



The trouble with *Adineta vaga* (Davis, 1873): a common rotifer that cannot be identified (Rotifera: Bdelloidea: Adinetidae)

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My purpose here is to highlight three long-standing problems in the taxonomy of *Adineta vaga* (Davis, 1873) and its subspecies: 1. The lack of unique morphological criteria to identify the morphological variant (morphovariant) Davis described; 2. The lack of an evolutionarily meaningful subspecies definition applicable to parthenogenetic bdelloid rotifers; 3. The lack of compliance with the applicable articles of the International Code of Zoological Nomenclature (ICZN; <https://tinyurl.com/y8f242an>) when subspecies are assigned to *A. vaga*.

Donner (1965) considered *A. vaga* to be the most common and cosmopolitan species in the genus. There are indeed many published records of it from various habitats. Several studies on the genetics of speciation of bdelloids have also used *A. vaga* as a model species (for example, Mark Welch & Meselson, 2000; Fontaneto *et al.*, 2011). Therefore, it is necessary to clear the taxonomic standing of this species not only to develop a more accurate picture of the zoogeography and the ecology of bdelloids, but perhaps also to assure the reproducibility of laboratory studies.

Adineta vaga (as *Callidina vaga*) was the first described bdelloid species characterized by a flat ciliated surface covering most of the ventral head (Fig. 1A); most other bdelloids carry on their heads a pair of ciliated disks. Although Davis's (1873) description was quite detailed in comparison with the contemporary descriptions of bdelloids, it is inadequate to help us recognize the morphovariant he had found, because Davis combined accurate and inaccurate observations and left out some of the traits now considered significant for the delineation of *Adineta* species (Örstan, 2018). For example, although remarkably Davis saw the rakes, which can be difficult to make out even with modern microscopes using the traditional brightfield illumination, he did not mention the number of denticles on them. His drawing shows seven denticles on one rake and six on the other (Fig. 1A). Asymmetric rakes are occasionally observed (Örstan, 2018), but it is not clear if Davis's drawing was meant to be a realistic rendition of the rakes. Davis neglected to describe the morphology of the spurs and to mention if the rostrum had setae, two traits that are taxonomically significant. Moreover, his claim that there was an unciliated median band on the ventral surface of the head was incorrect (Fig. 1A) and it is uncertain if he measured the lengths of his specimens (0.5–0.7 mm) correctly.

Subsequent authors contributed very little to make the identification of *A. vaga* more definite; they, in fact, added mostly contradictory information and opinions. For example, Hudson (in Hudson & Gosse, 1889) was uncertain about the presence of rakes in his *Adineta* specimens. Plate (1889) did see the rakes of a smaller morphovariant he identified as *A. vaga* (lengths, 0.28–0.34 mm) and counted “about five” denticles on them. Plate determined correctly that the ventral surface of the head was uniformly covered with cilia and showed setae exiting the rostral lamella in his drawing.

To make matters worse, Bryce (1893) introduced two varieties that have since been relabeled as subspecies. *Adineta v. major* was a large rotifer with a broad head, a distinct rostral lamella and posterior trunk pseudosegments sharply divided from each other; *A. v. minor* was smaller with an inconspicuous rostral lamella and trunk pseudosegments that decreased in width gradually. Later, Bryce (1897) added that the head of *A. v. minor* was elongated and claimed (apparently based on personal communication with Davis) that what Davis had described was *A. v. minor*. But this agreed neither with Davis's drawing (Fig. 1A), where the length and the width of the head were about the same, nor with the dimensions Davis gave. The majority of the described *Adineta* species are smaller than 0.5 mm and thus, one would not associate Davis's rather large morphovariant with a “minor” variety. Bryce never provided actual dimensions or drawings of these varieties. Weber (1898) published a drawing of what he thought was *A. vaga major* with the lengths of 0.5–0.6 mm. Thereafter, nothing significant appeared in the literature to contribute to the identification of *A. vaga* and its subspecies until Donner's monograph of 1965.

Donner (1965) provided drawings of morphovariants that he claimed represented *A. vaga minor* without explaining

his reasoning other than stating that the subspecies was the most common one. One of his morphovariants had long setae exiting its rostral lamella, while another did not have any; two morphovariants had short spurs, while a third one had long ones. Thus, by lumping different morphovariants under one subspecies name, Donner further confounded the issue.

Because of these shortcomings, it is difficult to accept Donner's drawings as being representative of Davis's or Bryce's morphovariants. When the associated uncertainties are taken into account, all descriptions and drawings of *A. vaga* and its subspecies from Davis (1873) to the present, apply equivocally to several *Adineta* morphovariants. Three examples are in Figs. 1B–D. Their body lengths, 330 µm to 490 µm, form a range more often encountered than that Davis gave for his specimens. We cannot pick one of them (or another morphovariant) with reasonable certainty as the one Davis described. Nor can we lump them all under *A. vaga*. A genetic analysis of specimens morphologically identified as *A. vaga* (without separation into subspecies) found 36 independently evolving entities (Fontaneto *et al.*, 2011). If each entity had one unique morphological trait, there would be 36 morphovariants. How would we decide which one was Davis's morphovariant? And which subspecies would it be?

Several species concepts applicable to sexually reproducing animals, for example, biological (Mayr, 1963) and genotypic cluster (Mallet, 1995), have proposed about the same definition for subspecies as geographically circumscribed populations that are morphologically and genetically distinct from other populations but with which they can interbreed in contact zones. Likewise, under the general lineage species concept (de Quieroz, 2007), two diverging populations of a species, before they turn into separately evolving lineages, may go through potentially interbreeding intermediate stages that may be labelled as subspecies (Braby *et al.*, 2012). Because bdelloids are asexual, any definition incorporating interbreeding is inapplicable to them. The species (not subspecies) of bdelloids may be defined as independently evolving populations phenotypically (and ultimately, genetically) different from other populations. The phenotypic cohesion of a bdelloid population is maintained not by gene exchange, but by genetic drift and selection (Templeton, 1989). However, in the absence of gene exchange, there does not appear to be an intermediate stage of a diverging bdelloid population that may be considered to be a subspecies of the original population (Örstan & Plewka, 2017).

Adineta v. minor and *A. v. major* indeed appear to be morphologically sufficiently unique to have been described as species (for brevity, I have left out two additional subspecies, *A. v. tenuicornis* Bryce and *A. v. rhomboidea* Bērziņš). However, the continuing use of the subspecies name *A. v. minor* in surveys (for example, Song & Lee, 2019) and the species name *A. vaga* in genetic studies (for example, Fontaneto *et al.*, 2011) is not only confusing but it also does not conform to the ICZN. If *A. vaga* is to have subspecies, then the ICZN Article 47.1 requires that the nominotypical subspecies Davis described be designated *A. vaga vaga*. But this name is rare in the literature; Donner (1965) did not use it and the only recent use of it that I know of was in a list of bdelloids recorded from Antarctica (Velasco-Castrillón *et al.*, 2014). Moreover, if we accepted Bryce's (1897) assertion that *A. v. minor* was in fact what Davis had described, then *A. v. minor* would become a junior synonym of *A. v. vaga* (ICZN Article 23.1). Otherwise, *A. v. vaga* and *A. v. minor* would remain separate subspecies, although it is not clear how they differ morphologically from each other.

To the problems I have discussed, I offer the following solutions:

1. Consider *A. vaga* an unidentifiable species and stop assigning the name to *Adineta* morphovariants. This would not have as drastic consequences as we might initially think. Because the majority of the literature records and the experimental studies give no pertinent drawings or morphological information, one cannot tell which morphovariant was identified as *A. vaga* anyway.

2. Otherwise, redescribe *A. vaga* by developing an unambiguous morphological (and molecular) characterization of it. Any *Adineta* population considered morphologically close to the original description may be used for the redescription. But if it is desired to fix the name *Adineta vaga* on a neotype, the requirements of the ICZN Article 75.3 must be met and the neotype specimen must come from an *Adineta* population at or near the original type locality, which Davis (1873) gave as the “stone vases in the grounds of Lord Osborne's house near Blanford [England]”.

3. Do not use the subspecies category with bdelloids, because, as I have argued, there is no current subspecies definition applicable to them. Redescribe the existing subspecies as separate species while complying with the ICZN.

4. If subspecies are retained, develop an evolutionary definition to guide taxonomists in determining whether a new bdelloid morphovariant may be described as a new species or a subspecies. Revise the existing subspecies accordingly and in compliance with the ICZN, especially the Articles 23 and 47.1.

Until these issues are resolved, I urge those considering to assign the name *Adineta vaga* or the names of any of its subspecies to a bdelloid morphovariant to take into account the arguments presented here.

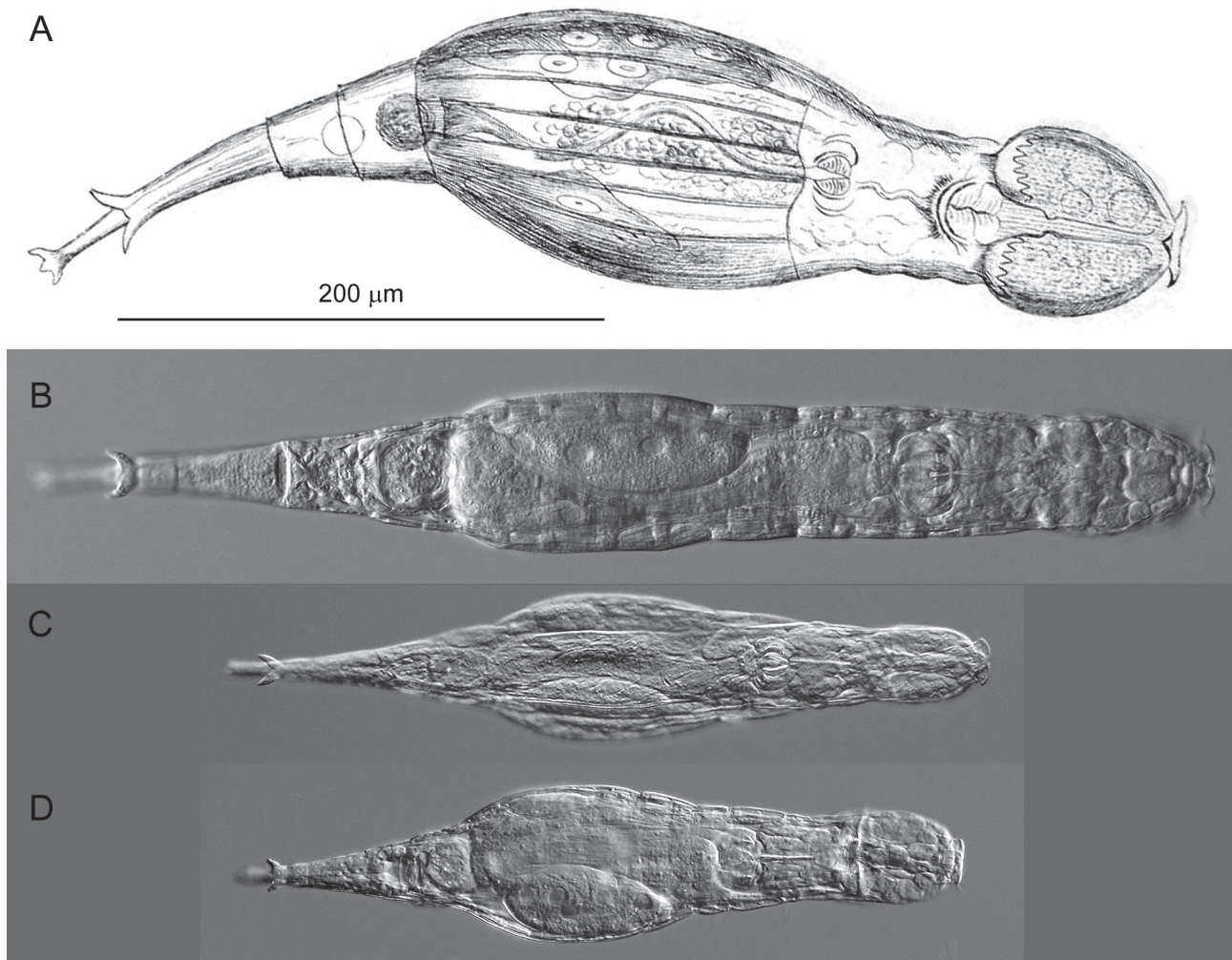


FIGURE 1: The original drawing of *Adineta vaga* by Davis (1873) compared to three undescribed morphovariants (original photographs). Davis's specimen was assumed to be 0.5 mm long and the other specimens were scaled proportionately. A, rake denticles 6–7, spurs medium, stone vase (England); B, denticles 7–7, spurs long, birdbath (USA); C, denticles 5–5, spurs long, outdoor container (USA); D, denticles 6–6, spurs short, moss (Canada).

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