



Fragilaria odeloucaensis sp. nov. (Bacillariophyta, Fragilariaceae) a diatom from temporary streams in southern Portugal

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Abstract

A new species of araphid diatom is described from a temporary stream in southern Portugal, *Fragilaria odeloucaensis* sp. nov., which belongs to the group of *Fragilaria* with widely linear to lanceolate valve outline, spaced striae, lacking spines, and with well-developed apical pore fields. The new taxon can be distinguished based on five unique features within this group, the lanceolate valves with capitate apices, the zig-zagged axial area, the central area with squared fascia, the apical pore fields clearly sunken into the valve apices and the heterovalvar frustules (with respect to striae distancing). Ecological features of the type locality and an additional sampling point where the new species was found are given, together with a discussion of the taxonomic position of the new species within *Fragilaria*, and the approach used herein for the identification of diagnostic features. This approach includes a detailed analysis of the internal and external characteristics of the axial area-virgae-striae complex, central area, apical pore fields and differences among valves of the same frustule, in addition to the traditional valve shape and morphometric features.

Keywords: Araphid diatoms, drylands, Iberian Peninsula, intermittent streams, taxonomy

Introduction

The recent revision of type material of several species of *Fragilaria* Lyngbye continues to elucidate the taxonomic identity and boundaries of many widely cited taxa (e.g. Tuji & Williams 2006a, b, 2008a, b, Tuji 2007, Heudre *et al.* 2019, Van de Vijver *et al.* 2020a, b, c, 2021a). This clarification has triggered the description of new taxa from different continents (e.g. Lange-Bertalot & Ulrich 2014, Delgado *et al.* 2015, 2016, Wetzel & Ector 2015, Almeida *et al.* 2016, Wengrat *et al.* 2016, Rioual *et al.* 2017, Cantonati *et al.* 2019, Novais *et al.* 2019, Van de Vijver & Ector 2020, Van de Vijver *et al.* 2020b, 2021c, Krahn *et al.* 2021).

The continued description of new taxa within *Fragilaria* shows that the diversity in the genus is higher than previously reported and that this diversity has remained masked due to force fitting and lumping (e.g. Tuji & Williams 2006b, Delgado *et al.* 2015) or because original descriptions still lack the support of detailed light (LM) and scanning electron microscopy (SEM) studies (e.g. Van de Vijver *et al.* 2020b). However, not only the revision of historical materials is yielding new taxa but also the study of material recently collected from regions that were previously studied (Morales 2003, Heudre *et al.* 2018, Cantonati *et al.* 2019, Van de Vijver *et al.* 2021b) or areas that are now receiving attention (Almeida *et al.* 2016, Wengrat *et al.* 2016, Chudaev *et al.* 2021).

In the case of Portugal, new taxa have been found, especially in rivers (Novais *et al.* 2014, 2019, Delgado *et al.* 2015, 2016). These studies have been important contributions in species delimitation since they included re- or new studies of type materials for comparative purposes. Recent research in Portuguese intermittent rivers carried out by

the Water Laboratory from the University of Évora, especially in the southern Alentejo and Algarve regions (Novais *et al.* 2014, 2020), have shown many new araphid taxa, including members of *Fragilaria*, some of which require to be described as new taxa for science.

With climate change and direct human-induced expansion of arid and semiarid regions, which already cover 41 % of the land surface, the study of the hydro-ecological dynamics and biodiversity in temporary streams has become one of the central points in contemporary ecology (Acuña *et al.* 2014, Datry *et al.* 2014, Barbosa *et al.* 2020). Temporary rivers represent about half of the river network at the worldwide level, being dominant in landscapes in southern Europe (Larned *et al.* 2010, McDonough *et al.* 2011). These streams are now being characterized as diversity hot spots for several groups such as algae, arthropods and plants, and due to the ecosystem services they provide (Acuña *et al.* 2014, Datry *et al.* 2018b), aside from water abstraction for different human activities (Datry *et al.* 2014). Since currently at least 1/3 of the human population lives in drylands, where intermittent streams dominate, protection, conservation and management of these systems with sustainability objectives is of outmost importance (Datry *et al.* 2014, 2018a, Bonada *et al.* 2020).

Conditions in temporary streams change dramatically after rain episodes disrupting not only the biological communities that live in them but also all the ecological processes, with the mosaic network of lotic, lentic and terrestrial habitats being in constant change during the wet-dry phase cycles (McDonough *et al.* 2011, Datry *et al.* 2014, Bonada *et al.* 2020). It has been shown that algae in general and diatoms in particular have adapted to these changes through different survival strategies and forming communities with marked spatial and temporal variability (Novais *et al.* 2014, Sabater *et al.* 2016, Várбірó *et al.* 2020). Studies in intermittent streams of southern Portugal showed that diatom communities have a high proportion of still undetermined species for which ecological preferences have not been determined, limiting biomonitoring and bioindication activities (Novais *et al.* 2014, 2020) but also impairing the study of the dynamics of populations and communities, which in turn are important in the determination of the biological functioning of intermittent systems.

Following the analysis of Novais *et al.* (2014), at least 12 % of the diatoms found in Portuguese temporary streams are endangered. But this percentage could be higher given that many of the diatoms identified from these streams are still not included in conservation lists (Lange-Bertalot & Steindorf 1996). This fact, together with the record of several taxa currently in need to be described as new, denotes the limited knowledge of the diatoms in intermittent streams of southern Portugal.

In order to continue with the description of araphid diatoms from southern Portuguese intermittent streams (Morales *et al.* 2021b), a new species is described herein from the Odelouca Stream in the Monchique municipality in the Algarve Region, a tributary of the Arade River in the basin of the same name. LM and SEM are combined for the description of the new taxon and ecological information is presented at the time that morphological features are compared with published information for morphologically related taxa.

Material and methods

Diatoms were collected in spring 2017 (March 20th) from the Ribeira de Odelouca (Odelouca Stream, Fig. 1). Simultaneously with diatom sampling, a thorough hydromorphological characterization of 500 m stretch of the stream (downstream of the sampling point) was carried out, following the River Habitat Survey Methodology (INAG I.P. 2008), including information on the type of substrate and vegetation present in the channel, flow types, land-use within 5 and 50 m of the left and right banktops, vegetation structure in banktops and bankfaces, bank profiles, height of banktop, and other dimensions such as the height above the water surface, channel (bankfull and water) width and depth, and presence of special features, as well as nuisance species and alders.

Water chemistry was determined in situ using the TROLL 9500 PROFILER XP (In-Situ Inc. Fort Collins, Colorado, U.S.A.), at the time the biological samples were collected. Nutrient data are usually collected by the Portuguese Water Agency (APA), but such data are lacking for the sampling date.

Biological samples were collected in the stream following methodology outlined in Novais *et al.* (2020). Five to seven hand-sized rocks were selected randomly and scrubbed with a toothbrush, rinsing with stream water and preserving with formaldehyde (1:1 v/v) right after collection. Aliquots from each sample were oxidized in the laboratory with hydrogen peroxide (35 %) in a sand bath (210 °C) for 36 h after which material was rinsed with distilled water until neutrality (INAG 2008). Permanent slides were mounted in Naphrax and diatom remains were identified to species level using a Leica DMLB light microscope equipped with a ×100 HCX PL APO oil immersion objective (N.A. 1.40)

and a Leica DC 500 camera. A minimum of 400 valves were identified and counted on each slide in order to assess the relative abundance of taxa composing the community (INAG 2008). The identification was based on reference floras (e.g. Krammer & Lange-Bertalot 1986, 1988, 1991a, b, Hofmann *et al.* 2011, Lange-Bertalot *et al.* 2017) as well as recent bibliographic sources, including the series “Diatoms of Europe”, “Iconographia Diatomologica”, “Bibliotheca Diatomologica” and relevant taxonomic papers, such as Reichardt (1997), Van de Vijver *et al.* (2011) and Novais *et al.* (2011).

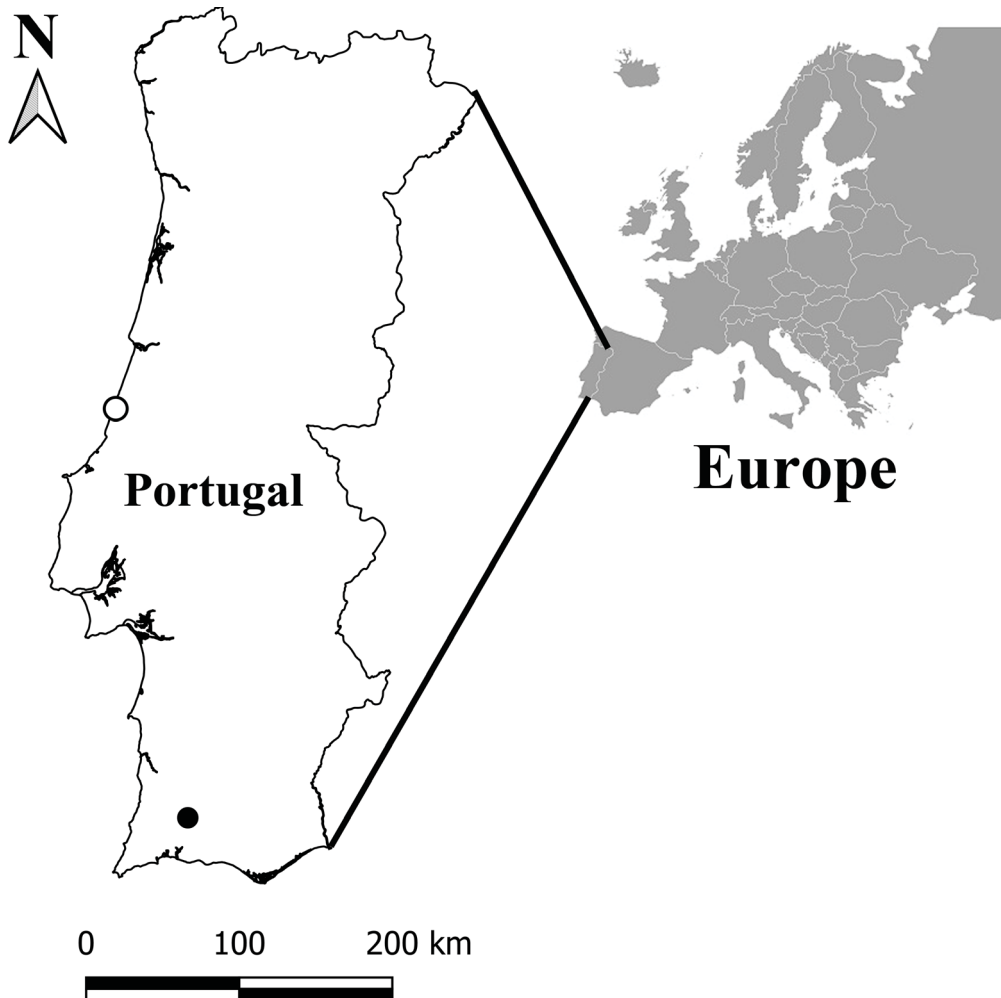


FIGURE 1. Location of type locality, Odelouca Stream, in southern Portugal. Black dot denotes the type locality: Odelouca Stream, Monchique Council, Algarve region. Open circle corresponds to St. Pedro stream in the Center Region of Portugal.

For SEM analysis, a portion of the oxidized material was rinsed with deionized water over a 3- μ m pore glass fiber filter and coated with platinum using a BAL-TEC MED 020 Modular High Vacuum Coating System for 30 s at 100 mA. A Hitachi SU-70 electron microscope operated at 5 kV and 10 mm distance was used for the analysis. All micrographs were digitally manipulated and plates containing LM and SEM pictures were mounted using Adobe® Photoshop CS3 v. 10.0.

The Specific Pollution Sensitivity Index (IPS) was calculated from diatom abundances (Coste in Cemagref 1982), using the OMNIDIA v. 5.5 software (Leconte *et al.* 1993). Additionally, the Ecological Quality Ratio (EQR) was calculated based on recommendations of A.P.A., I.P. (2016).

Morphological terminology follows Barber & Haworth (1981) for valve shape and stria pattern, Cox & Ross (1981) and Cox (2012) for lateral extensions (virgae) and cross bars (vimines), and Round *et al.* (1990) for areolar substructures, raphe and girdle bands.

Results

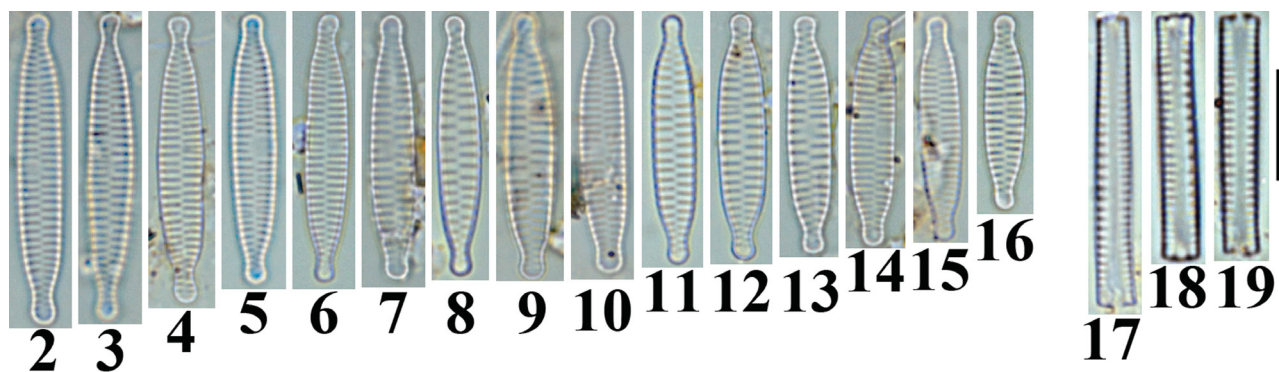
Fragilaria odeloucaensis E.Morales, Novais, C.E.Wetzel, Ector & Morais *sp. nov.* (LM: Figs 2–19, SEM: Figs 20–31)

Description:—Frustules rectangular in girdle view, frequently heterovalvar with respect to striation (Figs 17–19). Valves lanceolate with capitate apices (Figs 2–16). Length: 17.9–28.3 µm, width: 3.6–4.3 µm (n = 40). Axial area narrow and straight under LM (Figs 2–16), zig-zagged under SEM (Figs 20–25), delimited by elevated virgae that barely extend over sternum and by depressed striae (Figs 20, 21, 24). Axial area depressed in outer view (Figs 20–25), but raised in inner view (Figs 27–29), though this latter feature is less noticeable in valves with sparser striation (Fig. 26). Striae uniseriate, alternate and parallel in the middle of the valve (Figs 20, 21, 24), becoming slightly curved and radiate toward the apices (Figs 22, 23, 25). Stria density 11–16 in 10 µm. Each stria continues up to 1/2–2/3 of the valve mantle (Figs 27–29, 30, 31). Striae clearly depressed in outer and inner views (Figs 20–25, 27–29), though less depressed in internal views of valves with sparser striation (Fig. 26). Areolae round to elliptic (Figs 20–29), 6–7 in 1 µm. Volae small, growing from the internal contour of the areola (Figs 24, 31, black arrow heads). Spines absent. Virgae raised with respect to axial area and striae in outer view (Figs 20–25), also raised in internal view (Figs 27–29), although this feature is less prominent in inner view in valves with sparser striation. Central area with clear one-sided, square-shaped fascia infrequent, ghost striae faint, but clearer on valve face edges of the fascia (e.g. Figs 2, 5, 6, 8, 14). Blister-like depositions present along the abvalvar edge of mantle, irregular in shape and larger at the apices (Figs 30, 31, black wavy arrows). A single rimoportula present at one apex, oblique to apical axis of valve, with elliptic to squarish outer opening, aligned with a stria (Figs 20–22, white arrows), and parallel, raised, convex labia attenuated at the ends (Figs 26–28, white arrows). Apical pore fields well-developed, of the ocellulimbus type, composed of several rows of round pores entirely located on the apical valve mantle, externally framed by bulged borders (apical pore field is sunken) (Figs 20–23, 25, 31). Cingulum composed of several open elements (Figs 23, 30, 31, black arrows), perforated by a single row of round pores (Figs 22, 23, white arrow heads). Plastids unknown.

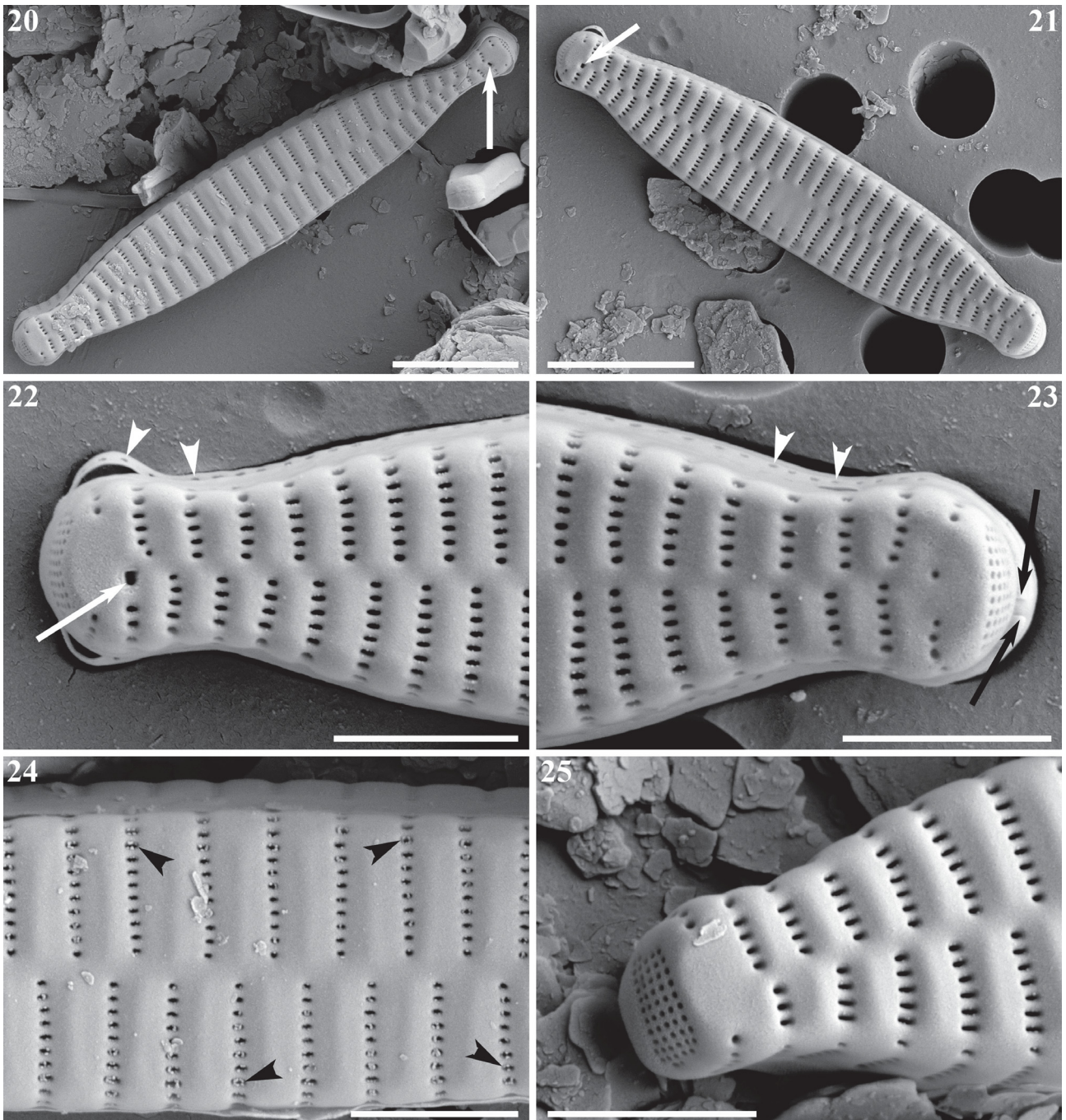
Type:—PORTUGAL. Algarve region, Monchique Council: Odelouca Stream, epilithon, sampling point in the stream, 37° 21' 19.87" N, 8° 26' 27.80" W, Josué Figueira, 20th March 2017 (holotype BR-4723 = Fig. 2).

Etymology:—The species epithet makes reference to the stream where the new taxon was found, the Odelouca (“ode” Arabic fem. for river, Portuguese “louca” and Arabic “lawqa” fem. for mad, insane).

Ecology and distribution:—The sampling site is located in a deep vee valley without natural terraces. The 500 m stretch was characterized by earth (crumbly) and bedrock in the banks, the channel substrate was mainly composed by cobble, gravel/pebble, the flow types were rippled, smooth and unbroken standing waves, there were some special features in the channel as exposed boulders, one unvegetated and two vegetated mid-channel bars, and the vegetation in the channel was composed by submerged broad-leaved plants, liverworts/moss/lichens, emergent reeds/sedges/rushes/grasses/horsetails and filamentous algae. The land-use within 5 m of the banktops included broadleaf/mixed plantations and scrub & shrubs, and within 50 m of the banktop consisted of *Eucalyptus* plantation mixed with shrubs and herbaceous plants, the vegetation structure within 1 m of the banktops and in the bank faces was composed of two or three vegetation types, there was a semi-continuous extent of trees in the margins, the reach is also located 100 m downhill from a main road. The stretch was characterized by a banktop 1.5 m in height, a bank to bank width of 8 m, a 10 m wide bankfull channel, and a 7 m wide water cover in the channel.

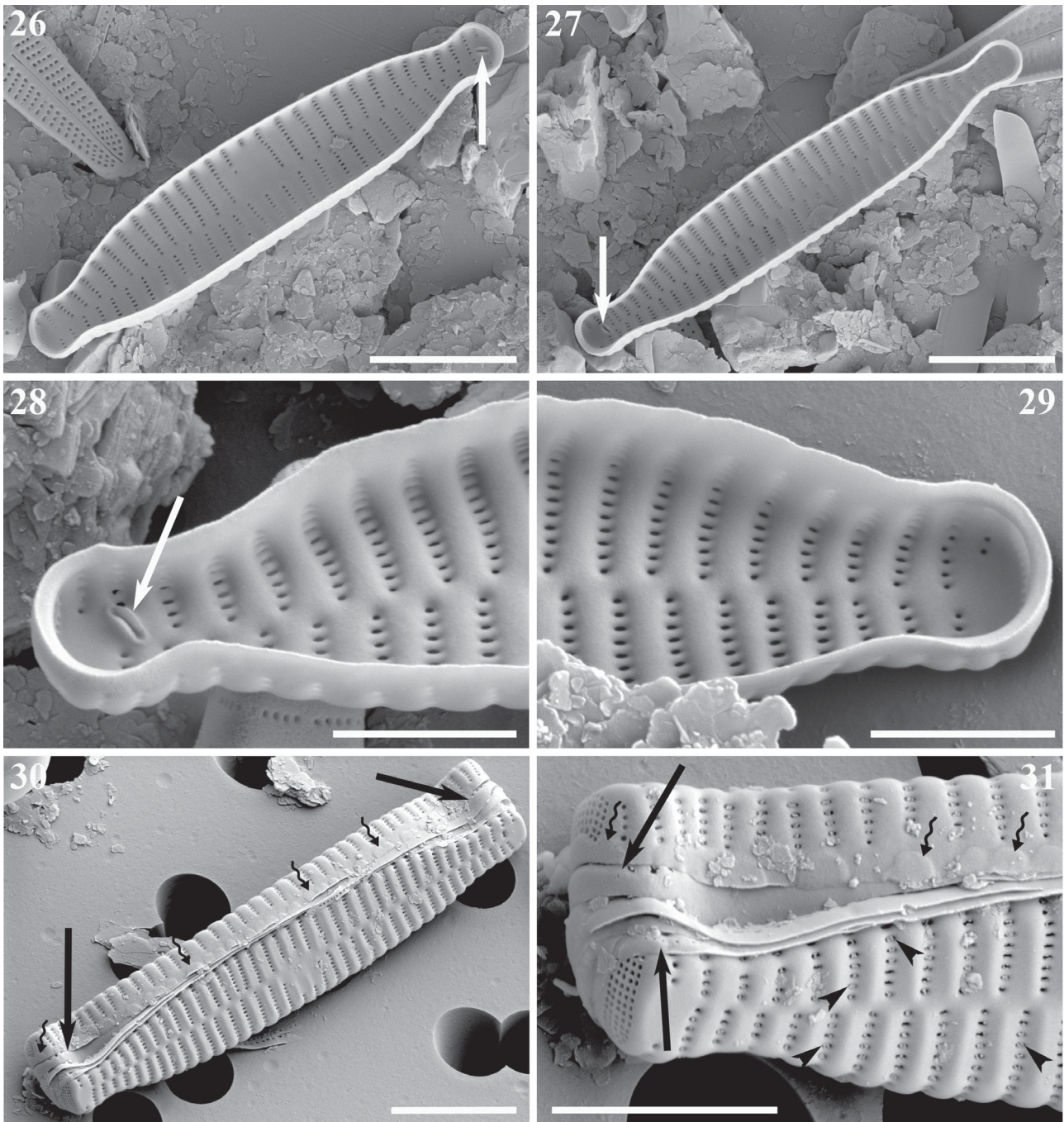


FIGURES 2–19. LM images of *F. odeloucaensis* *sp. nov.* from the type (BR-4723) from Odelouca Stream southern Portugal. Figure 2 corresponds to the holotype, while figures 17–19 are girdle views of the new taxon. Scale bar = 10 µm.



FIGURES 20–25. SEM images of *F. odeloucaensis* sp. nov. from type material from Odelouca Stream southern Portugal. 20, 21. Valve views of two different valves showing striation pattern, axial area and position of rimoportulae (white arrows). 22, 23. Details of apices of valve in figure 21. Notice outer opening of rimoportula (white arrow in 22), single row of areolae on cingulum elements (white arrow heads in 22 and 23) and open copula (black arrow in 23). 24. Detail of valve center of figure 20. Notice zigzag pattern of axial area and delicate volae (black arrow heads). 25. Detail of apex showing apical pore fields completely located on valve mantle and surrounded by a bulged frame. Scale bars = 5 μm (Figs 20, 21), 2 μm (Figs 22–25).

The Odelouca Stream is a temporary river that dries out completely at the end of the summer and is classified within the Mountainous Rivers in the South, according to the Water Framework Directive typology. At the time of sampling, there was flowing water with a velocity of $0.46 \text{ m}\cdot\text{s}^{-1}$ at the riffle where the scrubbed cobbles were collected. Depth of the transparent flowing water was 8 cm, water temperature was $14.1 \text{ }^{\circ}\text{C}$ (at 12:00 AM), pH 7.2, electrical conductivity $161.1 \text{ }\mu\text{S}\cdot\text{cm}^{-1}$, and dissolved oxygen 90.1 \% sat. , $9.2 \text{ mg O}_2\cdot\text{L}^{-1}$. At this site, the stream was classified as Excellent (IPS = 17.8, EQR = 0.96 since the reference value for this typology is 18.5).



FIGURES 26–31. SEM images of *F. odeloucaensis* sp. nov. from type material from Odelouca Stream southern Portugal. 26, 27. Internal views of two valves showing details of striation, narrow axial area and position of rimoportulae (white arrows). 28, 29. Internal view of apices of a single valve. Rimoportula is denoted by white arrow in 28. Notice raised costae and raised zigzag axial area, and depressed striae in 29. 30, 31. Collapsed frustule in side view (30) and detail of apex (31). Elements of cingulum are indicated by black arrows, blister-like depositions by wavy black arrows and volae in 31 by black arrow heads. Scale bars = 5 μm (Figs 26, 27, 30), 2 μm (Figs 28, 29), 3 μm (31).

Thus far, the presence of the new species was confirmed at Odelouca Stream (in this manuscript) and in epilithon of St. Pedro Stream (St. Pedro de Muel locality in the Ribeiras do Oeste hydrographic basin in the Center Region of Portugal), where it was collected in June 10th 2007 (Novais 2011, reported as *Fragilaria* sp. 2.). St. Pedro Stream is a permanent watercourse in a small watershed (ca. 38 km²). The sampling site is located 13.1 km from the source, and at the sampling time the water temperature was 16.4 °C, conductivity was 495.0 $\mu\text{S}/\text{cm}$, pH 7.5, dissolved oxygen 61.7 % sat, 6.13 mg·L⁻¹, alkalinity 73.0 mg CaCO₃·L⁻¹, ammonium 0.003 mg N·L⁻¹, chlorides 45 mg Cl⁻·L⁻¹, total organic carbon 20.8 mg C·L⁻¹, phosphates 0.006 mg P·L⁻¹, total phosphorus 0.025 mg P·L⁻¹, nitrates 1.5 mg N·L⁻¹, nitrites 0.015 mg N·L⁻¹, sulphates 60.1 mg SO₄·L⁻¹, total suspended solids 2.2 mg·L⁻¹, and a turbidity of 1.1 NTU.

Accompanying flora:—The new taxon reached a relative abundance of 5.2 % in the type slide. The most abundant accompanying species were *Achnantheidium minutissimum* (Kützing) Czarnecki (1994: 157; 36.4 % relative abundance), *Fragilaria gracilis* Østrup (1910: 190; 18.8 %), *Gomphonema truncatum* Ehrenberg (1832: 88; 6.8 %), *Brachysira microcephala* (Grunow) Compère (1986: 26, 28; 5.9 %), *Gomphonema tergestinum* (Grunow) Fricke in A.W.F.Schmidt (1902: pl. 234: figs 39–43; 4.9 %) and several additional taxa with abundances < 2 %.

Discussion

Fragilaria odeloucaensis sp. nov. has open girdle bands, which places it in *Fragilaria* as per the current definition of the genus (Williams & Round 1988, Tuji & Williams 2006a, 2008a, b, Williams 2011). Open girdle elements have remained as the single distinguishing feature (synapomorphic, following Williams 2011) of *Fragilaria*, which has held true after revision of type material and description of many new species (e.g. Van de Vijver & Ector 2020, Van de Vijver *et al.* 2022).

This grouping of taxa with open girdle bands now contains a more cohesive set of taxa since the recent erection of an epitype for *Bacillaria ulna* Nitzsch (1817: 99) (= *Ulnaria ulna* (Nitzsch) Compère (2001: 100)), the generitype of *Ulnaria* (Kützing) Compère (2001: 100), a genus that comprises taxa with closed girdle bands, has now been separated from *Fragilaria* (Krammer & Lange-Bertalot 1991a, Williams 1986, 2011). As it happens with open girdle elements, closed girdle bands in *Ulnaria* seem to be a reliable feature judging by the new species that have been described recently (e.g. Lange-Bertalot & Ulrich 2014, Cantonati *et al.* 2019, Liu *et al.* 2019, Williams & Van de Vijver 2021). Likewise, this same feature is present in many of the species which type material has been recently revised and that were formerly included in *Synedra* Ehrenberg (1830: 40) (e.g. Tuji 2009, Williams 2019), deeming *Synedra* a genus name restricted to marine species, though they have an ulnarioid bauplan (Williams 1986, Morales *et al.* 2014).

As the list of *Ulnaria* spp. grows, current ascriptions in this genus need revision as suggested by the work of Van de Vijver *et al.* (2021c) on type material of *Synedra cyclosum* Brutschy (1922: 184), which has open girdle bands (hence, it is a representative of *Fragilaria*). This taxon had been previously considered by Williams (1986, 2011) as a taxon with a closed cingulum belonging to a separate group within *Synedra*, a group that he suggested should be included in *Ulnaria* and many representatives of which were transferred to this latter genus.

Additionally, other newly erected species need to be revised from the morphological stand point since they have been described based on molecular information, but without assertion of the open/closed nature of the girdle bands, as is the case of *Ulnaria ferefusiformis* Kulikovskiy & Lange-Bertalot (in Kulikovskiy *et al.* 2016: 36) and *Ulnaria pilum* Kulikovskiy & Lange-Bertalot (in Kulikovskiy *et al.* 2016: 36).

Following Table 1, in which *F. odeloucaensis* sp. nov. is compared to morphologically closest relatives, i.e. taxa with linear to lanceolate valve outline, spaced striae, lacking spines, and having well-developed apical pore fields, the new species has the following unique distinguishing features: (1) lanceolate valves with capitate apices (Figs 2–16), (2) zig-zagged axial area (e.g. Figs 25, 29), (3) central area with squared fascia (Fig. 21), (4) heterovalvar frustules (Figs. 17–19), and (5) apical pore fields that are sunken into the valve apex (Figs 25, 21).

The feature lanceolate valves with capitate apices distinguishes the new taxon from the rest in Table 1, which have a variability of linear to lanceolate valves with rostrate to capitate apices valves. The closest taxon regarding this feature is *F. rinoi* Almeida & C.Delgado (in Delgado *et al.* 2016: 5), but instead of having capitate apices as in the new species, *F. rinoi* has rostrate apices.

Regarding the zig-zagged axial area, this feature is more notorious in internal views (Figs 28 and 29) since the virgae and the axial area are at the same level. Externally, virga and axial area are at different levels, the latter being depressed. However, the raised virgae faintly extend onto the axial area, and the latter appears associated at the same level to the depressed striae, producing a sinuous pattern (Figs 22–25).

As stated before, the central area with a one-sided squared fascia is not always present, as can be seen in Figs 2–16. The external bulge is absent in the new species, bulge that is present in a larger or lesser degree in the other species in Table 1, except in *F. irregularis* Chudaev, Jüttner & Van de Vijver (in Chudaev *et al.* 2021: 221), in which there is no clear central area. Given the degree of separation of the striae and general outline of the valves in *F. irregularis* and the new species, these two taxa are superficially the closest. However, following Table 1, additional separating features between the new species and *F. irregularis* are the shape of the valves, features of the axial area and axial area-virgae-striae complex, heterovalvy and shape and degree of subsidence of the apical pore fields.

TABLE 1. Comparison of *F. odeloucaensis* sp. nov. with morphologically similar, non-spiny species in *Fragilaria*. Asterisk in *F. uliginosa* column denotes incomplete data from original description, therefore no unique characters have been highlighted. Text in bolds and cursives denotes unique features to each taxon.

Taxon/features	<i>F. candidagilae</i> Almeida, C.Delgado, Novais & S.Blanco	<i>F. deformis</i> (W.Smith) Van de Vijver & Ector	<i>F. irregularis</i> Chudaev, Jüttner & Van de Vijver	<i>F. odeloucaensis</i> sp. nov.	<i>F. rinoi</i> Almeida & C.Delgado	<i>F. uliginosa</i> Kulikovskiy, Lange-Bertalot, Witkowski & Dorofeyuk*
Valve shape	Widely linear to lanceolate with subcapitate to capitate apices	Widely linear to lanceolate with rostrate to subcapitate apices	Linear to slightly lanceolate with rostrate to subcapitate apices	<i>Lanceolate with capitate apices</i>	<i>Lanceolate with rostrate apices</i>	Linear to lanceolate with rostrate to subcapitate apices
Morphometric data (L, W in µm, ST density in 10 µm, AR: density in 1 µm)	L: 13.0–25.8 W: 4.5–5.0 ST: 12–14 AR: 7	L: 11–29 W: 4.5–5.5 ST: 14–16 AR: 7–8	L: 14–27 W: 3.5–5.5 ST: 7–14 AR: 4.9–6.3	L: 17.9–28.3 W: 3.6–4.3 ST: 11–16 AR: 6–7	L: 8.8–24.1 W: 4.2–5.6 ST: 14–16 AR: 13–14	L: 15.3–20.0 W: 3.7–4.5 ST: 15–17 AR: n.d.
Axial area; axial area-virgae-striae complex	<i>Narrowly lanceolate</i> ; Externally, virgae elevated, axial area and striae depressed. Internally, virgae more elevated, axial area elevated, striae depressed	<i>Widely lanceolate</i> ; Externally, virgae elevated, axial area and striae depressed. Internally, virgae more elevated, axial area elevated, striae depressed	<i>Narrowly linear</i> ; <i>Externally and internally, virgae more elevated, axial area elevated, striae depressed</i>	<i>Narrowly zigzagged</i> ; Externally, virgae elevated, axial area and striae depressed. Internally, virgae and axial area at same level, striae depressed	Narrow at apices, <i>dilated at central area</i> ; Externally, virgae elevated, axial area and striae depressed. Internally, virgae and axial area at same level, striae depressed	Narrow at apices, dilated at central area; Externally virgae are elevated, axial area and striae depressed. Internal features unknown
Central area	Transapically half oval, one-sided fascia with external bulge	<i>Apically rectangular</i> , one-sided fascia with faint external bulge	Absent	<i>Square</i> , one-sided fascia without external bulge	Transapically half oval, one-sided fascia with external bulge	Transapically half oval, one-sided fascia with faint external bulge
Heterovalvy with respect to striation	No	No	<i>Rare</i>	<i>Yes</i>	No	Not apparent
Apical pore fields	Irregularly elliptic, several rows of round poroids, <i>sometimes extending onto valve face</i> , faintly sunken into valve apex	Irregularly elliptic, several rows of round poroids, restricted to the mantle, faintly sunken into valve apex	<i>Approximately transapically lanceolate</i> , several rows of round poroids, restricted to the mantle, not sunken into valve apex	Irregularly elliptic, several rows of round poroids, restricted to the mantle, <i>sunken into valve apex</i>	Irregularly elliptic, several rows of round poroids, restricted to the mantle, not sunken into apex	Apparently elliptic, several rows of poroids, restricted to the mantle, not sunken into the apex
Reference	Delgado <i>et al.</i> (2015), Van de Vijver <i>et al.</i> (2020)	Van de Vijver <i>et al.</i> (2020, 2021)	Chudaev <i>et al.</i> (2021)	This manuscript	Delgado <i>et al.</i> (2016)	Kulikovskiy <i>et al.</i> (2010)

Regarding the apical pore fields, two of the taxa included in Table 1, i.e. *F. candidagilae* C.Delgado, Novais & S.Blanco (Delgado *et al.* 2015: 3) and *F. deformis* (W.Smith) Van de Vijver & Ector (Van de Vijver *et al.* 2020a: 139) have apical pore fields that are barely sunken into the valve apices, and the change in relief from the borders to the apical pore field itself is not as noticeable as in the new taxon (Fig. 25).

Though there are no clear established cut offs in the number of features necessary to regard two species as different, we consider that the existence of two or more clearly distinguishing features, as is the case of the new taxon presented herein (Table 1), is sufficient to justify separation of two populations at the species level. Besides the long-chain polyamines and chitin fibres required for silica processing during valve morphogenesis, several genes are involved in the codification of silaffins, cingulins, silacidins, frustulins and pleuralins, which direct the formation of the different

frustule features, making it highly unlikely that a difference of two or more features between two populations is due to an exclusive environmental control (i.e. plasticity). Rather, these differences might be due to a truly genetic difference between the two populations (Mock *et al.* 2008, Brembu *et al.* 2017, Hildebrand *et al.* 2018).

As shown herein, species comparisons done at the group level, i.e., choosing all species within a genus that morphologically resemble the taxon being described, can yield a higher number of unique characters for each species than a one-on-one analysis of species randomly chosen from within the genus, as is usually done (e.g. Morales 2003, Morales *et al.* 2009, 2014). Species differentiation should not only be based on traditional measurement of valve dimensions and stria density (which actually do not separate the species included in Table 1), outline of valves, and other features such as shape of the axial and central areas, and presence or absence of spines and their general features. As shown in Table 1, consideration, for example, of the shape of the axial area, its elevation and interplay with the virgae and striae, both in internal and external views, can be revealing. This consideration clearly separates all taxa in Table 1 from each other, except in the case of *F. uliginosa* Kulikovskiy, Lange-Bertalot, Witkowski & Dorofeyuk (Kulikovskiy *et al.* 2010: 37), which was not clearly illustrated at the time of its first description (Kulikovskiy *et al.* 2010, p. 93, pl. 9, Figs 11–18, 20, 21).

Here, we have used an additional feature that is not usually considered but that might be informative in taxa with widely separated striae, that is the heterovalvy, herein referred to the lack of uniformity in the separation of the striae from one valve to the other in the same frustule. In this case, two taxa stand as different, the new taxon that exhibits a clear heterovalvy (Figs 17–19) and *F. irregularis* in which heterovalvy is present but it is rare.

Finally, it is worth mentioning that this detailed group-comparative approach has already been used successfully for other araphid taxa, e.g. *Punctastriata* D.M.Williams & Round (1988: 278) (Morales 2021), *Pseudostaurosira* D.M.Williams & Round (Morales *et al.* 2021a) but also for other groups, e.g. *Planothidium* Round & Bukhtiyarova (1996: 351) (Morales *et al.* 2021c).

Regarding the quality and completeness of the information included in Table 1, the majority of species are well illustrated in the literature, allowing for the proposed detailed analysis. In the case of *F. uliginosa*, although this species is different from *F. odeloucaensis* *sp. nov.* (based on valve shape, width of valves, features of the axial area, central area, and apical pore fields), more research on its type material is required to clearly show features of apical pore fields, areolar density, structure of rimoportulae and the axial area-virgae-striae complex, and to establish a concise difference with other taxa included in Table 1 (such as *F. rinoi* and *F. deformis*, for example).

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