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Ulnaria asymmetrica sp. nov. (Bacillariophyta), a new fossil species from the Trout Creek Miocene locality, Oregon, USA

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A new species of *Ulnaria* (Kützing) Compère is described from the Miocene Trout Creek fossil locality, situated in Harney County, Oregon, USA. The rock material from which the new species is described consisted of a subsample taken from the matrix harboring a plant fossil collected in 1932 or 1933 and archived at the Field Museum of Natural History, Chicago, Illinois, USA. The new species differs from all other taxa in the genus by possessing club-shaped valves that are asymmetric about the transverse axis, and frustules that are cuneate-shaped in girdle view. In addition to its unique shape, valves of the new species have a well-developed ocellulimbus (pore field) at each apex, a single rimoportula at one or both poles and closed girdle bands. The virgae are thick relative to the vimines, areolae possess exterior closing plates, and on larger specimens, the uniseriate striae can become biseriate near the valve margins. Material at the Trout Creek locality was deposited approximately 15.6–14 Ma during the Middle Miocene Climatic Optimum (MMCO). Given the diatom species co-occurring with the new *Ulnaria* species, it likely inhabited the plankton.

Keywords: *diatoms, fossil, Fragilaria, Miocene, Synedra, Trout Creek, Ulnaria*

Introduction

The complex taxonomic histories of the diatom genera *Synedra* Ehrenberg, *Fragilaria* Lyngbye and *Ulnaria* (Kützing) Compère are well documented and detailed by Compère (2001). Part of the taxonomic difficulty centers around *Synedra ulna* (Nitzsch) Ehrenberg and species deemed to be closely related to it, and the legitimate typification of the genus *Synedra*. In 1991, Lange-Bertalot (in Krammer & Lange-Bertalot 1991) believed *S. ulna* belonged in the genus *Fragilaria* and proposed the new subgenus *Alterasynedra* of *Fragilaria* to accommodate it and related taxa. Other authors (e.g. Round et al. 1990) argued that this group of species belonged to a genus separate from *Fragilaria*. However, Compère (2001) noted that because the genus *Synedra* is lectotypified by *S. balthica* Ehrenberg, and not by *S. ulna* as noted by some authors, that the latter species and the collection of related species could not be included in *Synedra*. As a result, Compère (2001) raised *Fragilaria* subgenus *Alterasynedra* to the rank of genus as *Ulnaria* (Kutzing) Compère and typified it with the species, *S. ulna* (Nitzsch) Ehrenberg.

Just like the complicated taxonomic history, the characters used to delineate *Ulnaria* from other genera, especially *Fragilaria*, can be confusing due to differences between diatomists (Zakharova et al. 2023). Williams (2011) and Liu et al. (2019) outlined three primary morphological characters that in their view represent synapomorphies for *Ulnaria*. The first is the relationship between the sternum, virgae and vimines. Second, is the presence of closed girdle elements. Third, are the features of the ocellulimbus, deemed more complex than the pore fields of *Fragilaria* taxa, including how it is fitted like a plate into the valve. These are the primary characteristics, along with details of the striae and closing plates, that were used in this study to make a generic determination and placement for an undescribed freshwater Miocene fossil species. The usefulness of these characters has recently been, and will undoubtedly continue to be, tested relative to molecular data (Morozov et al. 2023, Zakharova et al. 2023).

Currently, 82 species and subspecific taxa of *Ulnaria* are recognized (Guiry 2022). Of these, six taxa originally described as varieties of *U. ulna* have been elevated to the rank of species. None of the currently described species possess valves that are asymmetric about the transverse axis, nor have any been reported to be cuneate in girdle view. The objective of this communication is to describe a Miocene fossil species of *Ulnaria* that has distinctly club-shaped valves and frustules that are wedge-shaped in girdle view.

Sample and site information

The type material used in this investigation consisted of a small chuck of the rock matrix taken by P.A. Siver on

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31 May 2018 from a macro plant fossil specimen archived in the paleobotanical collection at the Field Museum of Natural History (FMNH), Chicago, IL, USA. The Miocene plant fossil, Sample FMNH UC 40854/UP 400, of an immature *Quercus* acorn with stem, was collected from the Trout Creek locality, Harney County, Oregon, by Percy Train in either 1932 or 1933 and archived at the Field Museum. The subsample is archived as Field #75 in P.A. Siver's collection.

The Trout Creek locality, situated in southeastern Oregon, has been extensively studied for its flora (Arnold 1937, Graham 1963, 1999) that dominated the region near the peak of the Middle Miocene Climatic Optimum (MMCO) approximately 15.6–14 Ma (Dillhoff et al. 2009, Nash & Perkins 2012). The MMCO was the warmest period since the Late Eocene and was represented by wet temperate forests with abundant lakes and cypress swamps in lowland regions. This was also a time period of intensive volcanic activity over a large portion of western North America, with lava and ash blocking streams and rivers resulting in the formation of numerous lakes, including at the Trout Creek site (Graham 1963, Nash & Perkins 2012). The sedimentary basins of many of the lakes, including ones from Sucker Creek, Mascall, Latah, Virgin Valley and Trout Creek, filled with lake sediment, watershed inputs, and sometimes deposits from other volcaniclastic events (Nash & Perkins 2012). The deposits contained remains of plants, animals, and lake microbes that fossilized, yielding a window into the MMCO period. Many of the lakes harbored extensive growths of diatoms over extended time periods, yielding diatomite deposits. Arnold (1937), who based his study on Train's collections, noted multiple diatomite layers ranging from 'a few inches to six feet or more in thickness separated by zones of weathered volcanic ash.' It is not known from which of these diatomite beds the sample (Sample 40854 UP400 W.C.) was taken, but all of the beds are representative of the MMCO period as noted above. Although Train believed that the Trout Creek locality represented an outcrop of the Mascall Formation, it is now known to be a separate formation also of MMCO age, and closely related to the Virgin Valley Formation (Nash & Perkins 2012).

Materials and methods

Chips (100–200 mg) of the Field #75 diatomite subsample were oxidized using 30% H_2O_2 under low heat for 1–2 h, rinsed a minimum of five times with distilled water, and the resulting slurries stored in glass vials at 4°C. This procedure resulted in the separation of numerous siliceous microfossils, including many diatoms, from the rock matrix. Although many specimens of the new species were uncovered from every chip processed, the valves were always broken. As a result, a second more gentle procedure was employed where a lower heat level was used and the sample allowed to settle between washings. Although this resulted in a higher percentage of larger valve fragments, whole valves were not uncovered. Lastly, direct examination of fragmented rock chips also did not yield views of whole valves.

One-ml aliquots of the clean slurries were air dried onto flat pieces of heavy-duty aluminum foil, trimmed and attached to aluminum stubs with Apiezon wax. Samples were coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and examined with a FEI Nova Nano SEM 450 field emission SEM. Additional aliquots were air-dried onto circular cover glasses, mounted onto glass slides using Naphrax, and examined with a Leica DMR light microscope equipped with a Zeiss Axiocam 506 color camera.

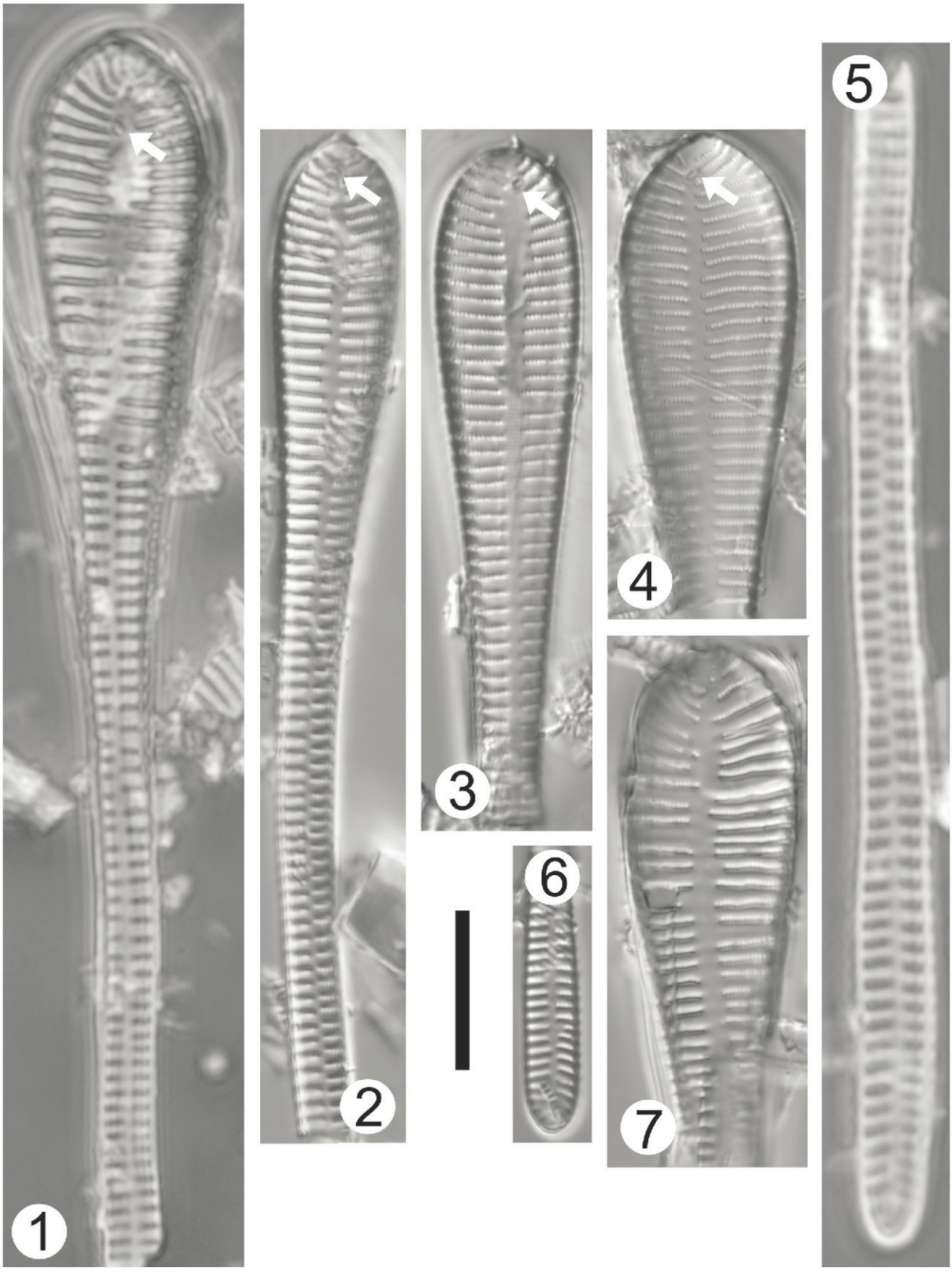
Morphometric measurements of the diameter of the head pole, foot pole and width of the narrow portion of the valve were made directly from SEM images. Stria density (the number per 10 μm) was measured both with the Leica light microscope and from SEM images.

Results

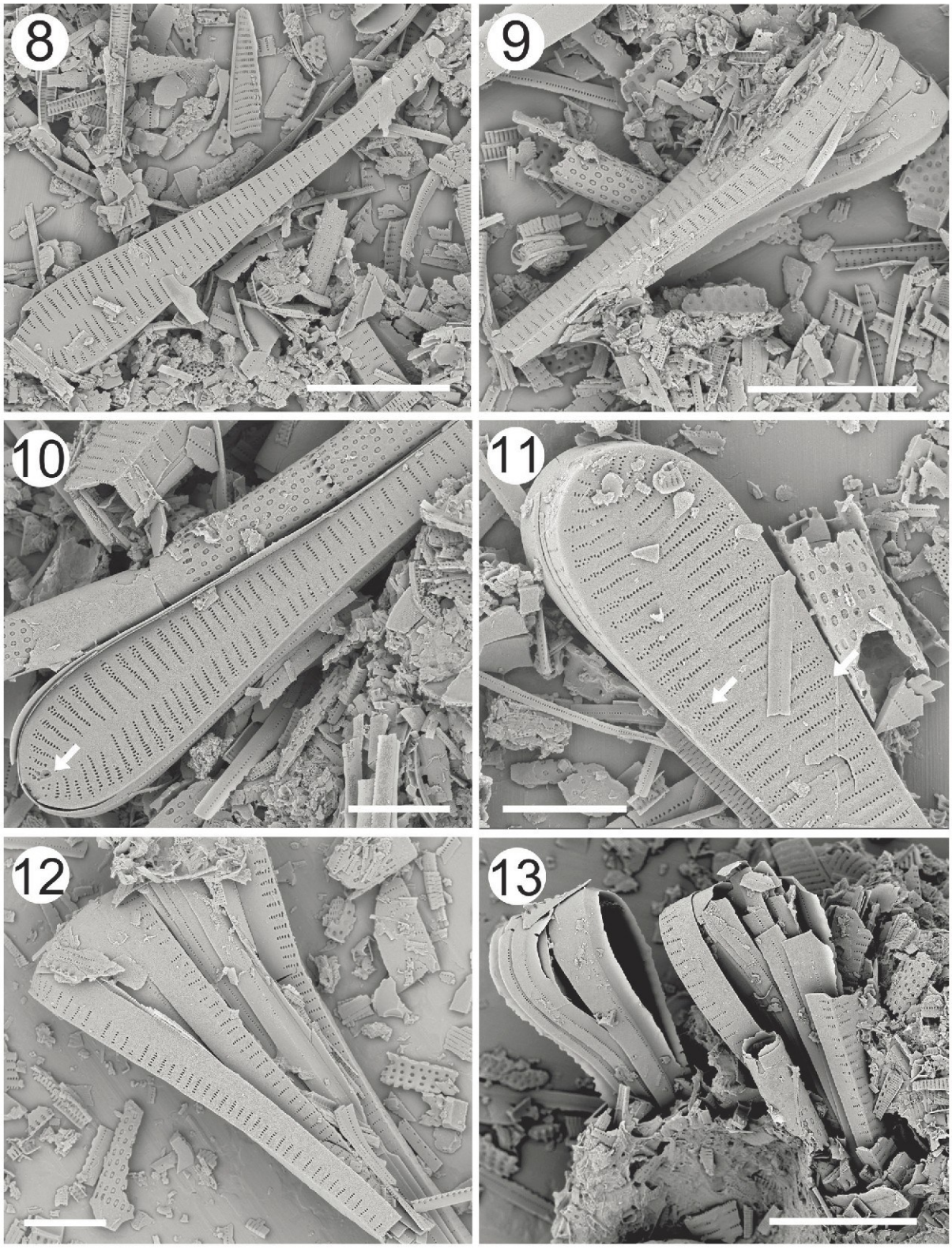
The rock matrix containing the plant macrofossil collected from the Miocene Trout Creek locality and archived at the FMNH (FMNH UC 40854/UP 400) contained numerous siliceous microfossils, mostly of diatoms. Remains of one taxon, an araphid pennate with a bulbous, club-shaped apical end (head pole) and a much narrower and rounded posterior end (foot pole), was a common element of the diatomite rock material. The fossil taxon represents a new-to-science species and is described below.

Ulnaria asymmetrica Siver sp. nov. Figs 1–19.

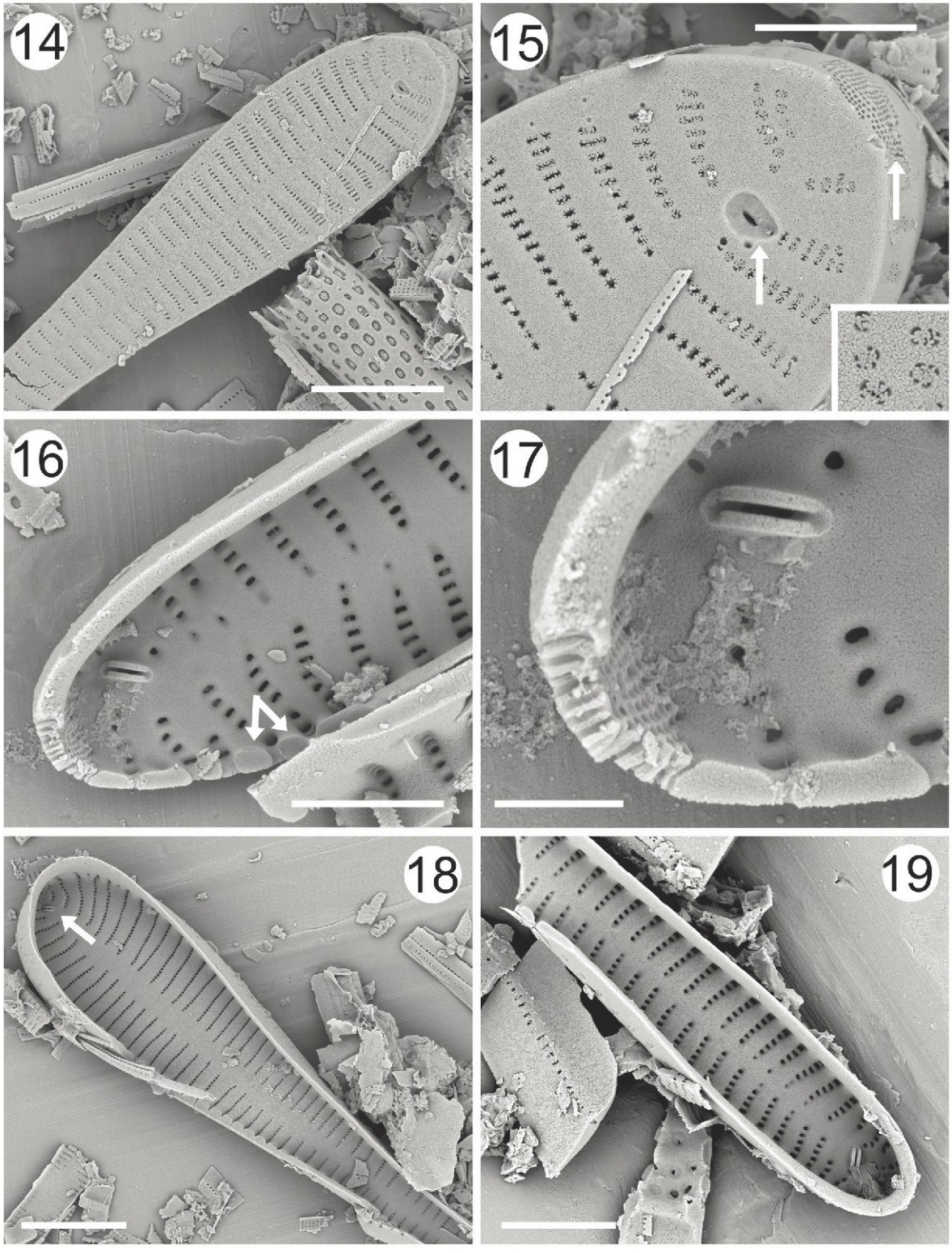
Description: Valves araphid, club-shaped, asymmetric about the transverse axis, with a wide capitate head pole (Figs 1–4, 7–11, 14–15), a slender shaft, and foot pole with a diameter similar to that of the shaft (Figs 5–6, 16, 19). Valves form a distinct right angle with the mantle (Figs 9, 11–12). In the girdle view, frustules are cuneate (wedge-shaped), asymmetric about the transverse axis, and widest at the head pole (Figs 9, 12). The diameter of the head and foot poles ranged from 7.1 to 14.7 μm and 2.7 to 5.0 μm, respectively. The mean diameters of the head pole, foot pole, and width at the middle of the valve shaft are 12.3 μm (n = 16), 4.1 μm (n = 10) and 3.8 μm (n = 10), respectively. The axial area, or sternum, is relatively wide, and of equal diameter throughout (Figs 10, 18). Striae are widely and equally-spaced, perpendicular to the apical axis, parallel, and with a density of 7–10 per 10 μm (mean = 8.4, n = 21) (Figs 8–11). Striae are interrupted at the valve margin, then continue onto the mantle. The vimine are evenly-spaced and much smaller than the virgae (Figs 16–17). Striae are uniseriate next to the axial region, and externally become elongated or biseriate at the valve margin on the head pole (Figs 10–11, 15). Areolae are open internally and covered externally with a



Figs 1-7. Light micrographs of *Ulnaria asymmetrica.* **Figs 1--4,** 7. Broken valves containing the wide capitate head pole portion, and various lengths of the slender valve shaft ranging from approximately 50)Iiii in length (Fig. 1) to a few microns (e.g. Fig. 4). The arrows in Figs 1--4 indicate the position of the rimoportula. Fig. 4 represents the holotype. **Figs 5-6.** Portions of valves containing the narrow foot pole and the slight increase in width relative to the slender shaft. Scale bar = 10)I!II.



Figs 8-13. Scanrting electron micrographs of *Ulnaria asymmetrica.* **Figs 8, 10--11.** External valve views depicting the wide capitate head pole and narrow shaft. Note the wide and evenly-spaced striae, position of the rimoportula (arrow on Fig. 10), and the biseriate nature of the striae near the valve margin (arrow, Fig. 11). **Figs 9 and 12.** Girdle views of specimens showing the cuneate shape of the fiustule and details of the mantle. Note the narrowing of the valve mantle with distance from the head pole. **Fig. 13.** Girdle views of several specimens partially embedded in the original rock matrix. Note the sculptured advalvar margin of the valvocopula that forms the pars interior portion of the band, and the single row of small pores. Scale bars= 10 lilll (Figs 10-12) and 20 lilll (Figs 8-9, 13).



Figs 14-19. Scanning electron micrographs of *Ulnaria asymmetrica.* **Fig. 14.** External view of a head pole. **Fig. 15.** Close-up of the specimen in Fig. 14 showing the depression containing the external opening of the rimoportula (left arrow), the large apical pore field, or ocellulirnbus, (right arrow), and a close-up (insert) of the external vola coverings. **Fig 16.** Internal view of the narrow foot pole. Note the thickened virgae (arrows), rimoportula and ocellulimbus. **Fig.17.** Close-up of the specimen in Fig. 16 showing details of the rimoportula, and the rows of straight pores penetrating the valve wall of the ocellulimbus. **Fig. 18.** Internal view of the head pole, narrowing shaft, and rimoportula (arrow). **Fig. 19.** Internal view of a foot pole with a rimoportula. Note the slight increase in valve width of the foot pole relative to the shaft. Scale bars = 1 lilll (Fig. 17), 3 lilll (Fig. 16), 4 lilll (Fig. 15), 511m (Fig. 19) and 10 lilll (Figs 14, 18).

vola consisting of a series of siliceous rod-like outgrowths attached to the margin of the areolae (Fig. 15). Costae, or virgae, between striae are thickened such that the areolae are slightly sunken from the valve surface both externally and to a greater degree internally (Figs 18–19). The mantle depth is widest at the head pole (mean = 6.7 µm, n = 10) and narrowest on the foot pole (mean = 3.7 µm, n = 10), with a mean ratio of 1.8. A single well-developed rimoportula can be found on either end of the valve (Figs 14–19), that opens externally within a depression (Fig. 15). Each end of the valve possesses a well-developed apical pore field (ocellulimbus), consisting of numerous rows of small poroids (Figs 15–17). Each valve is associated with a wide valvocopula that tapers in width from the head to foot poles. The advalvar margin of the valvocopula is sculptured such as to underlap the end of the valve mantle, forming the pars interior portion of the band (Fig. 13). There is a single row of small pores on the pars exterior adjacent to the pars interior portion, otherwise the band is solid.

Holotype specimen: Portion of a single gathering of cells on the microscope slide labeled 'Field #75, Siver A' archived at the Field Museum of Natural History, FMNH PP62125. The specimen illustrated in Fig. 4 is from the gathering.

Type material: Material taken from the matrix of the plant fossil sample archived at the Field Museum of Natural History, Catalog number: FMNH UC 40854/UP 400, collected by Percy Train in either 1932 or 1933.

Type locality: Outcrop of the Miocene-aged Trout Creek locality, Harney County, Oregon.

Isotypes: The gathering of cells on the microscope slide labeled 'Field #75, Siver 5A' archived at the Canadian Museum of Nature, CANA 131719. The specimen in Fig. 5 came from this gathering. The gathering of cells on the microscope slide labeled 'Field #75, Siver 2A' archived in Siver's personal collection. The specimen in Fig. 1 came from this gathering.

Co-occuring organisms: The diatomite sample is dominated by multiple species of *Aulacoseira*, with *U. asymmetrica* being the next most abundant species. In addition, the sample contains specimens of *Tetracyclus* spp., *Actinocyclus* sp. and chrysophyte cysts, all of which are rare. No synurophyte scales, testate amoeba plates or heliozoan scales were observed.

Further Analysis of Valve Apices: Despite observing literally thousands of broken specimens over multiple years and from numerous samples using both light and scanning electron microscopy, no intact whole valves were uncovered. This was frustrating and problematic. To examine the morphology in more detail, 50 valve apices were evaluated in each of five preparations and classified as having either a clearly swollen and bulbous apex (e.g. Fig. 14) or a rounded apex with a diameter similar to that of the valve shaft (Fig. 19). The ratio of these two apex morphotypes over all 250 specimens was 1.07, supporting a distinctly club-shaped nature of the valve.

Discussion

Because the species-rich genera *Synedra* Ehrenberg (now mostly *Ulnaria*) and *Fragilaria* Lyngbye share many characters, there has been a long and complicated history regarding whether they actually represent separate genera, more than two genera, or perhaps are one large clade (Patrick & Reimer 1966, Lange-Bertalot 1980, Williams & Round 1986, 1987, Williams 2011, Wengrat et al. 2016). Williams (2011) proposed that the presence of closed versus open valvocopulae was an important character that should be used to define a subgroup of species that included the common and widespread species *Synedra ulna* (Nitzsch) Ehrenberg. This subgroup of taxa is now formally recognized under the genus *Ulnaria* Compére (Compère 2001), based in part on the presence of closed girdle bands. Despite not being able to extract whole valvocopula bands from the rock matrix, hundreds of broken valvocopula bands were observed, including pieces that surrounded either the head or foot pole. Since all of the partial bands were solid and lacked openings or ligule, the conclusion is that *U. asymmetrica* possessed closed valvocopulae, supporting inclusion in the genus *Ulnaria* (Williams 2011, Liu et al. 2019).

Two additional synapomorphic characters used to define the genus *Ulnaria* are also found on *U. asymmetrica* specimens. First, is the close topology of the basal valve components, including the sternum, virgae and vimines (Williams & Round 1986, Liu et al. 2019). This is best described as a topology where the virgae are larger than the vimines and merge equally with the sternum, as discussed and illustrated in Figs 19–20 of Liu et al. (2017). Second, is the presence of an ocellulimbus, a plate-like apical pore field consisting of transapical and pervalvar rows of poroids (Williams & Round 1986, Liu et al. 2019). In addition, several short and blunt spines often overhang the apical pore fields on the fossil species, a feature found on other *Ulnaria* species. In summary, specimens of *U. asymmetrica* possess the three synapomorphic traits currently used to define *Ulnaria*, supporting placement into this genus (Williams 2011).

Several additional characters found on the fossil taxon are also thought to be more in line with *Ulnaria* than *Fragilaria*. First, the areolae on *U. asymmetrica* valves possess external closing plates. Although the fine structure of ribs composing the closing plate were broken and missing on some specimens, many specimens with intact structures or partially remaining ribs were observed and represent a vola type of velum. External closing plates are not often reported for *Fragilaria* species, and if they are

they are typically described as delicate and disc-shaped (Round et al. 1990, Almeida et al. 2016). Closing plates are found on *Ulnaria* species and they vary and include different types of vela (e.g. Tuji & Houki 2004, Liu et al. 2017, 2019). A second feature of the fossil taxon is the biseriate nature of the striae observed at the valve margins primarily on the swollen head pole. Other than species subsequently transferred to *Ulnaria*, *Fragilaria* species lack biseriate striae. In contrast, some *Ulnaria* species, for example *U. nyansae* (G.S. West) Williams, *U. goulardii* (Brebisson ex Cleve et Grunow) Williams, Potapova & Wetzel, and *U. oxybiseriata* Williams & Lui, possess partially or whole biseriate striae. To summarize, features of the closing plates and the formation of biseriate striae further support the placement of the fossil species in *Ulnaria*. However, the use of these two characters in defining and distinguishing between *Ulnaria*, *Fragilaria* and other araphid pennate genera needs further study.

Despite the placement of the new fossil taxon in *Ulnaria*, it differs from all other taxa in this genus with respect to valve symmetry, both in valve and girdle views. The club-shaped valves that are asymmetric in transapical view, and the crenate-shape of the frustule in girdle view are unique among *Ulnaria* species. The asymmetry of the valve about the transapical axis is similar to species belonging to the araphid pennate genus *Asterionella* Hassell, and frustules of some members of this genus can have a slightly cuneate-shape in girdle view (Patrick & Reimer 1966, Pappas & Stoermer 2001). In addition, valves of *Asterionella* taxa also possess rimoportulae and apical pore fields. However, unlike the fossil species, *Asterionella* taxa do not satisfy the synapomorphic characters used to define *Ulnaria* (Williams 2011). Specifically, the girdle bands of *Asterionella* species are open, the apical pore field is not of the ocellulimbus type, and the virgae are of similar structure and stature as the vimines. In addition, species of *Asterionella* lack biseriate striae, and either lack areola closing plates or they are said to be 'indistinct' (Round et al. 1990). For these reasons, the fossil taxon is not placed in *Asterionella*. The asymmetry of the frustule, and position of the rimoportula, are also slightly similar to that of the marine taxon *Licmophora* Agardh. However, the overall valve shape, lack of a true ocellulimbus, presence of open girdle bands, and the structure of the areolae are significantly different.

The type material used to describe *U. asymmetrica* was collected in the 1930s by Percy Train (Arnold 1937, Graham 1963). Train collected numerous fossils, most of which were archived at the University of Michigan, and subsequently used to reconstruct the flora of the region (Graham 1999). Some of Train's collections were also archived at the Field Museum of Natural History, including the type material used in this study. The data entry made at the time clearly indicates the collection site as the Trout Creek locality. It further suggests that it is part of the Mascall Formation, which is also a formation of Miocene age. However, subsequent work indicates the outcrop belongs to the Trout Creek Formation, and is a slightly younger deposit than the Mascall Formation (Nash & Perkins 2012). This was further supported by the fact that ash from the Mascall Formation was identified across eight other Miocene outcrops, but not at Trout Creek. Nonetheless, the MMCO age estimate of 15.6–14 Ma for Trout Creek is firmly established (Nash & Perkins 2012). All of the numerous specimens of *U. asymmetrica*, observed in this study, are broken at the narrow part of the valve. Despite this, the specimens are otherwise in excellent condition and exhibit no dissolution.

Based on the remains of other fossil taxa uncovered in the sample, it is likely that *Ulnaria asymmetrica* was a planktic organism. First, *Aulacoseira* spp. were the most dominant organisms in the sample. The *Aulacoseira* found in the Trout Creek sample were some of the same species reported from an extensive diatomite deposit within the Virgin Valley Formation composed of primarily planktic taxa (Siver in press). The Virgin Valley Formation is close to Trout Creek and of the same age (Nash & Perkins 2012). The presence of *Actinocyclus* sp. further supports the idea of a planktic habitat. In an extensive survey of both early and middle Miocene lacustrine localities in the western United States, Bradbury & Krebs (1995) reported *Actinocyclus* to be a dominant constituent of the phytoplankton communities in 70 of 115 sites examined. The collection of Miocene sites containing *Actinocyclus* ranged from small to large waterbodies, slightly acidic to alkaline, and often eutrophic. Bradbury & Krebs (1995) further noted that the waterbodies were likely warm monomictic, ice-free, and often co-dominated with *Aulacoseira*. Lastly, the lack of other microbes typically found in shallower waters or more littoral environments, including euglyphids and heliozoans (Siver & Lott 2023), provides additional support for a planktic habitat. Perhaps *U. asymmetrica* valves attached to one another to form a radial colony as in *Asterionella* or like the linear and zig-zag arrangement in *Tabellaria*.

Although the oldest fossil remains of *Actinocyclus* are marine, and radiation of marine species occurred early in the Miocene (Krebs & Bradbury 1995), the genus had invaded numerous lacustrine waterbodies over an expansive area of the western United States by the middle Miocene. Krebs & Bradbury (1995) list at least 12 obligate freshwater species of *Actinocyclus* in the Miocene deposits they investigated. Given that *Actinocyclus* was a common genus inhabiting freshwater lakes in the Miocene, coupled with the abundance of the obligate freshwater genus *Aulacoseira*, it is concluded that the Trout Creek locality does not include reworked marine sediments.

In summary, *Ulnaria asymmetrica* is a Miocene fossil diatom species with unique valve and frustule symmetries. It was a co-dominant along with *Aulacoseira* spp.

in diatomite uncovered at the Trout Creek locality in southeastern Oregon. The material was deposited near the peak of the Middle Miocene Climatic Optimum (MMCO) approximately 15.6–14 Ma. It will be interesting to see if this taxon, or its descendants, are eventually uncovered at other fossil localities to better appreciate the evolutionary history of this lineage.

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