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TRANSFER OF THE BENTHIC MARINE DIATOM *ANAULUS VALLUS* TO THE GENUS *DENTICULA*

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ANAULUS
DIATOMS
DENTICULA
EPIPHYTIC
TAXONOMY

ABSTRACT. – Examination of type material of the marine diatom *Anaulus vallus* Nikolaev with scanning electron microscopy revealed that it possesses a canal raphe. The “pseudosepta” seen with light microscopy are actually fibulae. Based on this information, *A. vallus* has been transferred to the genus *Denticula* as *Denticula vallus* (Nikolaev) Sullivan. This species is morphologically quite similar to *D. neritica* Holmes & Croll but differs in its lack of longitudinal ribs parallel to the raphe sternum. The two taxa can not be distinguished under LM. *Denticula vallus* and *D. neritica* have been collected in abundance from seaweeds, seagrasses, and sea birds.

INTRODUCTION

Nikolaev (1969) first described *Anaulus vallus* as an epiphyte on the red alga *Cytoseira crassipes* (Turner) C. Agardh and the brown alga *Sargassum* sp. from Valentin Bay in the Sea of Japan. Six light micrographs were provided which showed a hyaline diatom possessing rectangular frustules with rounded corners and linear-lanceolate valves with numerous transverse pseudosepta that gave the valve a segmented appearance. The pseudosepta were broadest at mid-valve and decreased in their transapical width toward the valve apices. No further details of the valve structure could be discerned. It was noted that living cells formed ribbon-like colonies and single cells were rare. Based on this information and the fact that scanning electron microscopy (SEM) had only rarely been applied to the study of diatoms at the time, Nikolaev's generic placement was quite logical.

Since Nikolaev's (1969) original description of *Anaulus vallus*, it has only been reported once, by Medlin (1981) from the stipe of the laminarian alga *Pterygophora californica* Ruprecht in Whale Cove, Oregon. Medlin provided a light micrograph of a valve at the lower end of the size range for *A. vallus* possessing only 4 pseudosepta.

Holmes & Croll (1984) described two new diatom species epizoid on body feathers of diving sea birds from California, one of which was *Denticula neritica*. Their light micrographs show valve and girdle views of a diatom morphologically similar to larger specimens of *A. vallus*. Observations with SEM and transmission electron microscopy (TEM) revealed that a central canal raphe was present and hence the placement of the new species in the genus *Denticula* Kützting. Holmes & Croll did comment, however, that “a resemblance of this taxon in LM to *Anaulus vallus* illustrated by Medlin (1981) collected from the Oregon coast is evident.”

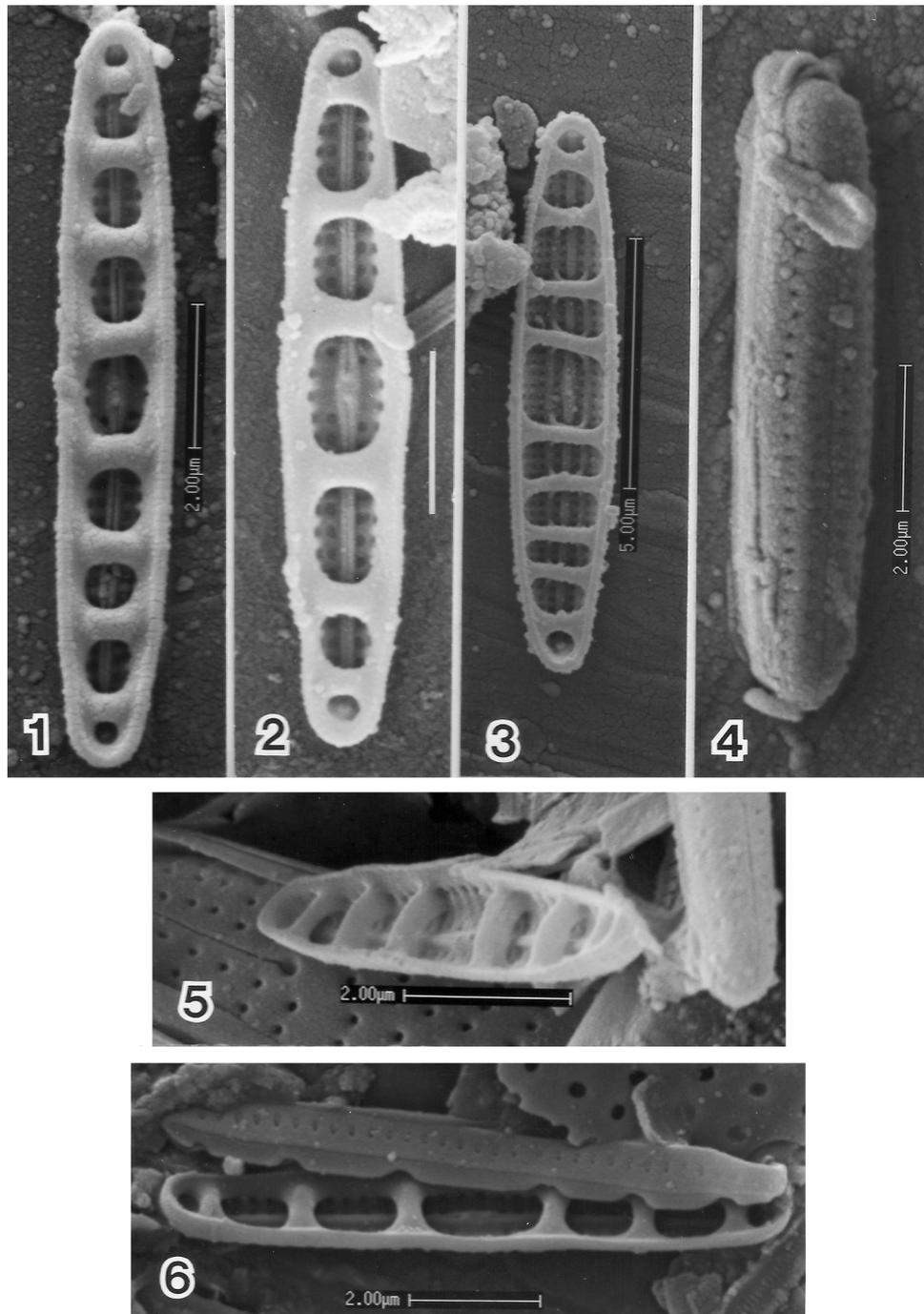
In May 1991 storms in the Gulf of Mexico blew large floating mats of the pelagic brown algae *Sargassum fluitans* Børgesen and *S. natans* (Linnaeus) Gaillon into Mississippi Sound. The author made collections of this material from Petit Bois Pass between Petit Bois and Horn Islands to study its epiphytic diatom flora. LM observations revealed that the dominant diatom was *Cocconeis diruptoides* Hustedt but a taxon similar to *Anaulus vallus* was an abundant form. Subsequent SEM observations revealed that these specimens possessed a canal raphe and hence *Anaulus* would be an inappropriate generic placement. The same sequence of events transpired in the author's later examination of the epiphytic diatom flora of the seagrass *Zostera marina* Linnaeus from Sequim Bay, Washington. In the present paper *Anaulus vallus* is formally transferred to the genus *Denticula*, and its relationship with *D. neritica* is evaluated.

MATERIALS AND METHODS

Original material of *Anaulus vallus* from the type locality in the collection of V A Nikolaev was obtained by the author. Part of the material was mounted in Hyrax for LM observations and part was examined in a Cambridge Stereoscan 360. Preparation of the *Sargassum* and *Zostera* materials described above for LM and SEM was as described in Sullivan (1983).

RESULTS

Examination of the type material of *Anaulus vallus* (Figs 7, 8), as well as the *Sargassum* and *Zostera* materials, with differential interference contrast optics (63x, NA = 1.4) revealed only valve and frustule shape and the number and position of the “pseudosepta”. All specimens were indistinguishable from those illustrated with LM by



Figs 1-6. – *Denticula* species, SEM. Scale bar = 2 μm (Fig. 2). Figs 1, 2, 4, 6, *Denticula vallus*, type material, Valentin Bay, Sea of Japan. Figs 1, 2, Internal valve views showing fibulae, raphe sternum and central pores, and helictoglossa at each pole. Fig. 4, External view of valve with attached valvocopula. Note filiform raphe flanked by areolae. Fig. 6, Internal view of valve with detached valvocopula. Note single row of areolae on *pars exterior* and that fibulae of valve fit into notches of *pars interior*. Fig. 3, *Denticula neritica*, Petit Bois Pass, Mississippi Sound. Internal valve view showing longitudinal ribs parallel to raphe sternum which fuse with overlying fibulae of canal raphe. Fig. 5, *Denticula* sp., Sequim Bay, Washington. Internal valve view showing thin, wafer-like fibulae forming archways over raphe.

Medlin (1981, Fig. 7) and Holmes & Croll (1984, Figs 38, 39). Under conditions of optimal resolution a line running along the apical axis of the valve could barely be discerned (Fig. 7 this paper; Fig. 38 in Holmes & Croll 1984). However, based on LM observations it is unclear

whether this line is a rib or a raphe. Length and width of specimens from the type material of *A. vallus* fell within that listed in its protologue (8-20 μm and 1.5-2 μm , respectively).

SEM observations of type material of *Anaulus vallus*

(Figs 1, 2, 4, 6) clearly show that a raphe is present. The raphe is straight, centrally positioned on the valve face, and is set within a narrow but conspicuous sternum. The central raphe endings are close to one another on a slightly enlarged central nodule, whereas the polar endings are present as small helictoglossae (Figs 1, 2, 4). The “pseudosepta” of the LM are in fact fibulae so that a canal raphe is present (Figs 1, 2). The number of fibulae per valve is 4-9 but the most common number appears to be 6. Usually an even number of fibulae is present. Interspaces between the fibulae are quadrate with rounded corners, except those at the valve ends where they are circular. Valvocopulae were the only components of the cingulum to be observed and these appear to be open at one end (Fig. 6). The *pars interior* is notched and it is clear that the fibulae of the valve fit into these notches in intact frustules. There is a single row of areolae on the *pars exterior* with a density of 36 in 10 μm . The density of areolae on the valve was determined as 36-50 in 10 μm .

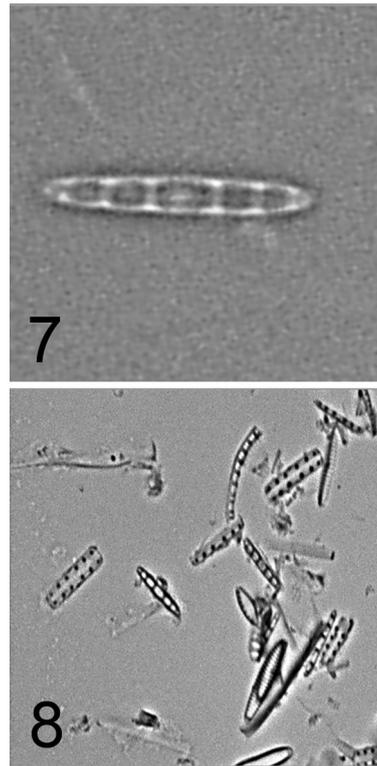
DISCUSSION

Based on the presence of a canal raphe, valve shape, and structure of the valvocopula, the following transfer is proposed:

Denticula vallus (Nikolaev) Sullivan comb. nov.

Basionym: *Anaulus vallus* Nikolaev 1969, p. 30, pl. 1, Figs 3-8

Holmes & Croll (1984) had reservations about the generic affiliation of their morphologically similar species *Denticula neritica*. The structure and arrangement of the girdle bands and centric arrangement of perforations in the hymenate pore occlusions were cited as differences between *D. neritica* and other *Denticula* taxa. In their circumscription of the genus, Round *et al.* (1990) wrote that the more advalvar girdle bands may possess a single row of transverse puncta and the valvocopula often extends beneath the fibulae to form septum-like structures; these features are present in the valvocopula of both *D. vallus* and *D. neritica*. In order for the latter to occur, the valvocopula would have to be notched to accommodate the fibulae. With regard to the pore occlusions in *Denticula*, Round *et al.* stated further that hymenes are present and Mann (1981) listed *D. tenuis* Kützing amongst those taxa possessing a hexagonal arrangement of the perforations of the hymenes rather than a centric arrangement as reported for *D. neritica* by Holmes & Croll (1984). It can only be stated here that the valve areolae of *D. vallus* appear to be occluded by hymenes but the perforation pattern is unknown. However, the arrangement of the perforations in the generitype *D. elegans* Kützing is also unknown to the author.



Figs 7, 8. – *Denticula vallus*, LM, type material, Valentin Bay, Sea of Japan. Fig. 7, Valve view 9 μm in length. Fig. 8, Several valve and girdle views. Valve view left of center is 9 μm in length.

Initial reservations of the author concerning generic placement included the central position of the canal raphe and the ecology of *Denticula vallus*. Round *et al.* (1990) described the canal raphe of *Denticula* to be nearly central to moderately eccentric; hence, the central position seen in *D. vallus* is only a matter of degree. Round *et al.* also stated that *D. neritica* is the “only marine, true *Denticula*”. The author has repeatedly found *D. subtilis* Grunow to be abundant in salt marsh sediments where salinity of the interstitial water may often exceed that of seawater. Therefore, as with the genus *Nitzschia* Hassall, *Denticula* as presently circumscribed includes freshwater, brackish water, and marine representatives. As stated by Holmes & Croll (1984), the significance of the differences between *D. neritica* (and I would add *D. vallus* as well) and other *Denticula* species is unknown at present and more detailed studies may lead to the erection of a new genus.

Denticula vallus and *D. neritica* appear to be two independent taxa. In the latter taxon there is a rib on each side of the raphe sternum that is lacking in the former taxon. Specimens collected by the author from floating mats of *Sargassum* in Petit Bois Pass, Mississippi Sound (Fig. 3) seem to be best classified as *D. neritica* (compare with Figs 45, 46 in Holmes & Croll 1984) as longitudinal ribs parallel to the raphe sternum are present. These ribs apparently fuse with the overlying fibulae to produce a

canal raphe more reminiscent of that in *Denticula* than that found in *D. vallus*.

A third taxon in this group may be represented by the specimen shown in Fig. 5, which was collected from leaves of the seagrass *Zostera marina* in Sequim Bay, Washington. It lacks the longitudinal ribs found in *Denticula neritica* but its thin, wafer-like fibulae contrast greatly with the highly prominent, septum-like fibulae of *D. vallus*. Therefore, it is probably best to identify this taxon as *Denticula* sp. for the present time.

The distribution of *Denticula vallus* and *D. neritica* is problematical because they can not be identified in LM. It is possible that both may be widely distributed epiphytic species in coastal marine waters, in some cases constituting a significant portion of the diatom assemblage. The type locality of *D. vallus* is the cold waters of the Sea of Japan (Nikolaev 1969) where it is epiphytic on seaweeds. Medlin (1981) reported *Anaulus vallus* as the second most abundant diatom (relative abundance = 13 %) on the stipe of the brown alga *Pterygophora californica* from Whale Cove, Oregon, but only LM was used in the identification. Holmes & Croll (1984) stated that numerous specimens of a diatom similar to *A. vallus* were present on the surfgrass *Phyllospadix* W J Hooker from Seal Rock, Oregon on a slide prepared by L Morris.

In warmer waters, Carpenter (1970) examined the epiphytic diatom assemblages of *Sargassum fluitans* and *S. natans* collected from seven stations in the western Sargasso Sea. His Fig. 1L shows a girdle and valve view of a diatom identified as *Navicula* sp. which is in all likelihood either *Denticula vallus* or *D. neritica*. He reported that a raphe was clearly seen with TEM but could not be resolved with LM. He further reported that 9-11 "craticula" per valve were present which are interpreted here as fibulae. The highest relative abundance of this form was 21 % in a *S. natans* sample. The author wrote to Dr Carpenter requesting slides and material but unfortunately both had been lost. In nearby waters *D. neritica* was the second most abundant diatom (relative abundance = 16 %) epiphytic on the pelagic brown alga *S. fluitans* in Mississippi Sound.

The type material of *Denticula neritica* was given as abundant diatom growths on the body feathers of diving sea birds from California by Holmes & Croll (1984). It

was listed as a dominant taxon so this taxon is apparently equally at home on animal substrata. Whether or not *D. vallus* has also adopted an epizoic habit is at present unknown. It is hoped that the present communication will result in additional records of these widespread epiphytic and epizoic marine diatoms.

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