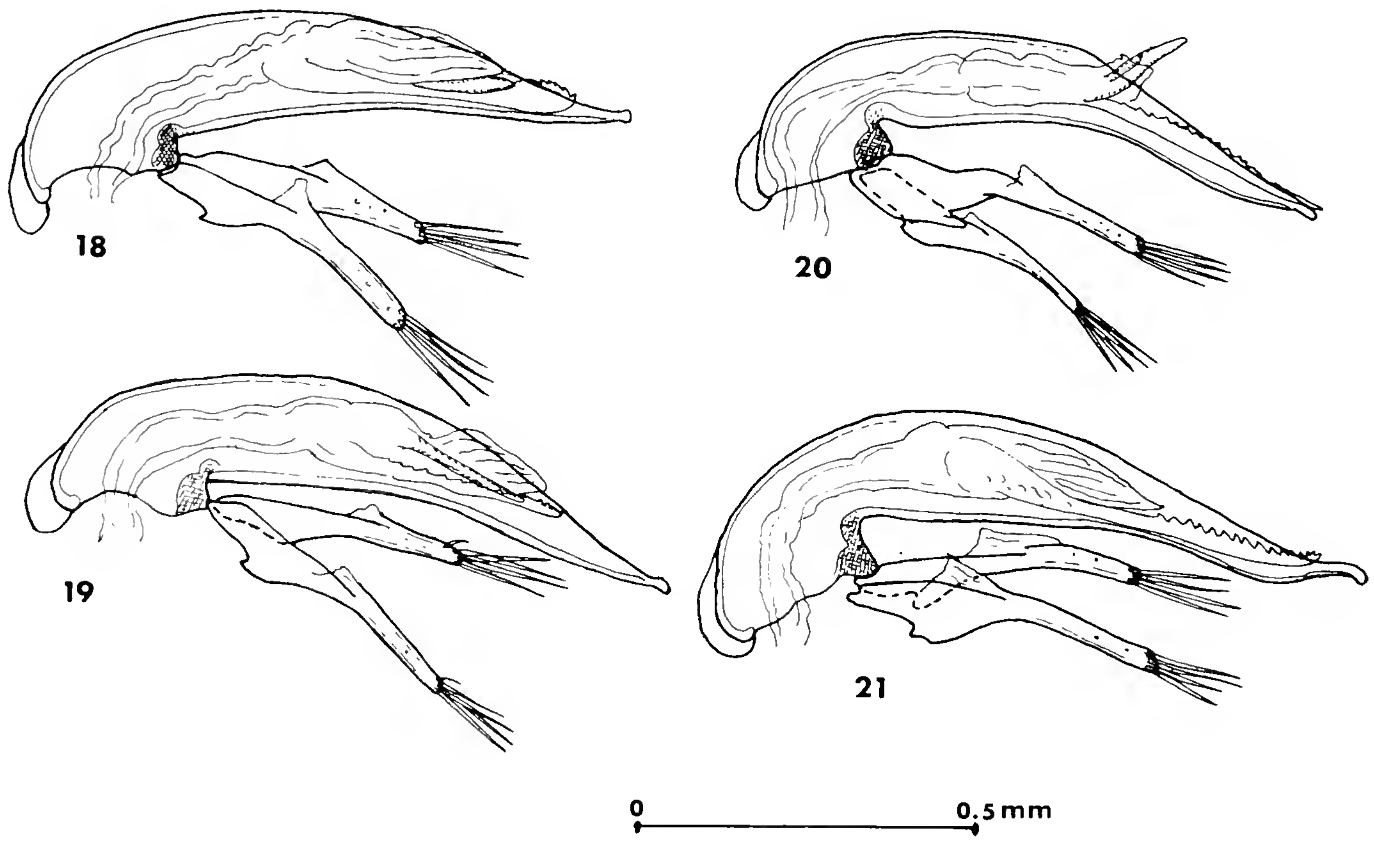
Trechus (Trechus) hydropicus hydropicus Horn, new status

Figs. 1, 18

Trechus hydropicus Horn 1883:273. Type locality, "Virginia"; type deposited in Academy of Natural Sciences, Philadelphia. Jeannel 1931:435. Barr 1962: 71.

Few specimens of typical *T. hydropicus* were available prior to 1960, most of them labeled "Va.", "W.Va.", and "Md." I suggested (Barr 1962:72) that *T. hydropicus* and *T. beutenmuelleri* Jeannel might eventually prove to belong to a widespread polytypic species, but did not then have sufficient fresh material to justify the recombination. The type of *T. hydropicus* bears the label, "Va., Ulke". I propose restriction of the type locality to Bald Knob, Mountain Lake, Giles County, Virginia; *T. hydropicus* is moderately abundant at that locality, and it is within the area known to have been visited by Ulke.

In comparison with other subspecies, *T. h. hydropicus* has an aedeagus of medium length (0.93-0.99 m), the apex of the median lobe straight and



Figs. 18-21. Aedeagi of *Trechus* species, left lateral view: 18. *T. hydropicus hydropicus* (Horn), Mountain Lake, Virginia. 19. *T. hydropicus avus* Barr, Grandfather Mountain, North Carolina. 20. *T. hydropicus beutenmuelleri* Jeannel, Mt. Mitchell, North Carolina. 21. *T. hydropicus canus* Barr, White Top Mountain, Virginia.

minutely knobbed in left lateral view. The pronotum is two-thirds as long as wide; the elytral disc is slightly flattened in the center, and its inner longitudinal striae are more deeply impressed.

New locality records for *T. h. hydropicus* are as follows; unlike the very general locations given on museum labels of 19th century collections, these localities suggest a distribution encompassing the Blue Ridge and western mountains of Virginia, eastern West Virginia, possibly north into western Maryland ("Md." labels must apply to specimens from the higher elevations in Maryland). VIRGINIA: *Giles County.* — Bald Knob at Mountain Lake, elevation 4350 ft. (1325 m) (T. C. Barr — restricted type locality); Cascades of Little Stony Creek, 2 mi. (3.2 km) nw of above locality, elevation 3000 ft. (900 m) (S. B. Peck). *Patrick County.* — Pinnacles of Dan, along Blue Ridge Parkway near Vesta (R. Hoffman and L. Knight). *Rockbridge County.* — Apple Orchard Mountain (R. Hoffman). *Tazewell County.* — Burkes Garden (R. Hoffman). WEST VIRGINIA; *Pocahontas County.* — Ravine n of Route 39, 4 mi. (6.4 km) nw Mill Point, elevation 3500 ft. (1100 m) (T. C. Barr); Falls of Hills Creek, 4 mi. (6.4 km) nw Lobelia, elevation 3300 ft. (1000 m) (S. B. Peck).

Trechus (Trechus) hydropicus avus Barr, new combination
Fig. 19

Trechus beutenmulleri avus Barr 1962: 72. Type locality, Grandfather Mountain, Avery County, North Carolina; type deposited in United States National Museum of Natural History (USNM).

This subspecies is known only from Grandfather Mountain and Three Top Mountain (Ashe County), North Carolina. It differs from *T. hydropicus hydropicus* in the slightly longer aedeagus (0.99-1.02), the apex of which is more conspicuously knobbed and reflexed. The pronotum is only 0.6 as long as wide, and the elytral striae are more feebly impressed. *Trechus h. avus* intergrades with *T. h. beutenmuelleri* on Beech Mountain, Avery County, North Carolina (see Barr 1962:73).

Trechus (Trechus) hydropicus beutenmuelleri Jeannel, new combination
Fig. 20

Trechus Beutenmülleri Jeannel 1931: 436. Type locality, Mt. Mitchell, Yancey County, North Carolina; type deposited in Museum National d'Histoire Naturelle, Paris (MNP) (not seen).

Trechus hydropicus: Schaeffer 1901: 212. Casey 1918:410. Jeannel 1927:191.

Trechus beutenmulleri beutenmulleri: Barr 1962:72.

This subspecies is abundant at higher elevations from the Black and Great Craggy mountains (Buncombe, Yancey, McDowell counties) of

North Carolina northward to the Bald Mountains along the Tennessee-North Carolina border. The northernmost limit appears to be Roan Mountain, Carter County, Tennessee—Mitchell County, North Carolina. The aedeagus is the smallest among the four subspecies of *T. hydropicus* (0.84-0.90 mm long), its apex slender, attenuate, slightly inflected but not knobbed. The pronotum is only 0.6 as long as wide, the elytral disc is convex, and the elytral striae are feebly impressed; the elytral apexes are more tapered than in other subspecies of *T. hydropicus.*

Trechus (Trechus) hydropicus canus Barr, new combination

Fig. 21

Trechus beutenmulleri canus Barr 1962:73. Type locality, Whitetop Mountain, Grayson County, Virginia (USNM).

Originally described from Whitetop Mountain in extreme southwest Virginia, *T. h. canus* has more recently been collected in Bowling Cave, 0.75 mile (1.2 km) southeast of Ben Hur, Lee County, Virginia, elevation 1700 feet (500 m) (J. R. Holsinger); from the summit of Big Black Mountain, Harlan County, Kentucky, elevation 4000 feet (1200 m) (T. C. Barr and S. B. Peck); and from the north slope of Pine Mountain, Kingdom Come State Park, Letcher County, Kentucky, elevation 2000 feet (600 m) (T. C. Barr). The range of the subspecies thus extends across the Appalachian valley floor from the Unakas to the Allegheny front; it probably intergrades with *T. h. hydropicus* farther north, but intermediate populations have not yet been discovered.

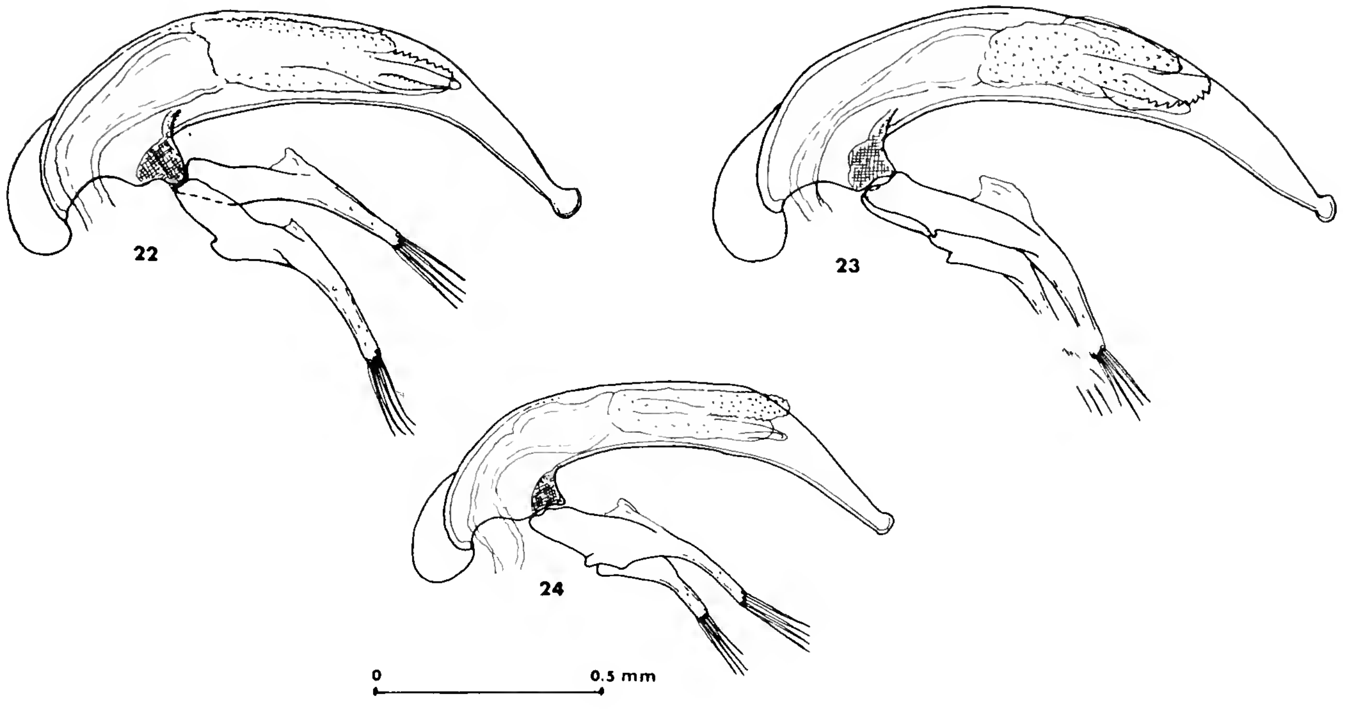
The aedeagus of *T. h. canus* is long (0.96-1.02 mm), the apex prominently inflected in left lateral view but not noticeably knobbed at the tip. Externally *T. h. canus* is virtually indistinguishable from *T. h. hydropicus*, with the pronotum fully two-thirds as long as wide, and the inner elytral striae rather deeply impressed.

Trechus (Trechus) schwarzi schwarzi Jeannel, new status

Figs. 3, 23

Trechus Schwarzi Jeannel 1931:437. Type locality, "Roan High Knob", but corrected to Retreat, Haywood County, North Carolina; type deposited in USNM. Barr 1962:74 (in part).

As previously noted (Barr 1962: 75), the type locality of *T. schwarzi* is Retreat, near the present site of Sunburst and Lake Logan, in the Great Balsam Mountains, Haywood County, North Carolina. Additional material which I recently collected at Mt. Pisgah, Haywood-Buncombe counties, and Buck Spring, Transylvania County, enabled me to make a



Figs. 22-24. Aedeagi of *Trechus* species, left lateral view: 22. *T. schwarzi scopulosus*, new subspecies, Craggy Dome, North Carolina. 23. *T. schwarzi schwarzi* Jeannel, Mt. Pisgah, North Carolina. 24. *T. schwarzi saludae*, new subspecies, Melrose, North Carolina.

careful comparison of topotypic *T. schwarzi* with similar populations in the Great Craggy and Black mountains north of the French Broad River valley. The latter proved to be taxonomically distinct and are described below. The nominate subspecies is thus restricted to populations of Pisgah Ledge, which is the eastern arm of the Great Balsams; *T. schwarzi* has not been taken at other localities in the Great Balsams.

My earlier description of *T. schwarzi* (Barr 1962) was based on a paratype from Retreat and is essentially correct, but the aedeagal sketch which accompanied it (Fig. 7) applies to *T. s. scopulosus* (described below). A female *Trechus* specimen from Tusquitee Bald, Clay-Macon counties, North Carolina, which I thought "may belong to *schwarzi*" (Barr 1962:75), is assigned to *T. (Microtrechus) luculentus wayahensis* (described below), a species and subspecies now known to be abundant in the Wayah Bald area, scarcely 10 miles (16 km) from Tusquitee Bald.

Nominate *schwarzi* is 3.8-4.4, mean 4.0 mm long. The hind angles are rather prominent and usually acute because of a relatively deep sinuosity in the lateral margins of the pronotum. Longitudinal striae of the elytra are rather shallowly impressed, the third through the sixth progressively obsolescent, the seventh absent. The aedeagus (1.31-1.39, mean 1.35 mm long) is weakly arcuate, with large basal bulb, a more or less straight middle portion, and reflexed, attenuate, and knobbed apex.

Trechus (Trechus) schwarzi scopulosus, new subspecies
Figs. 4, 22

Trechus schwarzi: Barr 1962:74, in part. NOT Jeannel 1931:437.

Etymology. — Latin *scopulosus*, "craggy;" a reference to the type locality.

Description. — Differs from *T. s. schwarzi* in smaller size, less prominent pronotal hind angles, deeper longitudinal striae of elytra; aedeagus slightly smaller, more arcuate, apical knob more prominent. Length 3.4-3.9, mean 3.6 mm. Sides of pronotum less deeply incised before hind angles, which are small, sharp, and usually more or less right. Inner two or three elytral striae distinctly and moderately impressed, outer striae progressively obsolescent. Aedeagus 1.25-1.29, mean 1.26 mm long, similar to that of nominate *schwarzi* but more arcuate, consequently shorter; parameres slightly shorter; apical knob much more prominent.

Type series. — Holotype male (American Museum of Natural History = AMNH) and 18 paratypes, below summit of Craggy Dome, elevation 5600 feet (1700 m), Buncombe County, North Carolina, 22 July 1960, T. C. Barr and M. C. Bowling.

Measurements (in mm). — Holotype male: total length 3.9, head 0.81 long × 0.84 wide, pronotum 0.71 long × 1.05 wide, elytra 2.33 long × 1.67 wide, antenna 1.92 long.

Distribution. — Known only from the Black and Great Craggy mountains and the adjacent Blue Ridge, in Buncombe, McDowell, and Yancey counties, North Carolina. Additional specimens, not made paratypes, were collected on Mt. Mitchell, elevation 6600 feet (2000 m), in the Black Mountains; and on the Pinnacle, elevation 5200 feet (1600 m), where the Blacks join the Blue Ridge, near the Buncombe-McDowell-Yancey county corner.

Trechus (Trechus) schwarzi saludae, new subspecies
Figs. 5, 24

Etymology. — Derived from Saluda, a town near the type locality.

Description. — Resembles *T. schwarzi scopulosus* in smaller size, less prominent hind angles of pronotum, deeper longitudinal striae of elytra; aedeagus smaller than in *T. s. schwarzi* or *T. s. scopulosus*, weakly arcuate and with small apical knob as in nominate *schwarzi*. Length 3.4-3.7, mean 3.5 mm. Pronotum and elytra about as in *T. s. scopulosus*. Aedeagus 1.08-1.16 mm long, weakly arcuate, apical knob small, apex rather sharply deflexed.

Type series. — Holotype male (AMNH) and 29 paratypes, one mile (1.6 km) east of Melrose, from small, wet ravines on the south side of the gorge of the North Pacolet River, elevation 1300 feet (350 m), Polk County, North Carolina, 13 July 1969, T. C. Barr.

Measurements (in mm). — Holotype male: total length 3.7, head 0.86 long × 0.74 wide, pronotum 0.74 long × 1.02 wide, elytra 2.14 long × 1.60 wide, antenna 1.66 long.

Distribution. — Known only from the type locality.

Discussion. — It is remarkable that this distinctive subspecies of *T. schwarzi* should occur at such a low elevation, since both of the other subspecies are known only at altitudes above 4500 feet (1400 m). The type locality lies in second-growth forest between U. S. 176 and the Southern Railway tracks a few miles southeast of Saluda. All specimens in the series were collected from beneath mosses and liverworts on stones in or at the edge of small, spring-fed brooks, where the cool temperature and high humidity apparently create a suitable microenvironment. *Trechus s. saludae* occurs farther from the eastern slope of the mountains and at a lower elevation than any other North Carolina *Trechus* species yet known. Melrose is approximately 35 miles (55 km) southeast of Mt. Pisgah, the easternmost locality at which *T. s. schwarzi* has been collected.

The three taxa here placed in polytypic *T. schwarzi* are probably all extrinsically isolated at the present time. However, survival of the *T. schwarzi* stock at a comparatively low elevation near Saluda suggests that other such insular populations may be scattered across the lowland areas separating the three subspecies, perhaps restricted to cool, wet ravines in the vicinity of springs. A gradual cooling of the regional climate could unite these populations again.

Trechus (Trechus) cumberlandus Barr

Barr 1962:76, Fig. 9. Type locality, 'Lish Steele Caves, Wayne County, Kentucky; type deposited in USNM.

Trechus cumberlandus, closely similar to *T. schwarzi* but without a distinct apical knob at the tip of the aedeagus, is a vicar species to *T. schwarzi*, occurring in the Cumberland plateau of eastern Kentucky and Tennessee. Elsewhere (Barr 1962, 1969) I interpreted the species as a Wisconsin relic. The range of *T. cumberlandus* extends along the western margin of the Cumberland plateau from Rockcastle County, Kentucky, to Grundy County, Tennessee. It has been collected in eleven localities, as follows: KENTUCKY: *Rockcastle County.* — Pine Hill Cave, at Pine Hill; Sinks of

Roundstone Cave, 0.8 mi. (1.3 km) ene Pine Hill. *Pulaski County.* — Hydens Cave, 1.3 mi. (2.1 km) ne Blue John. *Wayne County.* — 'Lish Steele Caves, 3 mi. (4.8 km) e Monticello (type locality); Johnson Fork Cave, 0.4 mi. (0.6 km) e Burfield; Upper Blowing Cave, at Sunnybrook. TENNESSEE: *Overton County.* — Falling Springs Cave, 1.25 mi. (2 km) wsw Hanging Limb. *Putnam County.* — Sinkhole in Calfkiller Valley, 0.7 mi. (1.1 km) se Bee Rock (near Monterey). *Cumberland County.* — Jewett Cave, 0.5 mi. (0.8 km) ese summit Hinch Mountain. *Van Buren County.* — Gorge below Fall Creek Falls (in State Park). *Grundy County.* — At spring in Savage Gulf, near Beersheba Springs. The last two localities are epigean. The Kentucky localities are at elevations of 800 to 980 feet (240 to 300 m) and those in Tennessee at 1100 to 2200 feet (335 to 670 m). The series are relatively small except in the case of Hydens Cave, where about 80 specimens were collected far back in the cave on wet, rotting leaves beside a deep pool.

Trechus (Trechus) mitchellensis Barr

Barr 1962:75, Fig. 8. Type locality, Celo Mountain, Yancey County, North Carolina; type deposited in USNM.

Trechus mitchellensis is known from three localities in the Black Mountains (Celo Mountain, Mt. Mitchell, and Big Tom, all in Yancey County), from the Pinnacle, where the Blacks intersect the Blue Ridge (McDowell County), and from Balsam Gap, where the Blacks join the Great Craggy Mountains (Buncombe County). All localities are at elevations between 4800 and 6500 feet (1460 to 2000 m) northeast of Asheville, North Carolina. This species is moderately large (3.6-4.2 mm), closely similar to *T. schwarzi scopulosus*, with which it is both sympatric and syntopic. From *T. s. scopulosus* it is distinguished by the sharp ventral cusp on the apical knob of the aedeagus and by the pronotum sides, which are very briefly but distinctly sinuate before the small, right, hind angles. The usual microhabitat is under moss carpets in spruce-fir forest.

Trechus (Trechus) carolinae Schaeffer

Schaeffer 1901:212. Jeannel 1931:439. Barr 1962:74, Fig. 6. Type locality, Mt. Mitchell, Yancey County, North Carolina; type deposited in AMNH.

Trechus carolinae is a very large (4.5-5.0 mm) species for the Appalachian area. It is relatively rare, inhabiting deep spruce and fir needle duff near the summits of the Black Mountains. On Mt. Mitchell I have taken a small number of specimens by prying back the duff layer at the bases of low, wet cliffs near the summit. It coexists with four other *Trechus* species (*T. schwarzi scopulosus, T. mitchellensis, T. hydropicus beutenmuelleri, T. vandykei vandykei*), but is easily distinguished by the large size. The apparent rarity is probably real but could possibly reflect the comparatively inaccessible microhabitat in which it occurs.

Trechus (Trechus) roanicus Barr
Fig. 2

Barr 1962:73. Type locality, Roan Mountain, Carter County, Tennessee; type deposited in USNM.

Trechus roanicus is known only from the type locality, where it occurs on Roan High Bluff, the highest point on Roan Mountain (elevation 6313 feet) (1924 m). It is closely similar to *T. hydropicus*, but is larger (3.8-4.4 mm) and coexists with the smaller and much more abundant *T. h. beutenmuelleri*. The species occurs under moss carpets on north-facing cliffs, in contrast to *T. h. beutenmuelleri*, which is found not only in the same microhabitat but also under wood chips, under moss on logs, and under stones near seeps.

Subgenus *Microtrechus* Jeannel

vandykei group

Trechus (Microtrechus) vandykei vandykei (Jeannel), new status
Figs. 6, 25

Microtrechus Vandykei Jeannel 1927: 587, Figs. 1280-1285; 1931: 443. Type locality, Black Mountains, North Carolina; type deposited in MNP (not seen).

Trechus (Microtrechus) vandykei: Barr 1962:77 (in part).

Although geographic variation among the smaller beetles of the *vandykei* group was previously noted (Barr 1962: 78), I separated out only the distinctive Smoky Mountains endemic, *T. bowlingi*, and incorrectly lumped the remainder into *T. vandykei*. Further study of older collections and much fresh material suggests that populations of the Great Balsams, Pisgah Ledge, and Cowee Mountains differ (at least) subspecifically from *T. vandykei* populations north of the French Broad valley, and that the populations of (a) the Tusquitee/Valley River, Snowbird, and Cheoah mountains and (b) the Unicoi Mountains, respectively, are best treated as distinct species.

From *T. bowlingi* and *T. tusquitee*, which have very obtuse hind angles on the pronotum, *T. vandykei* (s. lat.) is distinguished by the briefly but distinctly sinuate pronotum sides and the form of the aedeagus. From *T. haoe* it is distinguished by having only two instead of four distinct elytral striae; the aedeagus is less arcuate, and the parameres usually bear five rather than four apical setae. Nominate *vandykei* differs from *T. v. pisgahensis*, which occurs south of the French Broad River valley, in the nearly right hind angles of the pronotum and the slightly longer, slightly less arcuate aedeagus.

Both subspecies of *T. vandykei* are relatively common, but less so than the somewhat larger *T. hydropicus beutenmuelleri* or *T. barberi*. They occur in leafmold or under moss carpets. Nominate *vandykei* is known from several localities in the Black Mountains, the Great Craggy Mountains, at Balsam Gap between these two ranges, and from the Pinnacle at the point where the Blacks join the Blue Ridge (Yancey-Buncombe-McDowell counties, North Carolina). It also occurs on Camp Creek Bald and Unaka Mountain, in Greene and Unicoi counties, Tennessee, respectively. In the Black Mountains it is sympatric with four other species of *Trechus: T. schwarzi scopulosus, T. mitchellensis, T. carolinae*, and *T. hydropicus beutenmuelleri*.

Trechus (Microtrechus) vandykei pisgahensis, new subspecies
Figs. 7, 26

Trechus (Microtrechus) vandykei: Barr 1962:77 (in part).

Etymology.— From Mt. Pisgah, the type locality.

Description.— Length 2.5-2.8, mean 2.7 mm. Closely similar to *T. v. vandykei*, differing in more oblique sides and slightly obtuse hind angles of pronotum; aedeagus more arcuate and slightly smaller, 0.45-0.49 mm long.

Type series.— Holotype male (AMNH) and 29 paratypes, Mt. Pisgah, elevation 5000 feet (1524 m), Haywood-Buncombe counties, North Carolina, 21 May 1961, T. C. Barr; 15 additional paratypes, same locality and collector, 26 July 1960, 12 September 1964, and 17 August 1978.

Measurements (in mm).— Holotype male: total length 2.79, head 0.52 long × 0.55 wide, pronotum 0.51 long × 0.71 wide, elytra 1.54 long × 1.12 wide, antenna 1.22.

Distribution.— Occurs in the Great Balsam Mountains, Pisgah Ledge, and the Cowee Mountains, separated from the range of *T. v. vandykei* by the valley of the French Broad River. Additional localities other than Mt. Pisgah are Shining Rock Road and Graveyard Fields, Haywood County;

near Devils Courthouse, Transylvania County; and summit of Whiteside Mountain, Jackson County, North Carolina.

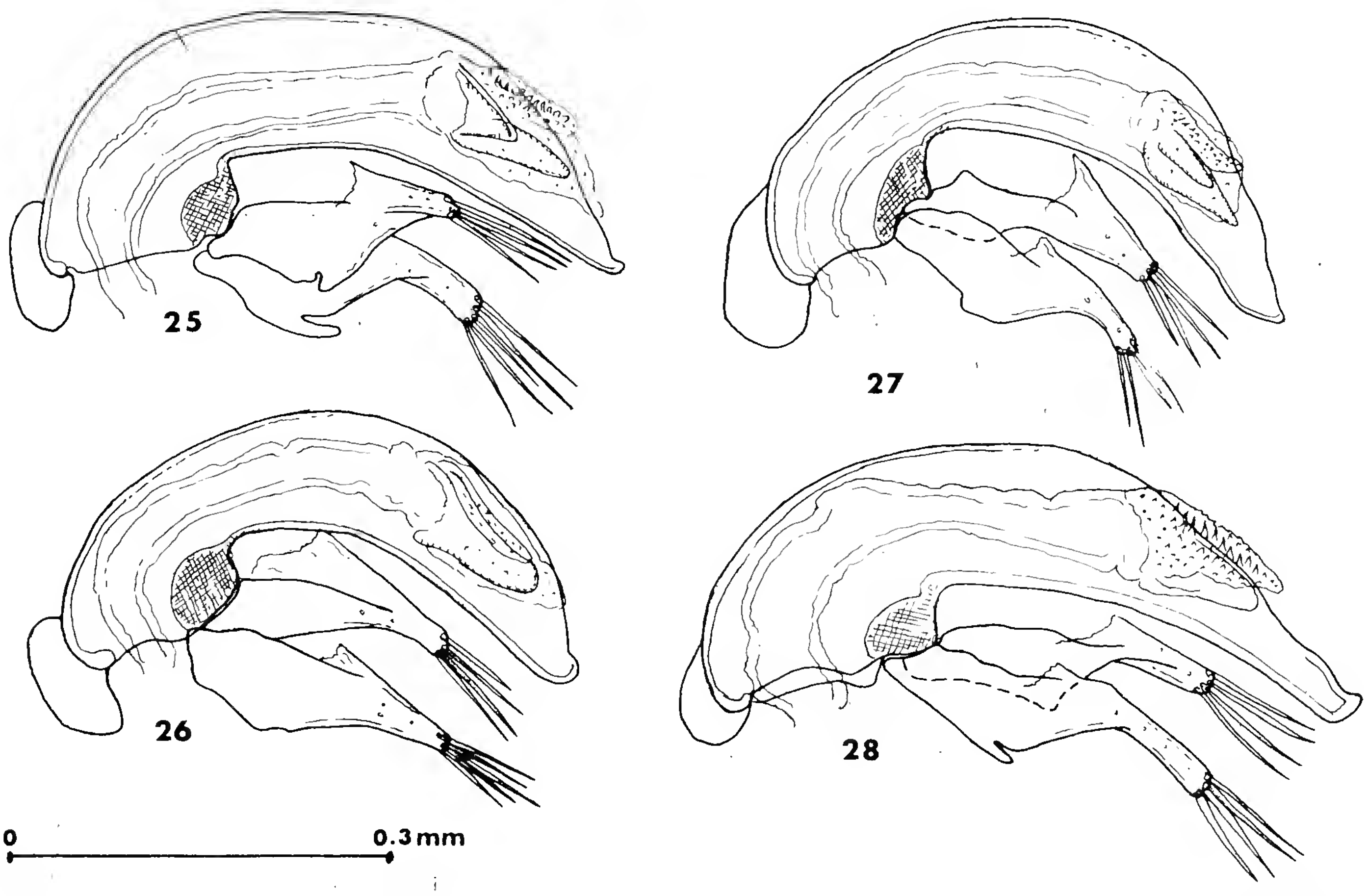
Discussion. — This subspecies commonly is found beneath carpets of moss on boulders. All collections have been made at relatively high altitudes, between 4700 and 5400 feet (1400 and 1600 m). Because of apparent altitudinal restriction there is, in my judgment, little or no gene flow between *T. v. vandykei* and *T. v. pisgahensis* at the present time. Syntopic *Trechus* species include *T. schwarzi schwarzi, T. aduncus aduncus*, and *T. barberi.*

Trechus (Microtrechus) haoe, new species
Figs. 8, 27

Trechus (Microtrechus) vandykei: Barr 1962:77 (in part).

Etymology.— From Haoe Lead, the type locality.

Diagnosis.— A small species of the *vandykei* group, with non-sinuate pronotum sides, small, obtuse hind angles, four elytral striae, and a short, evenly arcuate aedeagus the apex of which is neither produced, knobbed, nor truncate.



Figs. 25-28. Aedeagi of *Trechus* species, left lateral view: 25. *T. vandykei vandykei* (Jeannel), Balsam Gap, North Carolina. 26. *T. vandykei pisgahensis*, new subspecies, Mt. Pisgah, North Carolina. 27. *T. haoe*, new species, Haoe Lead, North Carolina. 28. *T. tusquitee*, new species, Tusquitee Bald, North Carolina.

Description.— Length 2.6-2.9, mean 2.7 mm. Form small, robust, subconvex; color piceous, shining, all appendages pale, contrasting. Head feebly transverse; labrum evenly emarginate; eye diameter 0.12-0.14 mm, a little less than or subequal to scape length. Pronotum about 0.7 as long as wide, sides arcuate apical two-thirds, then convergent and not sinuate before small, obtuse, hind angles; greatest width in apical fourth. Elytra 1.4 times longer than wide, oval, subconvex, four longitudinal striae present, outer striae obsolescent, apical groove wide and rather short, terminating a short distance anterior to anterior apical puncture. Aedeagus 0.45-0.48, mean 0.46 mm long, strongly arcuate and rather slender, more so than in *T. vandykei pisgahensis* which it most closely resembles; parameres with four apical setae.

Type series.— Holotype male (AMNH) and 21 paratypes, Haoe Lead, elevation 4800 feet (1460 m) above Joyce Kilmer Memorial Forest, Graham County, North Carolina, 25 July 1960, T. C. Barr and M. C. Bowling.

Measurements (in mm).— Holotype male: total length 2.70, head 0.49 long × 0.58 wide, pronotum 0.55 long × 0.80 wide, elytra 1.66 long × 1.19 wide, antenna 1.20 long.

Distribution.— Known only from the type locality in the Unicoi Mountains, along the Tennessee-North Carolina border.

Discussion.— Morphologically *T. haoe* is closest to *T. vandykei pisgahensis*, but the geographic ranges of *T. tusquitee* and *T. bowlingi* (two other closely similar species) intervene, suggesting complete genetic isolation. The entire type series was collected from beneath a moss carpet on a large boulder. Associated with *T. haoe*, but less abundant, were *T. talequah* and *T. barberi*. *Trechus luculentus unicoi*, the only other species of the genus thus far known from the Unicoi Mountains, has been collected nearby but not at the same spot.

Trechus (Microtrechus) tusquitee, new species
Figs. 9, 28

Trechus (Microtrechus) vandykei: Barr 1962:77 (in part).

Etymology.— From Tusquitee Bald, the type locality.

Diagnosis.— A small species of the *vandykei* group with obtuse, not rounded, hind angles of the pronotum, four elytral striae, the aedeagal apex produced and truncated.

Description.— Length 2.6-3.2, mean 2.8 mm. Form small, robust, subconvex; color piceous, shining, appendages all pale, contrasting. Head feebly transverse; labrum evenly emarginate; eye diameter 0.14-0.15 mm, a little less than or subequal to scape length. Pronotum less than 0.7 as long as wide, sides arcuate apical two-thirds, then convergent and barely sinuate or not sinuate before obtuse hind angles; greatest width in apical fourth. Elytra 1.4 times longer than wide, oval, subconvex, four longitudinal striae and trace of fifth present, apical groove wide and rather short, terminating at or a little anterior to level of anterior apical puncture. Aedeagus 0.49-0.58, mean 0.53 mm long, basal bulb large and bent at right angle to median lobe, apex narrowed, produced, abruptly truncate; parameres long, rather slender, each with four apical setae.

Type series.— Holotype male (AMNH) and 19 paratypes, Tusquitee Bald, Clay-Macon counties, North Carolina, 4 August 1960, T. C. Barr and M. C. Bowling.

Measurements (in mm).— Holotype male: total length 2.95, head 0.57 long × 0.60 wide, pronotum 0.54 long × 0.83 wide, elytra 1.71 long × 1.23 wide, antenna 1.28 long.

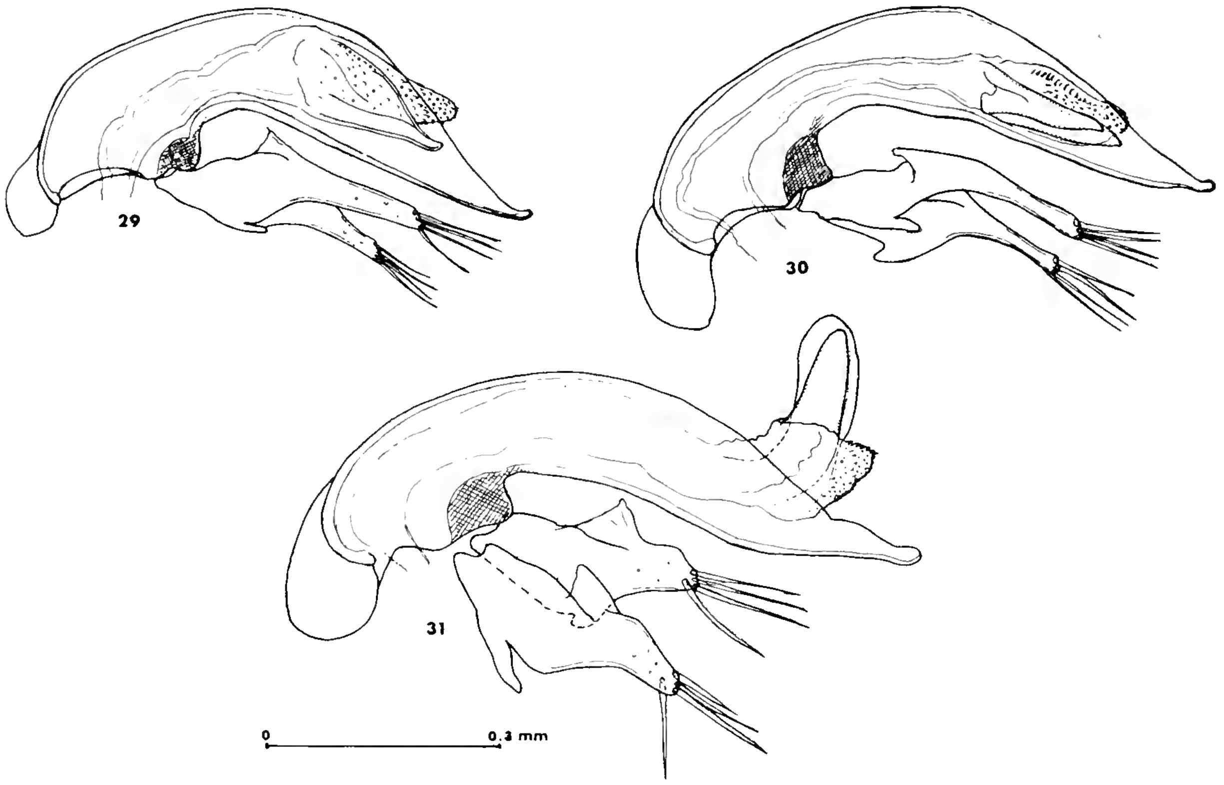
Distribution.— The species is known at present from three small mountain ranges in southwestern North Carolina, the Tusquitee/Valley River, Snowbird, and Cheoah mountains. Two additional localities from which I have collected *T. tusquitee* are Joanna (=Teyahalee) Bald, Graham-Cherokee counties, and Cheoah Bald, Graham-Swain counties. It may also occur in the adjacent Nantahala Mountains, although none of the small, *vandykei*-like species have yet been found there.

Discussion.— The altitudinal range of *T. tusquitee* is about 3500 to 5000 feet (1070 to 1525 m); it was collected near Old Road Gap on the slopes of Tusquitee Bald, on the north-facing cliff at the summit of Tusquitee Bald, at a spring on the same mountain at an intermediate elevation, at about 4500 feet (1370 m) near the summit of Joanna Bald, and at 5060 feet (1540 m) on the summit of Cheoah Bald.

The broadly transverse pronotum with obtuse hind angles and wide marginal gutter (Fig. 9) suggests affinity with *T. bowlingi*, which inhabits the Great Smoky Mountains northeast of the range of *T. tusquitee*, but the smaller and apically truncate aedeagus indicates probable status as a distinct species. Taken with *T. tusquitee* on Tusquitee Bald were two other species of *Trechus*, *T. barberi* and *T. luculentus wayahensis*.

Trechus (Microtrechus) bowlingi Barr
Figs. 10, 29

Barr 1962:78. Type locality, Mt. Kephart, Great Smoky Mountains, Sevier County, Tennessee; type deposited in USNM.



Figs. 29-31. Aedeagi of *Trechus* species, left lateral view: 29. *T. bowlingi* Barr, Mt. Kephart, North Carolina-Tennessee. 30. *T. barberi* (Jeannel), Sassafras Knob, North Carolina-South Carolina. 31. *T. tonitru* Barr, Thunderhead (Mountain), Tennessee.

Trechus bowlingi is limited to the Great Smoky Mountains, where it is a vicar species replacing the similar *T. vandykei, T. tusquitee*, and *T. haoe*. Like the latter species, it occurs in a variety of habitats, such as moss carpets, rotting leaf litter, and wet soil beneath stones. Its altitudinal range is about 3000 to 6500 feet (900 to 2000 m). Along the crest of the central Smokies, between Newfound Gap and Clingmans Dome, it coexists with two other small species, *T. barberi* and *T. uncifer*, and four larger species, *T. nebulosus, T. valentinei, T. luculentus*, and *T. novaculosus*. Characters useful in distinguishing *T. bowlingi, T. barberi*, and *T. uncifer* are given elsewhere in the present paper in the discussion of *T. uncifer*. Among the four small species of the *vandykei* group, *T. bowlingi* is easily differentiated by the large aedeagus and the blunt, obtuse hind angles of the pronotum.

Trechus (Microtrechus) barberi (Jeannel)
Fig. 30

Microtrechus Barberi Jeannel 1931:444, Figs. 55-57. Type locality, Retreat, Haywood County, North Carolina; type deposited in USNM.
Trechus (Microtrechus) barberi: Barr 1962:78.

Trechus barberi occupies a range which includes the Great Balsams and Pisgah Ledge, North Carolina, and extends southwestward to extreme eastern Tennessee, the mountains of northeast Georgia, and the South

Carolina border. Both altitudinally and geographically it is the most widely distributed of the Unaka assemblage of *Trechus* species, ranging from the highest summits in the Great Balsams, Plott Balsams, and Great Smokies down to 2400 feet (730 m) in the gorge of the Whitewater River. Additional collections made since 1962 serve firmly to establish its ubiquity in the main portion of its range, and I list only the southern peripheral records below.

GEORGIA: *Towns County.* — Summit of Tray Mountain, elevation 4400 feet (1340 m) near White-Habersham county corner. *Rabun County.* — Coleman River gorge, 0.4 mile (0.6 km) above mouth of the river in ravines on southwest slope of Straw Mountain. *Gilmer County.* — Quarry near summit of Betty Mountain, elevation 3300 feet (1000 m) on crest of Cohutta Mountain. *Murray County.* — Northeast slopes of Grassy Mountain along Mill Creek, elevation 3100 feet (945 m). NORTH CAROLINA—SOUTH CAROLINA: Sassafras Mountain, elevation 3500 feet (1070 m), Transylvania-Pickens county line. NORTH CAROLINA—TENNESSEE; 0.5 mile (0.8 km) south of Stratton Meadows on Johns Knob, elevation 4600 feet (1400 m), Graham-Monroe county line.

The larger species of the *vandykei* group include *T. barberi*, *T. tonitru*, and *T. subtilis*. The relationship of the latter two species to *T. barberi* is unclear, but probably they represent isolates whose range has been invaded by the ecologically more successful and more abundant *T. barberi*. The status of *T. tonitru* needs clarification: it is apparently well within the geographic range of *T. barberi*, but the two species have not been taken syntopically, and *T. tonitru* is still known from a single site. On the other hand, *T. subtilis* coexists with *T. barberi*, although it is much less abundant.

Trechus (Microtrechus) tonitru Barr
Fig. 31

Barr 1962:79. Type locality, Thunderhead, Great Smoky Mountains, Blount County, Tennessee; type deposited in USNM.

Trechus tonitru is known only from the summit of Thunderhead, elevation 5500 feet (1675 m) in the western Great Smoky Mountains, on the border between Blount County, Tennessee, and Swain County, North Carolina. The entire type series of 19 specimens was collected from beneath moss in a scrubby heath thicket just below the top of the mountain on the north (Tennessee) side. The species is closely similar to *T. barberi*, but the apex of the pronotum is a little wider than the base, the pronotum sides are slightly sinuate before the right to slightly obtuse hind angles, and the apical groove is longer and oblique to the suture. The aedeagus, 0.76-0.81 mm long, is a little larger than that of *T. barberi*; its apex is slender, slightly reflexed, and finely knobbed, the copulatory pieces are broader, and the parameres are conspicuously thicker and shorter.

Trechus (Microtrechus) subtilis Barr

Barr 1962:80, Fig. 15. Type locality, Mt. Sterling, Haywood County, North Carolina; type deposited in USNM.

This rare species is similar to *T. barberi*, with which it is sympatric and syntopic. Only nine specimens are known, six of them from the slopes of Mt. Sterling in the eastern Great Smoky Mountains, and three from Jones Knob (=Junaluska Balsam) in the Plott Balsam Mountains; both localities are in Haywood County, North Carolina. In comparison with *T. barberi*, *T. subtilis* is a little larger and more robust, with proportionately smaller eyes, slightly transverse head, more arcuate pronotum sides which are shallowly but distinctly sinuate before the right to slightly obtuse hind angles, proportionately wider elytra with five distinct longitudinal striae, and an oblique apical groove. The aedeagus, 0.85-0.92 mm long, is larger, more slender, and less arcuate than that of *T. barberi*, but shows the same general pattern.

uncifer group

Trechus (Microtrechus) uncifer Barr

Barr 1962:80, Fig. 16. Type locality, Clingmans Dome, Sevier County, Tennessee; type deposited in USNM.

This species is known only from the spruce-fir forests of the central Great Smoky Mountains and from Water Rock Knob, in the Plott Balsams, between altitudes of 5500 and 6500 feet (1675 and 2000 m). Males are immediately distinguished by the dense spines of the internal sac and the long, slender, produced, hooked aedeagal apex. In the Smokies, the only other species of *Trechus* in the same size range and same localities (Clingmans Dome, Mt. Buckley, Collins Gap, Mt. Collins, Sugarland Mountain) are *T. barberi* and *T. bowlingi*. *Trechus bowlingi* differs from both *T. uncifer* and *T. barberi* in slightly smaller size (2.6-2.9 mm, mean 2.7 mm), evenly convex elytra not flattened on the central part of the disc, and certain pronotal characters: pronotum very transverse, nearly a half wider than long, marginal gutter broad and extending past hind angles onto sides of base, hind angles very obtuse and slightly rounded, sides scarcely sinuate before angles. Externally *T. uncifer* can usually be distinguished from *T. barberi* by the following combination of characters: Color of body and appendages more contrasting; head, pronotum, and elytra dark piceous to black, appendages rather pale, testaceous, outer segments of antenna not darker than basal segments; femora slightly infuscated, and tibiae and tarsi paler. Pronotum sides convergent without trace of sinuation; hind angles obtuse. Eye small, its short diameter less than length of scape.

I have collected *T. uncifer* only under rocks in damp places, usually near seeps or small springs. It is apparently never abundant, with only one to four specimens occurring in the same spot where large numbers of *T. luculentus* or *T. valentinei* are found.

Trechus (Microtrechus) satanicus Barr

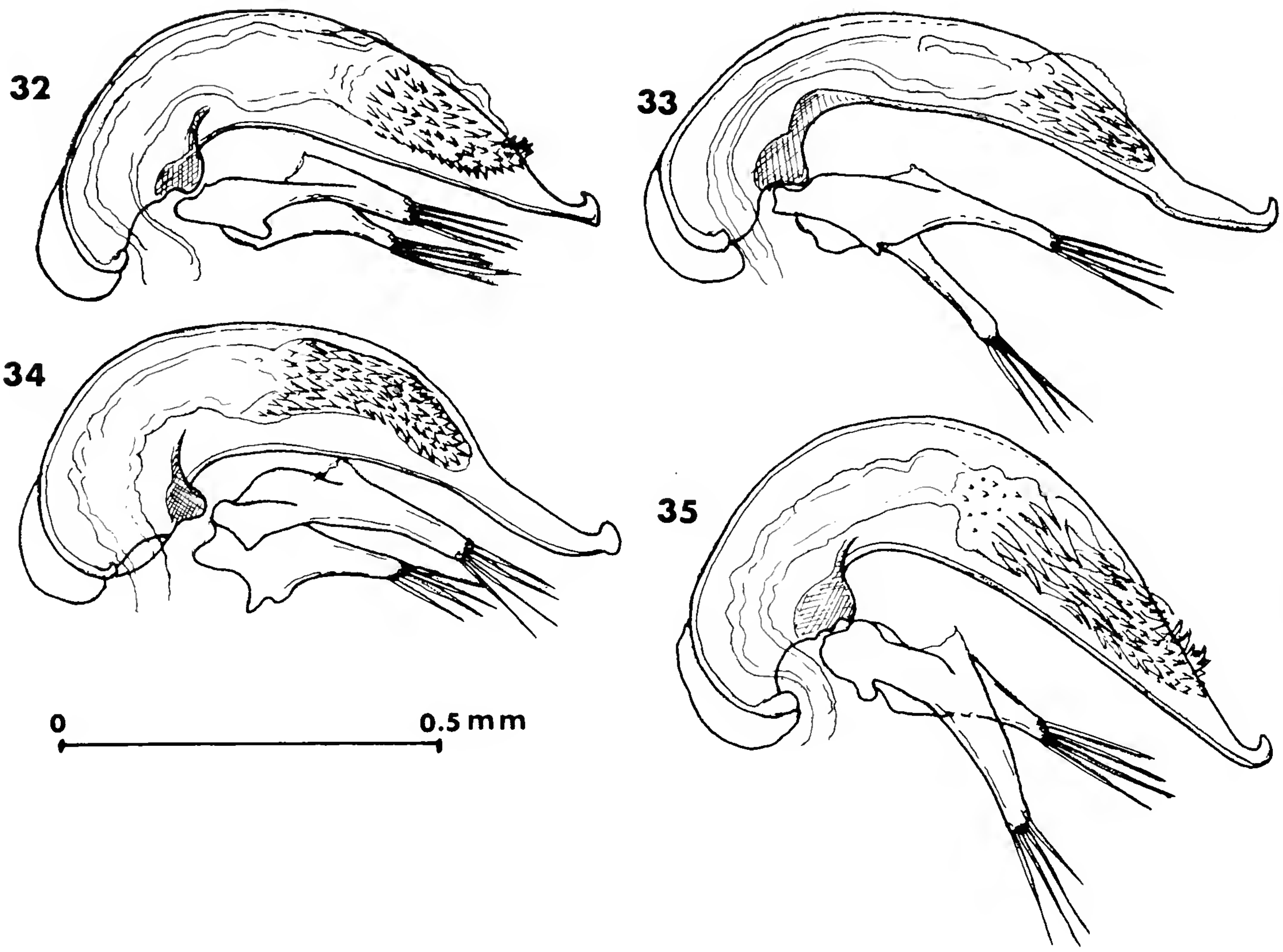
Barr 1962, Fig. 17. Type locality, Graveyard Fields, Haywood County, North Carolina; type deposited in USNM.

Superficially similar to *T. uncifer*, this species is known only from the west end of Graveyard Fields near Devils Courthouse, in the Great Balsam Mountains. It has not been taken farther west in the Balsams, nor on Pisgah Ledge to the east, despite careful search. *Trechus satanicus* is notable for the comparatively great length of the aedeagus, 1.47-1.49 mm long, despite the small body size (length 3.2-3.5 mm). Within the *uncifer* group, *T. uncifer* and *T. satanicus* form a subgroup and may be vicar species. The remaining species, *T. aduncus* and *T. talequah*, form another subgroup. Although *T. satanicus* lies within the range of nominate *aduncus*, the two species have not been collected syntopically.

Trechus (Microtrechus) aduncus aduncus Barr, new status
Fig. 32

Trechus (Microtrechus) aduncus Barr 1962:82. Type locality, Mt. Pisgah, Haywood County, North Carolina; type deposited in USNM.

Trechus aduncus is a medium-small (3.1-3.9 mm) species with eye diameter equal to or slightly less than the scape length, the pronotum 0.65-0.70 times as long as wide, pronotum apex and base widths subequal, the sides not or very feebly sinuate just before the small, right or slightly obtuse hind angles, the elytra with three inner striae clearly impressed and one to three additional, feebly impressed outer striae. The aedeagus is moderately arcuate to strongly arcuate, the apex more or less produced and terminating in a hook. The two copulatory pieces, which are normally obscured by the spiny armature of the internal sac, are simple, subequal, and have triangular apexes.



Figs. 32-35. Aedeagi of *Trechus* species, left lateral view: 32. *T. aduncus aduncus* Barr, Bearpen Gap, North Carolina. 33. *T. aduncus toxawayi*, new subspecies, Toxaway Mountain, North Carolina. 34. *T. aduncus coweensis*, new subspecies, Yellow Mountain, North Carolina. 35. *T. aduncus howellae*, new subspecies, Big Butt, North Carolina.

Nominate *aduncus*, which has only one elytral stria beyond the inner three and an aedeagus as in Figure 32, occurs along the crest of the Great Balsam Mountains, from Richland Balsam eastward to Mt. Pisgah, in Haywood, Transylvania, Buncombe, and Jackson counties, North Carolina. I have collected it at Mt. Pisgah, Buck Spring, Devils Courthouse, Bearpen Gap, Spot Knob, and Richland Balsam, at elevations ranging between 4600 and 6000 feet (1400 and 1800 m). Its usual habitat is wet moss in contact with a rock surface, and it is sympatric and syntopic at various localities with other *Trechus* species: *T. barberi*, *T. vandykei pisgahensis*, *T. schwarzi schwarzi*, and *T. rosenbergi*. The type (and only known) locality for *T. satanicus* lies near the middle of the range of *T. a. aduncus*, but the two species have not yet been collected at the same spot.

Four subspecies of *T. aduncus* are recognized in the present paper. All are probably extrinsically isolated populations which have diverged recently, and they are treated as a polytypic species to emphasize their close relationship. Intergrades between the subspecies have not been found, and (except possibly for nominate *aduncus* and *toxawayi*) are unlikely to be found because of the existence of low gaps between the ranges of the subspecies.

Trechus (Microtrechus) aduncus toxawayi, new subspecies
Fig. 33

Etymology.— From Toxaway Mountain, the type locality.

Description.— Length 3.2-3.3 mm. Elytra with three inner striae clearly impressed, at best a trace of fourth stria; elytra rather slender, elongate-oval. Aedeagus slender, 0.91-0.97 mm long, less arcuate than in the other subspecies of *T. aduncus*, apex slender and produced more than in nominate *aduncus*, terminating in reflexed hook.

Type series.— Holotype male (AMNH), two male and one female paratypes, 0.25 mile (0.4 km) west of the summit of Toxaway Mountain, elevation 4600 feet (1400 m), Jackson County, North Carolina, 24 June 1970, T. C. Barr, Jr., and T. C. Barr, III.

Measurements (in mm).— Holotype male: total length 3.25, head 0.62 long × 0.68 wide, pronotum 0.66 long × 0.89 wide, elytra 1.89 long × 1.31 wide, antenna 1.57 long.

Distribution.— Known only from the type locality, at the end of a divide (Tanasee Ridge) which extends 17 miles (27 km) south from the crest of the Great Balsams. The ridge possibly permits continuity between *T. a. toxawayi* and nominate *aduncus*, but no intermediate populations are known.

Discussion.— The type series was collected from beneath a mat of decaying leaves at the base of a low, sloping rock cliff, thus from very typical *T. aduncus* microhabitat. *Trechus barberi* was the only other species of the genus taken on Toxaway Mountain.

Trechus (Microtrechus) aduncus coweensis new subspecies
Fig. 34

Etymology.— From Cowee Mountains, where the type locality is situated.

Description.— Length 3.4-3.8, mean 3.7 mm. Elytra with at least five visible striae, inner three striae more deeply impressed. Aedeagus 0.84 mm long in paratype, median lobe thicker than in *T. a. aduncus* or *T. a. toxawayi*, apex slender, produced, slightly recurved, terminal hook knob-like.

Type series.— Holotype male (AMNH), three male and one female paratypes, summit of Yellow Mountain, elevation 5000 feet (1525 m), 4 miles (6.4 km) southwest of Glenville, Macon-Jackson counties, North Carolina, 28 June 1969, T. C. Barr.

Measurements (in mm).— Holotype male: total length 3.84, head 0.84 long × 0.74 wide, pronotum 0.68 long × 1.02 wide, elytra 2.17 long × 1.55 wide, antenna 1.61 long.

Distribution.— Known only from the type locality in the Cowee Mountains, North Carolina.

Discussion.— The five specimens of *T. a. coweensis* were taken from beneath wet leaves alongside the road to the fire tower, just below the summit of Yellow Mountain at an approximate elevation of 5000 feet (1525 m). A single *T. barberi* was collected at the same spot. This subspecies is geographically and morphologically a little closer to *T. a. howellae*, from the Nantahala Mountains farther west, than to either of the other two known subspecies of *T. aduncus*. The Cowees are separated from the Great Balsams by the valley of the Tuckasegee River and from the Nantahalas by the Little Tennessee River, thus there is every indication of complete extrinsic isolation of this taxon.

Trechus (Microtrechus) aduncus howellae, new subspecies
Fig. 35

Etymology.— Patronymic honoring Dr. Thelma Howell, director-emeritus of the Highlands Biological Station.

Description.— Length 3.3-3.9, mean 3.7 mm. Elytra with at least five visible striae, inner three striae more deeply impressed. Aedeagus 0.87-0.88 mm long, very strongly and evenly arcuate in median lobe, which is thick, as in *T. a. coweensis*; apex more evenly attenuate and terminal hook less reflexed than in *T. a. aduncus*, but not knob-like as in *T. a. coweensis*.

Type series.— Holotype male (AMNH) and seven paratypes, east face of Big Butt, elevation 4800 feet (1460 m), Coweeta Hydrologic Laboratory, Macon County, North Carolina, 21 July 1970, T. C. Barr, Sr., T. C. Barr, Jr., and T. C. Barr, III. Two paratypes, same locality, 26 July 1969, T. C. Barr, Jr.

Measurements (in mm).— Holotype male: total length 3.58, head 0.84 long × 0.68 wide, pronotum 0.68 long × 0.96 wide, elytra 2.05 long × 1.43 wide, antenna 1.61 long.

Distribution.— Known only from the type locality, in a research area maintained by the United States Forest Service, in the Nantahala Mountains.

Discussion.— The type series was collected from wet moss at the base of a vertical cliff face beside the Appalachian Trail on the east face of Big

Butt, a prominent peak in the Nantahala Mountains. The only other *Trechus* species associated with *T. a. howellae* was *T. barberi*, a pair of which was also taken at the Big Butt site.

Trechus (Microtrechus) talequah Barr

Barr 1962: 82, Fig. 20. Type locality, Haw Knob, Monroe County, Tennessee; type deposited in USNM.

Trechus talequah is a Unicoi Mountains vicar species to *T. aduncus*. Morphologically and geographically it is much farther removed from the subspecies of *T. aduncus* than they are from each other. It is smaller and flatter than *T. aduncus*, has deeply impressed elytral striae and a shorter apical groove. The aedeagus is shorter and straighter, but its form nevertheless suggests a close affinity with *T. aduncus*. The species coexists at Haw Knob (type locality) with *T. luculentus unicoi* and on Haoe Lead, Graham County, North Carolina, with *T. haoe*. Females and undissected males are easily separated from *T. haoe* by the depressed form and deep elytral striae.

nebulosus group

Trechus (Microtrechus) nebulosus Barr

Barr 1962: 86, Fig. 21. Type locality, Mt. Kephart, Sevier County, Tennessee, and Swain County, North Carolina; type deposited in USNM.

Trechus nebulosus is a species of medium size (3.3-4.0 mm) with large eyes, the sides of the pronotum not sinuate, and the hind angles obtuse and slightly reflexed. It is abundant beneath wet, fluffy moss which carpets north-facing cliffs along the crest of the Great Smoky Mountains from Clingmans Dome to Mt. Guyot, including the Mt. LeConte spur. In this region it coexists with three smaller species of *Trechus (T. barberi, T. bowlingi, T. uncifer)* and with four other species of the *nebulosus* group *(T. l. luculentus, T. valentinei, T. novaculosus*, and *T. verus)*. The only one of these species in the same size range and also having large eyes is *T. luculentus*, but in that species the sides of the pronotum are distinctly sinuate before the hind angles. Males of *T. nebulosus* are always easily determined if the aedeagus protrudes or is removed, because the tip of the right copulatory piece is large and twisted into the shape of a bird's head.

The lowest elevation at which I have collected *T. nebulosus* is about 4600 feet (1400 m) from mossy boulders along Ramsay Prong, above the Cascades, in Sevier County, Tennessee, on the north side of the Smokies. At higher elevations it is the most common of the larger species in the moss carpet assemblage.

Trechus (Microtrechus) balsamensis Barr

Barr 1962:87, Fig. 24. Type locality, Water Rock Knob, Haywood-Jackson counties, North Carolina; type deposited in USNM.

This species is known only from the type locality, at an elevation of 6200 feet (1900 m) in the Plott Balsam Mountains. It occurs beneath moss carpets and in spruce-fir needle duff at the base of low cliffs on the north face of Water Rock Knob, in spruce-fir forest. It is syntopic with *T. rosenbergi* and *T. barberi* at the type locality. Both *T. uncifer* and *T. subtilis* have been taken in the Plott Balsams, but not at the Water Rock Knob locality.

Trechus balsamensis resembles *T. nebulosus* in habitus and habitat selected. It is characterized by large eyes, pronotum sides feebly sinuate only in basal 0.05, hind angles small and approximately right, very feebly impressed elytral striae, only the inner two or three of which are present; aedeagus 0.93-1.05 mm long, of the same size and shape as that of *T. nebulosus*, but apex much broader in dorsal view, the right piece scoop-shaped, much larger than the left and without an apical twist.

Trechus (Microtrechus) valentinei, new species
Figs. 11, 36

Trechus (Microtrechus) verus: Barr 1962 (in part).

Etymology.— Patronymic honoring Dr. J. Manson Valentine for his early studies of North American trechines.

Diagnosis.— Distinguished from other species of the *nebulosus* group by small eyes, broad pronotum base with acute hind angles, pale coloration; aedeagal apex attenuate and produced, finely knobbed, twisted to left; parameres broad and non-styliform.

Description.— Length 3.6-3.9, mean 3.7 mm. Piceous, more or less pale, shining, form moderately robust and subconvex. Head slightly longer than wide; labrum shallowly emarginate; eyes small, their diameter 0.7 scape length; antenna about 0.45 body length. Pronotum three-fourths as long as wide, conspicuously transverse; apex 0.9 times as wide as base and only 0.7 maximum width, which occurs in apical third; margins convergent behind, not sinuous; hind angles small, sharp, acute, laterally produced, base slightly lobed; basal foveae large and deep. Elytra 0.4 longer than wide, disc subconvex, usually with five longitudinal striae, 4th and 5th more shallowly impressed; apical groove short, joining 5th stria a short distance anterior to anterior apical puncture; scutellar stria very short, obsolescent; anterior discal at level of fourth umbilicate.

Aedeagus 0.92-1.02, mean 0.97 mm long; thick, strongly arcuate, basal keel strong, apex attenuate, produced, curved to left, finely knobbed; copulatory pieces exserting to right, right piece much larger, heavily sclerotized, enfolding smaller left piece; internal sac armed with medial band of dense, slender spines; parameres broad, non-styliform (Fig. 36A), in left lateral view, with seta-bearing surfaces peculiarly elongate, obliquely truncate; usually only three setae on apex of each paramere, rarely four.

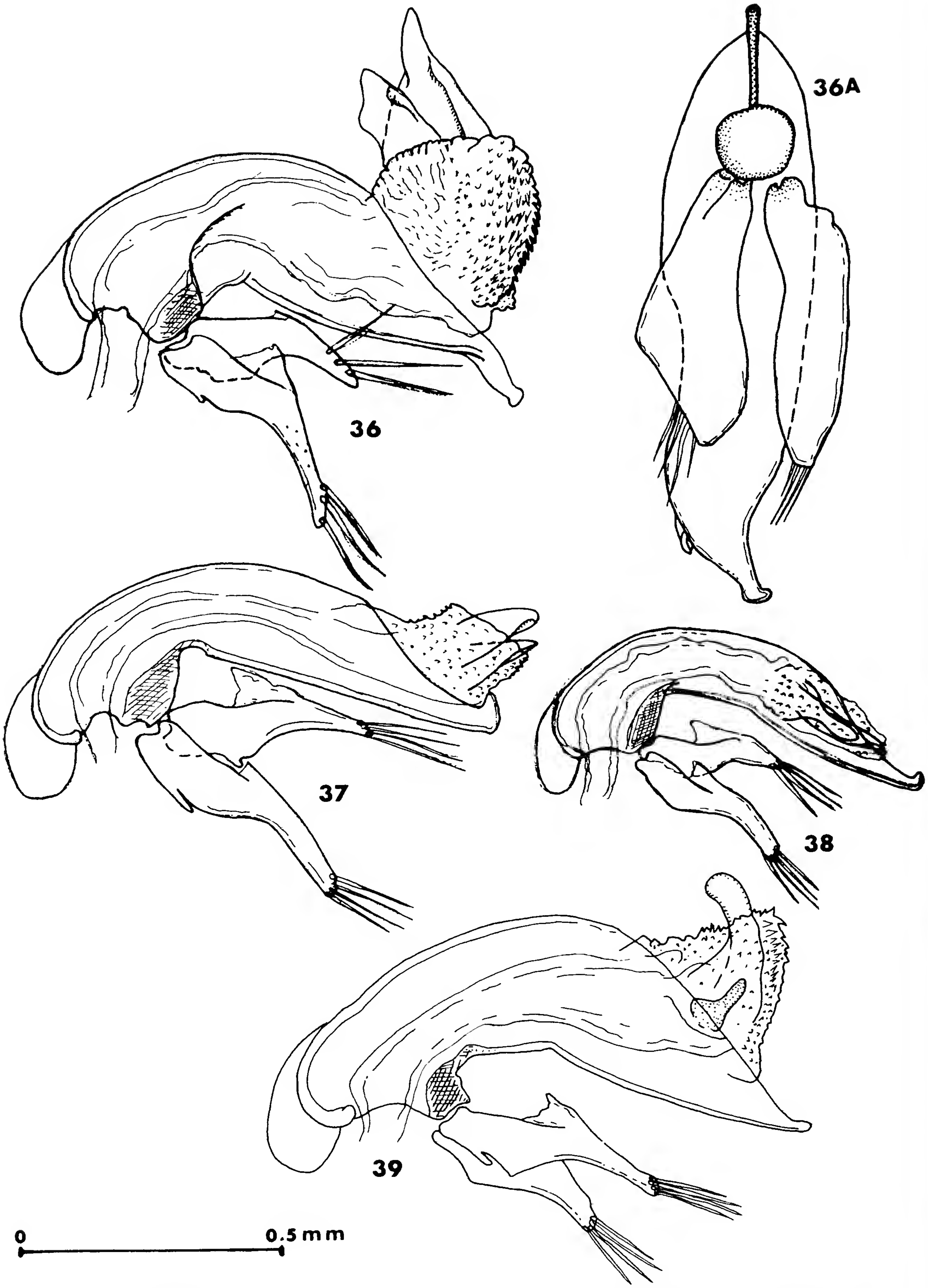
Type series.— Holotype male (AMNH) and 12 paratypes, Appalachian Trail near summit of Mt. Kephart, Sevier County, Tennessee, Great Smoky Mountains National Park, altitude approximately 6000 feet (1800 m), 1 July 1960, T. C. Barr, M. C. Bowling, Joyce and R. T. Bell.

Measurements (in mm).— Holotype male: total length 3.80, head 0.78 long × 0.71 wide, pronotum 0.78 long × 1.02 wide, elytra 2.23 long × 1.61 wide, antenna 1.74 long.

Distribution.— Known only from the central Great Smoky Mountains of Tennessee and North Carolina, from about 3500 to 6000 feet (1070 to 1830 m) in elevation.

Discussion.— In my earlier paper (Barr 1962) *T. valentinei* was confused with *T. verus*, another pale species with small eyes. The older records cited for *T. verus* at Clingmans Dome, Sugarland Mountain, and Mt. Kephart (Barr 1962:82) are incorrect and apply to *T. valentinei*. True *T. verus* is known only from Mt. Sterling, Cataloochee Balsam, and Old Black, in the eastern end of the Smokies.

Trechus valentinei is an inhabitant of the high spruce-fir forests of the Great Smokies, where it occurs under rocks beside streams and springs and in shallow ravines, often in company with the more abundant *T. l. luculentus* and occasionally with a rare specimen of *T. uncifer* or *T. novaculosus*. In addition to the type locality I have taken this species on Mt. LeConte, near the summit; Clingmans Dome, near the summit; Mt. Collins, near the summit; Sugarland Mountain, near its junction with the main crest of the Smokies. It can be readily distinguished from sympatric species of *Trechus* by the small eyes and paler color (*T. verus*, also pale with small eyes, is apparently allopatric), the broad pronotum base and acute hind angles, and the slender, produced, sinistrally twisted aedeagal apex (often visible without dissection). The non-styliform parameres are exceptional, duplicated in no other trechine species known to me (although rather different non-styliform parameres occur in Italian and Yugoslavian species of *Orotrechus* Müller).



Figs. 36-39. Aedeagi of *Trechus* species, left lateral view (except 36A): 36. *T. valentinei*, new species, Mt. LeConte, Tennessee. 36A. *T. valentinei*, ventral view, Ramsay Cascades, Tennessee. 37. *T. verus* Barr, Mt. Sterling, North Carolina. 38. *T. stupkai*, new species, Ramsay Prong, Tennessee. 39. *T. luculentus luculentus* Barr, Clingmans Dome, North Carolina-Tennessee.

Trechus (Microtrechus) verus Barr
Fig. 37

Barr 1962:81. Type locality, Mt. Sterling, Haywood County, North Carolina; type deposited in USNM.

When describing *T. verus* I placed it in the *uncifer* group, where it is readily distinguished by its large size and the absence of heavy, scaly armature on the internal sac. Both characters, so highly diagnostic in the *uncifer* group, are not at all out of the ordinary in the *nebulosus* group, where it more properly belongs alongside the closely similar species *T. valentinei*, with which I had earlier confused it. True *T. verus* is confined to the eastern end of the Smokies in Haywood County, North Carolina, and Cocke County, Tennessee, where it has been taken on Mt. Sterling, Old Black, and Cataloochee Balsam. Like *T. valentinei*, which it resembles, *T. verus* has small eyes and pale coloration and commonly occurs beneath rocks in wet places. The aedeagus of *T. verus* is more slender than that of *T. valentinei*, the apex is more conspicuously reflexed and not twisted to the left, and the parameres are styliform.

Trechus (Microtrechus) stupkai, new species
Figs. 12, 38

Etymology.— Patronymic honoring Mr. Arthur Stupka, former Park Naturalist and Research Biologist, National Park Service.

Diagnosis.— Eye diameter less than scape length; pronotum with apex and base widths subequal, sides briefly sinuate before small, right, hind angles; aedeagal apex briefly produced straight back, truncate at tip.

Description.— Length of unique holotype 3.3 mm. Form moderately robust and subconvex; dark piceous, appendages all pale. Head one fourth longer than wide; labrum evenly emarginate; eye diameter less than length of scape. Pronotum three fourths as long as wide, apex and base subequal, about 0.7 greatest width, which occurs in apical third; sides rounded apical two thirds, then convergent, shallowly but distinctly sinuate before small, about right, hind angles. Elytra 1.4 times longer than wide, oval, subconvex, inner two striae moderately impressed, third feebly impressed, fourth stria present only as evanescent trace; apical groove wide and short, ending slightly in advance of anterior apical puncture. Aedeagus of holotype 0.78 mm, basal bulb large and bent at right angles to median lobe, apex rather abruptly produced straight back and truncate with terminal button; copulatory pieces elongate-lobulate, left three fourths as long as right, internal sac weakly armed with small, indistinct scales; parameres slender and elongate, apexes with four setae each and not obliquely truncate as in *T. valentinei.*

Type series.— Holotype male (AMNH), a unique, in mossy rocks at edge of Ramsay Prong, about 150 yards (135 m) above Ramsay Cascades, elevation 4600 feet (1400 m), Sevier County, Tennessee, in Great Smoky Mountains National Park, 25 May 1969, T. C. Barr.

Measurements (in mm).— Holotype male: total length 3.29, head 0.74 long × 0.60 wide, pronotum 0.62 long × 0.83 wide, elytra 1.85 long × 1.28 wide, antenna 1.39 long, aedeagus 0.78 long.

Distribution.— Known only from the type locality.

Discussion.— Efforts to obtain additional specimens of this distinctive species have been unsuccessful. *Trechus nebulosus, T. valentinei*, and *T. bowlingi* were collected in the same microenvironment along Ramsay Prong, but even these otherwise common species are relatively rare at the site.

Trechus (Microtrechus) novaculosus Barr
Fig. 44

Barr 1962:89, Fig. 27. Type locality, Clingmans Dome, Sevier County, Tennessee; type deposited in USNM.

This large species, confined to the spruce-fir forests of the central Great Smoky Mountains, is the largest species of *Trechus* in the Smokies. The usual size range in the vicinity of Clingmans Dome is 4.4-4.8, mean 4.6 mm, but J. Manson Valentine took three very large specimens, fully 5.5 mm long, on Mt. LeConte in May 1934. Seventeen specimens from Mt. Kephart and along Anakeesta Ridge, which connects Mt. LeConte with the main crest of the Smokies, are intermediate in length, 5.1-5.5, mean 5.2 mm; these beetles, which I collected in August 1975, occurred several inches below the surface of wet scree piles along the trails.

The aedeagus of Clingmans Dome area specimens, 1.22-1.24 mm long, is smaller than the 1.23-1.32 mm length range seen in the Mt. LeConte-Anakeesta Ridge material, but the basic pattern is identical: rather strongly arcuate in lateral view, the median lobe sharply bent near the middle and produced and attenuate at the apex; in dorsal view the apex is simple and broadly spatulate. The copulatory sclerites are simple, spatulate, quite elongate and narrow, almost razor-like in shape.

From other species of the *nebulosus* group in the Smokies, *T. novaculosus* is readily distinguished by large size, small eyes, convergent (i.e., non-sinuate) pronotum sides, and large, obtuse hind angles. I found it only under and among rocks in wet places near seeps and springs at altitudes above 5500 feet (1675 m). In such microhabitats it is often associated with *T. valentinei*, which was always more abundant, and rarely with *T. uncifer*. The available specimens suggest a possible geographic cline in size, with total length increasing from Clingmans Dome along the crest to Mt. Kephart, then along the Boulevard across Anakeesta Ridge to Mt. LeConte. In the past three summers (1976, 1977, 1978) I have attempted to find intermediate populations (e.g., near Newfound Gap) but have been unable to do so. If the species is actually restricted to the very high elevations where it has thus far been taken, then one is faced with the alternative to a cline, that there are two genetically isolated populations less than 10 miles (16 km) apart. The only specimens known thus far from Mt. LeConte are those of Valentine, now in my private collection together with the series from Mt. Kephart and Anakeesta Ridge. In addition to Clingmans Dome the species has been taken on Mt. Buckley, Mt. Collins, and along the trail between Clingmans Dome and Andrews Bald; all specimens from these four localities fall into the 4.4-4.8 mm size range.

Trechus (Microtrechus) luculentus luculentus Barr, new status
Figs. 13, 39

Trechus (Microtrechus) luculentus Barr 1962:88. Type locality, Clingmans Dome, Swain County, North Carolina; type deposited in USNM.

Trechus luculentus s. lat. is characterized by large eyes, their diameter equal to or greater than the length of the scape, and distinctly sinuate sides of the pronotum. The apex of the aedeagus is not produced; the dorsal (right?) copulatory sclerite is large and scoop-shaped, and the ventral (left?) sclerite is a small, elongate-triangular spicule. Since collection of the type series in 1960, I have obtained specimens of *T. luculentus* from many other localities in the Great Smoky, Unicoi, and Nantahala mountains. Populations in the Unicois and Nantahalas differ subspecifically from Smoky Mountain *T. luculentus*. The nominate race is distinguished from the other subspecies by the combination of smaller hind angles of the pronotum, usually five longitudinal elytral striae, and the small aedeagus (length 0.63-0.73 mm).

In the central Smokies, *T. l. luculentus* has proven to be widely distributed altitudinally, occurring under rocks or debris beside seeps and springs or near water in little ravines. Near the summit of Clingmans Dome it is found under rocks in little wet ravines and under broken drain tiles near the septic disposal field. Along Roaring Fork and in Greenbrier Cove it was taken from beneath leaves and sticks beside small tributary streams at elevations of 3000 feet (915 m) and 2900 feet (885 m), respectively. A single specimen was found on Fish Camp Prong under moss carpeting a low ledge at an elevation of 2200 feet (670 m). On West Prong of Little Pigeon River (4000 feet) (1200 m) it occurred under rocks at the edge of the stream, with *T. valentinei* and *Bembidion carolinense* Casey. At the south base of the Smokies (Swain County, North Carolina) *T. luculentus* was extracted from leaves and wet gravels at 2250 feet (685 m), beside a small tributary stream crossing the Deep Creek Trail. A single female was collected on Kephart Prong under similar circumstances, at an elevation of 3350 feet (1020 m). These collecting data have been given in some detail to demonstrate that *T. luculentus* is by no means restricted to higher elevations, but should be able to bridge the low gaps between mountain ranges. A limited amount of gene flow between nominate *luculentus* and the other two subspecies is thus a reasonable proposition, although intergrading populations have not yet been discovered.

Wherever it coexists syntopically with *T. valentinei, T. luculentus* is always two to three times more abundant. It occasionally is taken together with *T. barberi* and *T. bowlingi*, both conspicuously smaller species, and rarely with *T. uncifer* and *T. novaculosus* at higher elevations. In the central Smokies the only other large species of *Trechus* with large eyes is *T. nebulosus*, an inhabitant of wet, fluffy moss carpets (consequently almost never syntopic with *T. luculentus*); in *T. nebulosus* the sides of the pronotum are simply convergent to the base, and males are readily determined by the distinctive shape of the apex of the dorsal copulatory piece which often protrudes from the apical orifice of the aedeagus.

Trechus (Microtrechus) luculentus unicoi, new subspecies
Figs. 14, 40, 41

Trechus (Microtrechus) luculentus: Barr 1962:88 (in part).

Etymology.— From Unicoi Mountains, where the type locality is situated.

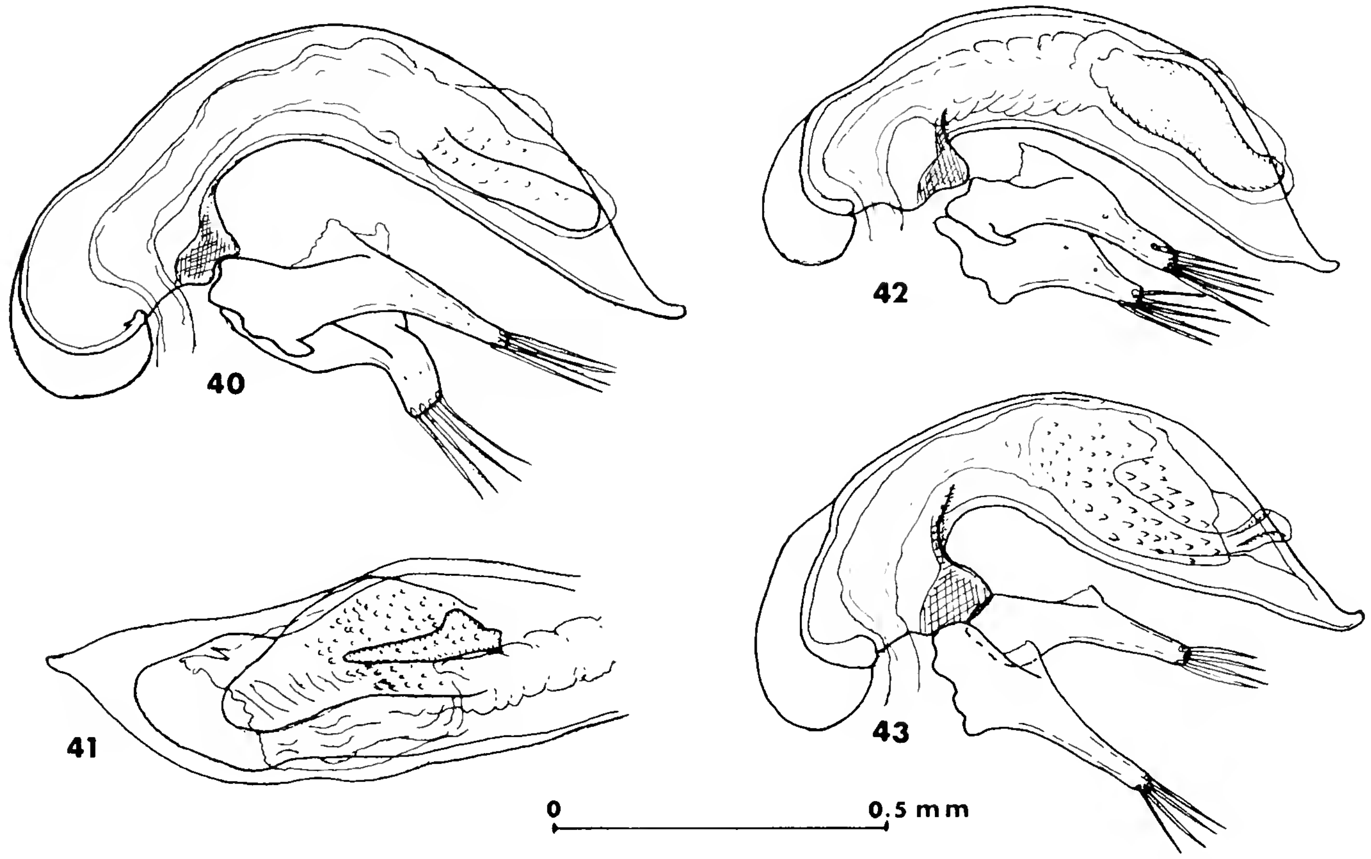
Description.— Length 4.3-4.5, mean 4.4 mm. Differs from other subspecies of *T. luculentus* in more prominently sinuous pronotum sides, which are subparallel in basal 0.12-0.15; more prominent, acute, hind angles of pronotum; more extensive longitudinal striation of elytra, with all striae usually present, although 5th through 8th progressively shallower; and larger aedeagus, 0.95-1.04, mean 1.00 mm long.

Type series.— Holotype male (AMNH) and 22 paratypes, Stratton Meadows, elevation 4900 feet (1494 m), Monroe County, Tennessee, and Graham County, North Carolina, 30 August 1964, T. C. Barr.

Measurements (in mm).— Holotype male: total length 4.48, head 1.00 long × 0.83 wide, pronotum 0.89 long × 1.19 wide, elytra 2.54 long × 1.89 wide, antenna 1.68 long.

Distribution.— In addition to the type series, I have seen specimens from the following localities. TENNESSEE: *Monroe County.* — Sugar Cove Creek, elevation 3000 feet (900 m) (T. C. Barr, 1964); Laurel Top, near Big Junction, elevation 5200 feet (1585 m) (T. C. Barr, 1960); Haw Knob, elevation 5400 feet (1645 m) (T. C. Barr, 1960). NORTH CAROLINA: *Graham County.* —Joyce Kilmer Memorial Forest, elevation 3000 feet (900 m) (J. M. Valentine, 1950-51); Bemis Lumber Company Camp (J. M. Valentine, 1951); Johns Knob, near Stratton Meadows, elevation 4800 feet (1465 m) (T. C. Barr, 1971). All localities are in the Unicoi Mountains, and specimens are at present in my private collection.

Discussion.— Previously (Barr 1962: 88) I noted the occurrence of this subspecies in the Unicoi Mountains but did not name it because insufficient specimens were available. I have now examined 55 specimens from the seven stated localities. The subspecies has the same microhabitat preferences of nominate *luculentus* and is prevalent beneath rocks and moss in wet ravines and near seeps and springs.



Figs. 40-43. Aedeagi of *Trechus* species, left lateral view (except 41): 40. *T. luculentus unicoi*, new subspecies, Stratton Meadows, North Carolina-Tennessee. 41. *T. luculentus unicoi*, apex, dorsal view. 42. *T. luculentus wayahensis*, new subspecies, Dirty John Creek, North Carolina. 43. *T. nantahalae*, new species, Burningtown Bald, North Carolina.

Trechus (Microtrechus) luculentus wayahensis, new subspecies
Figs. 15, 42

Etymology.— From Wayah Bald, a prominent topographic feature near the type locality.

Description.— Length 3.9-4.4, mean 4.1 mm. Differs from *T. l. luculentus* in having only four elytral striae and larger aedeagus, 0.84-0.95 mm long; differs from *T. l. unicoi* in having less prominent hind angles of pronotum, only four elytral striae, and smaller aedeagus.

Type series.— Holotype male (AMNH) and 30 paratypes, ravine at head of Dirty John Creek, southwest slope of Winespring Bald (near Wayah Bald), elevation 4900 feet (1500 m), Macon County, North Carolina, 3 July 1969, T. C. Barr.

Measurements (in mm).— Holotype male: total length 4.42, head 1.15 long × 0.87 wide, pronotum 0.84 long × 1.15 wide, elytra 2.48 long × 1.98 wide, antenna 2.11 long.

Distribution.— In addition to the type locality, this subspecies is known from two other sites in Macon County, North Carolina: Berties Falls, near Wayah Bald, elevation 4000 feet (1200 m); and Tusquitee Bald, near the Macon-Clay county line, elevation 4000 feet (1200 m). Tusquitee Bald, part of the Tusquitee/Valley River mountains, is 7 miles (11.3 km) west of Wayah Bald across the Nantahala River valley.

Discussion.— The occurrence of this subspecies in the Nantahala Mountains was first brought to my attention through the kindness of Dr. J. Manson Valentine, who gave me three females he had collected at Bertie Falls and Dirty John Creek in 1950. A single large female *Trechus* specimen which I collected on Tusquitee Bald in 1960 was earlier referred tentatively to *T. schwarzi* (Barr 1962:75), but this specimen properly belongs with *T. luculentus wayahensis.* Two other species of *Trechus, T. barberi* and *T. tusquitee*, have been collected syntopically with *T. wayahensis*, but *T. aduncus howellae* and *T. nantahalae*, which also occur in the Nantahalas, have not. *Trechus nantahalae* is readily distinguished from *T. luculentus* by the smaller eyes, pale color, and obtuse hind angles of the pronotum; the other three species are conspicuously smaller.

Trechus (Microtrechus) rosenbergi Barr

Barr 1962: 89, Fig. 26. Type locality, Water Rock Knob, Haywood and Jackson counties, North Carolina; type deposited in USNM.

Trechus rosenbergi is a large (4.5-5.0 mm) species, comparable in size only to *T. carolinae* (Black Mountains) and *T. novaculosus* (central

Smokies). It is known from only two localities: Water Rock Knob, in the Plott Balsam Mountains, and Richland Balsam, Haywood County, North Carolina, in the Great Balsam Mountains. At both collecting sites it was taken deep in the mat of spruce-fir needles piled up against wet, vertical rock faces. It is easily distinguished from the other species of *Trechus* with which it is sympatric (*T. aduncus, T. balsamensis, T. barberi, T. subtilis, T. vandykei*) by size alone.

Trechus (Microtrechus) tuckaleechee Barr

Fig. 16

Barr 1962:86, Fig. 22. Type locality, Tuckaleechee Caverns, Blount County, Tennessee; type deposited in USNM.

This species is known only from Tuckaleechee Caverns near Townsend, Tennessee, at the north side of the Great Smoky Mountains. It is distinguished from other members of the *nebulosus* group by small eyes, sinuate sides of the pronotum, hind angles sharp and nearly right, elytra with five clearly impressed striae and short apical groove, and the apex of the aedeagus broad, finely reflexed at the very tip. Morphologically it appears to be closest to *T. tennesseensis* and *T. nantahalae.*

Trechus (Microtrechus) tennesseensis tennesseensis Barr

Barr 1962:87, Fig. 23. Type locality, Berry Cave, Roane County, Tennessee; type deposited in USNM.

This taxon is at present known from a single locality in the floor of the Appalachian valley approximately 50 miles (80 km) west of the Great Smoky Mountains. Berry Cave is located a quarter of a mile (0.4 km) west of the Tennessee River (mile 578.4) near Wright Bend, 0.15 mile (0.24 km) west of Tennessee Route 72, at an elevation of 840 feet (255 m). *Trechus t. tennesseensis* resembles *T. tuckaleechee*, but the hind angles of the pronotum are sharp and acute, and the aedeagus is much larger. Neither *T. tuckaleechee* nor *T. tennesseensis* exhibit any regressive modifications that would restrict them to cave habitats. Presumably they are both relics of species that were more widely distributed during glacial maxima.

Trechus (Microtrechus) tennesseensis tauricus Barr

Barr 1962: 87. Type locality, Bull Cave, Blount County, Tennessee; type deposited in USNM.

This subspecies, known only from the sinkhole at the entrance to Bull

Cave, Blount County, Tennessee, at the edge of Great Smoky Mountains National Park (below the Rich Mountain Road, elevation 1840 feet [560m]), differs from nominate *T. tennesseensis* in the absence of internal clypeal grooves and outer elytral striae. The two taxa treated as polytypic *T. tennesseensis* are probably quite isolated, at least extrinsically, at the present time, but the morphological differences between them are so slight that I consider them relatively recent (post-Wisconsin?) relics of a previously more widely distributed species.

Trechus (Microtrechus) nantahalae, new species

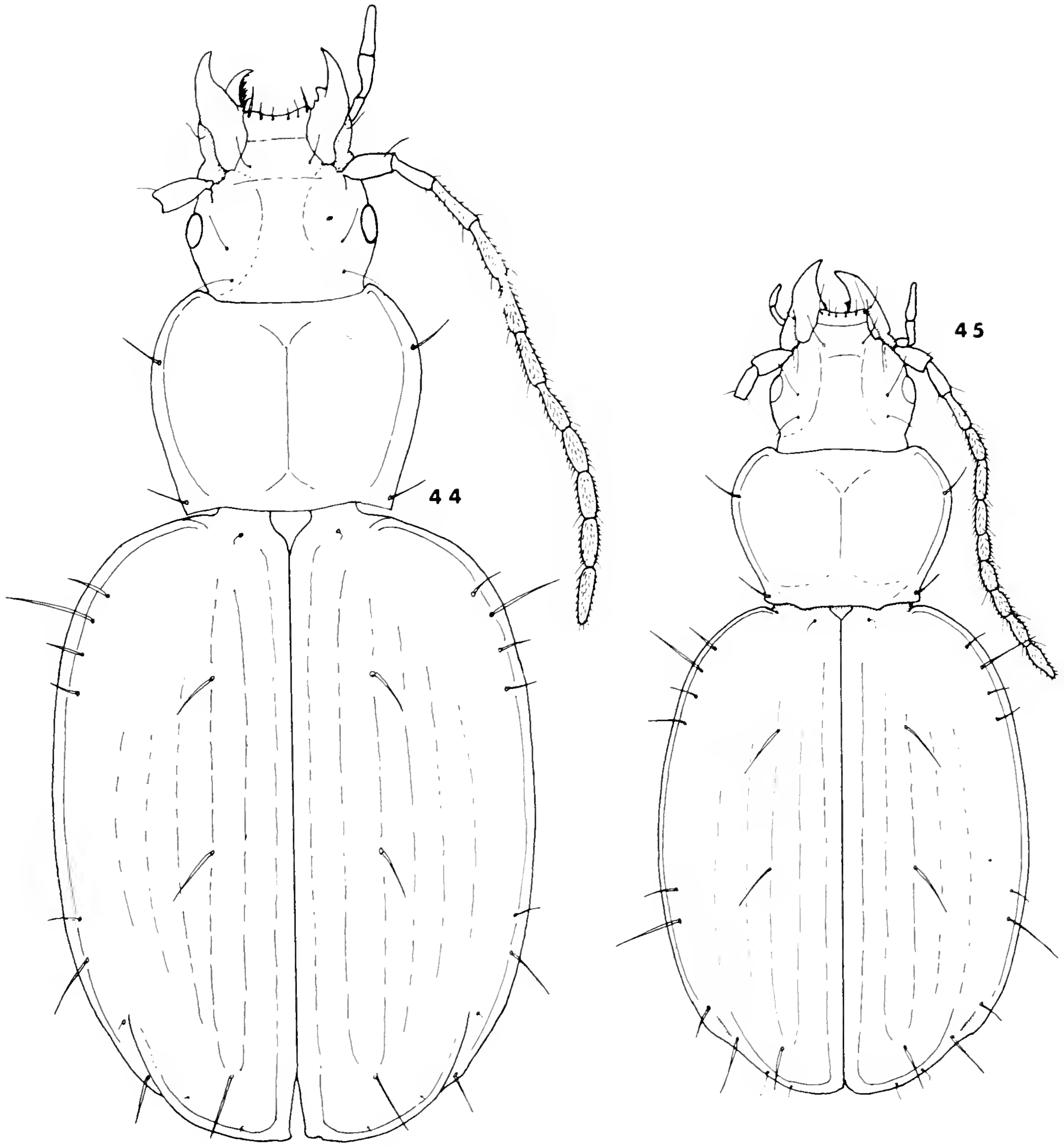
Figs. 17, 43, 45

Etymology.— From Cherokee *nantahala*, geographic name for the mountain range in which the type locality occurs.

Diagnosis.— Resembles *T. tennesseensis* in small eyes, pale coloration, sinuate sides of pronotum, and slender aedeagal apex; differs in obtuse hind angles of pronotum, shorter apical recurrent groove, smaller aedeagus, and knobbed right copulatory piece.

Description.— Length 4.2-4.4, mean 4.2 mm. Reddish piceous, shining; microsculpure obsolete on central elytral disc; form robust and subconvex. Head a little wider than long; labrum shallowly and singly emarginate; frontal grooves broad and deep; eyes small and subconvex, their diameter (about 0.15 mm) less than scape length; antenna about 0.45 body length. Pronotum 0.3 wider than long; apex and base subequal in width and about 0.7 maximum width; widest in apical third; sides arcuate, sinuous in basal sixth, hind angles small, sharp, slightly elevated, and obtuse; basal foveae broad and deep, separated from marginal gutter by low ridge; base oblique behind hind angles, thus slightly lobed. Elytra 0.75 as wide as long; inner three longitudinal striae moderately deep, inner intervals subconvex, 4th and 5th striae shallow, outer striae obsolete; apical recurrent groove attaining 5th stria a short distance in advance of anterior apical puncture; scutellar stria very short, obsolescent; anterior discal puncture slightly behind level of 4th umbilicate puncture. Aedeagus of paratype 0.94 mm long, similar to that of *T. tennesseensis* but a little shorter, apex slender in dorsal view; dorsal (right) copulatory piece with apex twisted into knob. Female unknown.

Type series.— Holotype male (AMNH) and 4 male paratypes, 0.4 mile (0.6 km) northwest of Burningtown Gap on the southwest slope of Burningtown Bald, at a seep along the Appalachian Trail, elevation 4300 feet (1300 m), Macon County, North Carolina, 5 July 1969, T. C. Barr.



Figs. 44-45. *Trechus* species, habitus sketch: 44. *T. novaculosus* Barr, large form (5.5 mm), Mt. LeConte, Tennessee. 45. *T. nantahalae*, new species (4.3 mm), Burningtown Bald, North Carolina.

Measurements (in mm).— Holotype male: total length 4.22, head 0.93 long × 0.81 wide, pronotum 0.84 long × 1.09 wide, elytra 2.45 long × 1.86 wide, antenna 1.92 long.

Distribution.— Known only from the type locality in the northern Nantahala Mountains, southwestern North Carolina.

Discussion.— *Trechus nantahalae* is readily distinguished from the other species of *Trechus* with which it is sympatric in the Nantahalas *(T. barberi, T. aduncus howellae, T. luculentus wayahensis, T. tusquitee)* by the small eyes, pale coloration, and peculiarly obtuse hind angles of the pronotum which

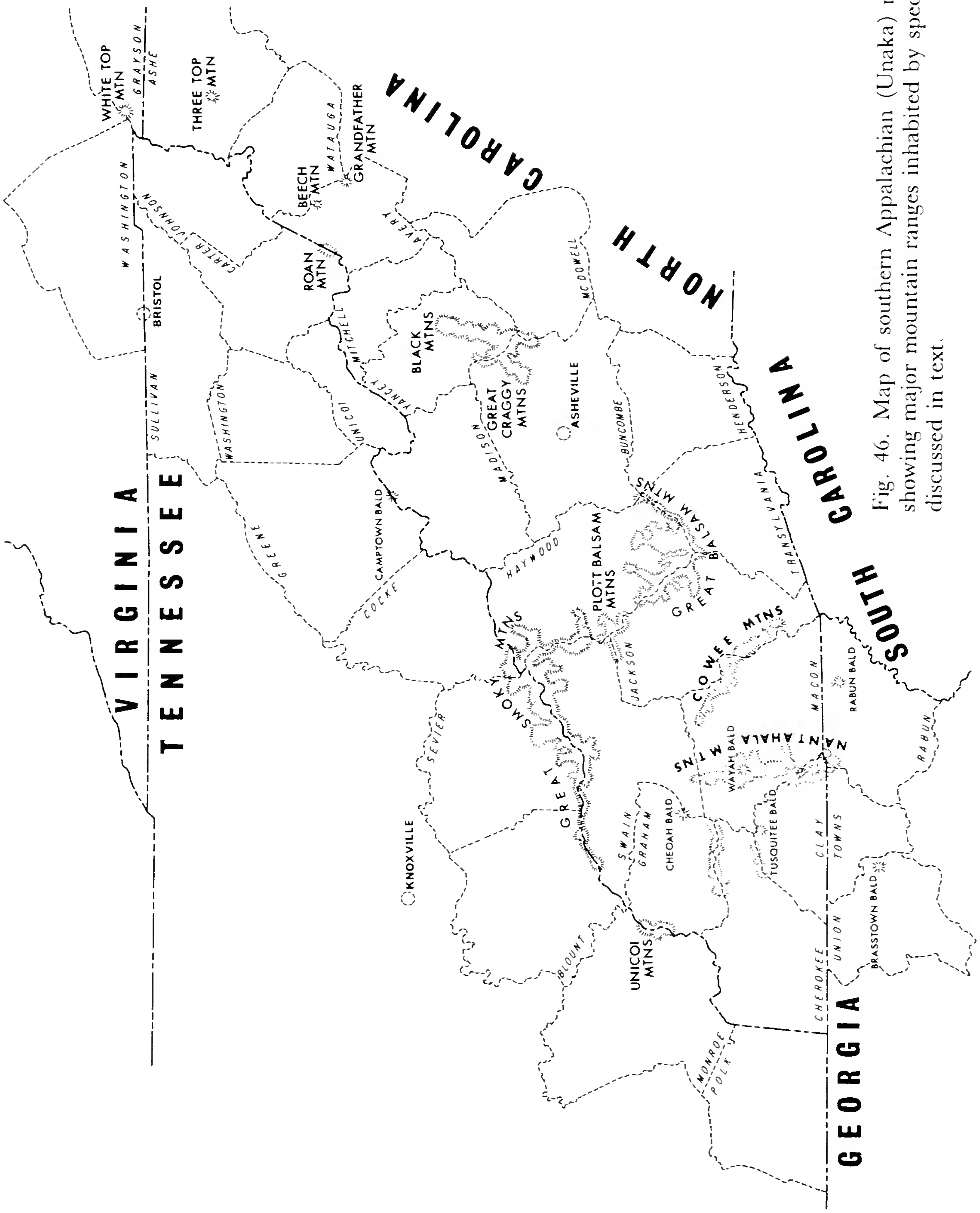


Fig. 46. Map of southern Appalachian (Unaka) mountain region, showing major mountain ranges inhabited by species of *Trechus*, as discussed in text.

result in a lobed base. The five specimens of the type series, all males, were collected from beneath stones in wet mud. No other *Trechus* species were found in the immediate vicinity, nor has *T. nantahalae* yet been found elsewhere in the Nantahala Mountains. In fact, the limited collections thus far made of *Trechus* in the Nantahala and Tusquitee/Valley River mountains suggest that the somewhat lower elevations along the crest and the absence of spruce-fir forest provide a restricted number of suitable microhabitats in contrast to the Great Smokies, Great Balsams, and Plott Balsams. Of the four endemic taxa known at the present time only *T. luculentus wayahensis* and *T. tusquitee* have been taken together (on Tusquitee Bald), in contrast to many syntopic species pairs known from the other ranges mentioned.

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Cretaceous Selachians from the Peedee Formation (Late Maestrichtian) of Duplin County, North Carolina[1]

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ABSTRACT.—A shark-tooth fauna of Late Cretaceous (Navarroan, Late Maestrichtian) age from the uppermost member of the Peedee Formation was recovered from three sites in southern Duplin County, North Carolina. Species represented include *Hybodus* sp. 1; *Squalicorax kaupi* and *S. pristodontus*; the goblin shark *Scapanorhynchus texanus; Odontaspis* sp.; *Cretolamna appendiculata lata; C. biauriculata* (the first New World record of this species) and *C. serrata; Plicatolamna* cf. *P. arcuata*; the sawfish *Ischyrhiza mira*; and the ray *Rhombodus* cf. *R. binkhorsti*. This Peedee assemblage adds significantly to the still-limited roster of Late Maestrichtian shark faunas of the world.

INTRODUCTION

The Peedee Formation is an Upper Cretaceous deposit of neritic marine origin (Heron and Wheeler 1964) which spans the Tayloran and Navarroan provincial stages (Brouwers and Hazel 1978), equivalent to the Late Campanian and the entire Maestrichtian stages of Europe. At the present time the deposit's various phases of regression and deposition are not named as members. This paper deals with the selachian fauna of an "uppermost" member of the Peedee that is Navarroan (Late Maestrichtian) in age. As shown below, the shark species of this member correspond to those known Late Maestrichtian faunas found elsewhere in the United States and other parts of the world.

The selachian fauna described here is distinct from that of the Black Creek Formation (Miller 1967, 1968; Baird and Horner 1979), which underlies the Peedee in North Carolina. A transition of several of the species from the Black Creek up into the Peedee is normal, but other species appear in the Peedee that were not present in the Black Creek.

The marine vertebrate fauna of the Maestrichtian in North America is poorly known. I have under study additional faunas of that age from widely separated localities (in Maryland and Texas) that should, when described, make our knowledge of the Late Maestrichtian much clearer. One of these faunas, like that of the Peedee described here, contains only megascopic species; the other contains a microfauna as well. Using this undescribed material for comparison I endeavor here to place on record

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[1] Additions to the fossil vertebrate fauna of North Carolina, Part I.

Brimleyana No. 2: 77-89. November 1979

for the first time a Late Maestrichtian/Navarroan shark fauna (incomplete as it is) from the state of North Carolina.

LOCALITIES

The sites from which the specimens in this report were recovered are all in southern Duplin County. Site 1, by far the most productive, is a borrow pit from which the county maintenance department extracts limestone for use as road fill. It is located on County Road 1148 approximately 3.2 km due east of its junction with the north-south U.S. Highway 117, about 2.4 km south of Rosehill. Its position is approximately 8.8 km diagonally northwest of the Angola Bay Game Preserve and the Northwest Branch of the Cape Fear River, at 34°52'30" north latitude and 77°90'0" west longitude. Fossils were first discovered at this locality by Mr. John C. Golden, Jr., of North Charleston, South Carolina.

At Site 1 the Peedee Formation is exposed at a depth of approximately 4.5 to 6.1 m and consists of limestone with little traces of glauconite. The lack of invertebrate steinkerns and foramnifera and the surficial wear on the shark teeth strongly suggest that the fossils were reworked after original deposition elsewhere and redeposited at their present location. Unconformably underlying the Peedee is the Black Creek Formation, which has yielded no fauna at Site 1 simply because the borrow pit has not yet been dug deep enough. The overburden is a mixture of Castle Hayne limestone (Claibornian, Upper Middle Eocene), Trent Marl (Aquitanian, Early Miocene) and Duplin Marl (= Yorktown, Sahelian, Late Miocene or more likely Early Pliocene) (Berry 1947; Richards 1950; Cooke et al. 1943; Baum and Wheeler 1977). The shark faunas of the Castle Hayne, Trent, and Duplin Marls at this locality will be described in subsequent parts of this series.

Site 2 is the spoil heap of an irrigation pond alongside the Rosehill Processing Plant (chicken renderers), approximately 2.4 km north of Rosehill on U. S. Highway 117. Several species of the Peedee fauna are quite common at this locality, although their condition is worn and abraded, indicating reworking and subsequent redeposition. The overlying material at this site is also the Castle Hayne Limestone.

Site 3, the Superior Stone Quarry, is situated 3.2 km west of U. S. Highway 117 at the Carroll intersection, approximately midway between the towns of Warsaw and Magnolia. The predominant material recovered from this now-defunct quarry is Castle Hayne Limestone with Late Eocene shark teeth and echinoids. The underlying formation is the Peedee, from which we obtained the same species as at Site 1. The vertebrate remains also have been worn and abraded by wave action.

SYSTEMATICS

Full synonymies for the species cited will be found in Cappetta and Case (1975b) and Case (1978). The illustrated voucher specimens are housed in the Museum of Natural History, Princeton University (PU); additional specimens are in the author's collection.

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Clade HYBODONTIFORMES
Order SELACHII
Hybodus Agassiz, 1837
Hybodus sp. 1

Hybodus sp. 1 - Cappetta and Case, 1975:5, Fig. 2.

Material: — PU 22418, one lower lateral tooth lacking roots (Figs. 1-2). Site 1.

Description: — An isolated central cusp showing little wear on the blade; the root is missing as it is in most specimens. Plications on either side of the blade, rising from the apron above the root separation to approximately 1/5 the total height of the blade; plications more pronounced on the labial face. The tooth faces inward and is slightly concave in lingual aspect. It resembles a similarly preserved specimen from the Navesink Formation (Middle Maestrichtian) of New Jersey (Cappetta and Case 1975b, Fig. 2), differing only in having a slight lateral apron.

Discussion: — Cappetta and Case described *Hybodus* sp. 1 on the basis of incomplete cusps, with or without lateral cusplet traces. More recently Case (1978) described as *Hybodus montanensis* a tooth from the Judith River Formation (Campanian) of Montana, which shows strong, quite deep plications occupying approximately 1/3 of the tooth cusps. This species from the Western Interior is quite different from *Hybodus* sp. 1. The latter will be named by Case on the basis of an almost complete specimen showing a partial root and two lateral cusplets on one side, found in central New Jersey in 1978.

Suborder ANACORACOIDEI
Family ANACORACIDAE
Squalicorax Whitley, 1939
Squalicorax kaupi (Agassiz)

Corax kaupi Agassiz, 1843:225, Pl. 26a, Figs. 25-34; Pl. 26, Figs. 4-8.

Material: — PU 22419A, an upper antero-lateral tooth (Figs. 3-4), and PU 22419B, a lower lateral tooth (Figs. 5-6); numerous additional teeth, anterior, lateral and posterior, from both upper and lower jaws. Sites 1 and 2.

Description: — Small-sized teeth, approximately 1 to 1.5 cm wide. The teeth of *Squalicorax kaupi* are about 1/3 the size of those of *Squalicorax pristodontus*. They show an indentation on the side of the blade directed towards the commissure of the mouth, whereas the teeth of *S. pristodontus* have a full, arcuate shape and no indentation of the blade. I assume that the upper and lower teeth are quite similar, showing no heterodonty, so it is difficult to be certain whether a given tooth comes from the upper or lower jaw.

Squalicorax pristodontus (Agassiz)

Corax pristodontus Agassiz, 1843:224, Pl. 26, Figs. 9-13.

Material: — PU 22420, a lower lateral tooth (Figs. 7-8). Site 1.

Description: — Teeth of fairly large size, averaging between 2 and 3 cm wide. Large crescent-shaped blade with no indentation, as distinct from *S. kaupi*. Roots, as with *S. kaupi*, are quite flattened, with or without an apical foramen on the lingual face, and with or without fenestration or multiple foramina on the upper portion of the root processes on the labial face. Upper and lower teeth are similar, as with *S. kaupi*.

Discussion: — The teeth of *S. pristodontus* are quite distinctive. Although some specimens have been recovered from formations as early as the Late Campanian, the species is quite uncommon in pre-Maestrichtian outcrops, and is by far more abundant in the Middle and Late Maestrichtian stages of the Upper Cretaceous. Its geographic range is much like that of *S. kaupi*. *Squalicorax pristodontus* is most abundant in the Middle Maestrichtian (Navesink Marl) of New Jersey, the Late Maestrichtian (Kemp Clay Member, formerly the "Littig," of the Navarro Group) in northeast and central Texas, and the Late Maestrichtian *("Couche trois" des phosphates)* of Morrocco, North Africa.

Clade EUSELACHIFORMES
Order EUSELACHII
Family MITSUKURINIDAE
Scapanorhynchus Woodward, 1889
Scapanorhynchus texanus (Roemer)

Lamna texana Roemer, 1852:29, Pl. 1, Fig. 7.

Material: — PU 22421A, an upper lateral tooth (Figs. 9-10), and PU 22421B, a lower anterior tooth (Figs. 11-12); about two dozen additional teeth, anterior, lateral and posterior, from both upper and lower jaws. Sites 1 and 3.

Description. — Teeth of large size, averaging between 2 and 5 cm in height from root tip to blade tip; upper and lower teeth are similar. The anterior teeth of both jaws are elongate and sigmoidal, with or without minute, sigmoidal lateral cusplets,with long striae on the lingual face of the blade. The antero-lateral and lateral teeth are more flattened on their labial and lingual faces and bear one or two lateral cusplets which differ from those of the anterior teeth in being flattened and spade-like. Long striae are seldom observed on the lingual face of the anterolateral, lateral, or posterior teeth, but the beginning of a striation pattern can be observed at the blade apron near the root on the labial face of well-preserved specimens.

Discussion: — *Scapanorhynchus texanus* is a very common and ubiquitous species in the Late Cretaceous of North America. It is most abundant in the Late Campanian to Middle Maestrichtian of New Jersey and Texas, and has recently been discovered in Late Campanian outcrops northeast of Taroudannt, Morocco (Pierre Zennaro, pers. comm.).

Until recently the description of teeth from the various mouth positions in *Scapanorhynchus* was quite haphazard, with numerous assignments to various erroneous genera, causing quite a problem with synonymic nomenclature in the literature. Capetta and Case (1975) compared the fossil teeth of *Scapanorhynchus* with those in the jaws of the modern "goblin shark," *Mitsukurina owstoni*. The teeth are basically the same, position for position, except that many teeth of *Mitsukurina* are devoid of lateral accessory cusplets. Consequently *Mitsukurina* has been relegated to synonomy and the living species should be cited as *Scapanorhynchus owstoni* (Jordan) (Bass et al. 1975:18). Now that the problem of differences between teeth from different positions has been cleared up, future authors should be able to assign occurrences correctly to *Scapanorhynchus* and avoid further synonymic confusion.

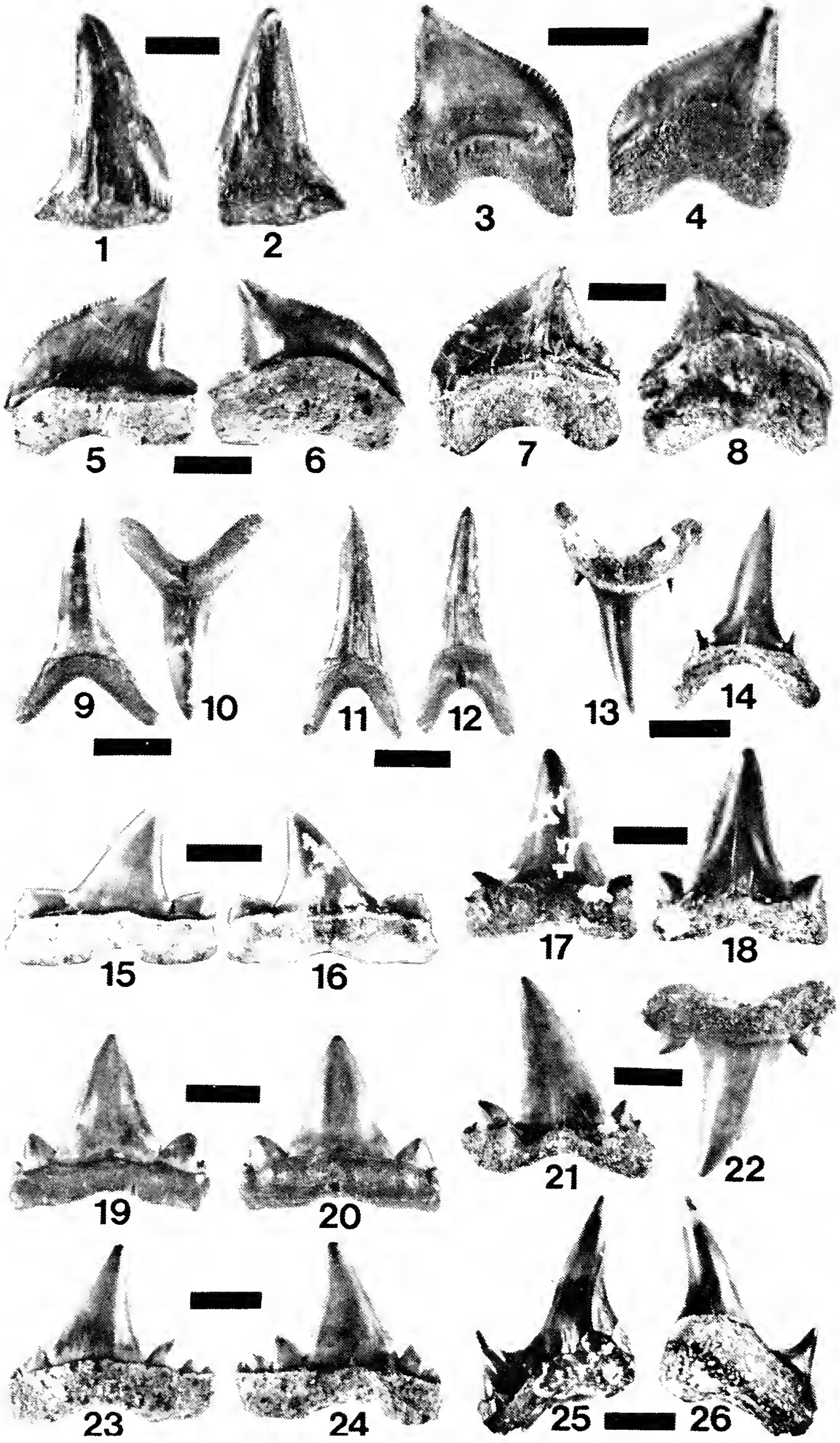
Scapanorhynchus texanus also occurs in the Black Creek Formation (Campanian) at Phoebus Landing on the Cape Fear River, Bladen County, North Carolina. The specimens, however, were mistakenly assigned to the Tertiary genera *Carcharias* and *Isurus* by Miller (1967:223, Figs. 1-5).

Family ODONTASPIDAE

Odontaspis Agassiz, 1838

Odontaspis sp.

Material: — PU 22422, a lower antero-lateral tooth (Figs. 13-14); about two dozen anterior and lateral teeth from both upper and lower jaws. Site 1.



Figs. 1-26. Selachian teeth from the Peedee Formation of Site 1, Duplin County, North Carolina, in labial and lingual views. Scale bar equals approximately 5 mm. **1-2**, *Hybodus* sp. 1 (PU 22418); **3-4**, *Squalicorax kaupi*, upper antero-lateral tooth (PU 22419A); **5-6**, *Squalicorax kaupi*, lower lateral tooth (PU 22419B); **7-8**, *Squalicorax pristodontus*, lower lateral tooth (PU 22420); **9-10**, *Scapanorhynchus texanus*, upper lateral tooth (PU 22421A); **11-12**, *Scapanorhynchus texanus*, lower anterior tooth (PU 22421B); **13-14**, *Odontaspis* sp., lower antero-lateral tooth (PU 22422); **15-16**, *Cretolamna appendiculata* var. *lata*, upper lateral tooth (PU 22423A); **17-18**, *Cretolamna appendiculata* var. *lata*, lower anterior tooth (PU 22423B); **19-20**, *Cretolamna biauriculata*, upper lateral tooth (PU 22424); **21-22**, *Cretolamna serrata*, lower antero-lateral tooth (PU 22425B); **23-24**, *Cretolamna serrata*, upper lateral tooth (PU 22425A); **25-26**, *Plicatolamna* cf. *P. arcuata* (PU 22426).

Description: — Teeth comparable in size and superficial appearance to those of the modern *Odontaspis (Carcharias) taurus* (Rafinesque). Erect central blade with or without striae or plications upon either the lingual or labial face; one or two lateral cusplets extending upward and outward from the base of the blade near the root apron; roots robust in teeth of the anterior and symphysial files, flattened in the lateral and posterior files. Tooth cuspidate or sigmoidal depending upon its position in the jaw.

Discussion: — Teeth of the Odontaspidae are quite difficult to sort and separate, as the species are sometimes similar in characteristics. The teeth from the Peedee Formation show no features of cusp design or root structure that would serve to distinguish them from previously-known species of *Odontaspis*, such as the Upper Cretaceous species *O. samhammeri*, *O. hardingi*, and *O. holmdelensis* described by Cappetta and Case from New Jersey. Until more and better material becomes available, the North Carolina teeth cannot be identified to species.

Family CRETOXYRHINIDAE

Cretolamna Glyckman, 1958

Cretolamna appendiculata lata (Agassiz)

Otodus latus Agassiz, 1843:271, Pl. 32, Fig. 26.

Material: — PU 22423A, an upper lateral tooth (Figs. 15-16), and PU 22423B, a lower anterior tooth (Figs. 17-18); two dozen anterior and lateral teeth from both upper and lower jaws. Site 1.

Description: — Teeth as described in Cappetta and Case (1975b: 21). The lower jaw teeth are more pointed and basically symmetrical, with pinched roots, while the roots of the upper jaw teeth are more flattened and their cusps are more squat. In the lateral to posterior files the blades are more slanted towards the commissure. There are two constricted accessory cusps, triangular in shape (not sigmoidal as in the Odontaspidae), on the anterior lower teeth, while the accessory cusps on the upper teeth are much wider and flatter. Roots in the lingual aspect are with or without an apical foramen, but all teeth lack a medial groove in that area. On certain specimens, mostly lateral to posterior teeth, there are vestiges of an additional and smaller accessory cusplet.

Discussion: — *Cretolamna appendiculata lata* is a most common species in the Cretaceous of the Atlantic Coastal Plain, while it is rare in the Gulf Coastal Plain (Texas in particular), and completely unknown in the Western Interior where *Plicatolamna* takes its place as the dominant form. It is common in the Maestrichtian of North Africa, especially in Morocco, and is present but uncommon in European Cretaceous deposits. In the

Cretaceous of New Jersey and Delaware *C. a. lata* ranks fourth in order of abundance, after *Scapanorhynchus texanus, Squalicorax (kaupi* and *pristodontus)*, and *Plicatolamna arcuata.*

Cretolamna biauriculata (Zittel *in* Wanner)

Otodus biauriculata (Zittel in MS) Wanner, 1902:148, Pl. XIX, Fig. 28.

Material: — PU 22424, an upper lateral tooth (Figs. 19-20); five other teeth, anterior and lateral. Site 1.

Description: — The teeth are basically similar to those of *C. a. lata* but differ conspicuously in bearing two divergent lateral cusps on either side of the central cusp, the outer ones being the smaller. The roots are flattened, with or without apical foramina, and lack a medial groove or furrow such as is found in the Odontaspidae.

Discussion: — This is the first reported occurrence of *C. biauriculata* in the New World. Its teeth are quite common in the Maestrichtian of Morocco, a bit scarcer in Algeria and Tunisia, and quite rare in Israel, where Raab (1963:27, Pl. 1, Figs. 1-18) claims to recognize *C. b. ?maroccana* Arambourg. It is extremely rare in European deposits.

Cretolamna serrata (Agassiz)

Otodus serratus Agassiz, 1838, Pl. XXXII, Figs. 27-28

Material: — PU 22425A, an upper lateral tooth (Figs. 23-24), and PU 22425B, a lower antero-lateral tooth (Figs. 21-22); about two dozen other teeth, anterior and lateral, from both upper and lower jaws. Site 1.

Description: — As described by Cappetta and Case (1975b), the typical tooth has two lateral cusps on one side of the central cusp and one lateral cusp on the other side. Otherwise the teeth are much like those of *Cretolamna appendiculata lata.*

Discussion: — Teeth of *C. serrata* are found only in Late Maestrichtian deposits. In North America the species ranges through the Atlantic and Gulf Coastal Plains, but has not turned up in the Western Interior nor west of the Rocky Mountains. It is quite common in North Africa (Morocco).

Plicatolamna Herman, 1974

Plicatolamna cf. *P. arcuata* (Woodward)

Lamna arcuata Woodward, 1894:198, Pl. VI, Fig. 10

Material: — PU 22426, a lower anterior tooth (Figs. 25-26). Site 1.

Description: — Tooth of average size, about 1 cm high and 8 mm maximum width (although the right lateral cusp and a small portion of the root are missing). It bears a sigmoidal lateral cusplet alongside a slender, slightly sigmoidal central cusp.

Discussion: — The teeth of *P. arcuata* are quite common in beds of Late Campanian to Middle Maestrichtian age but quite uncommon in the Late Maestrichtian. This specimen is not definitely identifiable as *P. arcuata*, and its temporal occurrence is very late for that species.

Order BATOIDEA
Suborder GANOPRISTINIDEA
Family SCLERORHYNCHIDAE
Ischyrhiza Leidy, 1856
Ischyrhiza mira Leidy

Ischyrhiza mira Leidy, 1856:221.

Material: — PU 22427A-B, two rostral teeth (Figs. 27-30); three other rostral teeth (no oral teeth). Site 1.

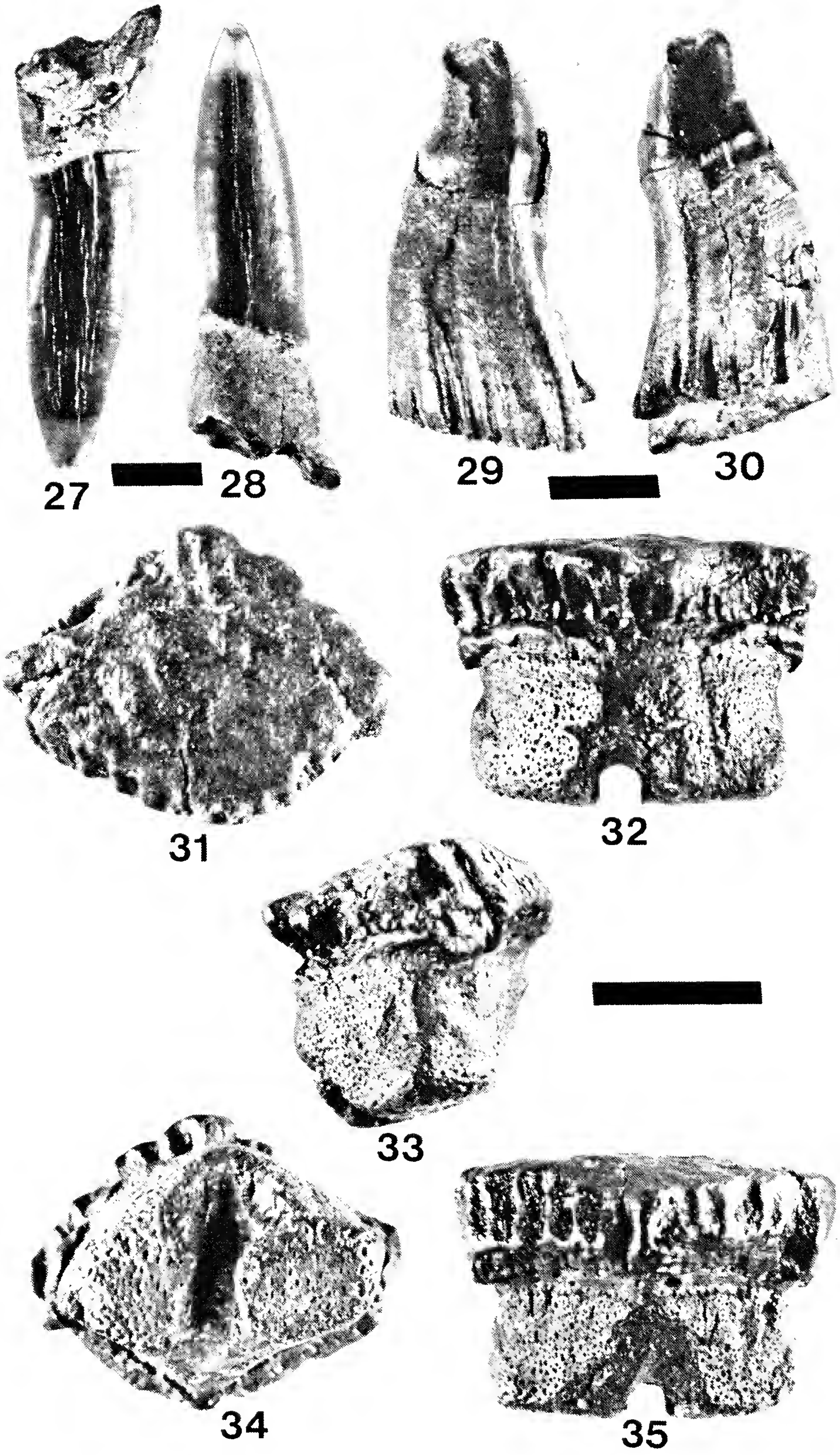
Description: — Rostral teeth of rather large size, ranging in length from 3.5 to 5.5 cm. No barb present on the lateral edge of the enameloid cusp (as in *Onchopristis*) and no plications or striations on the enameloid faces. The root base bears strongly rugose pleats which probably strengthened the attachment to the rostral cartilage. Otherwise the rostral teeth are characteristically sclerorhynchoid.

Discussion: — Rostral teeth of the sawfish *Ischyrhiza* are common in Upper Cretaceous deposits of North America, especially in the range from Late Campanian to Middle Maestrichtian. This genus is unknown outside the continental limits of the United States, for, as noted in previous work (Case 1967), *Sclerorhynchus* replaces *Ischyrhiza* in the Upper Cretaceous deposits of Europe and North Africa. Originally the rostral teeth of *Ischyrhiza* were thought to be the oral teeth of a teleost fish (Leidy 1856; Fowler 1911) but were later identified as belonging to a primitive sawfish that is known as a ganopristine because its denticles have a combination of enameloid and osseous structure.

Suborder DASYATOIDEI
Family MYLIOBATIDAE
Rhombodus Dames, 1881
Rhombodus cf. *R. binkhorsti* Dames

Rhombodus binkhorsti Dames, 1881:1, Fig. 1.

Material: — PU 22428, a pavement tooth (Figs. 31-35); and a dozen additional specimens. Sites 1, 2 and 3.



Figs. 27-35. Batoid teeth from the Peedee Formation of Site 1, Duplin County, North Carolina. Scale bar equals approximately 5 mm. **27-30**, *Ischyrhiza mira*, two rostral teeth in dorsal and ventral views (PU 22427A-B); **31-35**, *Rhombodus* cf. *R. binkhorsti*, pavement tooth in occlusal, anterior, lateral, basal, and posterior views (PU 22428).

Description: — Tooth-plates rhombic in outline, with short crowns containing enameloid material and with large, bifurcated roots that comprise approximately 2/3 of the total height. The crown has no rugose striation on its occlusal surface (such as occurs in *Myledaphus*), and its outer edge is crimped or milled, no doubt to facilitate interlocking between adjacent units in the tooth-pavement. Tooth-plates are of medium size, averaging less than 1 cm in diameter.

Discussion: — Because of their worn state the teeth from the Peedee Formation cannot be definitely assigned to the species *Rhombodus binkhorsti*. Despite its superficial similarity to *Myledaphus bipartitus* Cope, *Rhombodus* appears to be more closely related to the myliobatid *Hypolophus* than to the dasyatids, the skate family.

The isolated crushing teeth of *Rhombodus* are quite common in the Late Maestrichtian and are found in all marine deposits of that age, especially in Morocco, and in Texas, where they are second in number to the teeth of *Cretolamna serrata*.

FAUNAL COMPARISONS

The Late Maestrichtian stage of the Upper Cretaceous system is a most interesting period, and its vertebrate fauna is not very well known. Some of the shark species persisted into the Paleocene while others became extinct.

Table 1, based on data from nine states, shows the stratigraphic distribution of the shark species known from the Peedee Formation of North Carolina. This chart, of course, is not complete, but will require modification as further discoveries are made. On the basis of current information the shark species of the Peedee are characteristic of Late Maestrichtian time although some are seen to occur as early as the Cenomanian.

Considering the Late Maestrichtian shark fauna as a whole, the following forms are known to be of earlier origin: *Heterodontus, Lonchidion, Pseudocorax, Paranomotodon, Squalus, Ginglymostoma, Brachaelurus, Mesiteia, Rhinobatos, Sclerorhynchus, Ischyrhiza avonicola, Ischyrhiza mira, Ptychotrygon, Cretorectolobus*, and *Protoplatyrhina*. Appearing for the first time in the Late Maestrichtian are *Notorhynchus, Paleogaleus, Scyliorhinus, Dasyatis, Raja*, and *Rhombodus*, along with *Cretolamna biauriculata* and *C. serrata*. The only forms that survived into the Paleocene are *Odontaspis, Cretolamna appendiculata, Rhombodus, Squalus, Ginglymostoma*, and *Rhinobatos*.

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Table 1. Stratigraphic distribution of species in the United States Upper Cretaceous Formations*

Stages Species**	Cen	Tur	Con	San	Camp	Early Mas	Mid Mas	Late Mas
Hybodus sp. #1.						X	X	X
Squalicorax kaupi		X	X	X	X	X	X	X
Squalicorax pristodontus					X	X	X	X
Scapanorhynchus texanus					X	X	X	X
Odontaspis sp.	X	X	X	X	X	X	X	X
Cretolamna appendiculata	X	X	X	X	X	X	X	X
Cretolamna biauriculata								X
Cretolamna serrata								X
Plicatolamna sp.					X	X	X	X
Ischyrhiza mira					X	X	X	X
Rhombodus sp.								X

*Data from Upper Cretaceous faunal assemblages from the following states: *New Jersey; Maryland; North Carolina; Alabama; Arkansas; Texas; Montana; Wyoming and California.*

**Known species recovered from Rosehill, North Carolina.

Cen = Cenomanian San = Santonian
Tur = Turonian Camp = Campanian
Con = Coniacian Mas = Maestrichtian

his assistance in the field. My appreciation goes to Dr. Donald Baird, Department of Geological and Geophysical Sciences, Princeton University, for his kindness in reading the original manuscript and offering suggestions for the improvement of the paper. The excellent photography of the figures is the work of Mr. Richard E. Grant of Dallas, Texas. Appreciation is extended to Mr. Richard Hamilton, Rockaway, New York, for his kind assistance on the art preparation for the figures and tables.

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Freshwater Triclads (Turbellaria) of North America.

XII. Another New Cave Planarian from North Carolina, *Phagocata carolinensis* n. sp.

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ABSTRACT.—Phagocata carolinesis n. sp. from One Bat Cave, Burke County, North Carolina, is a slender, unpigmented species with two small eyes and is characterized by its peculiar penial anatomy and by the development of an enormous vagina with special histological differentiation. It belongs to a group of closely related species of *Phagocata* distributed in the Appalachian region.

Through the courtesy of Dr. Cato O. Holler, Jr. of Old Fort, North Carolina, I received some specimens of a new species of *Phagocata*, collected in a cave in Burke County, North Carolina. Dr. Holler is with the North Carolina Cave Survey and an investigator in the Biological Survey of North Carolina Caves.

Phagocata carolinensis, new species

Type-material (deposited in the U. S. National Museum of Natural History [USNM], Smithsonian Institution, Washington, D. C.).— Holotype, set of sagittal sections on 3 slides (USNM 58431); paratypes, sagittal and horizontal sections of 2 specimens on 12 slides (USNM 58432-58433).

External features (Figs. 1A, 1B). — The species is unpigmented (white), externally indistinguishable from *Phagocata angusta* Kenk (1977) or *P. holleri* Kenk (1979). In gliding locomotion the body is very slender, reaching up to 13 mm in length and about 1 mm in width. The truncate head has a somewhat wavy frontal margin and bears on each side a lateral projection, slightly more distinct than that of *P. holleri*. Posterior to these projections the head narrows, forming a kind of neck. Behind the neck the lateral body margins diverge again gradually to reach the maximum width, then run parallel for the greater part of the body length, to converge again and to meet at the rather rounded posterior end.

The two small eyes are situated close together at a considerable distance behind the frontal margin of the head. The intestine reaches

Brimleyana No. 2: 91-96. November 1979

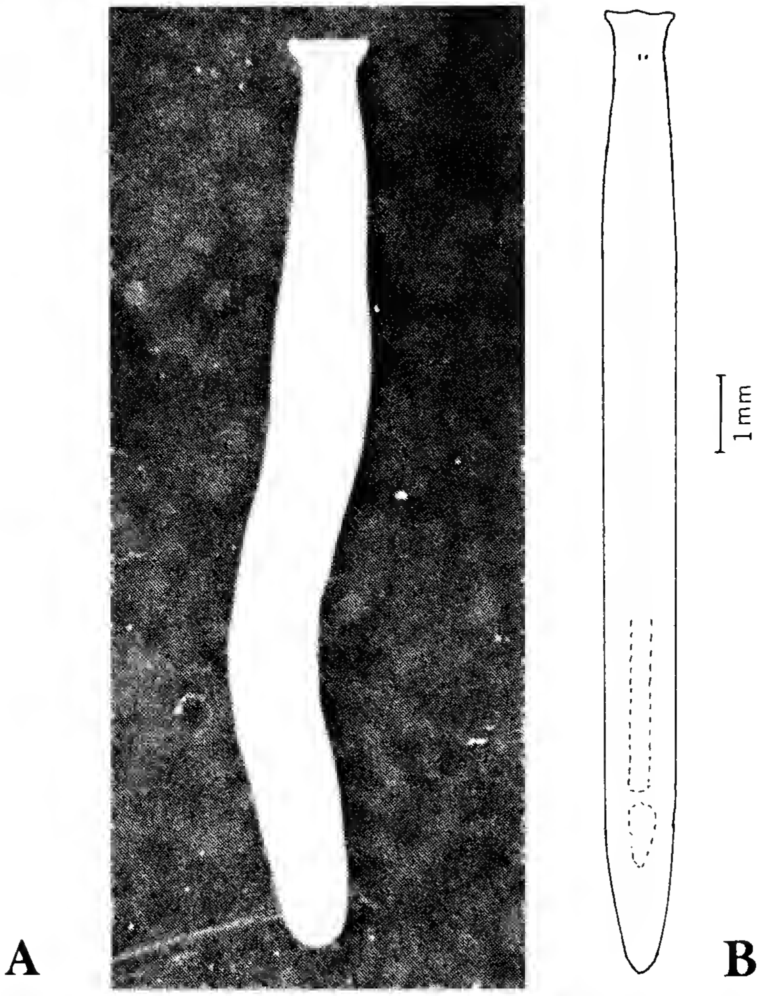

Fig. 1. *Phagocata carolinensis.* A, photograph of living animal, ×7; B, outline drawing of living animal, with indication of eyes, pharynx, and copulatory apparatus.

anteriorly to the level of the eyes. The pharnyx is rather long, about 1/5 body length, and its root is inserted at the beginning of the fourth fifth of the body. The copulatory apparatus is visible in the living specimen as a transparent area occupying the anterior half of the postpharyngeal region.

Anatomy. — The two eyes are rather small, the diameters of their pigment cups measuring 26-37 μm.

In the reproductive system, the two ovaries are situated behind the second or third lateral branches of the anterior intestinal trunk. Each ovary is equipped with a rather large, lobed parovarium, usually located laterally to the ovary. There are, however, cell accumulations also anterior to the ovaries that histologically resemble parovaria without being connected with either the ovaries or the true parovaria.

The numerous testes are essentially ventral, although at full maturity individual testicular follicles may extend almost to the dorsal body wall. They are arranged on either side of the body in a broad longitudinal zone beginning some distance behind the ovaries and terminating at the level of the pharyngeal root. In the region of the testes, the thin vas deferens or sperm duct on each side runs along the medial side of the ventral nerve cord, somewhat above the longitudinal layer of the ventral integumental

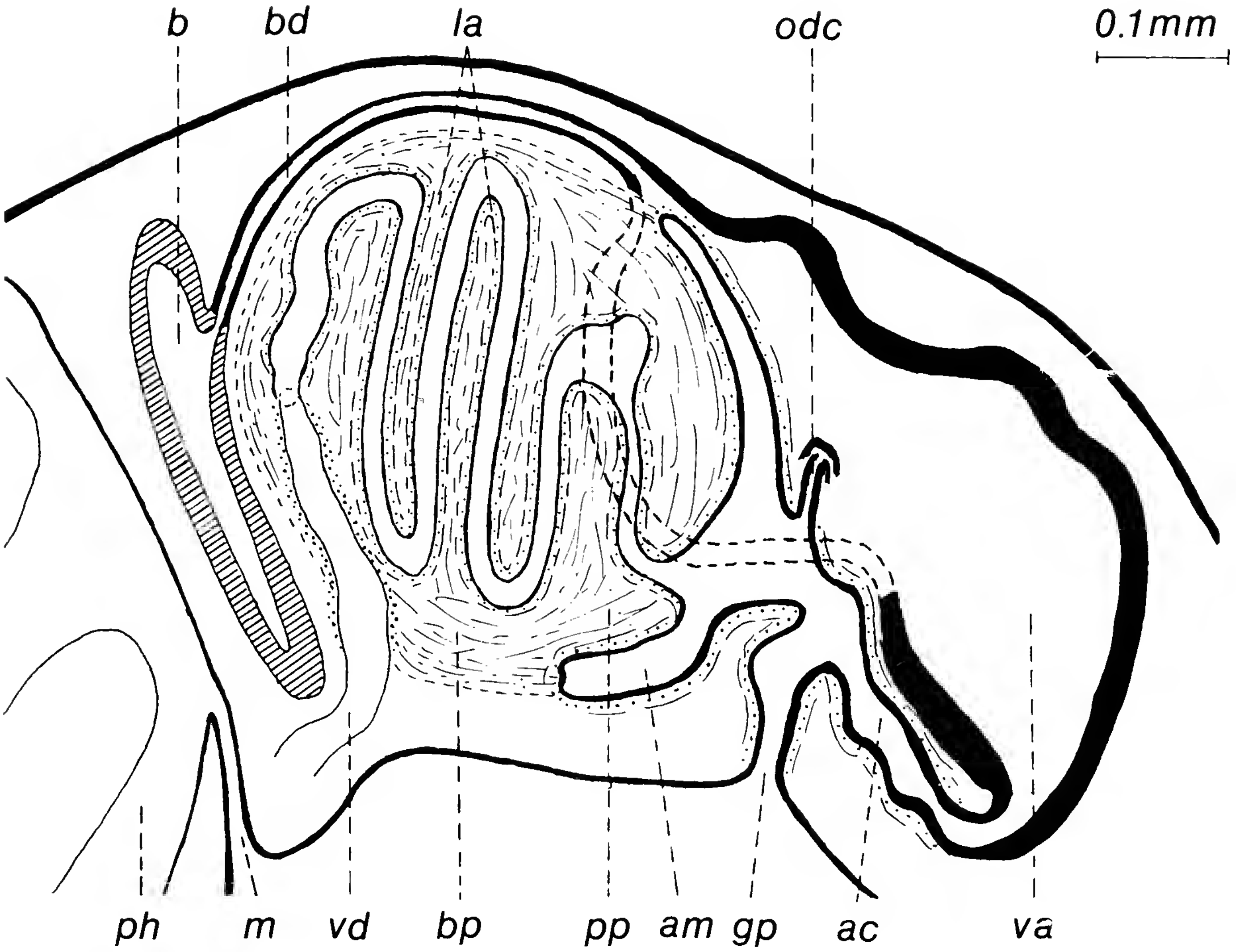

Fig. 2. *Phagocata carolinensis*, semidiagrammatic view of copulatory apparatus in sagittal section. *ac*, common atrium; *am*, male atrium; *b*, copulatory bursa; *bd*, bursal duct; *bp*, penis bulb; *gp*, gonopore; *la*, lamellae; *m*, mouth; *odc*, common oviduct; *ph*, pharyngeal pouch; *pp*, penis papilla; *va*, vagina; *vd*, vas deferens.

muscles. In the region of the pharynx, the vasa deferentia expand to form the tortuous false seminal vesicles or spermiductal vesicles, filled with sperm, which proceed posteriorly toward the copulatory complex.

The copulatory apparatus (Fig. 2) is located immediately behind the pharyngeal pouch (*ph*). The genital aperture or gonopore (*gp*) is situated about midway between the mouth (*m*) and the posterior end of the body. It leads through a short narrow duct into the common atrium (*ac*) which opens anteriorly into the male atrium (*am*) and posteriorly into the vagina (*va*) of the bursal duct. Both the male and common atria are lined with a nucleate and ciliated cuboidal epithelium.

The penis consists of a rather voluminous bulb (*bp*), the musculature of which is rather feeble and developed mainly near its periphery, and a short, bluntly conical papilla (*pp*) extending into the male atrium. The configuration of the penial lumen is quite unique. Three to five transverse lamellae (*la*) originate from the dorsal and ventral walls, alternatingly projecting downward and upward. Each lamella is attached to the lateral walls of the penis, as can be seen in horizontal sections through the organ.

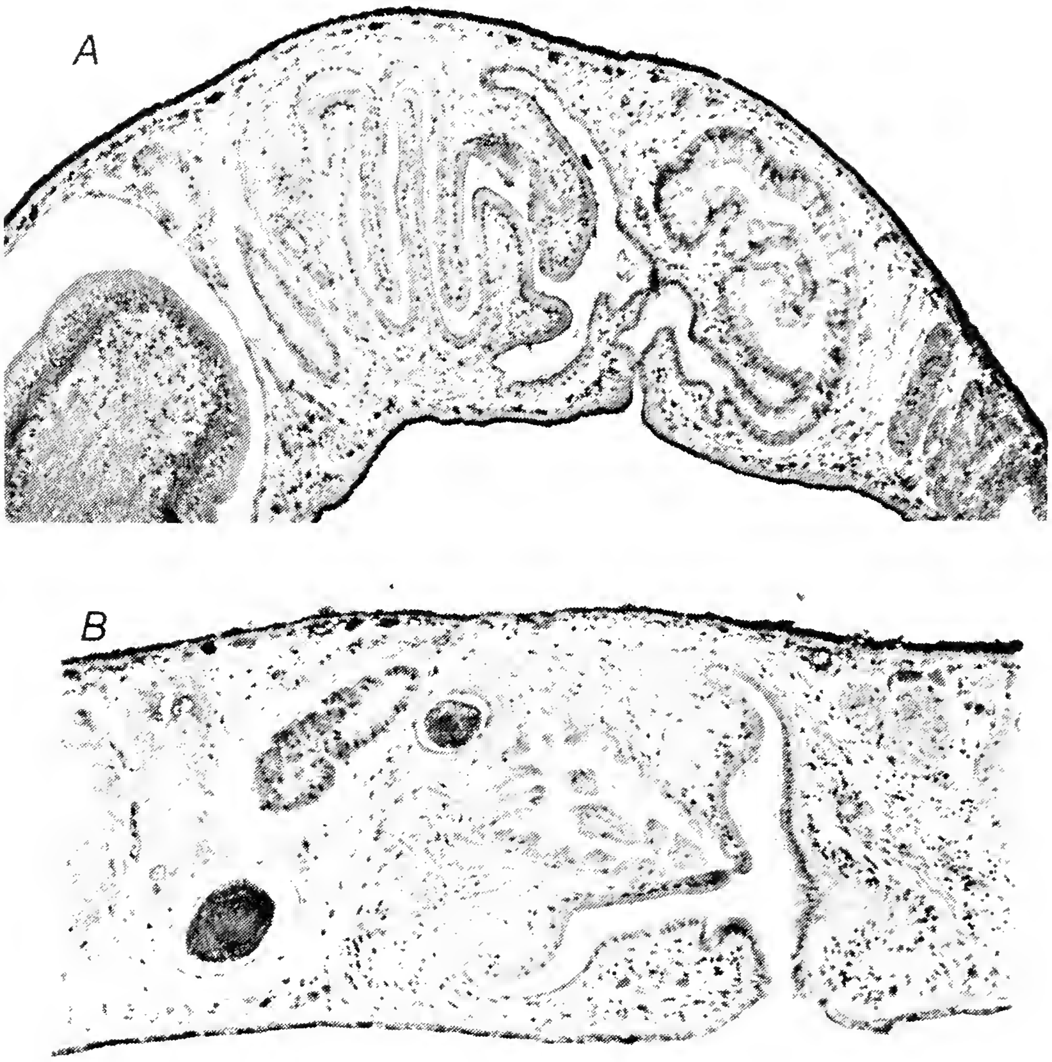

Fig. 3. Photomicrographs of copulatory organs in sagittal section. A, *Phagocata carolinensis*, ×60; B, *Phagocata holleri*, ×127.

This arrangement would permit the passage of sperm from the bulb to the tip of the penis papilla only in a serpentine fashion. It is possible, however, that the configuration of the penis lumen as it appears in the slides obtains only when the penis is retracted. When the papilla is extended during copulation the passage may well straighten out. Both the lamellae and the greater part of the outer surface of the papilla are covered by a thin infranucleate epithelium with two underlying muscle layers, a circular and a longitudinal one. There is no differentiation of the penial lumen into a seminal vesicle and ejaculatory duct. At most, a small anterior portion of the lumen may differ from the remaining part by having a ciliated and nucleate epithelium. The vasa deferentia (*vd*) enter the penis bulb ventrolaterally, turn dorsomedially, and unite at their opening into the anterior end of the penial lumen.

The copulatory bursa (*b*) adjoins the wall of the pharyngeal pouch (*ph*). Its outlet, the bursal stalk or duct (*bd*) proceeds posteriorly for a short distance as a narrow duct situated somewhat to the left of the midline and lined with a nucleate, ciliated epithelium. It then expands into a large, irregularly lobed sac, the vagina (*va*), the greater part of which is also located on the left side. The epithelium lining the vagina consists of large, apparently apocrine cells with basal nuclei (Fig. 3A), quite different from those of the anterior part of the bursal duct. It appears that one of the functions of the vagina is the resorption of superfluous sperm after copulation, a process that may take place at many locations in the turbellarians (cf. particularly Černosvitov 1931). Sperm was present in the vagina in two of the three specimens examined. The vagina connects with the posterior end of the common atrium (*ac*). At the transition, the nature of the epithelial lining changes from the vaginal glandular epithelium to the nonglandular, ciliated epithelium of the atrium.

The two oviducts or ovovitelloducts unite in the space between the bursal stalk and the atria and form a common oviduct (*odc*) that opens from the dorsal side near the junction of the male and common atria.

Distribution and ecology. — Four specimens were collected on 7 April 1979 by Dr. Cato O. Holler, Jr., Christopher Holler, and Keith Barnes in a small seep toward the rear end of One Bat Cave, located in the Linville Gorge Wilderness Area, Burke County, North Carolina. They were sent to me alive. Three of the specimens proved to be sexually mature.

Taxonomic position. — *Phagocata carolinensis* belongs to a group of closely related species of the genus distributed in the Appalachian region. Externally it cannot be distinguished from two other species, *P. angusta* and *P. holleri*. The three have in common the lack of body pigment, a slender shape, a truncate head end without prominent auricular projections, a pair of very small eyes, and anatomically prepharyngeal ventral testes. The principal differences are in the configuration of the copulatory complex. The penial lumen in *P. carolinensis* shows the peculiar transverse lamellae (at least in the retracted penis), while in *P. holleri* it contains finger-shaped villi (compare Figures 3A and 3B) and in *P. angusta* no special internal differentiations. *Phagocata carolinensis* has an extraordinarily large lobate vagina with a modified histology; *P. angusta*, a villous vagina of moderate size; and *P. holleri*, no distinguishable vaginal formation. In *P. holleri* the copulatory apparatus is situated considerably posterior to the pharyngeal pouch; in *P. carolinensis* the apparatus adjoins the pouch closely; while *P. angusta* has an intermediate position. Details in the histological differentiation of the epithelia of the copulatory complex also differ in the three species.

Etymology. — The species is named *carolinensis* after its habitat, North Carolina.

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Freshwater Fishes of Croatan National Forest, North Carolina, with Comments on the Zoogeography of Coastal Plain Fishes

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ABSTRACT.—In a survey of freshwater fishes in and near Croatan National Forest, eastern North Carolina, 94 collections at 51 localities yielded 5670 specimens representing 38 species. Sixteen additional species have been reported from the Forest, but at least four are considered questionable. Twenty species of estuarine fishes were collected during the study, including the first North Carolina record of the Fourspine stickleback, *Apeltes quadracus*.

Examination of the distribution of fishes in the nine major river systems draining the lower Coastal Plain of North Carolina reveals the absence of a number of species in the smaller drainages (e.g. Shallotte, New, White Oak and Newport rivers). Two possible reasons are lack of suitable ecological conditions and the irregular distribution patterns observed at the periphery of a species' range.

INTRODUCTION

The fishes of the lower Coastal Plain of North Carolina have not been as intensively sampled as those that occur in upland areas of the state, primarily because of apparent lower species diversity and high frequency of underwater obstructions. We initiated the survey on which this paper is based in 1973 to determine what freshwater fishes occur in the Croatan National Forest in eastern North Carolina. Observations on brackish water and marine fishes were also included.

Several prior fish surveys made in the general vicinity of the Croatan National Forest were either very localized (Bayless 1966; Turner and Johnson 1973), or covered a wide area of the state (Bayless and Smith 1962; Keup and Bayless 1964; Davis and McCoy 1965). Seehorn (1976)

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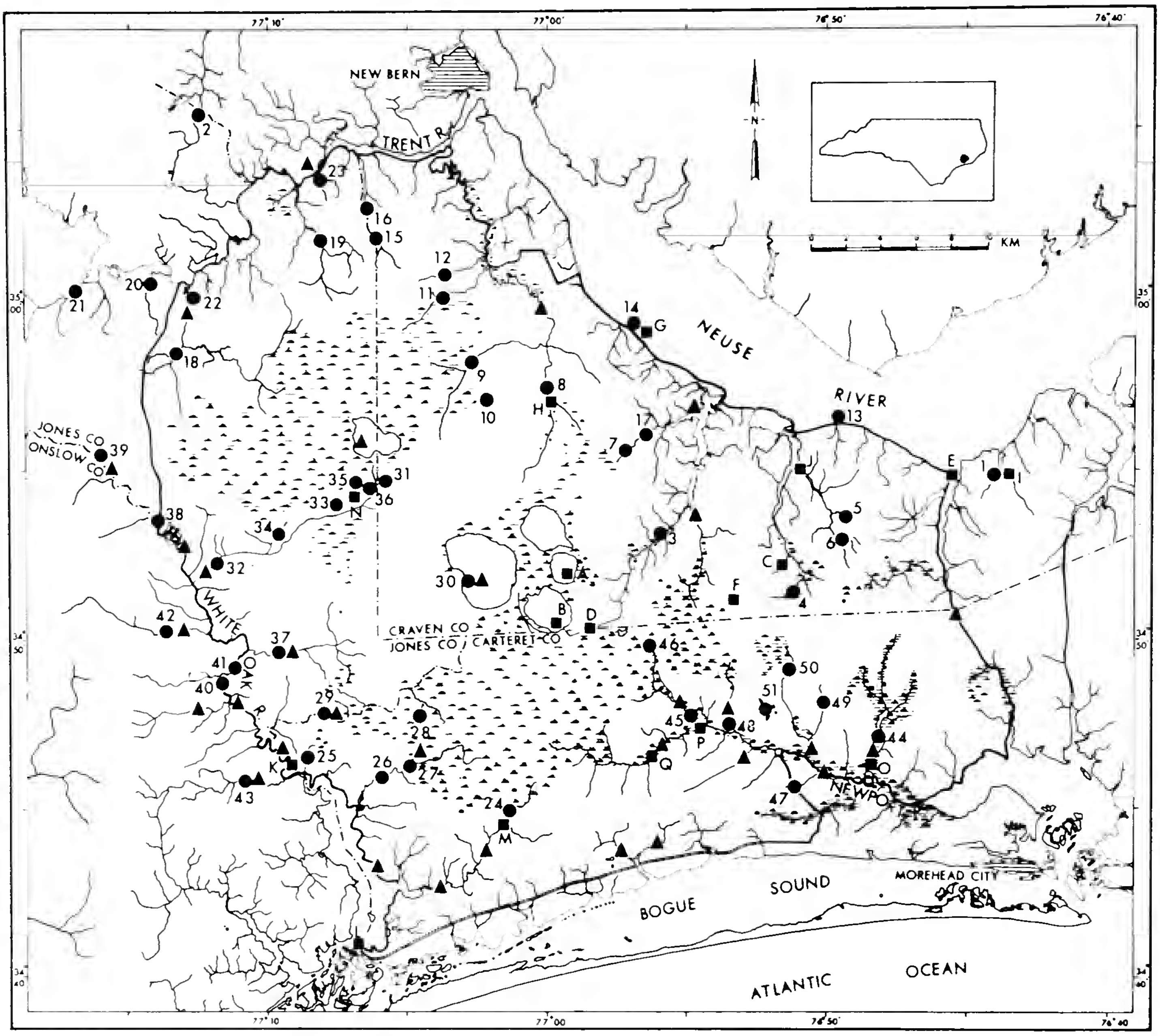

Fig. 1. Map of Croatan National Forest showing sampling stations. Heavy line depicts forest boundary. Circles denote stations in this study; squares represent collections made by Duke University Marine Laboratory (DUML) personnel or earlier workers at University of North Carolina - Institute of Marine Sciences (UNC); triangles indicate collections made by North Carolina Wildlife Resources Commission (NCWRC).

attempted to list all fishes known to occur or which might occur in southeastern national forests, but his Croatan list was based almost solely on a literature search (R. E. Jenkins, pers. comm.). We attempted to sample a large number of freshwater localities in the Croatan National Forest and adjacent streams in order to assess accurately the abundance and distribution of its fishes.

STUDY AREA

Croatan National Forest comprises 382,716 hectares and occupies parts of Carteret, Craven, and Jones counties (Fig. 1). It is drained by the Neuse, White Oak, and Newport rivers; a fourth river within the forest, the Trent, is tributary to the Neuse. Five natural lakes totaling 10,617 hectares are present there. Most of the land not forested is in agricultural use. There is little domestic or industrial pollution and, because the land is generally level, there is little evidence of soil erosion.

Water was tannin stained and acidic, as is typical of the Coastal Plain, and pH values of 4.6 - 9.0 have been recorded in the Neuse River within the forest, 5.1 - 8.2 in the White Oak, 4.9 - 8.1 in the Newport, and 4.5 - 4.7 in the lakes (Bayless and Smith 1962; Davis and McCoy 1965; Bayless 1966). Water temperatures in our study ranged from 3.0 C in January to 31.0 C in June, and the waters were usually clear.

Stream-side vegetation was typical for the Coastal Plain. Twenty aquatic plant species were observed in the area: filamentous algae; *Sphagnum* sp.; *Taxodium distichum; Typha* sp.; *Sparganium americanum; Potamogeton pectinatus; Najas* sp.; *Ruppia maritima; Sagittaria* sp.; *Scirpus* sp.; *Pontederia cordata; Juncus* sp.; *Saururus cernuus; Ceratophyllum demersum; Polygonum punctatum; Nymphaea odorata; Proserpinaca* sp.; *Myriophyllum brasiliense; Hydrocotyle* sp.; and *Utricularia purpurea.*

MATERIALS AND METHODS

From 3 September 1973 to 16 September 1978, 94 collections were made at 51 localities in and near the forest (Fig. 1). All specimens were collected either with a 3.0 m × 1.2 m, 3.1 mm mesh flat seine; a 6.1 m × 1.2 m, 6.4 mm mesh flat seine (used several times); or a 30.5 m gill net of varying mesh sizes (used only once). No attempt was made to standardize the collection methods used because of variations in physiography at the different sites. Fish were immediately preserved in 10% formalin and returned to the laboratory for identification. Representative specimens were deposited in the Institute of Marine Sciences - University of North Carolina (UNC) collection. Water and air temperatures and pertinent physical characteristics of each site were recorded. Although two sites were sampled intensively as part of several life history studies, most localities were sampled only once.

Data from collections made at 31 localities (Fig. 1) by the North Carolina Wildlife Resources Commission (NCWRC) (Bayless and Smith 1962; Davis and McCoy 1965; Bayless 1966) were summarized and are included. These collections were made with 5% emulsified rotenone. Data from seine and gill-net collections made at 17 localities (Fig. 1) by earlier workers at UNC-IMS and Duke University Marine Laboratory (DUML) are also included. Additional records were obtained from the fish collections at the North Carolina State Museum of Natural History (NCSM) and Duke University (DU). All localities at which collections were made are listed in Table 1.

Table 1. Sampling localities and dates (day/month/year). Numbers refer to our stations, letters to those of others (see text).

I. Neuse River drainage
  A. Craven County
    1. Long Creek on SR 1700, 7.8 km ne North Harlowe, 13/10/73.
    2. Bachelor Creek on SR 1224, 14.7 km w New Bern, 31/12/74.
    3. Southwest Prong of Slocum Creek on SR 1746, 2.7 km wnw Havelock, 4/1/75.
    4. Hancock Creek on dirt road s off NC 101, 5.1 km se Havelock, 1/6/75.
    5. Cahooque Creek on SR 1716, 7.7 km ne Havelock, 1/6/75.
    6. South Fork of Cahooque Creek on SR 1716, 7.7 km ne Havelock, 1/6/75.
    7. Tucker Creek on dirt road w of US 70, 7.5 km ene Havelock, 21/6/75.
    8. East Prong of Brice Creek on SR 1100, 3.2 km sw Croatan, 21/6/75, 31/1/76, 27/2/76, 12/3/76, 2/4/76, 30/1/77, 23/2/77, 23/4/77, 14/5/77, 16/9/78.
    9. Tributary to Brice Creek on Forest Road 121-2, 7.2 km w Croatan, 21/6/75.
    10. Drainage ditches on SR 1100 at jct. Forest Road 121-2, 4.8 km sw Croatan, 21/6/75, 9/4/77.
    11. Tributary to Brice Creek on Forest Road 170, 8.8 km nw Croatan, 31/1/76.
    12. Tributary to Brice Creek on Forest Road 170, 8.8 km nnw Croatan, 31/1/76.
    13. Neuse River at Cherry Point at end of SR 1716, 11.0 km ne Havelock, 18/5/76
    14. Neuse River at Flanner Beach at end of SR 1107, 2.4 km ne Croatan, 18/5/76, 16/9/78.
    15. Reedy Branch on SR 1004, 11.0 km ene Pollocksville, 31/1/76.
    16. Reedy Branch on SR 1340, 11.7 km se Pollocksville, 31/1/76.
    17. Tucker Creek on dirt road e of US 70, 5.0 km se Croatan, 17/7/77.
    A. Little Lake, 7.4 km wsw Havelock, 14/4/52, 29/4/52.
    B. Ellis Lake, 8.5 km sw Havelock, 24/4/52, 29/8/57.
    C. Tributary to Hancock Creek on NC 101, 3.7 km e Havelock, 14/4/52.

D. Drainage ditch tributary to outlet Ellis Lake, 7.8 km sw Havelock, 14/4/52.
E. Neuse River at North Harlowe, 29/8/57.
F. Drainage ditch along US 70, 3.2 km se Havelock, 29/8/57, 14/4/62.
G. See #14, 19/4/56.
H. See #8, 2/5/71, 7/10/72.
I. Long Creek on SR 1700, 7.8 km ne North Harlowe, 13/10/73.
J. Cahooque Creek at junction Hancock Creek, 6.7 km ne Havelock, 20/5/76, 24/8/76.

B. Jones County
18. Mill Creek on SR 1108, 3.2 km s Pollocksville, 22/8/74, 7/12/74.
19. Island Creek on SR 1004, 8.2 km ene Pollocksville, 22/8/74.
20. Tributary to Trent River on SR 1337, 1.4 km nw Pollocksville, 7/12/74.
21. Mill Run on NC 58, 5.4 km w Pollocksville, 7/12/74, 12/3/76, 28/8/76.
22. Mill Creek on SR 1004, 0.8 km se Pollocksville, 28/8/76.
23. Tributary to Trent River on SR 1340, 9.9 km ne Pollocksville, 14/6/77, 19/11/77.

II. White Oak River drainage
A. Carteret County
24. Pettiford Creek on Forest Road 128, 8.0 km ne Cape Carteret, 1/1/75.
25. Unnamed creek on SR 1101, 0.5 km e Stella, 1/1/75.
26. Hadnot Creek on NC 58, 8.8 km nnw Cape Carteret, 8/6/76.
27. Hadnot Creek on SR 1104, 8.8 km n Cape Carteret, 8/6/76.
28. Drainage ditch on Forest Road 176, 12.8 km n Cape Carteret, 8/6/76.
29. Hunters Creek on NC 58, 13.6 km nnw Cape Carteret, 8/6/76.
K. White Oak River at Stella, 3/3/56.
L. White Oak River on NC 24 at Swansboro, 17/8/71.
M. See #24, 31/7/72.

B. Craven County
30. Great Lake, sw corner at end Forest Road 126, 17.3 km se Maysville, 16/8/76.
31. Drainage ditch on SR 1100, 10.5 km e Maysville, 30/1/77.

- C. Jones County
  - 32. Black Swamp Creek on NC 58, 4.8 km se Maysville, 7/12/74.
  - 33. Drainage ditch along SR 1105, 9.8 km e Maysville, 31/12/74, 4/1/75, 16/8/75, 30/1/77, 23/2/77, 12/3/77, 19/3/77, 27/3/77, 3/4/77, 9/4/77, 16/4/77, 23/4/77, 30/4/77, 14/5/77, 14/6/77, 17/7/77, 14/8/77, 18/9/77, 16/10/77, 19/11/77.
  - 34. Tributary to Black Swamp Creek on SR 1105, 6.2 km ese Maysville, 4/1/75.
  - 35. Drainage ditch on SR 1105, 200 m w Black Swamp Creek, 9.9 km e Maysville, 16/8/75.
  - 36. Black Swamp Creek on SR 1105, 10.0 km e Maysville, 16/8/75, 9/4/77.
  - 37. Holston Creek on NC 58, 10.1 km se Maysville, 8/6/76.
  - 38. White Oak River on US 17, 2.2 km s Maysville, 28/8/76, 14/5/77.
  - 39. White Oak River on SR 1118, 3.2 km nw Maysville, 28/8/76.
  - 40. White Oak River, 0.5 km sw Haywood Boat Landing, 10.7 km se Maysville, 14/5/77.
  - 41. White Oak River at Haywood Boat Landing, 10.2 km se Maysville, 14/5/77.
  - N. See #33, 18/7/59.
- D. Onslow County
  - 42. Starkys Creek on SR 1434, 13.4 km nw Swansboro, 7/12/74.
  - 43. Webb Creek on SR 1435, 9.0 km nw Swansboro, 7/12/74.

III. Newport River drainage

- A. Carteret County
  - 44. Mill Pond and below spillway in Black Creek on SR 1154, 3.3 km e Newport, 3/9/73, 1/6/75.
  - 45. Northwest Prong of Newport River on SR 1124, 3.2 km wnw Newport, 22/8/74, 30/12/74, 4/1/75, 10/5/75, 16/9/78.
  - 46. Drainage ditch on SR 1125, 7.4 km s Havelock, 1/1/75, 1/4/75, 5/4/77.
  - 47. Unnamed tributary on US 70, 1.6 km s Newport, 1/3/75.
  - 48. Shoe Branch on SR 1124, 1.3 km wnw Newport, 1/3/75.
  - 49. Little Deep Creek on SR 1139, 2.9 km ne Newport, 1/3/75.
  - 50. Deep Creek on SR 1133, 3.7 km n Newport, 1/3/75.
  - 51. Pond, 0.5 km n of SR 1124, 1.3 km nw Newport, 1/3/75.
  - O. See #44, 17/8/56.

P. See #45, 31/7/72, 7/6/73.
Q. Southwest Prong of Newport River on SR 1124, 6.9 km w Newport, 7/6/73.

RESULTS

FRESHWATER FISHES

The following is a list of freshwater fishes collected in (or near) or reported from the forest, with comments on dubious records and records of interest. Table 2 provides a list of species by drainage and collector.

Lampetra aepyptera, Least brook lamprey

2 specimens, station 21. Menhinick et al. (1974) listed four localities for this species in North Carolina, one of which was station 21. Although three trips were made specifically to collect this lamprey, only two ammocoetes were captured. We also visited two of the remaining three localities and took lampreys (8 ammocoetes) at only the Pitt County site. The habitat at these sites was marginal for lampreys. Bailey et al. (1977) listed this species as of Special Concern in North Carolina. Because of lack of suitable habitat at the few known localities we feel that this species should be considered Threatened in the state.

Petromyzon marinus, Sea lamprey

One ammocoete (155 mm TL) was collected at station 21 on 21 October 1969 by J. R. Bailey, Duke University (DU uncat.). Two ammocoetes of *L. aepyptera* were taken concurrently.

Lepisosteus osseus, Longnose gar

4 specimens, stations 27, 38, 44. K, J, NCWRC.

Amia calva, Bowfin

NCWRC. Local fishermen reported this species from small ponds near Newport. Turner and Johnson (1973) collected it at their uppermost station in the Newport River.

Anguilla rostrata, American eel

237 specimens, stations 3-8, 16, 19, 21-27, 29, 36-39, 41, 42, 44, 45, 47-50. B, C, D, P, NCWRC.

Dorosoma cepedianum, Gizzard shad

1 specimen, station 38. J, NCWRC.

Umbra pygmaea, Eastern mudminnow

188 specimens, stations 5-7, 8, 10, 28, 31, 33, 35, 36, 44, 46. N, NCWRC.

Table 2. Species, total numbers of freshwater fishes collected (N) and locality numbers in and near Croatan National Forest, North Carolina, by drainage and study. Locality numbers in parentheses.

	Neuse River			White Oak River			Newport River		
	This Study	NCWRC	UNC-DUML	This Study	NCWRC	UNC-DUML	This Study	NCWRC	UNC-DUML
No. of localities	23	5	10	20	16	4	8	10	3
No. of collections	38	5	11	41	16	4	15	10	4
Species	N			N			N		
Lampetra aepyptera	2(1)	—	—	—	—	—	—	—	—
Lepisosteus osseus	—	(1)	(1)	3(2)	(5)	(1)	1(1)	(1)	—
Amia calva	—	(1)	—	—	—	—	—	—	—
Anguilla rostrata	105(11)	(5)	(1)	82(9)	(10)	—	50(6)	(8)	(2)
Dorosoma cepedianum	—	—	(1)	1(1)	(2)	—	—	(3)	—
Umbra pygmaea	13(5)	—	—	164(5)	(6)	(1)	11(1)	(3)	—
Esox a. americanus	43(10)	(2)	(1)	27(8)	(10)	—	30(5)	(7)	(1)
E. niger	17(5)	(4)	(1)	4(2)	(10)	(1)	—	(3)	(1)
Carassius auratus	—	—	(1)	—	—	—	—	—	—
Cyprinus carpio	—	—	—	—	—	—	—	(1)	—
Hybognathus regius	36(2)	(2)	—	—	—	—	—	—	—
Notemigonus crysoleucas	19(4)	(5)	—	13(4)	(11)	—	37(3)	(5)	(1)
Notropis amoenus	—	(1)	—	—	—	—	—	—	—
N. bifrenatus	—	(1)	—	—	—	—	—	—	—
N. chalybaeus	1(1)	(3)	—	65(5)	(8)	—	110(1)	(3)	(1)
N. cummingsae	23(4)	(1)	—	24(1)	(2)	—	—	—	—
N. hudsonius	3(1)	(1)	—	—	—	—	—	—	—
N. procne	—	(1)	—	—	—	—	—	—	—
Erimyzon o. oblongus	10(6)	—	(1)	59(2)	(7)	—	1(1)	(3)	—
E. sucetta	135(2)	(3)	(1)	3(1)	(2)	—	—	(3)	—

Moxostoma anisurum (?)	—	(1)	—	—	—	—	—	—	—
M. pappillosum (?)	—	—	—	—	(1)	—	—	—	—
Ictalurus catus	—	—	—	—	(5)	(1)	—	(1)	—
I. natalis	41(3)	—	(1)	23(4)	(6)	—	16(2)	(6)	(2)
I. nebulosus	8(2)	(1)	(1)	4(1)	(2)	—	—	(1)	—
I. punctatus	—	(2)	(1)	—	—	—	—	—	—
Noturus gyrinus	—	(3)	—	6(2)	(8)	—	9(3)	(2)	—
N. insignis	15(1)	—	—	—	(7)	—	8(1)	(2)	—
Chologaster cornuta	8(2)	(1)	—	774(4)	(2)	(1)	21(2)	(2)	—
Aphredoderus s. sayanus	209(9)	(3)	—	150(13)	(10)	—	117(5)	(7)	(1)
Fundulus d. diaphanus	6(1)	—	—	—	—	—	—	—	—
F. lineolatus	237(2)	—	(1)	—	—	—	—	—	—
Gambusia affinis holbrooki	751(12)	(3)	(2)	337(4)	(6)	—	41(5)	(5)	(2)
Acantharchus pomotis	31(2)	—	—	2(2)	(6)	—	8(4)	(5)	—
Centrarchus macropterus	114(6)	(1)	—	13(3)	—	(1)	9(2)	(2)	(1)
Elassoma zonatum	—	(1)	—	—	—	—	—	—	—
Enneacanthus gloriosus	500(14)	(4)	(1)	169(11)	(10)	(1)	66(4)	(6)	(1)
E. obesus	7(3)	(4)	(1)	41(5)	(11)	—	78(1)	(6)	(2)
Lepomis auritus	7(2)	(1)	—	8(1)	(7)	—	7(4)	(3)	(1)
L. gibbosus	60(11)	(4)	(1)	7(3)	(8)	—	3(2)	(2)	(1)
L. gulosus	54(4)	(2)	(1)	26(3)	(11)	—	9(2)	(5)	(2)
L. macrochirus	33(3)	(2)	—	87(3)	(11)	—	52(3)	(4)	(1)
L. microlophus	—	—	—	—	(1)	—	—	—	—
Micropterus s. salmoides	5(3)	(4)	(1)	9(3)	(7)	—	10(3)	(3)	(2)
Pomoxis nigromaculatus	5(1)	(2)	—	—	—	—	3(1)	(1)	—
Etheostoma f. fusiforme	10(4)	(3)	—	9(1)	(5)	—	19(1)	(4)	—
E. o. olmstedi	146(5)	(1)	—	17(2)	(7)	—	13(2)	—	(1)
E. serriferum	25(2)	(1)	—	87(4)	(6)	—	40(6)	—	(1)
Perca flavescens	2(1)	(2)	—	2(1)	(6)	—	—	—	(1)
Percina crassa roanoka	4(1)	—	—	—	—	—	8	—	—
Total Species	35	35	18	30	33	7	26	30	19
Total Specimens	2685	—	—	2216	—	—	769	—	—

Esox americanus americanus, Redfin pickerel
100 specimens, stations 4, 6-10, 17, 18, 21, 22, 26, 27, 33, 35-37, 45-47, 49, 50. C, F, M, P, NCWRC.

E. niger, Chain pickerel
21 specimens, stations 1, 6, 8, 23, 27, 37. B, I, J, NCWRC.

Carassius auratus, Goldfish
B. Local fishermen reported it as present in a small pond near Newport.

Cyprinus carpio, Carp
NCWRC. One specimen taken in the Newport River.

Hybognathus regius, Silvery minnow
36 specimens, stations 18, 23. NCWRC. The status of this form as a full species and its relationships with other *Hybognathus* species requires further investigation.

Notemigonus crysoleucas, Golden shiner
69 specimens, stations 6, 7, 8, 18, 25, 27, 32, 38, 40, 44, 45, 50. P, NCWRC.

Notropis altipinnis, Highfin shiner
Reported by Seehorn (1976) from the forest, but R. E. Jenkins (pers. comm.) says it was included by mistake. Hubbs and Raney (1948) recorded it from a tributary on the north shore of the Trent River.

N. amoenus, Comely shiner
NCWRC. Taken only in Trent River and tributaries. Representative specimens are in the NCSM fish collection.

N. bifrenatus, Bridle shiner
NCWRC. Three Tucker Creek specimens represent the southernmost record for the species (Jenkins and Zorach 1970). We made collections at two separate sites without success. Station 17 is close to the NCWRC site, but we encountered high salinities (8 ppt) which had apparently forced most freshwater fishes upstream. Bailey et al. (1977) said that *N. bifrenatus* is probably extirpated at this locality.

N. chalybaeus, Ironcolor shiner
176 specimens, stations 18, 22, 27, 32, 38, 39, 45. C, P, NCWRC.

N. cummingsae, Dusky shiner
47 specimens, stations 16, 18, 19, 32. NCWRC.

N. hudsonius, Spottail shiner
3 specimens, station 23. NCWRC. Found only in Trent River and tributaries.

N. procne, Swallowtail shiner
NCWRC. Taken only in Trent River and tributaries. Representative specimens are in NCSM collection.

Erimyzon oblongus oblongus, Creek chubsucker
70 specimens, stations 3, 6, 7, 19, 21, 23, 29, 38, 45, 46. J, NCWRC.

E. sucetta, Lake chubsucker
138 specimens, stations 8, 10, 33. H, NCWRC. We encountered some difficulty in identifying certain Croatan specimens. Hanley (1976) stated that *E. oblongus oblongus* and *E. sucetta* hybridize in the drainage ditches of the forest probably as a result of habitat alteration.

Moxostoma spp., Redhorses
NCWRC tentatively recorded *M. collapsum (=anisurum)* from a Trent River tributary and *M. papillosum* from the White Oak River. R. E. Jenkins (pers. comm.) believes that either *M. anisurum* or *M. macrolepidotum* may be present in Forest waters, as both have been collected from the lower Neuse in the vicinity of New Bern. We did not collect either species.

Ictalurus catus, White catfish
K, NCWRC.

I. natalis, Yellow bullhead
92 specimens, stations 7, 8, 10, 30, 32, 33, 36, 38, 45-47. B, H, P, NCWRC.

I. nebulosus, Brown bullhead
J, NCWRC.

I. punctatus, Channel catfish
H, NCWRC. Possibly introduced to Neuse drainage (Jenkins et al. 1972).

Noturus gyrinus, Tadpole madtom
15 specimens, stations 29, 38, 45, 49, 50. NCWRC.

N. insignis, Margined madtom
23 specimens, stations 21, 40, 45. NCWRC.

Chologaster cornuta, Swampfish
803 specimens, stations 8, 10, 24, 33-35, 37, 45-47. N, NCWRC. Most

specimens were collected at station 33 as part of an investigation into the life history of this species.

Aphredoderus sayanus sayanus, Pirateperch
476 specimens, stations 3-8, 20-25, 27, 29, 32, 33, 35-39, 41, 42, 44-47, 49, 50. P, NCWRC.

Fundulus diaphanus diaphanus, Banded killifish
6 specimens, station 23. Taken only in a tributary of the Trent River.

F. lineolatus, Lined topminnow
237 specimens, stations 8, 10. H, NCWRC. Found only in drainage ditches along Catfish Lake Road (SR 1100), where it is abundant. Wiley (1977) recently revised the *Fundulus notti* species group. He considered *F. lineolatus* a full species and resurrected the name *F. escambiae* for the Florida panhandle populations. However, Ralph Yerger (pers. comm.) has found what he believes to be intergradation of the two forms in the median portions of several panhandle systems. Additional study of this complex problem is certainly required.

Gambusia affinis holbrooki, Mosquitofish
1129 specimens, stations 1, 5, 6, 8, 10, 11, 17, 18, 21, 23, 25-27, 30, 38, 44, 45, 47, 49, 50. A, B, C, E, H, NCWRC.

Acantharchus pomotis, Mud sunfish
41 specimens, stations 4, 8, 33, 34, 45-47, 50. NCWRC.

Centrarchus macropterus, Flier
136 specimens, stations 4, 7-9, 15, 18, 32, 35, 36, 45, 47. M, Q, NCWRC.

Elassoma zonatum, Banded pygmy sunfish
NCWRC. One specimen collected at a site on the Trent River.

Enneacanthus chaetodon, Blackbanded sunfish
Sweeney (1972) reported the Blackbanded sunfish from a locality near the forest, but indicated that the record is probably erroneous because numerous efforts by collectors in this region have failed to collect the species. Seehorn (1976) and Jenkins et al. (1975) perpetuated this possible error. The closest known records, according to Menhinick (ms), are in Duplin, Lenoir, and Pender counties.

E. gloriosus, Bluespotted sunfish
735 specimens, stations 1, 3-10, 15, 17, 21, 23-25, 27-31, 33, 35-39, 41, 44-47, 50. H, M, P, NCWRC.

E. obesus, Banded sunfish
126 specimens, stations 8, 10, 31, 33, 35, 36, 45, 46. A, C, D, P, NCWRC.

Lepomis auritus, Redbreast sunfish
22 specimens, stations 18, 21, 38, 44, 45, 49, 50. P, NCWRC.

L. gibbosus, Pumpkinseed
70 specimens, stations 5-8, 17, 18, 20, 21, 23, 25, 29, 38, 41, 45, 48. J, P, NCWRC.

L. gulosus, Warmouth
89 specimens, stations 3, 7, 8, 10, 30, 37, 38, 44, 45. B, C, D, Q, NCWRC.

L. macrochirus, Bluegill
172 specimens, stations 8, 18, 21, 25, 26, 38, 43-45, 50. B, C, D, Q, NCWRC. Possibly introduced to the Neuse system (Jenkins et al. 1972).

L. marginatus, Dollar sunfish
Although reported by Seehorn (1976) as occurring in the forest, there are no records to substantiate this. Closest verified localities are in northern Craven County.

L. microlophus, Redear sunfish
NCWRC. Stocked by the NCWRC in the White Oak River.

Micropterus salmoides salmoides, Largemouth bass
24 specimens, stations 1, 23, 25, 32, 37, 38, 44, 45, 50. I, J, O, P, NCWRC.

Pomoxis nigromaculatus, Black crappie
8 specimens, stations 8, 44. NCWRC. Possibly introduced into Newport drainage (see Discussion).

Etheostoma fusiforme fusiforme, Swamp darter
38 specimens, stations 3, 6, 7, 21, 38, 44. B, NCWRC.

E. olmstedi olmstedi, Tessellated darter
176 specimens, stations 3, 16, 18, 21, 22, 38, 39, 45, 48. P, NCWRC.

E. serriferum, Sawcheek darter
152 specimens, stations 6-8, 22, 33, 38, 39, 44-47, 50. P, NCWRC.

Perca flavescens, Yellow perch
4 specimens, stations 8, 36. A, NCWRC. Possibly introduced to Neuse system (Jenkins et al. 1972).

Percina crassa roanoka, Piedmont darter

4 specimens, station 21. This species, rarely encountered on the lower Coastal Plain, was collected over gravel in swifter portions of the creek. Station 21 represents the easternmost known locality in North Carolina.

ESTUARINE FISHES

Twenty estuarine fishes were taken within the forest (Table 3). Most were sporadic visitors during periods of increased salinity. One item of note is the capture of a Fourspine stickleback, *Apeltes quadracus*, at station 23 on 14 June 1977, the first published record of a stickleback in North Carolina.

Table 3. Species, numbers (N) and station numbers of estuarine fishes collected in (and near) Croatan National Forest, North Carolina, in this study.

Species	N	Station
Alosa aestivalis	21	23
Brevoortia tyrannus	2	14
Anchoa mitchilli	3	17
Fundulus heteroclitus	1	14
Lucania parva	17	17
Membras martinica	31	13, 14
Menidia beryllina	48	13, 14, 17, 23
Menidia menidia	103	13, 14
Apeltes quadracus	1	23
Syngnathus fuscus	1	1
Morone americana	3	14
Eucinostomus argenteus	12	17, 26
Lagodon rhomboides	31	1, 13, 14, 17, 26
Bairdiella chrysura	13	17
Leiostomus xanthurus	72	13, 14, 17
Mugil cephalus	5	14, 17
Mugil curema	4	14
Dormitator maculatus	2	23, 26
Gobiosoma bosci	5	17
Trinectes maculatus	11	25, 27, 38, 41, 44, 45, 48

DISCUSSION

Fifty-one species of freshwater fishes representing 16 families have been identified as occurring in or near the Croatan National Forest (Table 2, plus *Petromyzon marinus*). Four additional species *(Notropis altipinnis, Enneacanthus chaetodon, Lepomis marginatus, L. punctatus)* possibly occur there. Sunfishes (Centrarchidae), well suited to the slow-moving, vegetated waters of the Croatan National Forest, are the most speciose family with 12 species. Minnows (Cyprinidae) are also well represented with ten species, but none is common.

Although major sections of the White Oak and Newport rivers are contained in the forest, their faunas do not contribute as much to the overall diversity as does the fauna of the Neuse River, which drains only a very small part of the overall area. Forty-six species were collected in the Neuse drainage, including 12 not taken in the Newport or White Oak rivers. The Trent River, a tributary of the Neuse, forms the northern boundary of the forest and accounts for much of the diversity. Eight of the 12 species confined to the Neuse drainage were taken only in the Trent or its tributaries. The Newport and White Oak rivers had 33 and 34 species respectively, of which only 3 were unique to one or the other system.

Our examination of fishes in the three Croatan National Forest drainages prompted a review of the distributions of lowland (lower Coastal Plain) fishes throughout North Carolina. Most distributional data were obtained from regional faunal summaries (Jenkins et al. 1972; Jenkins et al. 1975; Menhinick, ms) and systematic revisions (e.g. Collette 1962; Snelson 1968; Yerger and Relyea 1968; Sweeney 1972), but some unpublished records are based on collections of ours. Nine major rivers drain into coastal North Carolina estuaries, including one (the Cape Fear) that is composed of two systems on the Coastal Plain (Fig 2). Some (e.g. the Shallotte, New, White Oak, and Newport rivers) are small drainages confined to the lower reaches of the Coastal Plain, whereas others (e.g. the Cape Fear, Neuse, Tar, and Roanoke rivers) are more extensive and originate in the Piedmont or the Appalachian Mountains. The following discussion concerns fishes of those rivers lying totally or in part below the Fall Line in North Carolina.

Nineteen species reach the northern termini of their distribution ranges on the Coastal Plain of North Carolina or in nearby southeastern Virginia (Table 4, plus *Micropterus salmoides salmoides* and *Etheostoma serriferum*). The greatest faunal break occurs between the Cape Fear and the more northern drainages, with eight terminations in the combined Cape Fear-Northeast Cape Fear systems (see Jenkins et al. 1972 for additional discussion of this break). Five species terminate in the Chowan River in North Carolina and Virginia (Jenkins et al. 1975). Only four fishes

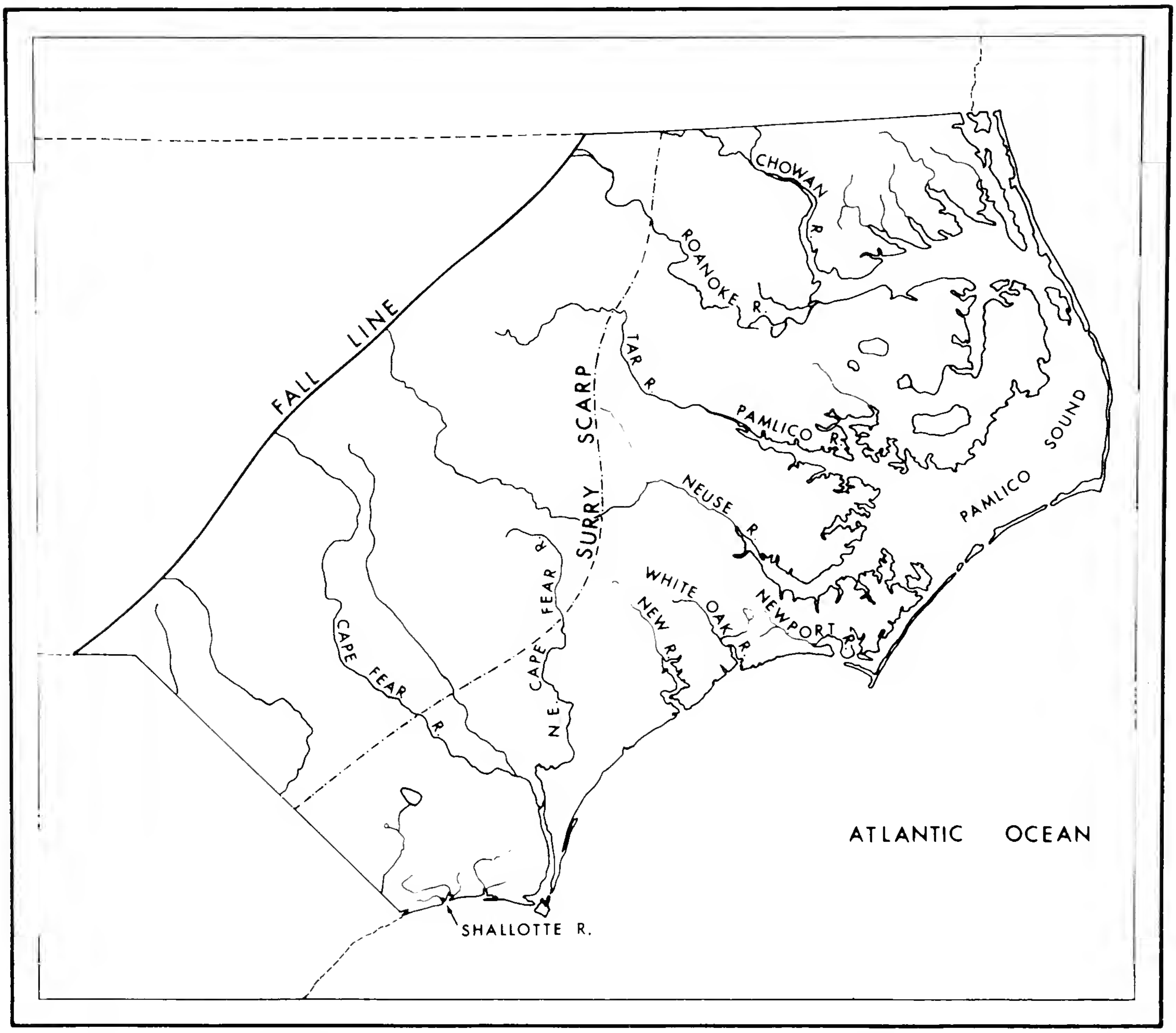

Fig. 2. Coastal drainages of eastern North Carolina lying below the Fall Line. Surry Scarp drawn from White (1966).

(Lampetra aepyptera, Notropis bifrenatus, Etheostoma vitreum, Percina peltata nevisense) have southern termini in the Coastal Plain drainages. *Noturus furiosus* is confined to the Neuse and Tar drainages (Taylor 1969), but may have been present in the Roanoke prior to habitat destruction by dams and pollution (C. R. Gilbert, pers. comm.). *Menidia extensa* and *Etheostoma perlongum* are endemic to Lake Waccamaw, and *Fundulus waccamensis* is confined to lakes Waccamaw and Phelps (see zoogeographic discussions in Hubbs and Raney 1946; Jenkins et al. 1972; and Bailey et al. 1977). Phelps Lake *F. waccamensis* have not been critically examined, and introduction from Lake Waccamaw is considered a possibility.

Twenty-four native species are uniformly distributed throughout coastal North Carolina drainages: *Lepisosteus osseus, Dorosoma cepedianum, Anguilla rostrata, Umbra pygmaea, Esox americanus americanus, E. niger, Notemigonus crysoleucas, Notropis chalybaeus, Erimyzon oblongus oblongus, Ictalurus natalis, Noturus gyrinus, N. insignis, Aphredoderus sayanus sayanus, Gambusia affinis holbrooki, Acantharchus pomotis, Centrarchus macropterus, En-*

neacanthus gloriosus, Lepomis auritus, L. gibbosus, L. gulosus, L. macrochirus, Micropterus salmoides salmoides, Etheostoma olmstedi olmstedi, and *E. serriferum*. Of these, only *M. s. salmoides* and *E. serriferum* terminate in the Chowan (Jenkins et al. 1975); all others extend farther northward. No southern terminations are involved.

Using available distributional information, 41 species are known to be absent from one or more Coastal Plain drainages in North Carolina. Based on habitat preferences and distributional patterns of the species involved, we believe that 13 of these will eventually appear in collections from those drainages where they are now unknown (Table 4). Three others *(Elassoma evergladei, Notropis petersoni, N. cummingsae)* have northern termini in North Carolina and are not expected in more northerly drainages. The remaining 25 species have what appears to be real distributional gaps. These may be further separated into two groups: a lowland contingent composed of 5 species of sunfishes, and a larger group of 20 species with predominantly upland affinities (Table 4). All are missing from the New, White Oak, and Newport rivers, and all but *Lepomis marginatus* and *L. punctatus* are also absent from the Shallotte or Northeast Cape Fear, or both.

The absence of the 5 lowland species of sunfishes *(Lepomis marginatus, L. punctatus, Elassoma zonatum, Enneacanthus chaetodon, Pomoxis nigromaculatus)* from the New, White Oak, and Newport rivers is enigmatic. Since the first three species reach terminations in nearby northern drainages (Table 4), it is possible that their absence in these intermediate rivers merely reflects the irregular distribution pattern often observed at the periphery of a species' range. *Enneacanthus chaetodon* is often absent from habitats for which it is seemingly well-suited and its distribution is spotty throughout most of its range (Jenkins et al. 1975; Burgess et al. 1977). *Enneacanthus chaetodon* is likely to be discovered in one or more of these drainages with further collecting. We have two records of *Pomoxis nigromaculatus* from the Newport drainage, but since both are from a single pond (Mill Pond) owned by a fishing club, we suspect introduction. Although *P. nigromaculatus* is a common lowland form in much of North Carolina (Table 4), its apparent absence in these three coastal drainages may prove real.

The remaining 20 species' distributions are perhaps more easily explained. Most species involved are forms that prefer swifter flowing, upland streams, habitats which are scarce or absent in the New, White Oak, and Newport drainages. The 30 meter high stand in sea level (represented today by the Wicomico Shoreline or Surry Scarp, Fig. 2) that occurred in the Pleistocene may have influenced the distribution of these fishes. The area occupied by the present-day Shallotte, New, White Oak,

Table 4. Distributions of selected elements of the North Carolina Coastal Plain ichthyofauna. See text for explanation of categories. X = documented record, (X) = questionable record, *X* = terminus of range, E = expected.

CONTINUOUS DISTRIBUTIONS	Shallotte	Cape Fear	Northeast Cape Fear	New	White Oak	Newport	Neuse	Tar-Pamlico	Roanoke	Chowan-Albemarle	Comments
Heterandria formosa	E	*X*									
Notropis maculatus	E	X	*X*								
Elassoma evergladei	X	X	*X*								
Notropis petersoni	X	X	X	*X*							
Notropis cummingsae	X	X	X	X	X	X	X	*X*			
Fundulus lineolatus	X	X	X	E	E	X	X	X	X	*X*	
Chologaster cornuta	X	X	X	E	X	X	X	X	X	*X*	
Ictalurus catus	X	X	X	E	X	X	X	X	X	X	
Etheostoma f. fusiforme	X	X	X	E	X	X	X	X	X	X	
Ictalurus nebulosus	E	X	X	X	X	X	X	X	X	X	
Enneacanthus obesus	E	X	X	X	X	X	X	X	X	X	
Erimyzon sucetta	E	X	E	E	X	X	X	E	E	X	
Amia calva	E	X	X	X	E	E	X	X	X	X	
Perca flavescens	X	X	X	X	E	X	X	X	X	X	All possibly introduced
Notropis amoenus		*X*	X	X	E	E	X	X	E	X	
Notropis bifrenatus							*X*	E	E	X[1]	[1] Fall line only

DISJUNCT DISTRIBUTIONS										
LOWLAND FORMS										
Lepomis punctatus	X	X	X			*X*				
Lepomis marginatus	X	X	X			X	*X*			
Elassoma zonatum		X	X			X	X	*X*		
Enneacanthus chaetodon		X	X			X	X	X	X	
Pomoxis nigromaculatus	X	X	X		X[1]	X	X	X	X	[1] Prob. introduced
UNFAVORABLE HABITAT										
Hybopsis n.sp.		*X*								
Notropis scepticus		*X*								
Ictalurus brunneus		*X*								
Noturus n.sp.		*X*								
Minetryma melanops		X	*X*							
Ictalurus platycephalus		X				X		*X*		
Notropis hudsonius	X	X				X	X	X	X	
Percina crassa		X[1]	X[1]			X[2]	X[2]	E[2]	X[2]	[1] *P.c. crassa*, [2] *P.c. roanoka*
Hybognathus regius		X				X	X	X	X	
Notropis altipinnis		X				X	X	X	X	
Notropis analostanus		X				X	X	X	X	
Notropis procne longiceps		X				X	X	X	X	
Moxostoma anisurum		X				X	X	X	*X*	
Moxostoma macrolepidotum		X				X	X	X	X	
Moxostoma pappillosum		X		(X)[1]		X	X	X	X	[1] NCWRC - no specimen
Ictalurus punctatus		X				X	X	X	X	All probably introduced
Fundulus d. diaphanus		X				X	X	X	X	
Etheostoma vitreum						*X*	X	X	X	
Percina peltata nevisense						*X*	X	X[1]	X	[1] Above Fall Line only
Lampetra aepyptera						*X*	X			

and Newport rivers and most of the Northeast Cape Fear River was inundated by encroaching seas; colonization by stream fishes began as the sea regressed and rivers developed. Most species with preferences for slow-moving, lowland waters were probably able to enter these newly developing systems, but others with upland affinities undoubtedly found the ecological conditions unsuitable and never became established.

The distribution of *Fundulus diaphanus diaphanus*, a secondary freshwater species (Myers 1938, 1951) that tolerates brackish waters, is not explainable by lack of upland habitat. However, *F. d. diaphanus* prefers gravel or sand bottoms and avoids areas of heavy siltation (Shapiro 1947), and most lowland North Carolina rivers are heavily silted. In addition, the species is at the southern periphery of its range in North Carolina, and records are few south of the Neuse River. *Ictalurus punctatus* is similarly distributed, but the extensive introductions of this species throughout its range prevents assigning any significance to the pattern.

The diversity of fishes in the Croatan National Forest is quite high compared to studies made on other Coastal Plain regions. Jenkins et al. (1975) found 25 species in the Dismal Swamp and 43 species in the Chowan system on the Coastal Plain. Both areas are considerably larger than Croatan National Forest.

At present there is little evidence of degradation of the Forest waters, and with proper management practices these waters should continue to support a diverse ichthyofauna.

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Genetic Variation in Cave-dwelling and Deep-sea Organisms, with Emphasis on *Crangonyx antennatus* (Crustacea: Amphipoda) in Virginia.

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ABSTRACT.—Genetic variation was analyzed through electrophoretic techniques in six populations of the troglobitic (i.e. obligatory cave-dwelling) amphipod *Crangonyx antennatus* from Lee County, Virginia. From the results of this investigation and those tabulated from previous studies on a number of cave-dwelling species, genetic variability does not appear to be substantially reduced in populations inhabiting subterranean environments. The origin of normal levels of genetic variability in cave-dwelling species may differ from those organisms inhabiting another relatively stable environment, the deep-sea. The high levels of genetic variability recorded in many deep-sea invertebrates are thought to be due in part to the presence of large populations of these species. In contrast, the small population sizes observed in cave-dwelling organisms may allow species to expand their niches with an associated increase in genetic variability.

INTRODUCTION

Similarities in the physical environments of caves and the deep-sea have led to the suggestion that similar selection pressures may be operating on their respective faunas (Poulson 1971). Caves and the deep-sea share several important characteristics including absence of light, reduced food supply, and relative stability of chemical and physical properties. Similar biological adaptations have been observed in organisms inhabiting abyssal (Menzies et al. 1973) and subterranean

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(Poulson 1964) areas. The deep-sea and cave environments probably lie at the extreme end of a continuum of environmental stabilities.

Several theories relating the level of genetic variability maintained in a natural population to the degree of environmental heterogeneity have been proposed (Levins 1968; Grassle 1972; Selander and Kaufman 1973; Valentine 1976). The basis for these hypotheses is that increased genetic variation would allow individuals to be better suited to spatial and temporal heterogeneity of the environment. A population in a heterogeneous physical environment or a population which perceives its environment as coarse-grained, would be expected to maintain greater genetic variability than a population living under a more homogeneous regime (Nevo 1976). These hypotheses have received some support in experimental laboratory populations of *Drosophila* maintained under constant versus variable conditions (Powell 1971; McDonald and Ayala 1974). Genetic studies of deep-sea and cave faunas should permit tests with natural populations of the proposed correlation between genetic variability and environmental heterogeneity.

Electrophoretic techniques may be employed to survey products of structural genes chosen without prior bias with respect to level of variability. Such studies have been conducted on various deep-sea invertebrates including mollusks, echinoderms and crustaceans. A recent review of these studies compiled by Siebenaller (1978) indicated that abyssal fauna contain levels of genetic variability similar to those of species living in other aquatic habitats.

In one of the first genetic studies of a cave organism, Avise and Selander (1972) observed exceptionally low genetic variability in certain cave populations of the fish *Astyanax mexicanus*. Results identified an additional complicating factor influencing genetic variability but unrelated to selection pressures *per se*: drift and founder effect in the frequently small cavernicole populations. Since that time several other studies of genetic variation in cave species have been published. Because of the possibility of drift lowering genetic variation in many cave populations, tests of the proposed relationship between environmental and genetic heterogeneity using cave organisms are likely to be one-sided. That is, the observation of normal or high levels of genetic variability would tend to refute the proposed correlation, while the observation of low variability could often be attributed to either selection pressures or stochastic events.

Our investigation was conducted (1) to examine genetic variability in another cave organism, the troglobitic (i.e. obligate cave-dwelling) amphipod crustacean *Crangonyx antennatus* Packard, and (2) to summarize the available literature concerning genetic variation in other cave species.

METHODS AND MATERIALS

In this study, populations of the troglobitic amphipod crustacean, *C. antennatus*, were examined electrophoretically. This species is one of the most common and widespread aquatic troglobites in the eastern United States. It occurs in the Appalachian region of Virginia, Tennessee, Georgia and Alabama (Holsinger 1969, 1972). *Crangonyx antennatus* occupies two distinctly different habitats within its range: gravel-bottom streams and mud-bottom pools. Significant differences in morphology (Dickson 1977a), behavior (Dickson 1977b) and population structure (Dickson and Holsinger, in press) were observed between populations living in these habitats.

Populations of *C. antennatus* were sampled from six caves in Lee County, Virginia (Fig. 1). Although the populations are relatively large in caves of this area, small collections were taken from each cave to minimize population disruption (Table 1). Three of the populations sampled inhabited gravel-bottom streams (Spangler, Cope and Gallohan No. 2 caves) and three inhabited mud-bottom pools (Roadside No. 1, Molly Wagle and Sweet Potato caves). Mud-bottom pool habitats generally contained greater quantities of available food, fewer predators and smaller numbers of potential competitors than stream habitats. Additional ecological data on these habitats were given elsewhere (Dickson and Kirk 1976; Dickson 1977a); geological data are found in Holsinger (1975).

After collection, amphipods were transported live to the laboratory and stored at −70°C until analyzed. Amphipods were electrophoresed on horizontal starch gels using conditions and staining procedures similar to those of Selander et al. (1971) and Ayala et al. (1972). Of 21 enzyme systems screened on six gel types, eight allowed consistent scoring, with two of those exhibiting polymorphic allozyme patterns interpreted as segregating electromorphs. As previously noted by Gooch and Hetrick (in press), amphipods are not well suited for electrophoretic study, probably because of the release of inhibitory enzymes from the hepatopancreas during homogenization.

The monomorphic systems included glucose-6-phosphate dehydrogenase (G-6-P), indophenol oxidase (IPO), aldehyde oxidase (AO), malate dehydrogenase (MDH), and general proteins I-II (GP-1, GP-2). The polymorphic systems scored were phosphoglucose isomerase (PGI) and phosphoglucomutase (PGM). The PGI locus exhibited three-banded heterozygote patterns, suggesting that this enzyme is a dimer. Two-banded heterozygote phenotypes were observed at the PGM locus, as expected for a monomeric enzyme. These enzyme structures are consistent with those recorded in other crustaceans, including lobsters (Tracey et al. 1975) and crayfish (K. Stueck, in prep.). To determine

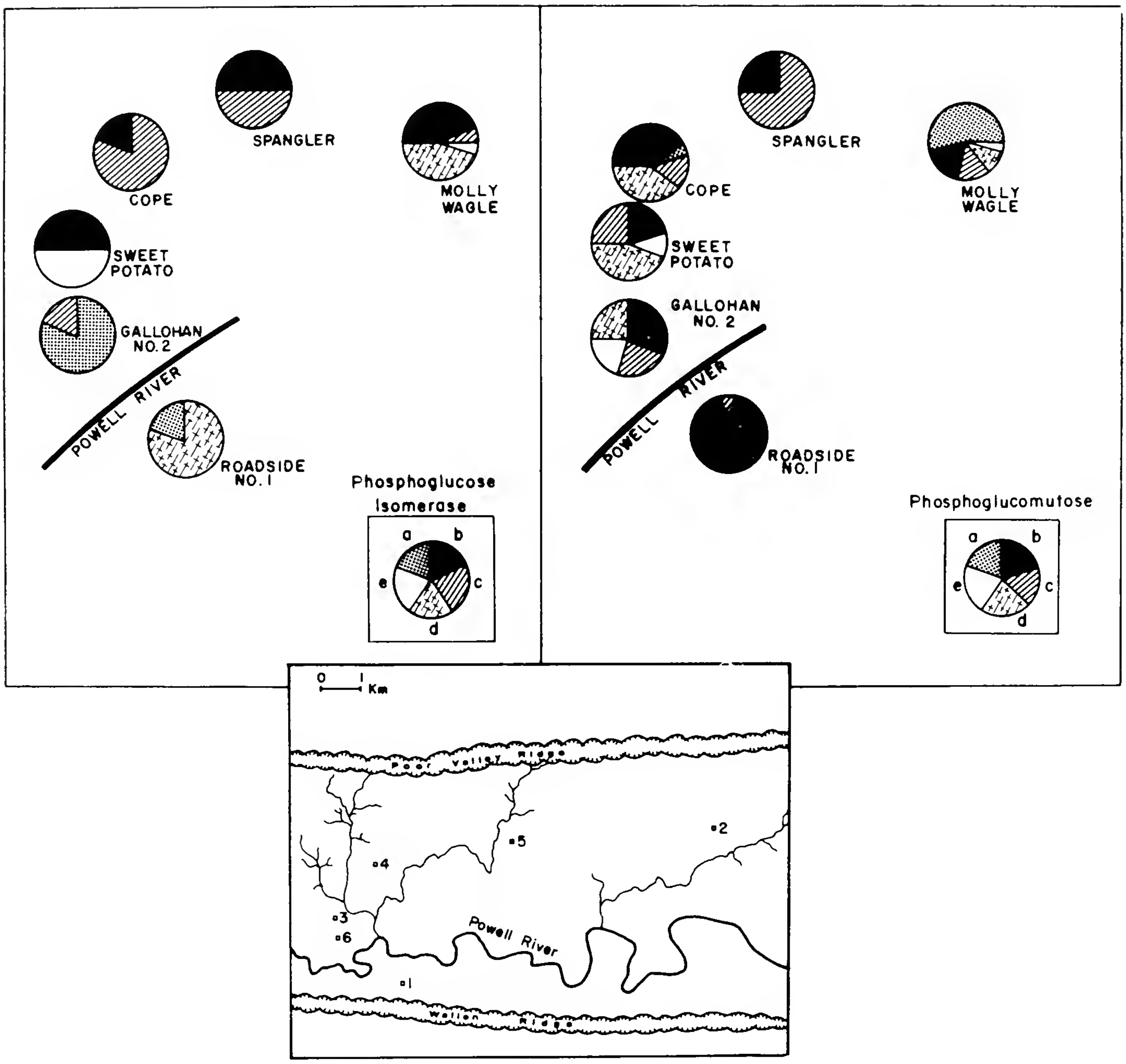

Fig. 1. Allele frequency distributions for phosphoglucose isomerase and phosphoglucomutase in the study area. Insert shows location of the six caves sampled for *Crangonyx antennatus* in relation to the major surface drainage in the Powell Valley, Lee County, Virginia. 1. Roadside No. 1 Cave (RD), 2. Molly Wagle Cave (MW), 3. Sweet Potato Cave (SP), 4. Cope Cave (C), 5. Spangler Cave (S), and 6. Gallohan No. 2 Cave (G).

whether electromorphs produced at the same locus in different populations were identical or different, amphipods from all six populations were run on the same gels.

RESULTS

All population samples were monomorphic for the same electromorph at six loci (G-6-P, IPO, AO, MDH, GP-1 and GP-2). Electromorph frequencies for the two polymorphic loci are given in Table 1. A total of five allelic products were distinguished for both PGI and PGM, although in only one case (PGM, Molly Wagle Cave) were all five electromorphs observed in a single cave. For eight loci in *C. antennatus*, polymorphism (proportion of loci polymorphic) equals 0.25. The mean proportion of loci

Table 1. Allele frequencies at polymorphic loci in *Crangonyx antennatus* populations. (N) = number of individuals examined. Abbreviations as in Fig. 1.

Locus	allele	RD	MW	SP	S	C	G
PGM	a	—	0.536	—	—	0.043	—
	b	0.923	0.155	0.203	0.250	0.391	0.281
	c	0.077	0.155	0.250	0.750	0.196	0.188
	d	—	0.107	0.391	—	0.369	0.250
	e	—	0.036	0.141	—	—	0.156
	(N)	(26)	(42)	(32)	(36)	(23)	(16)
PGI	a	0.200	—	—	—	—	0.800
	b	—	0.400	0.500	0.500	0.200	—
	c	—	0.100	—	0.500	0.800	0.200
	d	0.800	0.400	0.500	—	—	—
	e	—	0.100	—	—	—	—
	(N)	(5)	(5)	(5)	(5)	(5)	(5)

heterozygous per individual (heterozygosity) can be estimated in two ways: by direct count, and by expected heterozygote proportions in each population assuming Hardy-Weinberg equilibrium. Heterozygosity values per cave range from 0.021 (counted) and 0.058 (expected) to 0.276 (counted) and 0.124 (expected) (Table 2), and overall mean heterozygosities ($\bar{H}$), weighted by sample size, in *C. antennatus* equal 0.118 and 0.136, respectively. The greater spread in values for the counted heterozygosities primarily results from assay in some populations of only small numbers of specimens at the apparently monomorphic loci. At the PGM locus there was a consistent tendency for pool populations to exhibit significant heterozygote deficiencies relative to Hardy-Weinberg

Table 2. Heterozygosity ($\bar{H}$) values in populations of *Crangonyx antennatus*. Abbreviations as in Fig. 1.

Population	Frequency of heterozygous loci in an average individual	
	Counted	Expected ±1 Standard Error
RD	0.021	0.058 ± 0.042
MW	0.130	0.161 ± 0.106
SP	0.102	0.149 ± 0.099
S	0.183	0.109 ± 0.073
C	0.276	0.124 ± 0.087
G	0.216	0.107 ± 0.073

Table 3. Levels of electrophoretically detectable genetic variability in organisms inhabiting caves[1]. Troglobite — obligatory cavernicole; troglophile — facultative cavernicole. N = number of individuals examined. N.P. = data not presented.

Organism	N	No. of Loci	($\bar{H}$) Heterozygosity	% Loci Polymorphic	Source
Astyanax mexicanus (Pisces) — Troglophile[2]	91	17	0.016	0-11.7	Avise and Selander 1972
Eurycea lucifuga (Caudata) — Troglophile	331	12	0.022	1.2-13.9	Merkle and Guttman 1977
Rhadine subterranea (Coleoptera) — Troglobite	158	N.P.	N.P.	Considerable Variability	Avise and Selander 1972
Ptomaphagus spp. (Coleoptera) — Troglobite	132	5	N.P.	50.0	Carmody et al. 1972
Ptomaphagus hirtus (Coleoptera) — Troglobite	900-Approx.	13	0.048	15.4	Laing et al. 1976a
Neaphaenops tellkampfii (Coleoptera) — troglobite	103-Approx.	12	0.121	25.0-42.0	Giuseffi et al. 1978
Scoterpes copei (Diplopoda) — Troglobite	44	10	0.068	10.0-20.0	Laing et al. 1976b
Ceuthophilus gracilipes (Orthoptera) — Troglophile	330-Approx.	26	0.027	8.0	Cockley et al. 1977
Dolichopoda geniculata (Orthoptera) — Troglophile	1468	1	N.P.	Considerable Variability	Sbordoni et al. 1976
Meta menardi (Arachnida) — Troglophile	N.P.	15	0.027	9.6	Johnston and Carmody, in press.
Asellus brevicauda (Isopoda) — Troglophile	N.P.	11	N.P.	81.8	Steiner et al. 1977
Niphargus spp. (Amphipoda) — Troglobite	N.P.	Utilized Hemolymph Proteins		Considerable Variability	Gibert 1971
Gammarus minus (Amphipoda) — Troglophile[2]	500-Approx.	13	0.119	0-23.0	Hetrick 1975; Gooch and Hetrick, in press.
Crangonyx antennatus (Amphipoda) — Troglobite	150	8	0.118	25.0	Present Study

[1] Tabular values were either reproduced directly or computed from data presented in the listed citations.

[2] Populations reported possessed characteristics associated with obligatory cave existence; the species as a whole could be considered troglophilic.

expectations. Heterozygosity values displayed no correlation with distance from the Powell River.

Sample sizes and numbers of loci scored were small for reasons noted earlier, so the results must be interpreted with extreme caution. Estimates of genetic variability fall near the middle of the range of values previously reported in crustaceans from other aquatic habitats ($\bar{H}$ ranges from 0.038 in the lobster, *Homarus americanus*, to 0.211 in the krill, *Euphausia distinguenda*; see reviews in Nevo 1978 and Powell 1975). Heterozygosity values in *C. antennatus* are considerably above mean values reported for eight other cave species ($\bar{H} = 0.056$, Table 3).

A striking aspect of the data is the high degree of allele frequency heterogeneity among *C. antennatus* populations, particularly at the PGM locus where sample sizes were fairly large (Table 1, Figure 1). Heterogeneity among localities can be expressed by the standardized genetic variance ($\bar{F}_{ST}$), which provides a common scale for comparing the relative levels of interlocality allele frequency heterogeneity at different loci, or in different sets of populations (Wright 1978). For five electromorphs at the PGM locus, weighted $\bar{F}_{ST} = 0.300$ among populations of *C. antennatus* inhabiting the approximately 60 km^2 area of the study. This variance in allele frequency is greater than mean values among snail, *Helix aspersa*, populations in different California cities or house mice, *Mus musculus*, populations on different farms in Texas (Selander and Kaufman 1975). It is comparable to observed values between bluegill sunfish, *Lepomis macrochirus*, populations inhabiting distinct reservoirs within large southeastern drainages (Avise and Felley, in press). The microgeographic heterogeneity in *C. antennatus* is consistent with the contention that caves may be highly partitioned habitats, analogous to islands or archipelagos (Culver 1971).

Genetic similarity values were calculated between pairs of cave populations using Nei's (1972) identity statistic ($\bar{I}$). This statistic can assume values from 0 (no electromorphs shared) to 1 (identical electromorph frequencies). For the populations of *C. antennatus* studied, $\bar{I}$ values fell between 0.858 and 0.968, within the range typical of conspecific populations in other invertebrates. The identity matrix was employed to generate a biochemical dendrogram (Fig. 2) according to the unweighted pair-group method with arithmetic means (Sneath and Sokal 1973). There is no clear tendency for stream and pool populations to cluster distinct from one another. Based on the relatively distinct pattern of allele frequencies in the population from Roadside No. 1 Cave (Figs. 1, 2; Table 1), it appears that the Powell River has acted as a partial barrier to gene flow.

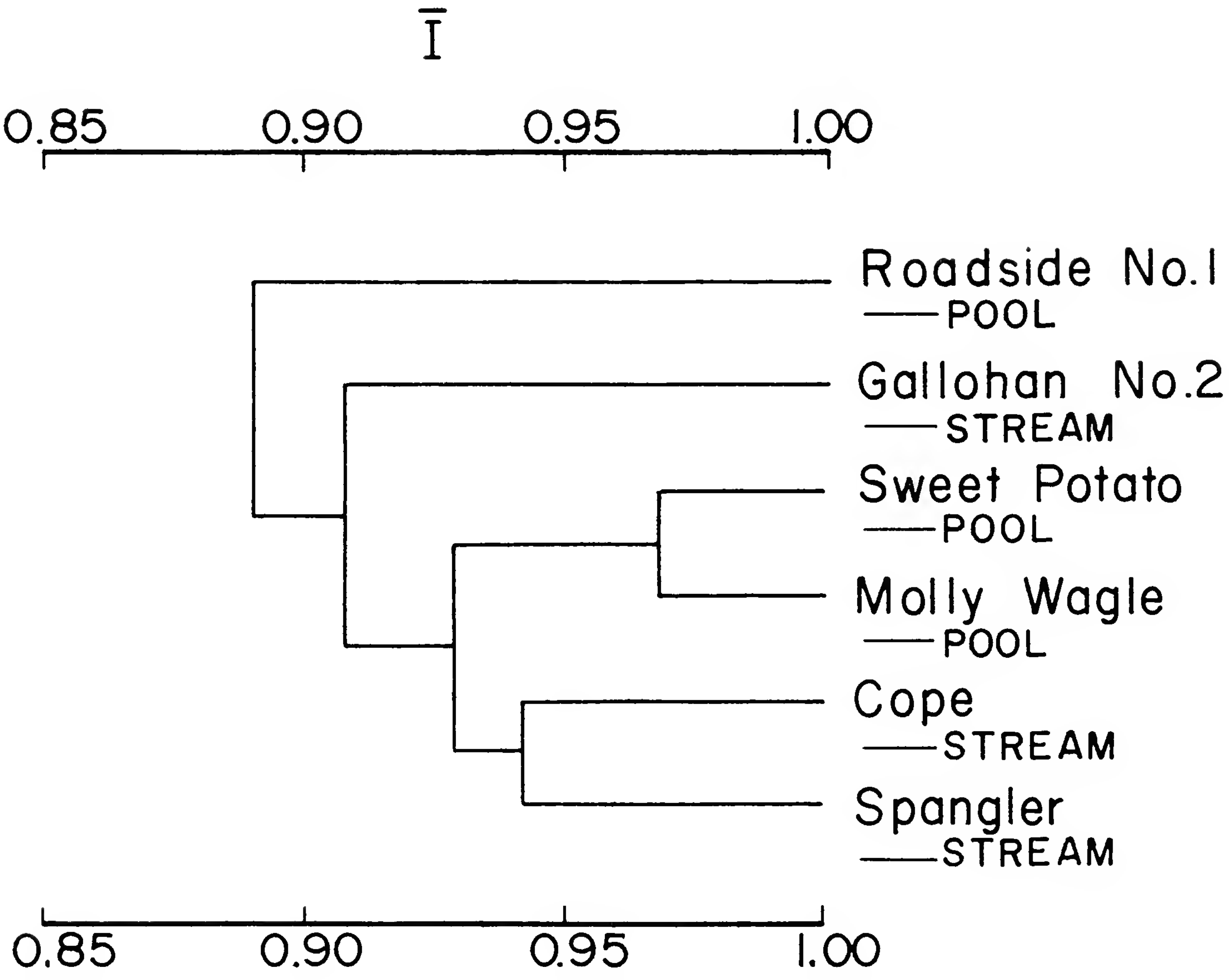

Fig. 2. Dendrogram of *C. antennatus* populations based on genetic similarity values derived from eight loci. Scale is in units of genetic identity, Ī. Cophenetic correlation equals 0.79

DISCUSSION

In addition to measurements of physical and chemical parameters, studies of troglobitic organisms have yielded biological evidence which attests to the relative environmental stability of cave systems. In general, troglobitic species exhibit K-selected population characteristics including late maturity, low reproductive rates, large size at hatching and increased longevity (see reviews in Vandel 1965; Dickson and Holsinger, in press). Population characteristics of this type have been associated with relatively stable (i.e. predictable) habitats (MacArthur and Wilson 1967). Of these characteristics, perhaps the most remarkable is the extremely long life span reported for various troglobites (Poulson 1964; Cooper 1975; Dickson and Holsinger, in press). Increased longevity has also been described in deep-sea organisms (Turekian et al. 1975; Engemann 1978).

From the results of the present investigation and previous studies on a number of different cave species (Table 3), genetic variability does not appear to be substantially reduced in populations inhabiting subterranean habitats. Values of genic heterozygosity in many cavernicolous populations are comparable to those of species from epigean environments (Nevo 1978). However, a cautionary note is required. Studies on troglobitic organisms are still few in number, and generally have included only a small number of loci. Results are not yet sufficient to eliminate the possibility of a mild quantitative decrease in genic variation in cavernicolous populations. It does appear very likely that the genetic response of troglobitic organisms to their environment (at least as evidenced by level of genetic variability) is not qualitatively different from that of other species. Analogous conclusions have been reached from studies of organisms inhabiting abyssal areas (Siebenaller 1978; Costa and Bisol 1978).

The genetic variability observed in populations inhabiting stable environments (i.e. caves and deep-sea) may have different origins. Siebenaller (1978) proposed that the relatively high variability observed in many deep-sea invertebrates could be due to the presence of large population sizes and to interactions predicted by the time, population size and divergence hypothesis of Soulé (1976). In cave organisms, species and population numbers are normally smaller than in most faunal counterparts living in other habitats, including abyssal areas (Poulson 1964). The normal levels of genetic variability in these subterranean species could be due to a process described as ecological release (Avise and Selander 1972). In the generally depauperate cave communities, troglobites could expand their niches and exploit resources which would normally be shared by two or more species. Relatively high levels of genetic variability might be maintained under these conditions.

If genetic variation is not neutral with respect to fitness, normal levels of genetic variability in deep-sea and cave organisms could also be maintained by selection due to spatial or temporal heterogeneity. Although caves and the deep-sea are considered more stable than most other aquatic and terrestrial areas, physical habitat variability and seasonal fluctuations in certain parameters are present (Poulson and White 1969; Menzies et al. 1973). It is possible that the threshold of environmental heterogeneity below which significant genetic variability is no longer favored is still lower than the level of environmental variation in the proverbially stable environments of caves and the deep-sea.

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A Photographic Technique to Study Tadpole Populations

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ABSTRACT.—Although the use of photography to estimate the numbers of vertebrates in wild populations is a well established wildlife management technique, it has not been previously used in studies of tadpoles in shallow breeding ponds. A pond used by the American toad, *Bufo americanus*, was monitored through the breeding season of 1977 in Fairfax County, Virginia. Tadpole clusters were photographed and the prints used to evaluate this technique for working with such populations. An example of how the technique may be used is provided. While especially valuable in certain types of studies (for instance, those involving tadpoles in shallow ponds without much vegetation and containing one or a few species), photographic analysis is probably of use in many field studies.

INTRODUCTION

Use of photography to estimate the numbers of vertebrates in wild populations is a well established wildlife management technique (Watson 1969; also see references in Caughley 1977 and Giles 1969) although it has generally been employed in connection with aerial censuses. However, photography has not been previously used to estimate the numbers of larval amphibians in breeding ponds. Since many species of amphibians breed in shallow ponds where the larvae are readily visible, such populations should be amenable to analysis by photographic methods. I attempted to determine if photography could be used to study one of these populations of tadpoles.

METHODS AND MATERIALS

The study area encompassed a shallow (initially 70 mm maximum depth) temporary pond, 42.8 m^2 in surface area, located near the confluence of Indian Run and Back Lick Run, Fairfax County, Virginia. Characteristic vegetation in and surrounding the pond included sedges (Cyperaceae), *Juncus* sp., *Bidens* sp., *Aster* sp., *Lespedeza* sp., willow (*Salix* sp.) and river birch (*Betula nigra*); individual plants often formed clumps and were scattered along the bottom and around the edges of the pond. The pond was surrounded by a rather well-defined margin consisting of a thick growth of vegetation on one side and a mud bank on the other. This

Brimleyana No. 2: 131-136. November 1979

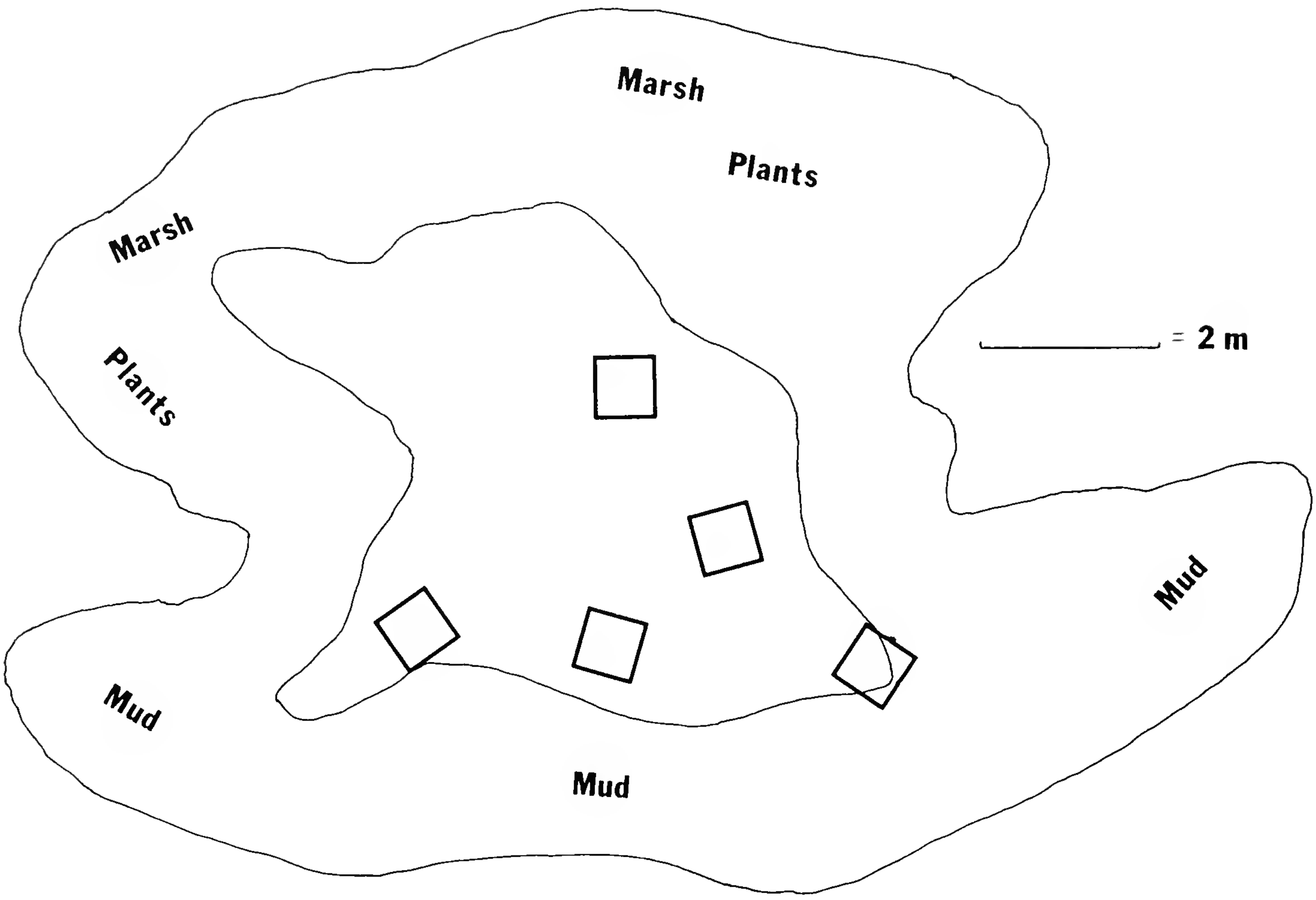


Fig. 1. Diagram of the study pond showing location of quadrats.

margin apparently represents the limit to which the pond fills during periods of maximal rainfall. Tadpoles remained in the pond and were not observed in any of the small pockets of water located in the margin.

Five study quadrats were selected and photographed with Kodachrome 64 slide film using a Nikon F camera with a 55 mm micro lens. A one meter ruler was placed at the top of each area photographed to insure uniformity of quadrat size; each quadrat measured 25 x 40 cm (see Fig. 1 for location of quadrats). The camera was hand held directly over the area to be photographed, in such a way as to assure that the film plane was parallel to the surface of the water and the scale of reference. If this is not done the resulting shift in parallax could cause a scaling problem, thus affecting area, and therefore density, estimates. Care was taken to insure that movements of the observer and placement of the meter ruler did not disturb the tadpoles and cause them to change their position.

Each slide was enlarged to a 17 x 25.5 cm print and the 25 x 40 cm quadrat was marked off (Fig. 2). A clear plastic sheet was overlain on the photograph and tadpoles marked onto the sheet as they were counted. Thus, both the exact position and number of tadpoles could be scored for each quadrat.

Fig. 2. Quadrat B showing the meter rule and the 25 x 40 cm study plot.

RESULTS AND DISCUSSION

Results of the photographic overlays are provided in Fig. 3. Tadpoles were easily counted and marked; seldom was there a question as to whether a black mark on the photograph should be counted. However, tadpole shadows are a potential problem. Densities of tadpoles were generally D-2 (20-50% of area covered by tadpoles, tadpoles within 1-5 cm of one another) or D-3 (51-89% of area covered, tadpoles mostly in contact) in the sense of Beiswenger (1975); if densities greater than this are encountered, photographic analysis might prove difficult.

Although the five study plots were apparently selected at random, I made no attempt at complete objectivity, such as using a table of random numbers to preselect quadrats. Therefore, an estimate of population size based on total numbers of tadpoles from these sites would not provide a statistically accurate picture of tadpole numbers. Methods for the estimation of population sizes via direct counts within randomly selected quadrats are available. Caughley (1977) provided several methods which might be useful, notably the use of stratified random sampling as applied to aerial surveys.

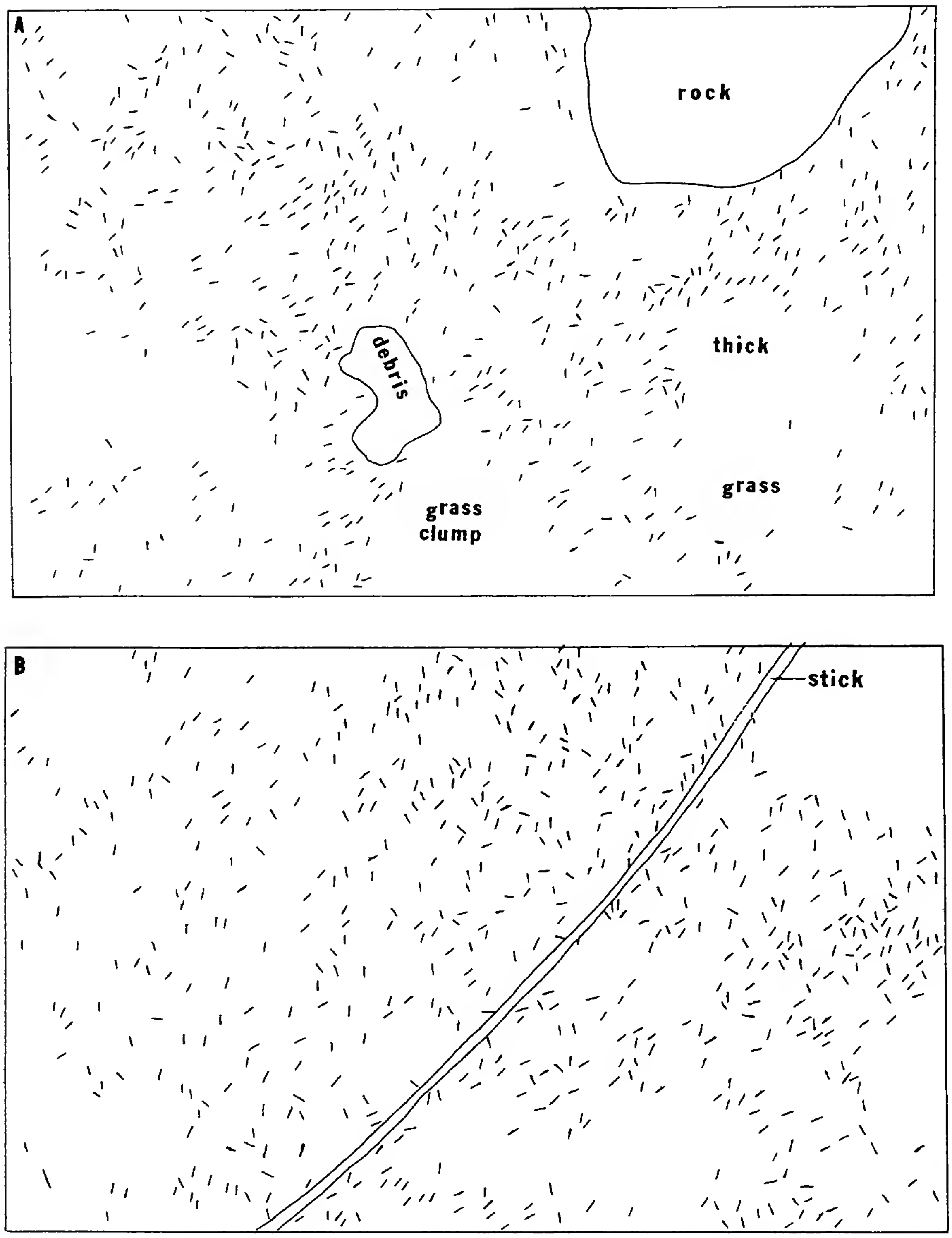
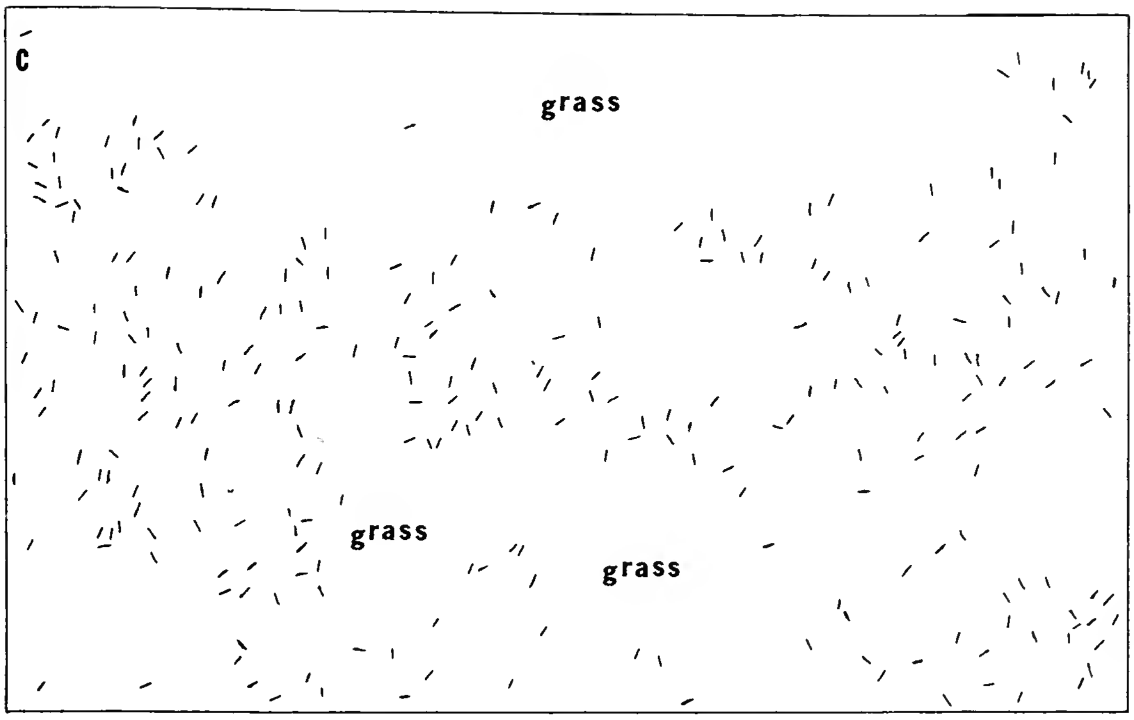


Fig. 3. Positions of tadpoles in each of the study plots as determined from photographs. The number of tadpoles in each quadrat is: A) N=545, B) N=599, C) N=268, D) N=213, E) N=480.

As an example, had the quadrats used in this study been randomly preselected, the stratified random sampling method would have yielded a value of $Y_h = 180{,}188$. The standard error rounded off to 34,000 would give a population estimate (with 95% confidence) between 116,200 and 244,200 tadpoles. The literature on toads reports a wide range of eggs deposited per female (2000 to 20,600). Therefore, using the high figure, 6 to 12 females produced these tadpoles; using the low figure, 58 to 122 females produced them. Other data gathered preliminary to this study showed that 12 females actually bred at the pond. Assuming 100% successful hatch of eggs, this number was therefore within the admittedly large estimate predicted by tadpole numbers. On the other hand, if eggs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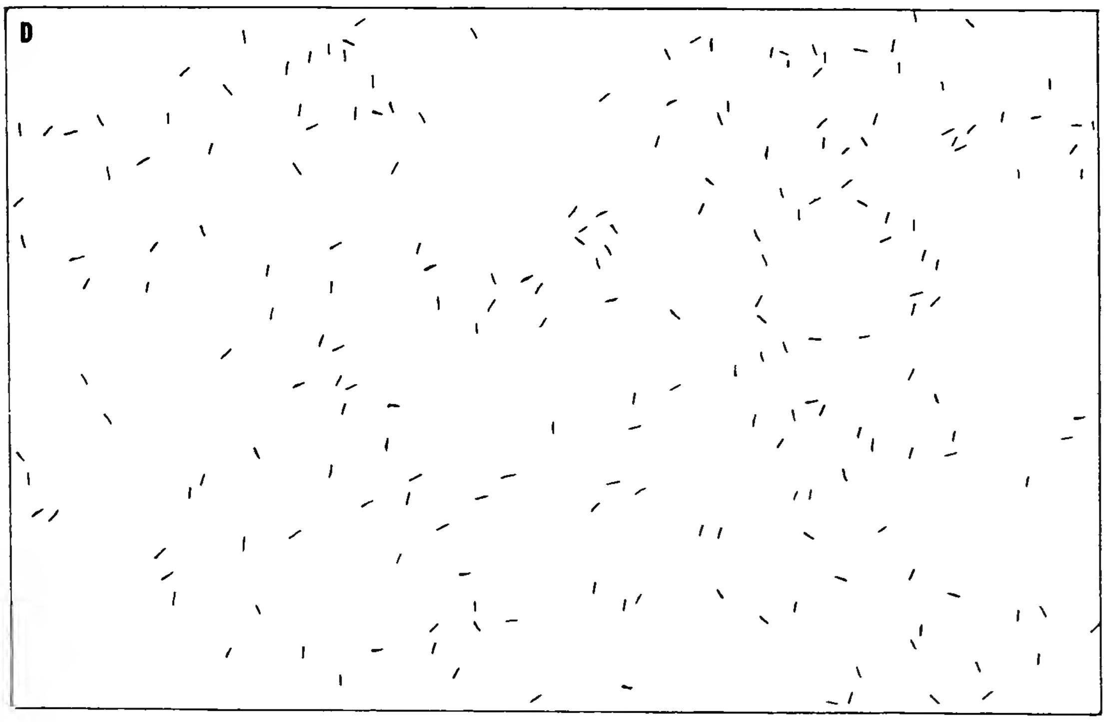
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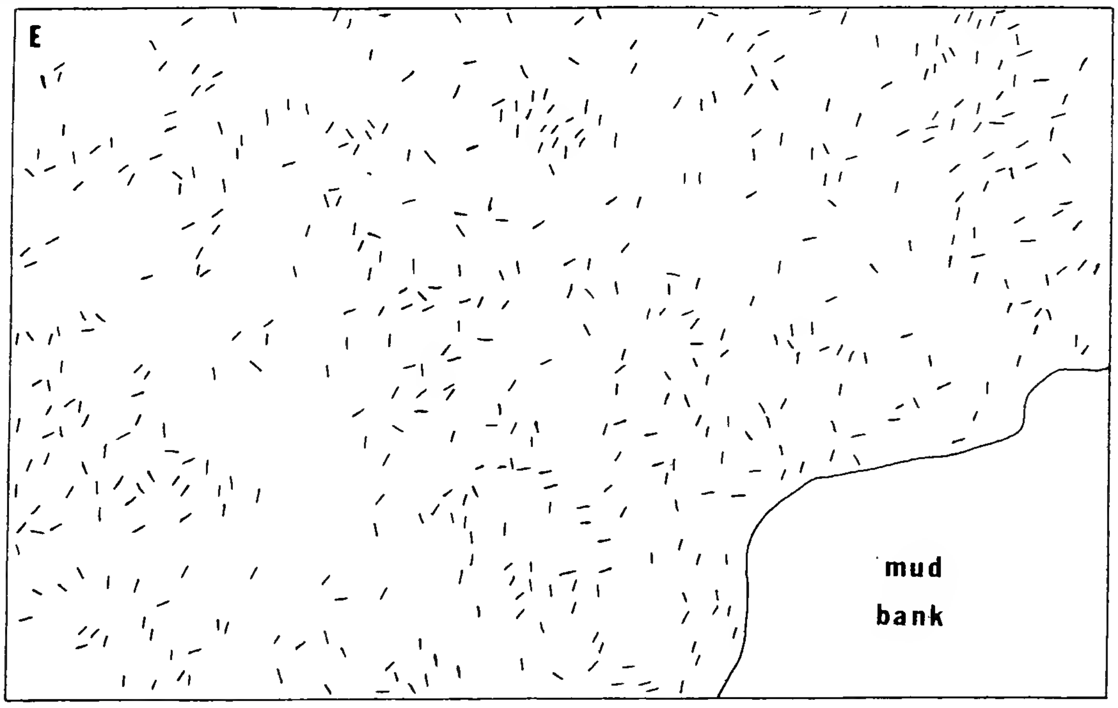
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per female were estimated, then each female would have deposited between 9680 and 20,350 eggs, again within the range of literature reports. Obviously, knowledge of other aspects of a species' biology would severely limit basing predictions about anuran population breeding characteristics solely on tadpole counts. However, depending on species, photographic analysis of a tadpole population could be substituted for, or used to supplement, counts in the field. Thus, photography could provide a valuable technique for the estimation of certain amphibian population parameters.

There are obvious problems with the method. Deep ponds or those that are very murky or clogged with vegetation would not be suitable for such analysis, nor would ponds that harbor many species of tadpoles, since tadpoles are difficult to identify without examining certain key characteristics (Altig 1970). However, many types of tadpole populations would seem to be particularly suited to photographic analysis, notably tadpoles of those species which use shallow and/or temporary water sources, especially in xeric habitats. In addition, photographic analysis could be valuable in monitoring the breeding status of species considered endangered or threatened, such as the Houston toad, *Bufo houstonensis*. The animals could be left undisturbed, thus avoiding the harassment which may be prohibited by law without a special permit. Sequential photography might also prove valuable in studies of the orientation behavior of tadpoles over a period of time.

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Rediscovery of the Sharphead Darter, *Etheostoma acuticeps*, in North Carolina (Pisces: Percidae)

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ABSTRACT.—Etheostoma (Nothonotus) acuticeps, the Sharphead darter, was known prior to October 1975 on the basis of only 37 specimens from the South Fork Holston River, Tennessee, and the North Toe River, North Carolina. The populations at all of these localities are either extremely tenuous or extirpated by impoundments and strip mining runoff. In 1975 a TVA field crew discovered a healthy population in the lower Nolichucky River below Davy Crockett Reservoir. A search of the upper tributaries of the Nolichucky revealed a small population in the lower 6 km of the Cane River, North Carolina. The Sharphead darter inhabits the swiftest portion of riffles in water 15-40 cm deep. The substrate is typically cobble and small boulders 8-20 cm in diameter, well covered with riverweed, *Podostemum ceratophyllum.* Because of the small size of the Cane River population and various threats to the water quality of the river, the Sharphead darter warrants endangered status in North Carolina.

INTRODUCTION

The Sharphead darter, *Etheostoma acuticeps*, is a poorly known member of the subgenus *Nothonotus*. In fact, until October 1975, only 37 specimens of this fish had been collected and the species was considered extinct. It was not recognized as distinct until 1947, when two specimens were collected in the South Fork Holston River, Tennessee. A last attempt to obtain the darter prior to the impoundment of South Holston Reservoir resulted in only four specimens, indicating a meager population. The species was described by Bailey (1959) on the basis of these six specimens, and at that time the only known locality was under 58 m of water.

In the 1960s L.W. Knapp and T. Zorach independently uncovered four misidentified collections of *E. acuticeps* at the Academy of Natural Sciences of Philadelphia totaling 28 specimens (Zorach 1972). These had been labeled by Fowler (1936a,b) as *Nothonotus rufilineatus*. The collections were made in June 1930 by J.G. Carlson and T. Kerr in the South Fork Holston River, Tennessee, and the North Toe River, North Carolina. Apparently the collections were not very exhaustive, as they included only a few species. *Etheostoma acuticeps* was caught in respectable numbers, however, indicating much healthier populations than at the type locality, but these populations are also undoubtedly now extirpated. The South Fork Holston localities are either impounded or are tailwaters supporting cold-adapted fishes (Jenkins and Burkhead 1975). The North Toe River has been subjected to extensive siltation from mica strip mining in North Carolina (Jenkins and Burkhead 1972, Saylor and Etnier 1976). The mica and feldspar dust smothers the eggs and eliminates the interstitial microhabitat of the darters. In recent years siltation of the North Toe has been aggravated by highway construction that parallels the river nearly to its headwaters.

Exhaustive attempts by Jenkins and Burkhead (1975) to obtain *E. acuticeps* in the Holston drainage in 1972 resulted in only three specimens. These were taken in the South Fork Holston River just above the impounded portion of South Holston Reservoir, where there apparently is enough habitat to support a small and extremely tenuous population. In the fall of 1975, Charles Saylor and a TVA field crew looking for the Snail darter, *Percina tanasi*, discovered the Sharphead darter in the Nolichucky River between Davy Crockett and Douglas Reservoirs (Saylor and Etnier 1976). Davy Crockett Reservoir had acted as a settling basin and protected the lower Nolichucky population from the siltation that eliminated the North Toe population. The discovery of this very healthy population allowed better understanding of the exact microhabitat of the Sharphead darter and fueled speculation by D. Etnier (pers. comm.) that the species may exist in larger tributaries of the Nolichucky that are relatively free of siltation. Bailey (1977) considered the Sharphead darter extirpated in North Carolina, however, as it had not been collected in the state in 47 years.

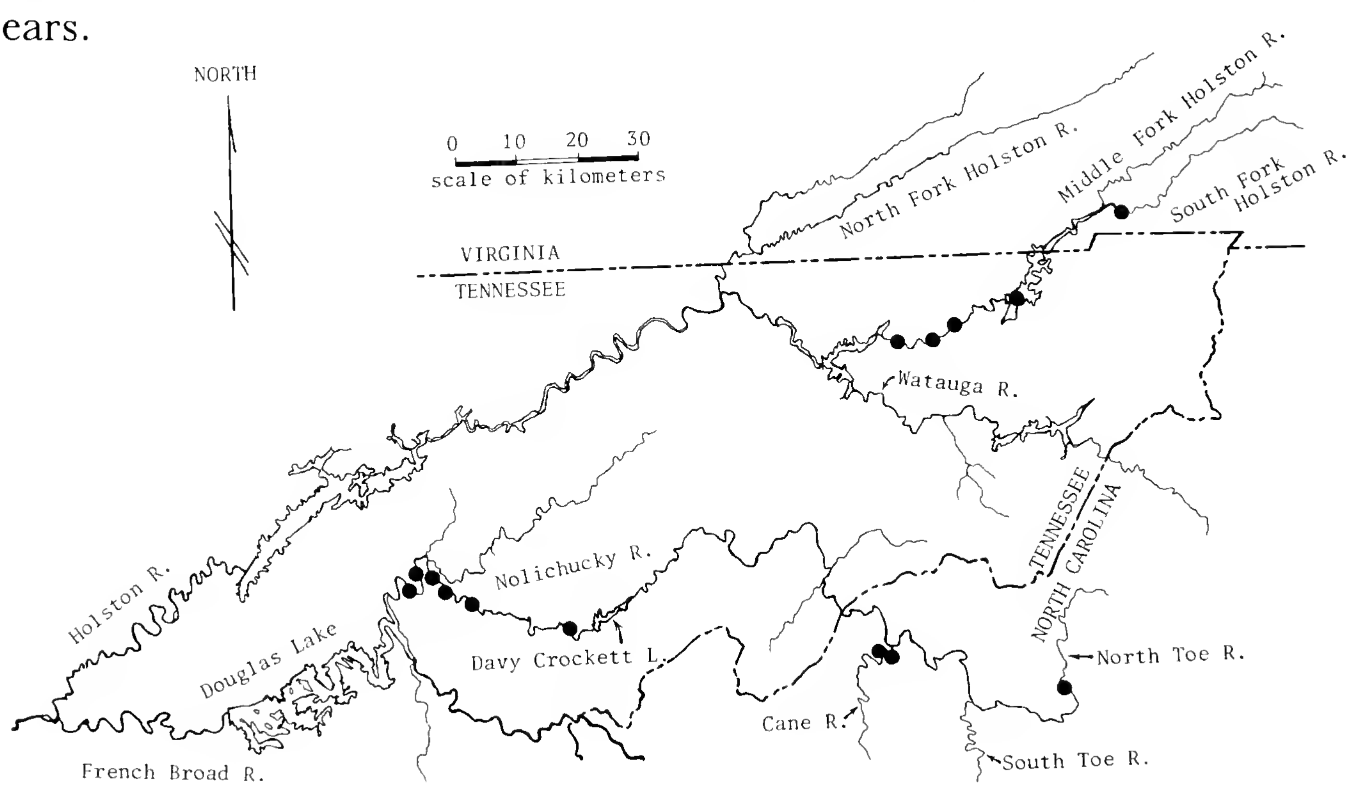

Figure 1. All known localities of *Etheostoma acuticeps*.

RESULTS AND DISCUSSION

We collected *Etheostoma acuticeps* on 14 July 1977 in the Cane River just below the US hy. 19W bridge, 1 km se of Sioux, Yancey County, North Carolina. It has since been collected at several sites between the 19W bridge and the confluence with the Toe River by E. F. Menhinick and his ichthyology class from the University of North Carolina at Charlotte, and by the authors. Attempts by both groups to find the fish above the 19W bridge have been fruitless, leading us to believe that this is its upstream limit.

The river above the bridge is slightly higher in gradient than below, with larger rocks and less riverweed, *Podostemum ceratophyllum*. The only member of the subgenus *Nothonotus* found there was the Greenfin darter, *Etheostoma chlorobranchium*. The habitat below the bridge is more like that in the lower Nolichucky. The Sharphead darter is found in the main body of riffles, in fairly swift water 15-40 cm deep. The substrate is cobble and small boulders, 8-20 cm in diameter, usually well covered with riverweed. The lower Nolichucky has slightly smaller substrate and lower current velocity. The lower Cane River drops about 2.3 m/km and the lower Nolichucky only 1 m/km. The riffles are typically shaded by large trees and bordered by beds of waterwillow, *Justicia americana*. *Etheostoma acuticeps* is not a numerous species at any of these sites. The largest collection made by Menhinick and class at the 19W bridge included only 14 specimens in a sample containing 80 other darters.

During November 1977 a flood in the Cane River watershed washed away a road, a house and a service station at the 19W bridge. In order to replace the road bed, bulldozers were used in the vicinity of the bridge, an action which inadvertently eliminated Sharphead darter habitat. The shade trees, waterwillow beds, and thick riverweed growth are gone, and the area is broad, bare gravel. Just how much of this destruction is due to the bulldozing is difficult to assess, but riffles above and below the bridge seem to be unchanged and normal habitat. Intensive sampling at the bridge on 23 September 1978 revealed mostly Gilt darters, *Percina evides*, a few *E. chlorobranchium* and only one *E. acuticeps*. In addition, Big Creek, which enters the Cane just above the bridge, has been channelized for several kilometers upstream. This may have detrimental effects on the lower Cane. Other problems upstream of the *E. acuticeps* population include two gravel washing operations, one of which, according to a local game warden, was the source of a chemical spill that resulted in a fish kill 5 km long.

Etheostoma acuticeps is known in North Carolina from only the lower 6 km of the Cane River. It apparently is not numerous and its continued existence is not assured. Channelization, gravel washing, and possible chemical spills may have detrimental effects on this species, as well as others inhabiting the lower Cane River. The Sharphead darter should be considered an endangered species in North Carolina.

ACKNOWLEDGMENTS.—The authors would like to thank Dr. E. F. Menhinick, University of North Carolina at Charlotte, for the use of his excellent field notes, and Dr. J. F. McCormick and the Ecology Program at the University of Tennessee for support and the use of a vehicle.

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Nesting Biology of *Andrena (Larandrena) miserabilis* Cresson and Description of the Prepupa (Hymenoptera: Andrenidae)

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ABSTRACT.—Andrena (Larandrena) miserabilis Cresson was found nesting in the sandy soil of the amphitheater in Highlands Hammock State Park, Highlands County, Florida. Observations were made on 31 December 1975, 1-3 January 1977, and 4-7 March 1977. Circular tumuli marked nest entrances and an average density of 11 nests per 15 cm^2 area was found. Nest tunnels were ca. 5 mm in diameter and extended from 28.5 cm to 47.0 cm deep. A single cell ca. 5.7 mm in diameter was constructed, lined, and provisioned. Pollen balls averaging 2.9 mm in diameter were dark yellow and consisted of *Acer rubrum* pollen. Prepupa were cream-colored, C-shaped, and 5.2 mm to 7.3 mm long. *Sphecodes* sp. and *Solenopsis* sp. were found in association with the nesting bees, and evidence of nest destruction by the armadillo, *Dasypus novemcinctus*, was noted.

Although the Holarctic genus *Andrena* is a common, extensive taxonomic group, little is known about the biology of many species (Rozen 1973, Davis and LaBerge 1975). A large colony of *Andrena (Larandrena) miserabilis* Cresson in Florida provided an opportunity to observe nest biology on 31 December 1975, 1-3 January 1977, and 4-7 March 1977. Adults and larvae also were collected during these visits for later laboratory examination. All specimens retained are in the Entomology Collection, Towson State University.

Study Site.—Andrena miserabilis was nesting in the soil of the amphitheater in Highlands Hammock State Park, Highlands County, Florida. The amphitheater consists of an oblong clearing ca. 9.0 m × 15.0 m in the mature hardwood hammock. It contains 12 rows of wooden benches (Fig. 1) and is surrounded by hydric hammock dominated by broadleaved evergreen trees including *Liquidamber styraciflua, Persa palustris, Godonia lasianthus, Ulmus floridana, Nyssa sylvatica, Sabal palmetto*, and *Citrus aurantium.* Epiphytes of the genera *Epidendrum, Tillandsia*, and *Polypodium* are common on the trunks and limbs. All nests were located within the clearing, 2 to 3 m inward from the peripheral vegetation, and this was the only nesting site found within the park.

Nests of *A. miserabilis* were scattered throughout the clearing, beneath

Fig. 1. Study site, March 1977.

benches as well as in open walkways. As pointed out by Osgood (1972), sites with well drained soil, good surface flow, and sparse plant cover are most often selected for nest construction by solitary bees. The sandy soil of the amphitheater provided these characteristics, while the hammock floor was densely matted with plant debris. The loose leaf litter covering the amphitheater floor presented no obstacle for bees to crawl beneath. Davis and LaBerge (1975) suggested that loose debris protects nests against beating rain and parasites, and may aid *Andrena* in nest recognition.

The amphitheater soil is classified as Sunniland-Bradenton which consists of fine sand down to marl hardpan. It is moderately wet and has a pH of 5.0-6.5. The sand is dark gray and contains fine carbon particles from fires of previous years. The soil is permeated by a complex network of roots at a depth of 2 to 5 cm below the surface. These roots, originating from hammock trees, hindered excavation.

Nest Construction.—The density of nests was determined by counting the number of nest openings within a 15 cm^2 wire frame, placed at 1 m intervals along a line transect diagonally crossing the amphitheater. An average of 11 nests per 15 cm^2 area (N = 30) was found, and the nests were slightly more numerous toward the rear of the amphitheater. This distribution is perhaps influenced by morning sunlight which reaches the rear area earliest. Early warmth after cool January nights may allow more foraging time.

Conspicuous, circular tumuli were usually present at nest entrances. They ranged in diameter from 2.0 cm to 4.3 cm ($\bar{x}$ = 3.2 cm, N = 30). Tumuli height ranged from 0.9 cm to 2.0 cm ($\bar{x}$ = 1.6 cm). Most nests were clustered in groups of 2 to 5, with many tumuli overlapping. Solitary nests were seldom found.

Nests were excavated with the aid of plaster of Paris poured into the entrances. Tunnels descended vertically except to circumvent roots. They were circular in cross-section, ca. 5.0 mm in diameter, and their walls consisted of unlined, slightly compacted, moist sand.The main shaft extended from 28.5 cm to 47.0 cm deep ($\bar{x}$ = 37.8 cm, N = 46). At the bottom of the vertical tunnel a lateral tunnel ca. 1.5 cm long terminated in a single cell. Although additional cells may have existed, none was located. Thorp and Stage (1968) reported difficulty in finding laterals of *Andrena placida* which also nests in sand.

Most cells were oriented horizontally to the main tunnel. They were slightly larger in diameter than the descending shaft ($\bar{x}$ = 5.7 mm, N = 18) and were lined with a thin, transparent waterproofing material. Cells were shiny, smooth, and jet-black from soil carbon wetted as the cell was lined. Microscopic examination showed that individual sand grains were cemented together by the hardened lining material.

Provisioning.—Pollen balls were spherical, dark yellow, and uniformly moist. Completed balls ranged in diameter from 2.5 mm to 3.2 mm ($\bar{x}$ = 2.9 mm, N = 25). As previously noted for other *Andrena* (Michener and Rettenmeyer 1956, Linsley and MacSwain 1959, Davis and LaBerge 1975), incomplete balls were smaller, less smooth, and drier than completed balls.

Slides were prepared of provisions taken from three different nests ca. 3 m apart. Microscopic examination of several hundred pollen grains proved them to be of a single type, probably *Acer rubrum*, typically a wind pollinated species. We never observed bees upon the flowers as it was not possible to follow them outside the amphitheater and no *A. rubrum* were in the immediate area. The bees never flew through the hammock, but always left or entered the area from above the surrounding trees. As noted by Graenicher (1930), bees are seldom found in a shaded hammock interior.

Adult bees were actively foraging when the study site was first visited on 31 December 1975. A steady progression of individuals left the

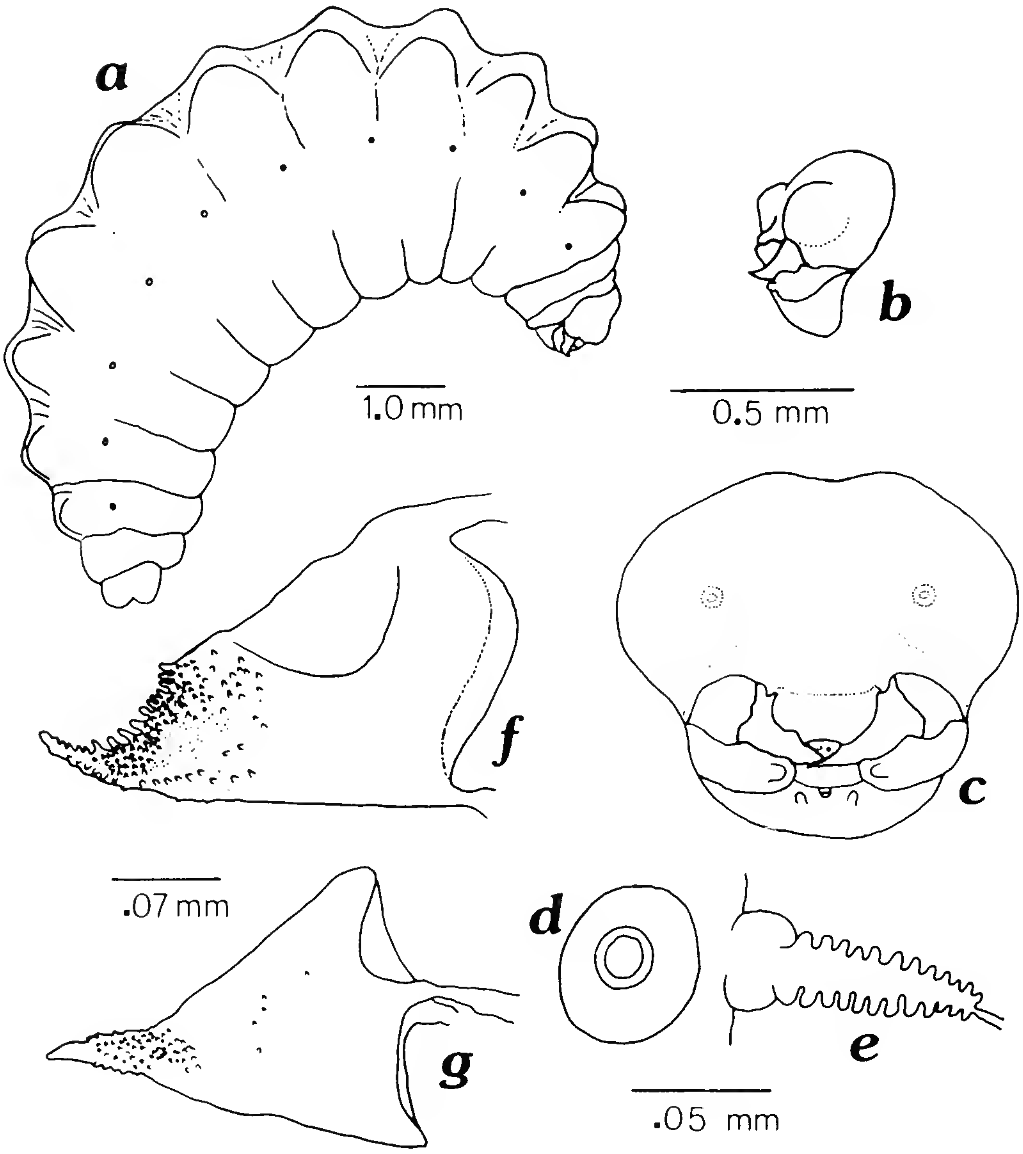

Fig. 2. Prepupa of *Andrena miserabilis*. a. Larva, lateral view. b. Head, lateral view. c. Head, frontal view. d. Spiracle, frontal view. e. Spiracle, longitudinal section. f. Right mandible, ventral view. g. Right mandible, inner view.

amphitheater and returned to the nesting site, usually carrying pollen. Flight activity of several hundred bees became concentrated in a region directly above their nests to a height of ca 1.5 meters. Zig-zag flight patterns exhibited within this region by exiting and returning bees suggested that they were conducting orientation maneuvers. Once above this region they followed a straight line of flight.

Observations on 1-3 January 1977 were made during cooler temperatures (7-9°C) under overcast skies and during intermittent showers. Under these conditions activity was noticeably reduced, with little or no zig-zag flight activity above the nests. Returning bees flew to the vicinity of their nests, landed, and crawled (seldom directly) to their burrows. When departing, bees remained on the sand outside their nests for several minutes, then crawled 3 or 4 cm before taking flight. Males were found crawling along the ground beside females, and in two instances males occupied burrows with females during a shower.

Description of Prepupa (Fig. 2).—Cream colored, C-shaped, 5.2 mm to 7.3 mm long (N = 15), with prominent transverse, dorsolateral tubercles. Intersegmental furrows distinct. Head lacking setae, weakly sclerotized; cleavage lines indistinct. Vertex rounded with two small paramedian convexities. Antennae represented by low convexities arising from large, rounded prominences. Parietal bands not apparent. Posterior thickening of head capsules inconspicuous; hypostomal and pleurostomal thickenings more pronounced. Posterior tentorial pits distinct. Epistomal suture weak; labroclypeal suture distinct. Labrum bearing two small convexities with clustered sensillae; tubercles absent. Mandibles robust; moderately sclerotized, most heavily at cusp; apex attenuate and sharply pointed; upper apical margin with dense row of teeth; lower margin with row of smaller denticles; ventral surface with row of denticles near lower margin, denticles and spicules scattered distally; adductor apodeme twice as long as abductor apodeme. Maxillae with indistinct separation of cardines and stipites. Maxillary palpi very pronounced, twice as large as labial palpi. Labium with prementum and postmentum undefined. Salivary opening a U-shaped slit. Body naked; spiracular atria extending slightly above body surface.

Predators and Parasites.—On 2 January 1977, three adult *Sphecodes* sp. were noted in the nesting area, two of which were observed leaving *Andrena* nest burrows. Members of this genus are frequently nest parasites of bees (Bohart 1970). Also present at *Andrena* nest entrances were ants of the genus *Solenopsis*, and an adult female *Andrena* was collected on 3 January 1977 with an ant firmly grasping both right wings (Fig. 3). The bee crawled from a nest hole, attempted flight, then crawled along the ground dragging the ant.

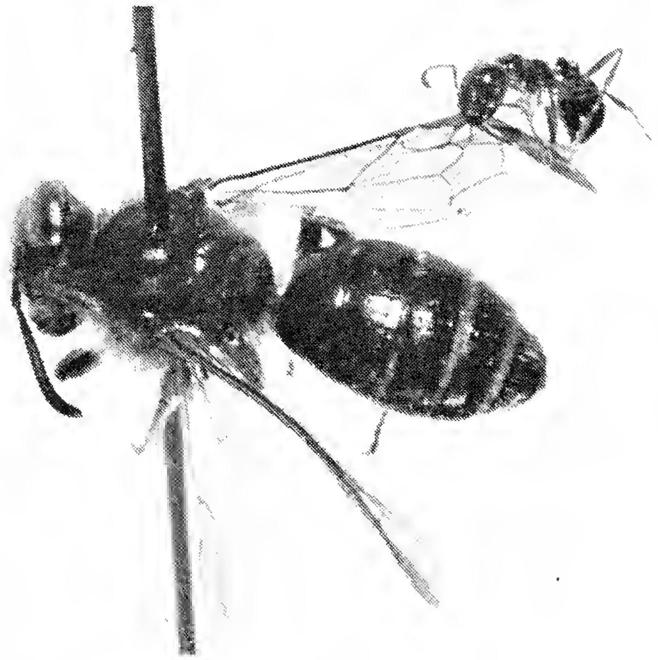

Fig. 3. Female *Andrena miserabilis* with *Solenopsis* attached to wings.

On the mornings of 5 and 6 March 1977, tracks and feeding excavations of the Nine-banded armadillo, *Dasypus novemcinctus*, were found in the area containing the highest density of *Andrena* burrows. The armadillo excavations extended to the depth of larval bee cells and fragments of opened cells were present. It is doubtful that bee larvae were being sought by armadillos; but if encountered larvae would likely be consumed, and nests were destroyed by the digging.

ACKNOWLEDGMENTS.—We gratefully acknowledge the contributions of the following persons: Drs. W. E. LaBerge, Illinois Natural History Survey, Urbana; S. W. T. Batra, U.S.D.A., Beltsville, Md.; and E. S. Deevey, Florida State Museum, Gainesville, for bee, ant, and pollen identifications respectively; and Dr. R. Shoemaker, M. Brenner, T. Bladen, R. Franz, and A. Norden for technical assistance.

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COVER DESIGN

The cover of *Brimleyana* was designed by Ray Hodges and Tim Dove.

ERRATA

A few typographical errors were missed in proofing *Brimleyana* No. 1, but only one substantive error has been brought to our attention.

In the essay, "The Brothers Brimley: North Carolina Naturalists," by John E. Cooper (p. 8, para. 2, line 8) the statement was made that illustrations by Roger Tory Peterson appeared in the 1919 edition of *Birds of North Carolina.* Peterson's illustrations actually first appeared in the 1942 edition. We are grateful to Eloise H. Potter, editor of *The Chat*, for bringing this error to our attention.

PRODUCTION

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REVIEWERS OF MANUSCRIPTS

We are indebted to many scientists who served as referees for manuscripts. Their names and institutional affiliations will be provided in every third issue.

INDEX AND TABLE OF CONTENTS

An index of scientific names and a table of contents for 1979 will appear in *Brimleyana* No. 3, which will appear in the spring of 1980.

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Crocker, Denton W. and D. W. Barr. 1968. Handbook of the Crayfishes of Ontario. Univ. Ontario Press, Toronto. 158 pp.

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