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(Branchiopoda: Anostraca)

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UNTANGLING CONFUSION BETWEEN *EUBRANCHIPUS VERNALIS* AND *EUBRANCHIPUS NEGLECTUS* (BRANCHIOPODA: ANOSTRACA)

Denton Belk, Graziella Mura, and Stephen C. Weeks

ABSTRACT

Despite illustrations in Garman (1926) clearly showing the different antennal appendages of *Eubbranchipus vernalis* and *Eubbranchipus neglectus*, Creaser (1930) published erroneous drawings of the antennal appendages of these two species that led to more than 65 years of taxonomic confusion between them. We untangle this confusion, and show that these species have nonoverlapping areas of occurrence with *E. vernalis* to the east and *E. neglectus* to the west of the Appalachian Mountains. In addition, we present evidence supporting the use of resting-egg (cyst) morphology in studying evolutionary relationships among anostracan species. An important part of this usefulness is due to the independence of cyst morphology from sexual selection. Since the primary taxonomic characters of anostracans are all strongly influenced by sexual selection, cyst morphology can supply a reasonably independent set of characters for testing hypotheses of species relationships.

Nine of the 16 anostracan species described in the genus *Eubbranchipus* are endemic to North America (Belk and Brtek, 1995). Of these nine, two species pairs, *bundyi-intricatus* and *holmanii-moorei*, were involved in taxonomic problems that have already been cleared up. Here we reveal and correct confusion involving a third species pair, *vernalis-neglectus*. In addition, we show that the morphology of the cyst shell reflects the apparent close evolutionary relationship between the sister species of each pair.

Hartland-Rowe (1967) pointed out that two taxa were being confused under the name *Eubbranchipus bundyi* Forbes, 1876. He documented the morphological differences, and described a new species, *Eubbranchipus intricatus* Hartland-Rowe, 1967. Brtek (1967) demonstrated that the taxon from southern Louisiana referred to in several studies by Dr. Walter G. Moore as *Eubbranchipus holmanii* (Ryder, 1879) was in fact a new species which he named *Eubbranchipus moorei* Brtek, 1967. We point out below that a mistake in fig. 3 of Creaser (1930) resulted in confusion between *Eubbranchipus vernalis* (Verrill, 1869) and *Eubbranchipus neglectus* Garman, 1926. Creaser's error was picked up and perpetuated in popular identification keys by Penak (1953, and later editions) and by Dexter (1959). Brtek (1966) incorrectly placed these two in synonymy, while hesitantly suggesting the *neglectus* form might be a subspecies. Confusion between the taxa within each of these three pairs resulted from morphological

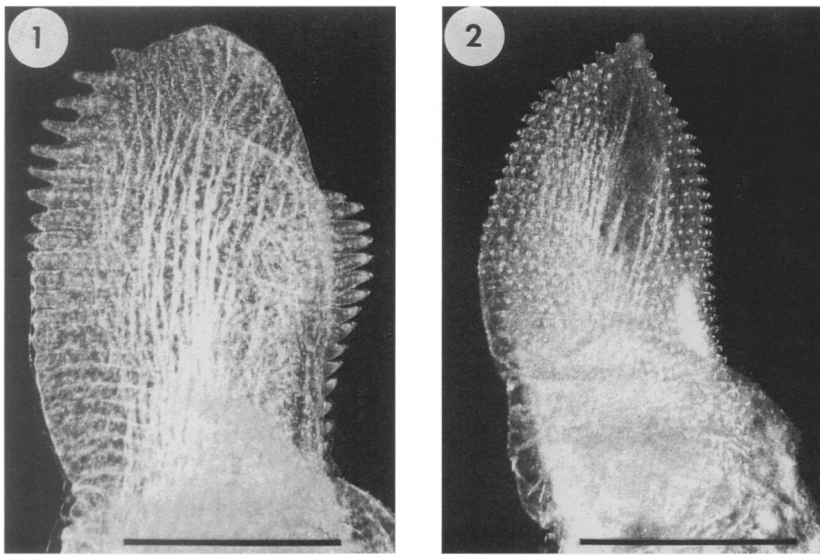
similarity, a situation that usually indicates close relationship.

Brendonck *et al.* (1992) found that four African species in the anostracan genus *Streptocephalus* produce uniquely shaped tetrahedral cysts. Their morphological analysis of the taxonomically important male antennae suggested these four streptocephalids form a closely related group. Thus, as it turned out, the unique tetrahedral cyst represented the most striking of a cluster of morphological characters indicating close evolutionary relationship. Brendonck *et al.* formally recognized this situation by assigning the four species to a new subgenus, *Parastreptocephalus*. This is the first example of cyst morphology aiding in the discovery of a group of closely related anostracans.

As was the case in the group of related species which Brendonck *et al.* (1992) named *Parastreptocephalus*, we found each of the three pairs of problem species of *Eubbranchipus* produce cysts that look alike in comparisons made between the members of each pair. The three species that have not been confused with other taxa (*Eubbranchipus oregonus* Creaser, 1930, *Eubbranchipus ornatus* Holmes, 1910, and *Eubbranchipus serratus* Forbes, 1876) produce cysts that look different from each other, and from cysts of all the other North American species.

MATERIALS AND METHODS

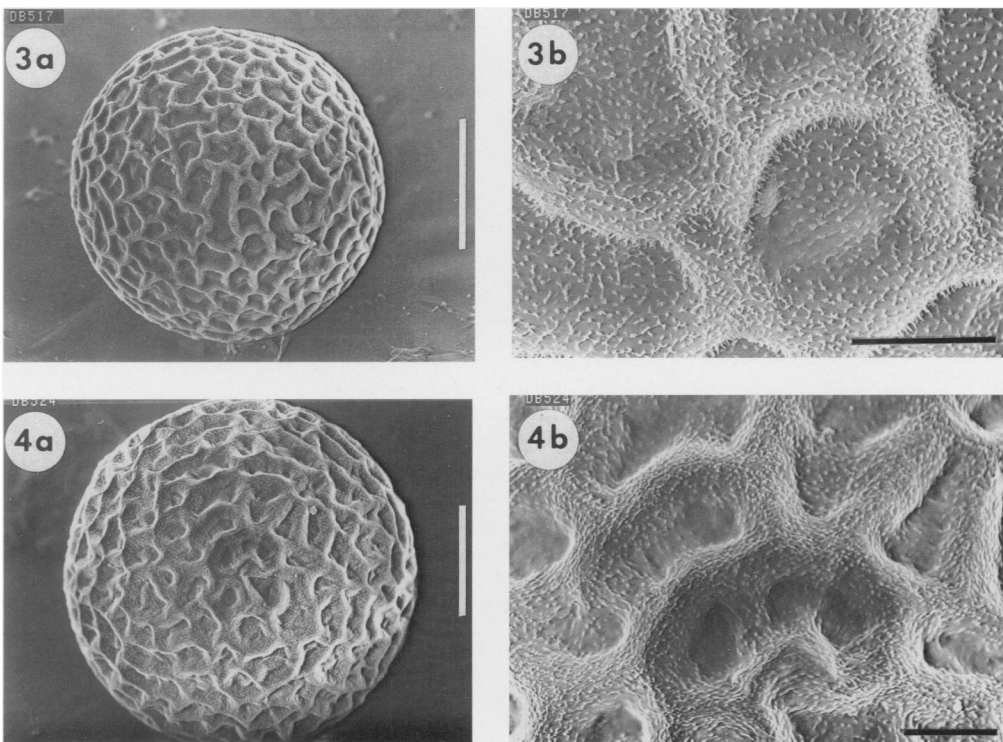
All cysts used in this study were removed from the brood pouches of preserved specimens. We chose only cysts that



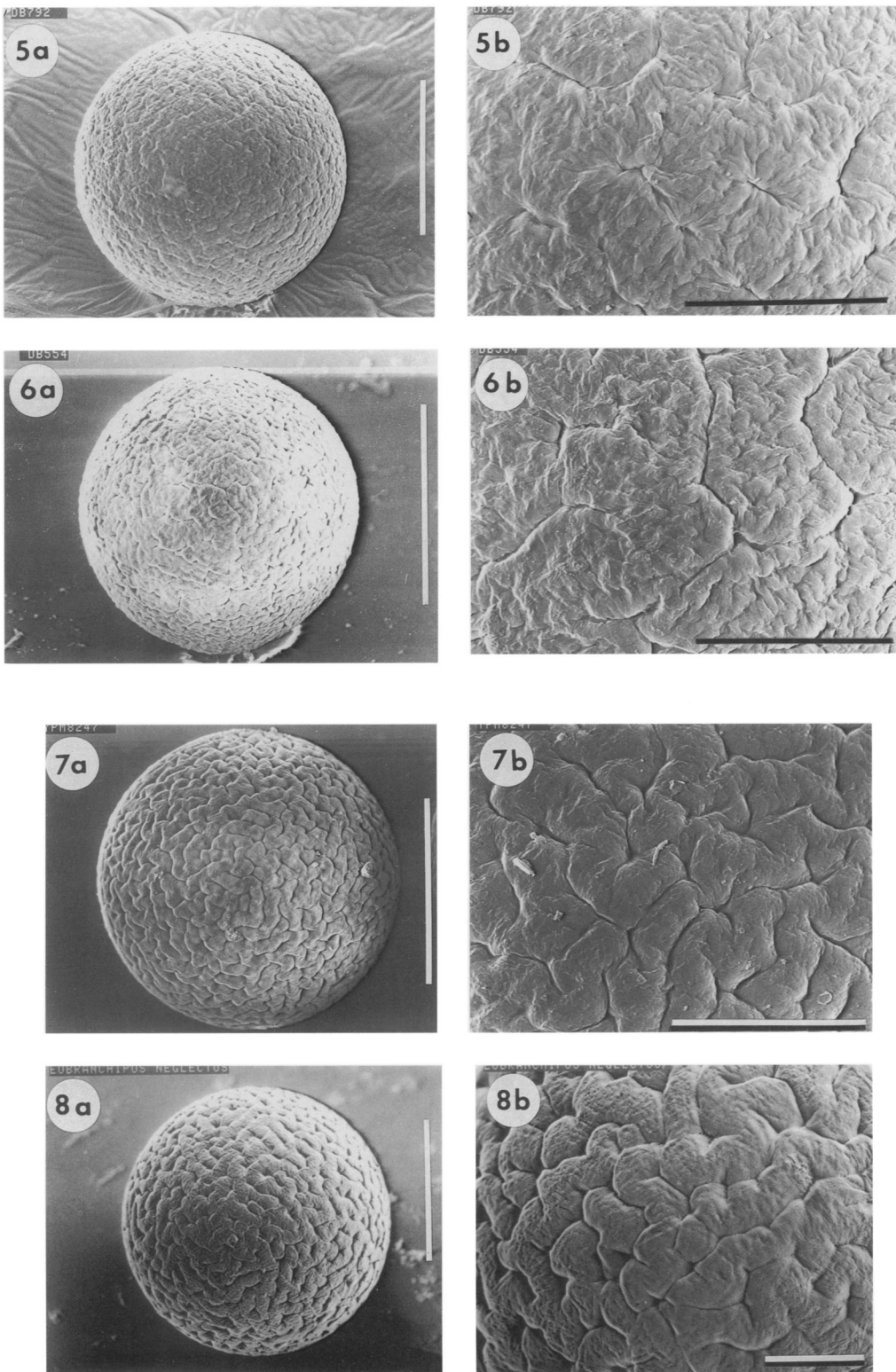
Figs. 1, 2. Dorsal views of left antennal appendages. 1, *Eubbranchipus neglectus*, antennal appendage from a 25-mm male collected in Cuyahoga County, Ohio, U.S.A. (DB146); 2, *Eubbranchipus vernalis*, antennal appendage from a 20-mm male collected in New London County, Connecticut, U.S.A. (DB1095). Scales = 1 mm.

appeared to be mature and of normal morphology, so as to avoid problems like those discussed in Mura (1992). The selected cysts were prepared for SEM analysis as described in Mura (1986). We used cysts of 1–5 females from each location, and examined more than 4 cysts from each fe-

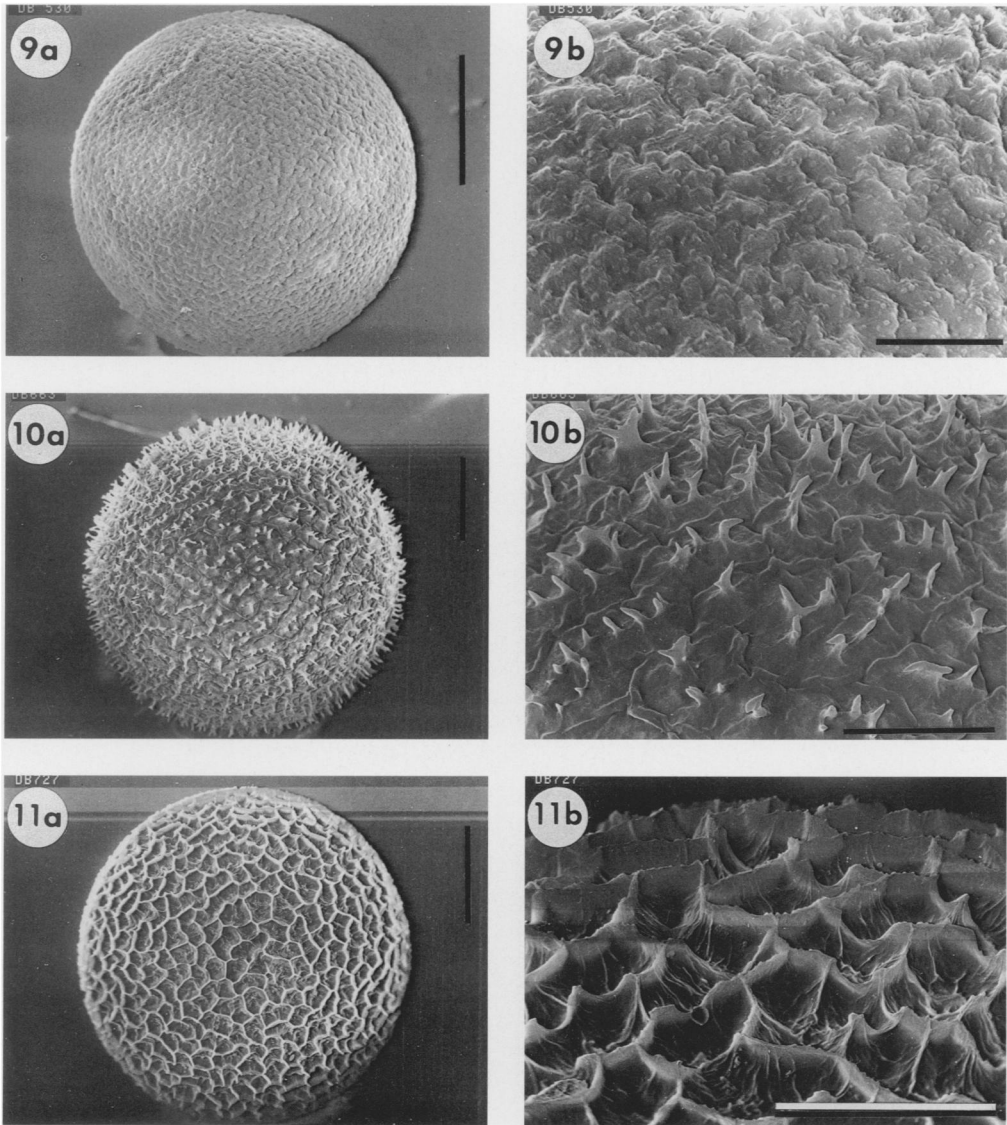
male by SEM. When material was available, we used cysts from several populations, choosing especially those distant from each other. For our figures, we selected the SEM photographs that most accurately illustrated the typical morphology of the cyst produced by each species.



Figs. 3, 4. Cysts, whole view (a) and close view of surface (b). 3, *Eubbranchipus holmanii*; 4, *Eubbranchipus moorei*. Scales: a = 100 μ m; b = 20 μ m.



Figs. 5–8. Cysts, whole view (a) and close view of surface (b). 5, *Eubbranchipus bundyi*; 6, *Eubbranchipus intricatus*; 7, *Eubbranchipus vernalis*; and 8, *Eubbranchipus neglectus*. Scales: a = 200 μ m; b = 50 μ m.



Figs. 9–11. Cyst, whole view (a) and close view of surface (b). 9, *Eubbranchipus ornatus*; 10, *Eubbranchipus serratus*; and 11, *Eubbranchipus oregonus*. Scales: a = 100 μ m; 9b = 20 μ m; 10b and 11b = 50 μ m.

We used cysts from the following sources and localities during the SEM portion of our study. For *E. bundyi*: DB222 (DB = collection of Denton Belk) Apache County, Arizona, U.S.A.; DB229 Coconino County, Arizona, U.S.A.; DB528 Alberta, Canada; and DB792 Northwest Territories, Canada. For *E. holmanii*: DB517 Madison County, Alabama, U.S.A. For *E. intricatus*: DB554 Alberta, Canada, and DB557 Alberta, Canada. For *E. moorei*: DB521 Mobile County, Alabama, U.S.A., and DB524 (paratypes) St. Tammany Parish, Louisiana, U.S.A. For *E. neglectus*: DB146 Cuyahoga County, Ohio, U.S.A.; DB518 Madison County, Alabama, U.S.A.; DB880 Madison County, Alabama, U.S.A.; and accession no. IZ1994–12 (Milwaukee Public Museum, Milwaukee, Wisconsin, U.S.A.) Jefferson County, Kentucky, U.S.A. For *E. oregonus*: DB727 King County, Washington, U.S.A. For *E. ornatus*: DB530 Alberta, Canada. For *E.*

serratus: DB152 Coconino County, Arizona, U.S.A.; DB581 British Columbia, Canada; and DB663 Beaverhead County, Montana, U.S.A. For *E. vernalis*: DB1095 New London County, Connecticut, U.S.A. and YPM8247 (YPM = Peabody Museum of Natural History, Yale University) New Haven County, Connecticut, U.S.A.

Data for the map in Fig. 12 came from field work by Stephen Weeks in Ohio during the period 26 July 1995 and 1 May 1996, and locality data on collections in the holdings of the National Museum of Natural History, Smithsonian Institution; the Milwaukee Public Museum, Milwaukee, Wisconsin, U.S.A.; the Peabody Museum of Natural History, Yale University; the Canadian Museum of Nature, Ottawa, Ontario; the personal collection of Denton Belk; and specimens examined by Belk for Harp *et al.* (in press). These specimens are divided among the Smithsonian Institution, Arkansas State University Mu-

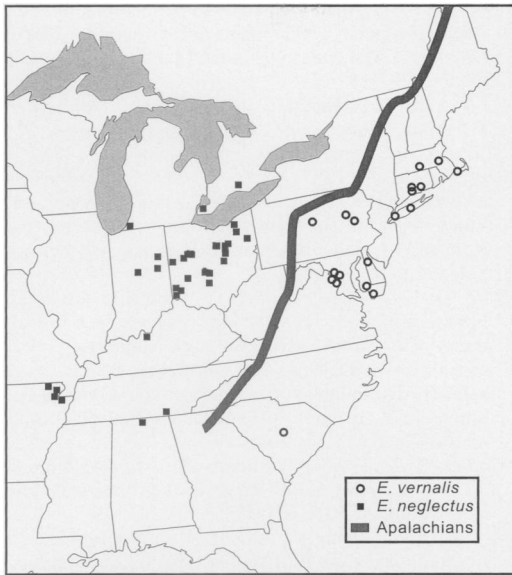


Fig. 12. Distribution of *Eubbranchipus neglectus* and *Eubbranchipus vernalis*, based on specimens in museum and private collections (see Materials and Methods for details).

seum, and Denton Belk (DB1231, 1232, 1250, 1251). All museum collections were personally examined by Denton Belk.

RESULTS AND DISCUSSION

Our Figs. 1 and 2 show that *Eubbranchipus neglectus* and *E. vernalis* are reliably identified by the differing morphology of their antennal appendages. Garman (1926) understood this, and accurately illustrated the antennal appendages of both these species (compare his figs. C and D to ours). Problems began when Creaser (1930) misidentified the specimen that he used to draw his fig. 3 to illustrate the antennal appendage of *E. vernalis*. The specimen he used for the drawing was actually one of *E. neglectus*. Creaser published his 1930 paper as a revision of the genus *Eubbranchipus*, giving it standing as authoritative. Thus, not unexpectedly, the widely used identification keys of Pennak (1953, and later editions) and Dexter (1959) reproduced Creaser's drawing, and further clouded the separate identity of these two species.

The grouping of our cyst photographs on the basis of morphological similarity brought together each of the pairs of species that have generated the most taxonomic confusion. This can be seen for *holmanii-moorei* by comparing Figs. 3 and 4, for *bundyi-intricatus* by comparing Figs. 5 and 6, and for *neglectus-*

vernalis by comparing Figs. 7 and 8. In addition, very similar ridge development, differing only in width, suggested that *bundyi*, *intricatus*, *neglectus*, and *vernalis* may be a cluster of related species (Figs. 5–8). Each of the three species of *Eubbranchipus* that have not been subjects of taxonomic problems had a unique cyst-shell pattern in comparison to all the other North American species (Figs. 9–11). For these three, cyst morphology offered no suggestion of their relationships among the North American *Eubbranchipus* fauna.

Our study of the distributions of *E. neglectus* and *E. vernalis* shows that they have nonoverlapping areas of occurrence separated by the Appalachian Mountains (Fig. 12). All verified records of *E. vernalis* were east of the Appalachians, from Connecticut south to Columbia, South Carolina. All verified records of *E. neglectus* were confined to the area between the western slope of the Appalachian Mountains and the Great Plains from Ontario in Canada south to northern Alabama in the United States, and as far west as Arkansas.

Our study of specimens collected throughout eastern North America reveals that the Appalachian Mountains separate the ranges of *Eubbranchipus neglectus* and *Eubbranchipus vernalis*. Thus, it seems clear that the information reported in Dexter (1946), Dexter and Kuehnle (1951), Dexter (1967), and many of the papers cited in these works, actually applies to *E. neglectus*, and not to *E. vernalis*. We know for certain that this is the situation in Modlin (1982, 1983, 1985) and Belk and Milne (1984), because we have examined specimens from these studies. Ferguson (1935) reported the first Canadian record for what he thought was *E. vernalis*. Fortunately, he placed specimens at the Canadian Museum of Nature. These allow us to determine that he was dealing with *E. neglectus*.

After presenting new observations and reviewing the data on anostracan cyst morphology, Thiéry *et al.* (1995) concluded that cyst morphology can provide new taxonomic information useful in defining natural groups. We concur. In addition, we point out that characters based on cysts may be particularly useful, because they are independent of sexual selection, unlike the other morphological characters used in anostracan taxonomy (for discussion, see Belk, 1991; Brendonck, 1995). Thus, they likely offer a reasonably in-

dependent set of characters against which hypotheses of relationship may be tested.

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