

argue for its continued recognition as a subgenus. Although derivable from *Boleosoma*, reproductive behavior in *Ioa* is unique among darters (Winn and Picciolo, 1960), another reason for maintenance of its subgeneric status.

Ioa was held to be distinctive partly on the basis of possessing one rather than two anal spines (Jordan and Brayton, 1878:88). However, Bailey and Richards (1963) noted that one or two spines occur in certain populations of *Ioa* as in a species of *Boleosoma*. Richards (1966) stated that prevomerine and palatine teeth are absent in *Ioa* and present in *Boleosoma* (apparently, *sensu lato*), but whether in all species of the latter was not made clear.

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- ROBERT E. JENKINS, Department of Biology, Roanoke College, Salem, Virginia 24153.

NUPTIAL TUBERCULATION AND ITS SYSTEMATIC SIGNIFICANCE IN THE PERCID FISH *ETHEOSTOMA (IOA) VITREUM*.—The glassy darter, *Etheostoma vitreum* (Cope), occurs on the central Atlantic slope from the Patuxent drainage in Maryland to the Neuse drainage of North Carolina (Jenkins *et al.*, in press). Sandy substrates in streams are its preferred habitat. It composes the monotypic subgenus *Ioa* Jordan and Evermann of the percoid tribe Etheostomatini. A comprehensive study of nuptial tubercles in percids (Collette, 1965) and of reproduction in *E. vitreum* (Winn and Picciolo, 1960) did not reveal the presence of tubercles in this species. These structures develop in both sexes and their distribution is unique among percids. A description and discussion of their bearing on the systematic placement of *Ioa* is thus merited.

Material.—Numbers in parentheses refer to

tuberculate and/or adult specimens and their standard length in millimeters. Virginia, Roanoke drainage: CU (Cornell University) 11879 (3, 31-42) Dinwiddie Co., Stony Cr., 21 March 1948; CU 11927 (1, 46) Brunswick Co., Great Cr., 21 March 1948; CU 16914 (3, 32-40) Sussex Co., Sappony Cr., 27 March 1949; CU 50989 (1, 52) Brunswick Co., Totaro Cr., 27 March 1949; CU uncataloged (21, 36-46) Nottoway Co., Little Nottoway R., 30 March 1968. Rappahannock drainage: CU 9900 (7, 36-49) Stafford Co., Rappahannock R., 28 March 1941.

Tuberculation.—Tubercles were found only on the pectoral and pelvic fins in all ripe specimens studied of both sexes. On the pectoral fin, they are restricted to the anterior (outer) surface of the rays, occurring on all 12-13 rays in highly tuberculate specimens to as few as the medial five rays in specimens with weak tuberculation. They are best developed proximally on the distal one-third of rays, generally absent from the proximal half and tip of rays, and extend over a greater length of medial than upper and lower rays. Tubercles are small, generally ovoid, firm (not hard), uniserial, and occur almost always one per segment. In most specimens they appear as low elevations with a rounded surface; in highly tuberculate males many are pointed with an erect or, less often, retrorse tip.

On the pelvic fin, tubercles similar to those on the pectoral occur on the distal one-third to half of the ventral (inner) surface of rays 2-4 or 1-5. On a highly tuberculate male those of rays 2-3 had apparently fused to produce a low ridge. Tubercles are generally absent from the dorsal surface of the rays; tiny ones occur on rays 4-5 of a highly tuberculate male. None was found on the pelvic spine. Tubercle distribution and size is greater on both fins in males than in females of about equal size taken in the same collections.

Tubercles in darters are believed to function primarily as an aid in maintenance of spawning position and in sexual stimulation of the female, by apposition of roughened fin, body, and head surfaces (Winn, 1958; Collette, 1965; Braasch and Smith, 1967; Wiley and Collette, 1970). Based on observations by Winn and Picciolo (1960:189-190) of spawning behavior in *E. vitreum*, tubercle function in this species is probably the same as in other tuberculate darters. Spawning occurs with a male or group of males gen-

erally beside an ovipositing female. Individuals in this position probably have their apposed pectoral fin usually adducted posteriorly permitting tubercle contact. Winn and Picciolo (1960:190) noted a male holding one pectoral over a female during a spawning act, but did not state whether the (tuberculate) outer or (atuberculate) inner surface made contact; such acts may partly serve a stimulatory function. The long pectorals in this species are possibly an adaptation for spawning, by providing increased surface area for tubercles, as well as to maintain position on the substrate and, perhaps, for burrowing into sand bottoms. The function of the pelvic fin tubercles remains uncertain since no data are available on the relation of this fin to the spawning act. Perhaps males sometimes mount females for spawning, as the ventral rather than dorsal surface of pelvic rays are the most tuberculate. Then, however, it becomes difficult to explain the occurrence of pelvic tubercles in females.

Other characters best developed during the reproductive period in *E. vitreum* are a dusky or blackish color over the head and body, a small knob-like thickening at the tip of the pelvic fin spine and anterior soft rays, integumental thickening over head and ventro-lateral body scales, somewhat oblique imbedment of the anterior field of these scales resulting in an elevation of their posterior margin, and a genital papilla and anal mound profusely covered with fleshy villi (in part, Winn and Picciolo, 1960; Cole, 1967). These features occur in both sexes; the first four are generally better developed in males, the latter in the female. Integumental thickenings upon scales in *E. vitreum* may be histologically similar to nuptial tubercles on scales of other darters. They differ in *E. vitreum* by being poorly or undeveloped over the ctenoid scale margins, leaving the cteni free. Since spawning individuals have lateral and/or ventro-lateral parts adjacent to each other, the elevated cteni likely function with tubercles in contact maintenance. This would be analogous to the enlarged spinous mid-ventral scales in some darters of the genus *Percina* (New, 1966:26-27, fig. 4).

Spawning period.—The glassy darter spawns in early spring. Tubercles were present on gravid or partly spent specimens collected from 21 to 30 March in south and central eastern Virginia. Earlier collections

were not seen. Some specimens in these collections were spent and had poorly developed tubercles or lacked them. Specimens taken on 12 April 1947 and 2 April 1949 from the upper Piedmont section of the James drainage, central Virginia were spent and lacked tubercles. Winn and Picciolo (1960) found that four spawning seasons occurred between about mid-March and mid-April farther northward, near Washington, D.C. Collette (1965) probably failed to find tubercles in *E. vitreum* because most of his specimens were spent; his study material was collected from 28 March to 17 May.

Systematic significance.—*E. vitreum* has a unique tubercle distribution for darters: tubercles occur on the pectoral fin, are distributed distally rather than proximally, and they are apparently absent from the body. Of the approximately 120 valid species of darters (in part, Collette, 1967), 46 or more in the three genera and in 12 of the 25 subgenera develop breeding tubercles (Collette, 1965). Tubercles were found on the pectoral fin of only two species, *Percina (Imostoma) uranidea* (Collette, 1965) and *Etheostoma (Oligocephalus) spectabile* (Collette, 1965; Distler, 1968). The pectoral tubercles appear in both species after all or nearly all other tuberculate areas have developed tubercles and do not achieve a wide distribution. Distler (1968) did not find pectoral tubercles in two of five subspecies of *E. spectabile*. These data indicate that the pectoral in these species may be only a secondary center of tuberculation. The pectoral is the largest tuberculate area in *E. vitreum*. Collette's (1965:fig 7) illustration of *E. spectabile* shows tubercles only on the proximal portion of rays. They were stated to occur on the ventral 2-5 rays of *P. uranidea* but whether located proximally or distally was not shown in Collette's fig. 3. Tubercles are primarily distributed distally in *E. vitreum*. This species also differs from *P. uranidea* and *E. spectabile* by apparently lacking body tubercles. The possession and distribution of pelvic fin tubercles in *E. vitreum* are not unusual; these are commonly found on the ventral surface in numerous species of tuberculate darters (Collette, 1965).

E. vitreum is also distinctive from the standpoint that females develop tubercles. Tubercles were recorded on females of only five darter species, all in the *E. variatum* species-group of the subgenus *Etheostoma*;

their tubercles are on the body (Collette, 1965).

Tubercles are profusely developed on the body and certain fins including the pectoral in males and females of species of the European tribe Romanichthyini (Collette, 1965; pers. obs.).

The monotypic *Ioa* Jordan and Brayton, consisting of *E. vitreum*, was long recognized as a genus. Bailey (*In* Bailey and Gosline, 1955) ranked it as a subgenus of *Etheostoma* and placed it distant from the subgenus *Boleosoma* De Kay in his arrangement. Winn and Picciolo (1960) indicated that the ancestor of *Ioa* was johnny darter-like, resembling *Etheostoma olmstedii* and *E. nigrum* of the subgenus *Boleosoma (sensu stricto)*. Evidence was provided from their similarity in habitat (sandy streams), morphology (body form; subdivided or emarginate genital papilla and anal mound), and coloration (speckled pattern of juveniles and blackish nuptial color). A hypothesis was given deriving the unusual communal reproduction of *E. vitreum*, with spawning performed in an upright position, from a pattern of spawning in which a single male and female spawn in an inverted position beneath rocks, as in johnny darters. The two groups also share fleshy enlargements (small in *E. vitreum*) over the tip of the pelvic spine and rays. For some of these reasons Collette (1965:570, 587) shifted the systematic position of *Ioa* to follow *Boleosoma* directly, an arrangement with which I concur. The longer and sharper snout, more elongate body, smaller orbit (Eddy, 1969:fig. 548), more translucent flesh, and slight reduction of the non-breeding pigmentation pattern of *Ioa* are probably advancements for arenicolous life. In at least some of these respects, *Ioa* converges with species of the sand darter genus *Ammocrypta*.

Boleosoma (sensu lato) consists of a non-tuberculate group and a tuberculate group of species (Collette, 1965). The latter group was elevated and subdivided into two subgenera, *Doration* Jordan and *Vaillantia* Jordan and Brayton, by Cole (1967:29). Thus five nontuberculate species (Cole, 1967) remain in the subgenus *Boleosoma*. Collette (1965), unaware that tubercles occur in *Ioa*, suggested its eventual synonymization with *Boleosoma* on the basis of absence of tubercles and shared character states noted above. However, the possession of tubercles by *Ioa* and their unique distribution pattern