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# *Fallacia californica* sp. nov. (Bacillariophyta), a new freshwater diatom species from streams in California, USA

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## Abstract

Small naviculoid diatoms remain largely taxonomically unexplored in the United States, due to the inability for clear differentiation of unique characteristics under light microscope magnification during routine identification. In a recent study of benthic stream diatoms from California and as a part of taxonomy data quality assurance and quality control process it became evident that taxonomic reevaluation of a common *Fallacia* species is needed. A new small-celled *Fallacia* species is described here and compared to similar taxa. Nomenclatural and ecological discussions, based on historical and current literature, are presented for each taxon. Type materials were consulted for taxonomic evaluation and comparison. The new taxon is described with light microscopy and scanning electron microscopy. *Fallacia californica* could be distinguished from other small *Fallacia* species with coarse areolae by the unique combination of following features: 1) distinct lyre-shaped sternum, 2) asymmetrical central area, and 3) variable central striae with one to four inner areolae absent, and unilateral gap between the central striae on the mantle. The new freshwater species was distributed in warm alkaline waters with medium conductivity and elevated nutrients content.The majority of populations have been recorded in coastal streams, where they could be abundant, but the species could be scattered in other inland running waters as well.

**Keywords:** *Fallacia*, Bacillariophyta, diatom, streams, California, new species, scanning electron microscopy

## Introduction

Small naviculoid diatoms are widely distributed in periphyton, can vary in abundance, and provide important information towards the ecological assessment of each habitat (Van Dam *et al*. 1994, Wetzel *et al*. 2015). Taxonomic evaluation using high quality research microscopes, while estimating relative abundance of diatom taxa within site, remains a necessary step in bioassessment (Manoylov 2014). The taxonomic composition of the freshwater algae in California, particularly from streams and rivers has been reported as part of national programs and state surveys. In the last decade, the extensive bioassessment sampling by the Surface Water Ambient Monitoring Program (SWAMP) of the California Water Resource Control Board allowed a more complete picture of the local diatom flora from streams. Taxonomic analysis of the data led to the description of new-to-science species belonging to the diatom genera *Amphora* Ehr. ex Kütz., *Halamphora* (Cleve) Levkov, *Rhoicosphenia* Grunow, *Gomphonema* Grunow, and *Gomphoneis* Cleve (Stepanek & Kociolek 2013, Thomas & Kociolek 2015, Stancheva *et al.* 2016), with more in progress. A recent diatom quality assurance and control process, similar to the USEPA (2013) procedures, indicated that taxonomic reevaluation of a common, and often locally abundant *Fallacia* species is needed.

The diatom genus *Fallacia* Stickle & D.G. Mann was described in Round *et al*. (1990) with transfer of 59 species from *Navicula* Bory. The unique combination of characters combine H-shaped chloroplast, lateral depressed sterna interrupting the striae, and a finely porous conopeum (Li *et al.* 2014b; Spaulding *et al.* 2010). Most *Fallacia* taxa are characteristic of marine and brackish benthic habitats, where they often form rich epipsammic communities in coastal and estuarine intertidal areas (Witkowski 1993, Sabbe *et al*. 1999, Witkowski *et al*. 2000). Currently, there are 89 *Fallacia* species recognized (Guiry & Guiry 2018). Taxa ascribed to the genus *Fallacia* have been increasing recently with transfer and description of several new species (e.g., Sabbe *et al*. 1999, Witkowski 1991, Procopiak & Fernandes 2003, Metzeltin *et al*. 2005, Li *et al*. 2015, Van De Vijver & Cox 2015, Genkal & Yarushina 2017),

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but the morphological variation and diversity of the freshwater species remain poorly understood. Taxonomic and autecological characteristics of intertidal marine and brackish species from this genus were analyzed in depth (i.e., Sabbe *et al*. 1999). The species diversity of *Fallacia* in freshwater habitats is much lower, for instance, 17 species were reported from central Europe (Cantonati *et al*. 2017), the same number of species from Uruguay (Metzeltin *et al*. 2005), 15 species presented from Baikal with 47% of those described as new to sciences (Kulikovskiy *et al.* 2012), and 23 species are known from streams in California (SWAMP Master List).

The most prominent morphological feature of the genus *Fallacia* is the lyre-shaped hyaline marking (sternum, canal), located on either side of the raphe. The markings represent hollow canals which are formed between the depressed sterna and the finely porous conopeum, which covers the valve surface (Liu *et al*. 2012). Striae are uniseriate, interrupted by lateral sterna (rib) internally and composed by round internally-closed areolae (Liu *et al*. 2012) (see Fig. 1). Sabbe *et al*. (1999) separated three complex morphological clusters within *Fallacia*: 1) species with predominantly marginal striae; 2) species with distinctly panduriform lyre, and 3) species complex around *Fallacia tenera* (Hust.) D.G. Mann, characterized by striae split to two coarse areolae by longitudinal hyaline rib.

Recently, Liu *et al*. (2012) separated several species into the new genus *Pseudofallacia* Y. Liu, J. P. Kociolek & Q. X. Wang, based on the presence of a longitudinal rib on either side of the axial area, which interrupts the striae internally, in contrast to the lyre-shaped canal in *Fallacia*. Also, the central area in *Pseudofallacia* is large, expanded transversely to the valve margins, in contrast to the small central area in *Fallacia*. The striae in *Pseudofallacia* have one elongated, externally closed areola.

The common freshwater species *F. tenera* was transferred to the new genus *Pseudofallacia* by Liu *et al.* (2012). This new taxonomic position was accepted in several publications (Ector *et al.* 2015, Genkal & Yarushina 2017), but some recent authors used the genus name *Fallacia* (i.e. Li *et al.* 2014, Miscoe *et al.* 2017). Li *et al*. (2014) provided ultrastructural evidence that *F. tenera* does possess the typical characteristics of *Fallacia,* the most important of which is the lyre-shaped canal, which does not have areolae in it, as illustrated for *Pseudofallacia occulata* Krasske (Liu *et al*. 2012, Fig. 15). The complicated taxonomy and nomenclature of *F. tenera* are discussed in detail by Li *et al*. (2014) and further in this paper, because it is closely related to the diatom species presented here. As part of the required taxonomic reconciliation process (USEPA, 2013) it became evident that all taxonomists recognized a potentially new taxon, which combines the coarse areolae, characteristic for *Fallacia* cf. *tenera* with distinct panduriform lyre-shaped markings and dense areolae, typical for *Fallacia* cf. *cryptolyra* (Brockmann) Stickle & D.G. Mann.

The goal of this study was to describe the most common, and often locally abundant *Fallacia* taxon in coastal streams in California. The new species is illustrated with light microscopy (LM) and scanning electron microscopy (SEM) and compared with closely related taxa. Distributional and ecological data from stream locations in California are also presented.

## Material and methods

For this study we used diatom samples obtained between 2013 and 2017 as part of the SWAMP program in California. The diatom samples were collected along with environmental variables using the multihabitat sampling protocol (Fetscher *et al.* 2009). For LM observations, the preserved diatom samples were cleaned by the hydrogen peroxide method, mounted in Naphrax®, and 600 diatom valves were identified to species level and counted (for details see Stancheva *et al.* 2015). The original analysis of the samples was performed at the California State University San Marcos and EcoAnalysts Inc. For this study, diatom slides were scanned additionally after diatom enumeration, in order to obtain a size ranges a minimum of 50 *Fallacia* valves. LM imaging of the specimens was performed using a Leica DM2500 microscope with differential interference contrast opticsand Leica DFC295 Camera attached to the microscope (Leica Microsystems, Wetzlar, Germany) at the Georgia College and State University.

SEM was performed with cleaned specimens air dried onto cover glasses, attached to aluminum stubs, sputter-coated with 5 nm of iridium or platinum. Initial observations of frustular ultrastructure were performed with JEOL SEM (JSM-IT100) at Georgia College and State University. The diatom material was examined and pictured in high vacuum mode using a ZeissSIGMA 500 (Carl Zeiss Microscopy, Thornwood, NY, USA) with an accelerating voltage of 5 k at the Nano3 Facility at the University of California, San Diego. Holotype slides and material are deposited at the Georgia College and State Natural History University Museum Algae Collection, diatom collection and isotype slides and type material are maintained by the author Rosalina Stancheva at the California State University San Marcos.

In addition, we observed three slides from Hustedt collection at the Friedrich Hustedt Zentrum für

Diatomeenforschung Institute for Polar and Marine Research: 1) Slide N8/50 *Navicula tenera* Hust., R. S. Java, Ranu Klindungan Lake 1, 1930. St., 2) Slide 230/70 R. M. Kamerun Lagune 1b, 1939. H.2. (for *Navicula auriculata* Hust.), and 3) Slide 397/94, R. M. Arcachon, 1960. H. (for *Navicula dissipata* Hust.). Terminology used followed Anonymous (1975), Ross *et al.* (1979), and Round *et al*. (1990).

## Results

*Fallacia californica* Stancheva & Manoylov, sp. nov. (Figs. 1–38)

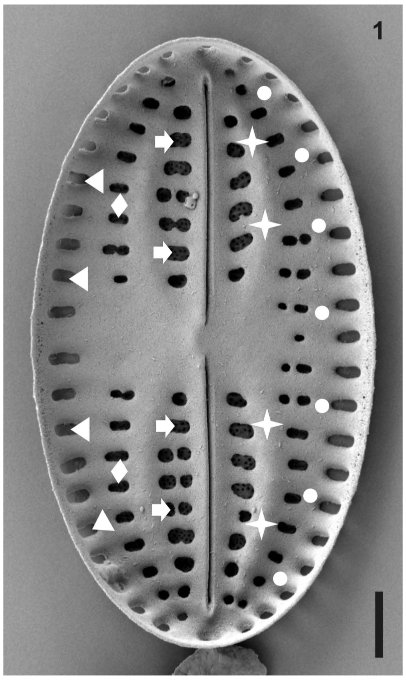


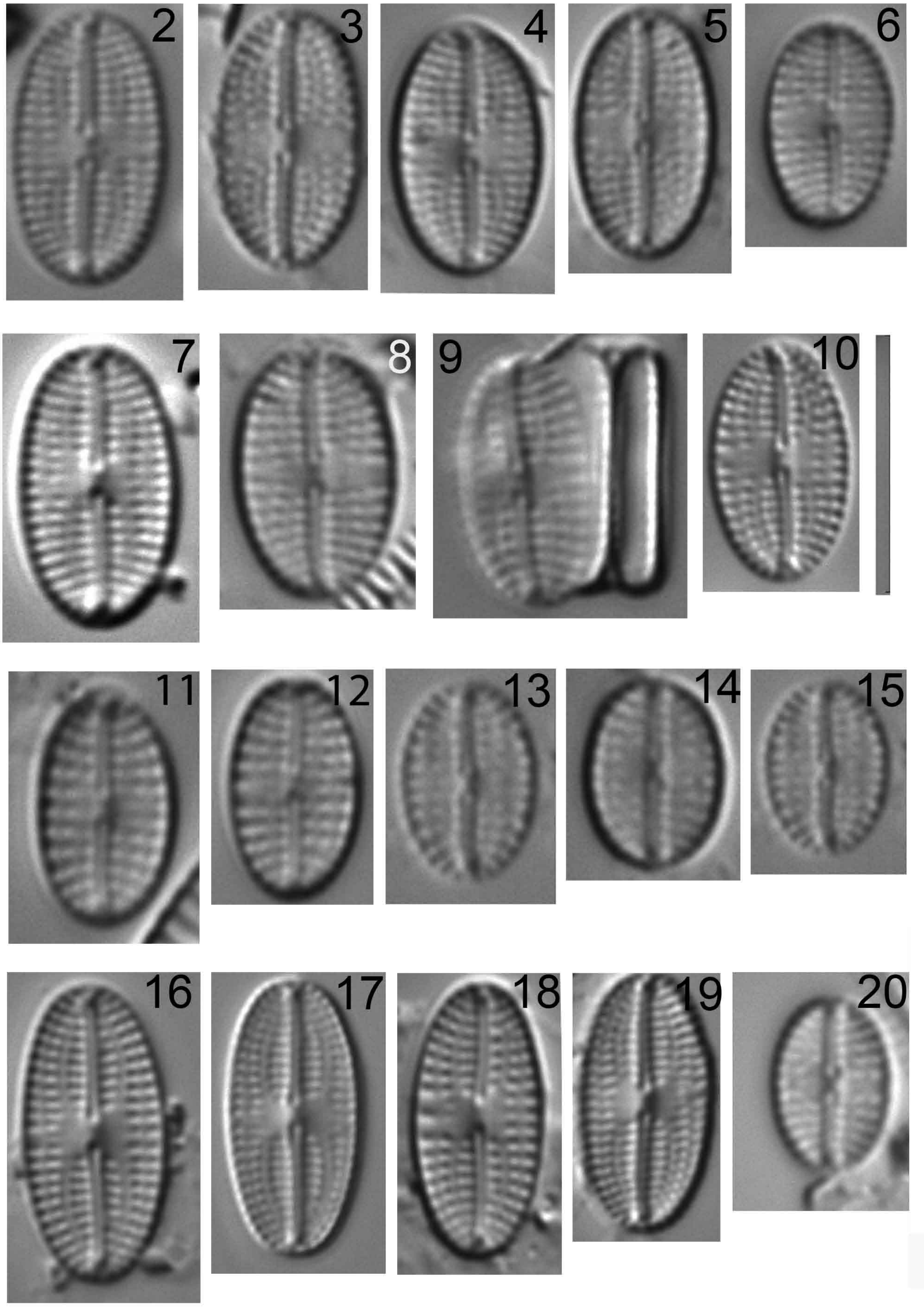

**FIGURE 1**. SEM image of *Fallacia californica* Stancheva & Manoylov, *sp. nov.* with indication of main structural elements of the valve as follow: stars—lyre-shaped sternum; dots—hyaline rib interrupting the striae; arrows—areolae adjacent to the raphe branches; diamonds—inner areolae; arrowheads—areolae near the mantle. Scale bar 1 µm.

**Description**

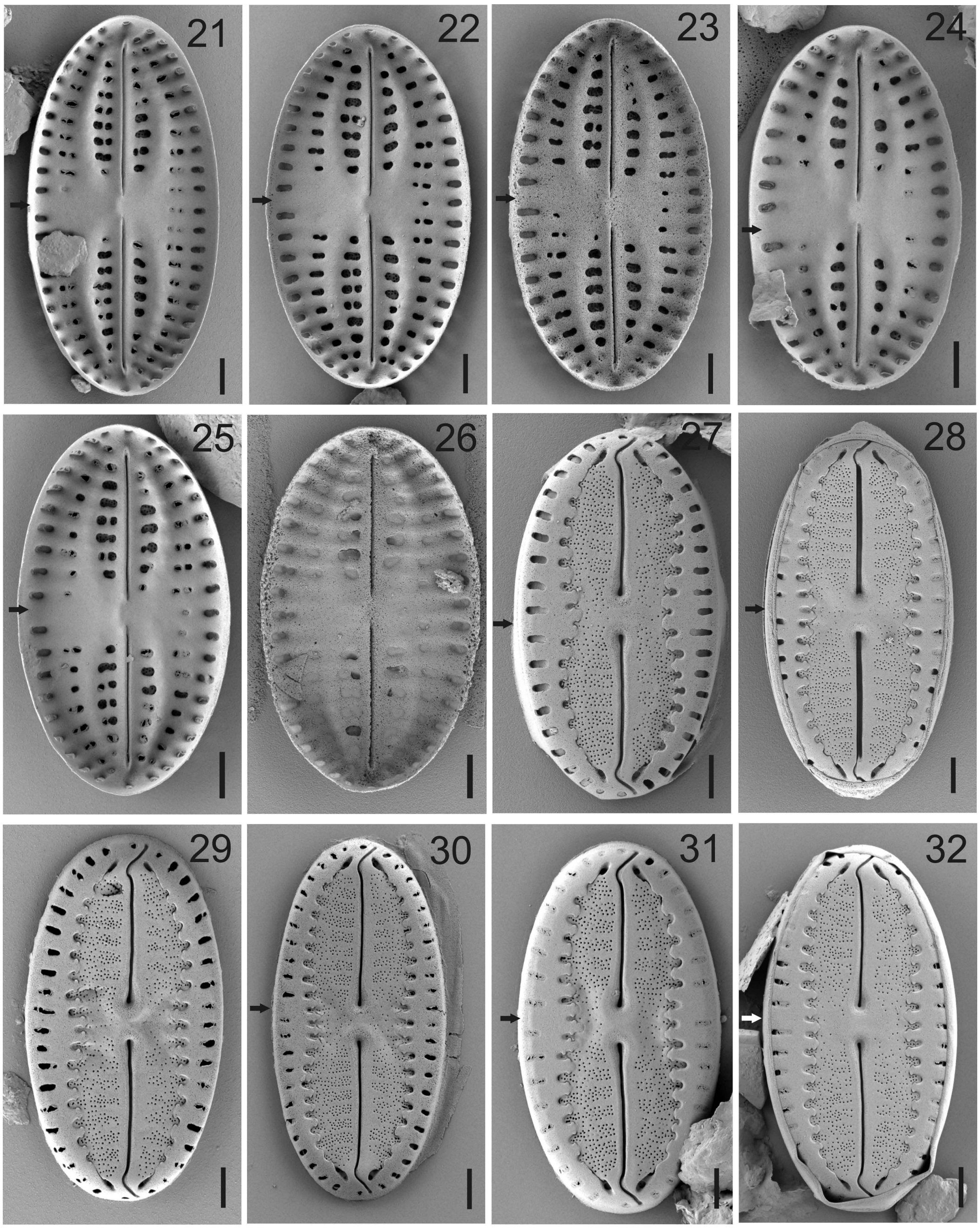
Valves are elliptical with rounded poles, 4–5.6 µm wide, 6–14.5 µm long (Figs 2–20). In girdle view (Fig. 9) ends look rounded too. The raphe is filiform and slightly arched toward the primary side of the valve. Terminal raphe fissures curved toward the secondary side of the valve. The striae are parallel in the center, radiate near the poles, 21– 10 µm, composed of coarse areolae resolvable with LM. The lyre-shaped sternum distinctly panduriform, constricted in the center (Figs 3, 4, 10, 16, 17, 19), often clearly visible in the smallest valves (Fig. 15). Striae longitudinally interrupted by a hyaline rib which split the striae into two or three areolae of different sizes. The hyaline rib is often enlarged to fan-shaped near the valve center (Figs 2, 7, 8, 10, 15, 18). The areolae closer to the mantle are larger, transapically elongated, one per stria, uniform and equally spaced through the valve; occasionally the central two areolae are slightly distant and form unilateral gap (Figs 2–6, 8, 10, 12, 15–19). The inner areolae are smaller, one or two per stria, forming a longitudinal line which is curved inwards near the center (Figs 7, 10, 16, 18). The inner areolae are asymmetrical on both sides of the central area, smaller, variable in size and position, weakly developed, widely spaced or absent, or sometimes longer than the other areolae (Figs 10, 20). The central area is asymmetrical, small or transapically expanded to unilateral fascia in some specimens. Areolae adjacent to the raphe branches are well developed, single or double, forming equally long lines on both sides of the raphe (Figs 7, 10, 15, 16, 19).

**SEM observations**

Internally, small helictoglossae are visible at the polar terminals of the raphe, slightly curved to the primary side of the valve (Figs 21, 24). On both sides of the raphe, depressed lyre-shaped lateral sternum is interrupting the striae




**FIGURES 2–20.** *Fallacia californica* Stancheva & Manoylov, *sp. nov.* Figs. 2–15, type material from Aliso Creek, California, USA (site 901M14126), Fig. 9 girdle view. Figs 16–20 from Soquel Creek (site 304PS0338). Note the distinct panduriform lyre sternum (Figs 2–4, 15); the hyaline rib, which is enlarged to fan-shaped near the valve center (Figs 2, 7,10,18) and enlarged central area on the opposite side (Figs 2, 5, 10, 18). LM images, scale bar 10 µm.

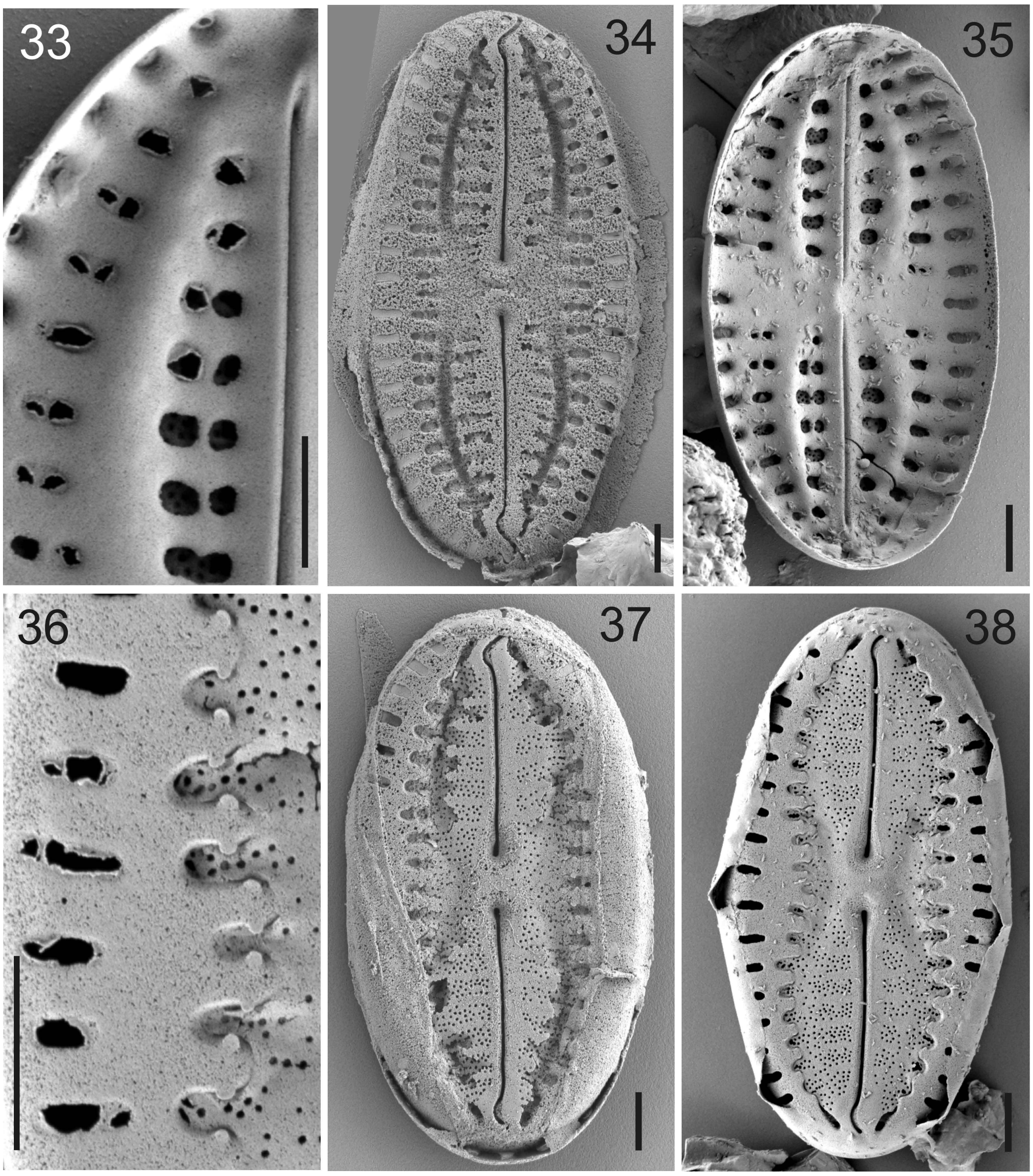



**FIGURES 21–32.** *Fallacia californica* Stancheva & Manoylov, *sp. nov.* type material from Aliso Creek, California, USA and from Soquel Creek (Figs 26–28). Figs 21–26 internal valve view. Figs 27–32 external valve view. Arrowheads show the gap between central striae. SEM images, scale bars 1 μm.

(Figs 21–25, 35). The striae outside the sternum are crossed by longitudinal hyaline rib, which does not appear to be depressed (Figs 22–26). A longitudinal row with transapically elongated large areolae is positioned on the valve mantle (Figs 21–25). These areolae are equidistant, except for the two central areolae on the primary side, which are separated by larger gap (Figs 24, 30–32). The inner areolae are positioned on the valve face. They are smaller and vary from elongated in a single row to circular in a single or double row near the center of the valve (Figs 21–25). One to four central striae on the primary side are absent (Figs 24, 25). The striae between the raphe and lyre-shaped sternums are transapically elongated, constricted, in a single row, or circular in pairs (Figs 22, 23, 35). The rows with areolae on both sides of the raphe branches are relatively symmetrical. Internally, the areolae are occluded by thin hymenes, which are often dissolved, but partially visible on Figs 24, 25, 33.

Externally, the areolae on the valve face are covered by a finely porous conopeum from the raphe sternum to the valve mantle (Figs 27–32). The edge of mantle possesses finger-like protrusions, each with two to four "pegs", which fasten the connection of the conopeum and the mantle (Figs 30, 31, 36). The central 4–6 finger-like mantle protrusions are longer and more pronounced than the other (Figs 29, 31). The images with broken conopeum (Figs 34, 37) show that the lyre-shaped lateral depressed sterna and the finely porous conopeum comprised two longitudinal canals that connect with the exterior by pores on both sides of terminal raphe fissure. The cingulum is composed of at least one wide open girdle band (Figs 28, 32, 37, 38).

**Type:** USA. California: Aliso Creek, Orange County, 33.54743949, -117.72230590, *Jim Mann, May 17, 2016* (holotype GCP4211 circled specimen on the slide; isotype RS! 015, circled specimen on slide and material, CSUSM, USA).




**FIGURES 33–38.** *Fallacia californica* Stancheva & Manoylov, *sp. nov.* type material from Aliso Creek, California, USA and from Soquel Creek (Figs 34, 37). Figs 33, 35 internal valve view. Figs 34, 36–38 external valve view. Fig. 33 shows areolae with remnants from thin hymens. Figs 34, 37 eroded valves with degraded conopeum show the canal of lyre-shaped sternum. Fig. 35 internal valve showing distinctly depressed lyre-shaped sternum. Fig. 36 finger-like protrusions, each with two to four "pegs", which fasten the connection of the conopeum and the mantle. Fig. 38 shows girdle band. SEM images, scale bars 1 μm.

**Etymology:—**The epithet refers to the state of California, USA, where the species was first observed.

**Distribution and ecological notes:—**Distributed in twenty one coastal streams in central and southern California and in Rock Creek located at the foothills of the Sierra Nevada Mts. *F. californica* was locally abundant in seven coastal stream sites with relative abundance ranging from 6.2 to 16.6% in diatom counts. The salinity in *F. californica* habitats was below 0.5 ppt, except for the type locality with elevated salinity1.8 ppt. Specific conductivity was 39–1567 μS $cm^{-1}$ and 3434 μS $cm^{-1}$in the type locality, pH range was 7.1–8.6. Total nitrogen concentrations ranged from 0.1 to 2.2 mg $L^{-1}$, and total phosphorus from 0.06 to 0.16 mg $L^{-1}$. The distribution data and environmental variables are presented in Table 1.

**TABLE 1**. Stream locality data and environmental variables in the habitats of *Fallacia californica* Stancheva & Manoylov, *sp. nov.* NA – not available.

| Site ID | 901M14126 | 304PS0338 | 304WDCAH1 (SEM) | 204PS0358 | 201LAG140 | 201LAG150 | 201LAG165 | 201LAG210 | 201LAG241 | 201LAG280 | 201WLK098 | 201WLK120 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Sapling date | 5/17/2016 | 5/17/2016 | 5/17/2016 | 5/23/2016 | 09-Jun-16 | 01-Jun-16 | 14-Jun-16 | 07-Jun-16 | 06-Jun-16 | 31-May-16 | 24-May-16 | 23-May-16 |
| ***Fallacia californica*** relative abundance (%) | 12.2 | 16.7 | 6.3 | 9.5 | 4.5 | 0.2 | 3.2 | 1.2 | 2.3 | 9.3 | 4.0 | 0.3 |
| Stream name | Aliso Creek | Soquel Creek | Waddell Creek | Crow Creek | Nicasio Creek | Halleck Creek | Lagunitas Creek | Lagunitas Creek | San Geronimo Creek | San Geronimo Creek | Walker Creek | Chileno Creek |
| Latitude | 33.54743 | 36.99348236 | 37.113717 | 37.69543831 | 38.07034 | 38.06669 | 38.05839 | 38.01861 | 38.008307 | 38.013003 | 38.215233 | 38.20764 |
| Longitude | -117.28263 | -121.955562 | -122.26978 | -122.058428 | -122.77051 | -122.70264 | -122.76522 | -122.73306 | -122.703405 | -122.660755 | -122.864597 | -122.79456 |
| Alkalinity as $CaCO_3$ (mg $L^{-1}$) | 288 | 190 | 95 | 350 | 85.6 | 73.1 | 80.2 | 74.3 | 170 | 213 | 59.8 | 147 |
| Ammonia as N (mg $L^{-1}$) | 2.18 | 0.0194 | 0.0098 | 0.0068 | 0.0166 | 0.0058 | 0.0086 | 0.0042 | 0.0064 | 0.0057 | 0.0153 | 0.0269 |
| Ash Free Dry Mass (mg $cm^{-2}$) | NA | 6.08 | 6.61 | 6.51 | NA | NA | NA | NA | NA | NA | NA | NA |
| Chloride (mg $L^{-1}$) | 486.2 | 48 | 21.5 | 66.5 | 11.1 | 20.7 | 10.3 | 9.48 | 21.2 | 21.8 | 15.5 | 29.1 |
| Chlorophyll a (μ $cm^{-2}$) | NA | 20.3 | 17.3 | 21.3 | 1.03 | 0.49 | 0.11 | 0.36 | 0.31 | 1.22 | 0.93 | 1.78 |
| Dissolved Organic Carbon (mg $L^{-1}$) | NA | 2.31 | 5.08 | 5.6 | 2.93 | 2.08 | 2.90 | 2.06 | 1.29 | 2.27 | 6.11 | 12.1 |
| Hardness as $CaCO_3$ (mg $L^{-1}$) | 1182.3 | 108 | 99.4 | 400 | 93.7 | 89.7 | 88.2 | 81.4 | 197 | 236 | 68.4 | 165 |
| Nitrate + Nitrite as N (mg $L^{-1}$) | 1.39 | 0.0102 | 0.147 | 0.2 | 0.0248 | 0.0433 | 0.0382 | 0.0644 | 0.277 | 0.230 | 0.159 | 0.292 |
| Nitrogen, Total (mg $L^{-1}$) | NA | 0.109 | 0.219 | 0.494 | 0.153 | 0.170 | 0.165 | 0.162 | 0.427 | 0.370 | 0.525 | 1.26 |
| OrthoPhosphate as P (mg $L^{-1}$) | 0.418 | 0.112 | 0.0668 | 0.148 | 0.0239 | 0.0185 | 0.0233 | 0.0167 | 0.0454 | 0.0797 | 0.0609 | 0.158 |
| Oxygen, Dissolved (mg $L^{-1}$) | 8.29 | 9 | 9.2 | 10.7 | 8.43 | 9.67 | 9.05 | 10.75 | 9.52 | 6.41 | 9.31 | 5.74 |
| pH | 7.85 | 8.4 | 7.9 | 8.6 | 7.47 | 8.07 | 7.82 | 8.81 | 7.94 | 7.38 | 7.65 | 7.21 |
| Phosphorus as P (mg $L^{-1}$) | 0.349 | 0.0875 | 0.0623 | 0.156 | 0.0301 | 0.0204 | 0.0156 | 0.0160 | 0.0402 | 0.0700 | 0.0728 | 0.251 |
| Salinity (ppt) | 1.8 | 0.4 | 0.2 | 0.4 | 0.10 | 0.12 | 0.10 | 0.09 | 0.20 | 0.23 | 0.09 | 0.19 |
| Specific Conductivity (uS $cm^{-1}$) | 3434 | 830 | 330 | 883 | 204.1 | 246.3 | 200.7 | 186.4 | 407.6 | 473.7 | 188.1 | 390.7 |
| Sulfate (mg $L^{-1}$) | 1026.5 | 155 | 37.4 | 103 | NA | NA | NA | NA | NA | NA | NA | NA |
| Suspended solids (mg $L^{-1}$) | 2.8 | 0.4 | 0.7 | 8.1 | 23.8 | NA | NA | 13.1 | 15.4 | 3.5 | 12.8 | 2.9 |
| Temperature (°) | 19.4 | 14.7 | 14.9 | 15.3 | 14.969 | 16.95 | 14.014 | 12.819 | 15.290 | 14.810 | 13.842 | 14.57 |

NA - not available

*...continued on the next page*

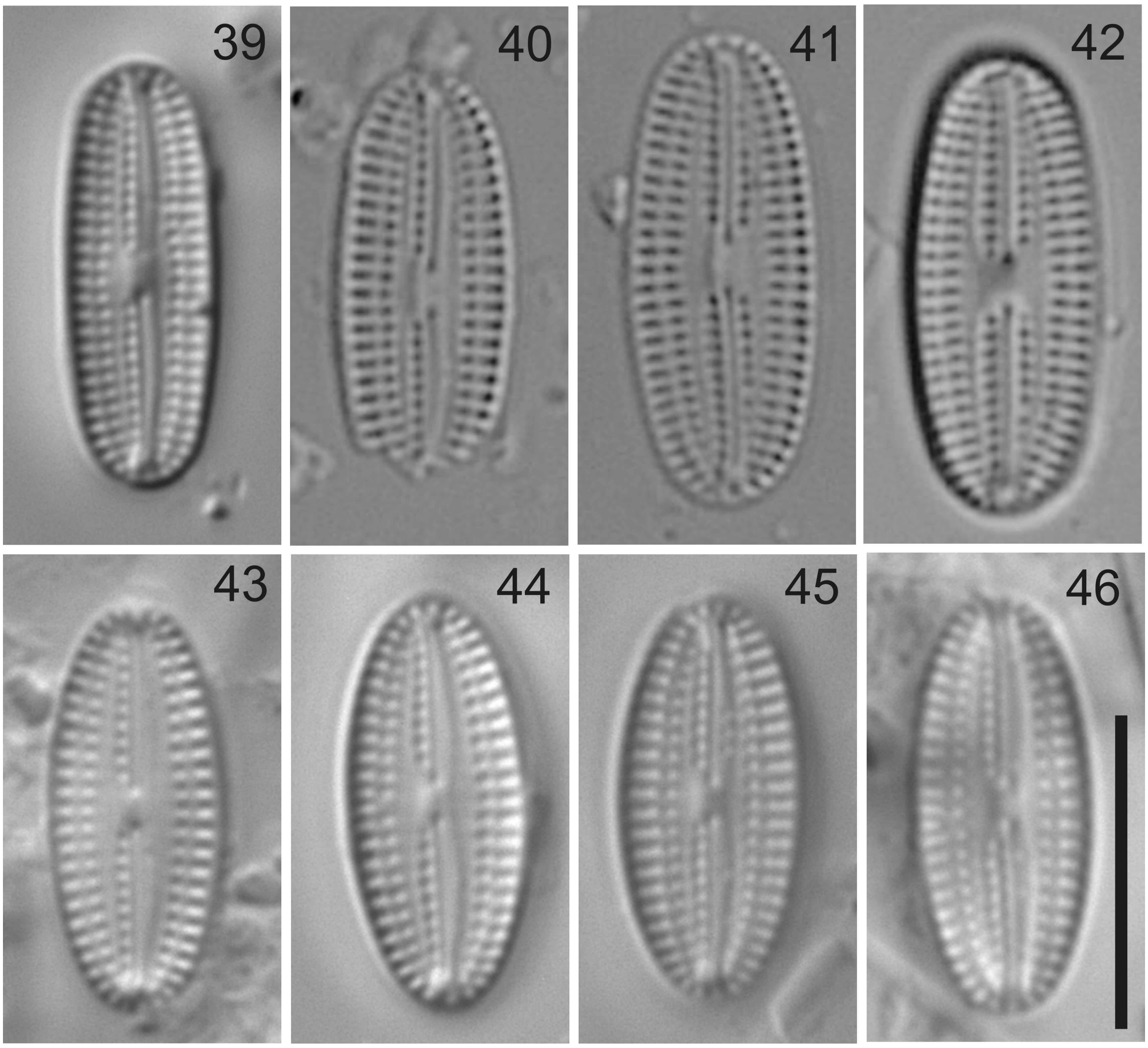
**TABLE 1**. (Continued)

| Site ID | 201WLK160 | 201WLK178 | 201WLK230 | 206PET400 | 304GZR | 308SBCAH1 | 404M07360 | 404M07361 | 403FCA022 | 517FCA222 | 535CR1051 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Sapling date | 18-May-16 | 16-May-16 | 25-May-16 | 10-May-16 | 6/5/2017 | 18/May/2016 | 6/8/2017 | 6/6/2017 | 5/29/2013 | 7/10/2013 | 6/25/2014 |
| ***Fallacia californica*** relative abundance (%) | 6.2 | 3.8 | 0.3 | 0.2 | 0.8 | 0.3 | 0.7 | 16.3 | 0.3 | 3.0 | 0 |
| Stream name | Walker Creek | Walker Creek | Arroyo Sausal | Lichau Creek | Gazos Creek | Soberanes Creek | Medea Creek | Topanga Canyon | Santa Clara River | Rock Creek | Tuolumne River |
| Latitude | 38.17545 | 38.163658 | 38.14342 | 38.29444 | 37.175211 | 36.455100 | 34.15478 | 34.10139 | 34.354720 | 39.300000 | 37.5929 |
| Longitude | -122.82044 | -122.783144 | -122.72472 | -122.66629 | -122.353366 | -121.922610 | -118.75924 | -118.62114 | -119.022500 | -120.968890 | -121.061 |
| Alkalinity as CaCO3 (mg $L^{-1}$) | 50.8 | 47.7 | 83.4 | 172 | 120 | 125 | NA | NA | NA | NA | NA |
| Ammonia as N (mg $L^{-1}$) | 0.0160 | 0.0113 | 0.0050 | 0.0340 | NA | 0.009 | NA | NA | 0.12 | NA | NA |
| Ash Free Dry Mass (mg $cm^{-2}$) | NA | NA | NA | NA | NA | 18.4 | NA | NA | 7.49 | 2.27 | NA |
| Chloride (mg $L^{-1}$) | 13.2 | 13.0 | 31.7 | 60.0 | NA | 40.4 | NA | NA | 80 | 1.4 | NA |
| Chlorophyll a (μ $cm^{-2}$) | 1.14 | 1.48 | 3.25 | 5.94 | NA | 5.2 | NA | NA | 40.7 | 5.5 | NA |
| Dissolved Organic Carbon (mg $L^{-1}$) | 6.66 | 7.75 | 5.52 | 8.45 | NA | 2.8 | NA | NA | 1.9 | NA | NA |
| Hardness as $CaCO_3$ (mg $L^{-1}$) | 56.6 | 54.9 | 94.9 | 272 | NA | 102 | NA | NA | 764 | 12.3 | NA |
| Nitrate + Nitrite as N (mg $L^{-1}$) | 0.265 | 0.289 | 0.0022 | 0.164 | NA | 0.05 | NA | NA | 2.1 | 0.05 | NA |
| Nitrogen, Total (mg $L^{-1}$) | 0.717 | 0.781 | 0.326 | 0.624 | NA | 0.1 | NA | NA | 2.25 | 0.05 | NA |
| OrthoPhosphate as P (mg $L^{-1}$) | 0.0871 | 0.105 | 0.0550 | 0.274 | NA | 0.08 | NA | NA | 0.06 | 0.04 | NA |
| Oxygen, Dissolved (mg $L^{-1}$) | 9.51 | 9.87 | 9.25 | 5.77 | 10.22 | 10 | NA | NA | NA | NA | NA |
| pH | 7.91 | 7.82 | 8.66 | 7.67 | 7.91 | 8.4 | NA | NA | 8.1 | 7.13 | NA |
| Phosphorus as P (mg $L^{-1}$) | 0.0989 | 0.122 | 0.0963 | 0.333 | NA | 0.045 | NA | NA | 0.027 | 0.011 | NA |
| Salinity (ppt) | 0.08 | 0.08 | 0.13 | 0.36 | 0.13 | 0.1 | NA | NA | NA | NA | NA |
| Specific Conductivity (uS $cm^{-1}$) | 164.4 | 159.7 | 277.8 | 738.4 | 304.5 | 168 | NA | NA | 1567 | 39 | NA |
| Sulfate (mg L-1) | NA | NA | NA | NA | NA | 9.1 | NA | NA | | 0.36 | NA |
| Suspended solids (mg $L^{-1}$) | NA | NA | 21.1 | 6.7 | NA | 3.5 | NA | NA | 1.3 | 2.4 | NA |
| Temperature (°) | 14.36 | 12.70 | 14.582 | 13.69 | 15.2 | 12.9 | NA | NA | NA | NA | NA |

NA - not available

**Comments:—**We used two large *Fallacia* populations from southern California (Aliso Creek) and the central coast (Soquel Creek discharging into Monterey Bay) for detailed LM and SEM observations to illustrate the morphological variation in this species. The silica thickness of diatom valves of this species varies significantly depending on different water chemistry, in addition to the valve diminution (see Figs 16–19). The LM appearance of the hyaline lyre in *F. californica* is similar to *F. cryptolyra*. However, the striae in *F. cryptolyra* are much finer and denser (26 to 36 in 10 µm according to Sabbe *et al.* 1999), and are not interrupted by hyaline rib longitudinally. *F. californica* could be distinguished from other small *Fallacia* species with course areolae by the unique combination of following features: 1) distinct panduriform lyre-shaped sternum; 2) asymmetrical central area; and 3) variable central striae with one to four inner areolae absent, and unilateral gap between the central striae on the mantle.

The species with most similar morphology, i.e. *F. tenera*, has distinctly different valve structure, besides the larger valves and the lower number of striae. It is easily distinguished by the uniform striae along the valve margins and particularly near the central area, narrower lanceolate lyre, and a single or incomplete double row of areolae along the raphe. In the studied data set, *F. tenera* was recorded with a single valve in Aliso Creek (Fig. 39) and with several valves in Tuolumne River in the Central Valley (Figs 40–42), showing considerable variation in valve outline and the pattern of areolae adjacent to the raphe branches. A comparison of morphological features of *F. californica* with similar species from *F. tenera* group is presented in Tables 2 and 3.




**FIGURES 39–46.** *Fallacia tenera* (Hust.) D. G. Mann. Fig. 39 specimen from Aliso Creek, Orange County, California. Figs 40–42 specimens from Tuolumne River, Central Valley, Stanislaus County, California. Figs 43–46 specimens from Ranu Klindungan Lake, Java, Hustedt`s slide N8/50 *Navicula tenera*, R. S. Java, Ranu Klindungan Lake 1, 1930. LM images, scale bar 10 µm.

*Navicula tenera* Hust. 1937 (Figs 43–46)

Type locality: Ranu Klindungan Lake, Java, Indonesia.

Valve are 5–6.5 µm wide, 12–14 µm long with striae 16–18 in 10 µm according to Hustedt (1937). In Hustedt slide N8/50 we observed 17 valves, which corresponded to *N. tenera*. Valves are 4.9–6 µm wide, 12–14 µm long, with 18–20 striae in 10 µm. Marginal striae are uniform along the valve, in some specimens there was a shorter single central stria (Figs 44 and 46). There is a single row of circular areolae on concave side of the raphe branches, and occasionally few isolated areolae on the other side of the raphe (Figs 43, 45, 46).

In Hustedt`s slides 230/70 and 397/94 we did not observe diatom valves corresponding to descriptions and size ranges of *Navicula auriculata* and *N. dissipata* (see Table 1).

## Discussion

LM species identification within *Fallacia* is based on shape, size and structure of the valve, hyaline lyre, lateral hyaline areas and longitudinal ribs, along with striae structure and density (Sabbe *et al*. 1999). *F. californica* is closely related to species from *F. tenera* group, because of the presence of a longitudinal rib on the valve face outside the lyre, which is splitting each stria to 2–3 coarse areolae. The hyaline lyre in *F. californica* is well developed, depressed, panduriform and distinct under LM even in the smallest specimens. However, in some species of this group, for instance in *F. tenera* and *F. arenaria* Sabbe & Vyverrman, there is a tendency for obligate or facultative absence of depression on the lyre-shaped sternum (Sabbe *et al*. 1999). According to Sabbe *et al*. (1999), the distinguishing of the species belonging to *F. tenera* complex is based mainly on the structure, number and position on the valve of the hyaline areas. *F. californica* is distinguished from all close species based on specific appearance of the distinct panduriform lyre, in combination with longitudinal rib typically enlarged towards the center, and unilaterally expanded central area.

The current understanding about the morphological variation of *F. tenera* is unclear (Li *et al.* 2014), since Schoeman & Archibald (1979) lumped freshwater *Navicula tenera* (syn. *N. uniseriata* Hust.) from Ranu Klindungan Lake in Indonesia (Hustedt 1937), with *Navicula insociabilis* var. *dissipatoides* Hust. from the Weser River in Germany (Hustedt 1957) and marine *Navicula auriculata* from Cameroon lagoon (syn. *N. dissipata*, Hustedt 1966). Besides the size and valve outline differences, the freshwater species have unilateral row of areolae near the raphe, in contrast to well developed two rows of areolae on both sides of the raphe in marine species in combination with weakly developed or absent inner puncta of the central striae (see Table 2). This broad concept has been accepted by Krammer & Lange-Bertalot (1986), Sabbe *et al*. (1999), Witkowski *et al*. (2000), Cantonati *et al.* (2017) which resulted in morphologically and ecologically heterogeneous *F. tenera* species complex. Reevaluation of the type materials of the freshwater species of *Fallacia* is needed, in conjunction with ecological, morphological and molecular data, in order to clarify the infrageneric concepts.

In North America, Patrick & Reimer (1966) illustrated *N. tenera* with single row of coarse puncta on concave side of the raphe and reported it for California. Specimens with two rows of puncta on both sides of the raphe were defined as *N. auriculata*. The newly described species *Fallacia californica* shows similarity in striae position and structure to the marine *N. auriculata* by having two rows of puncta bordering the raphe and variable differentiation of the central striae and inner areolae on both sides of the raphe (feature not recognized by Patrick& Reimer 1966), in contrast to the uniform striae in *F. tenera* from our data set (see Figs 39–42). However, *F. californica* differs from both taxa by its smaller valves, denser striae, distinct panduriform lyre and asymmetrical central area (Table 2 and 3). During the routine analysis of samples from California, *F. californica* should be carefully compared with other sporadically reported finely-striated taxa, e.g. *F. cryptolyra*, *F. insociabilis* (Krasske) D.G. Mann, *F. monoculata* (Hust.) D.G. Mann, *F. sublucidula* (Hust.) D.G. Mann, *F. omissa* (Hust.) D.G. Mann. *F. californica* shares some structural similarities also with a small-sized *F.* cf. *teneroides* (Hust.) D.G. Mann, recorded from sandy sediments in the mouth of the Westerschelde estuary, The Netherlands (Sabbe *et al.* 1999).

The new species can be found in running alkaline waters in California with medium conductivity, elevated nutrient concentrations and salinity below 0.5 ppt, occasionally inhabiting streams with higher electrolyte content.The majority of populations have been recorded in coastal streams, where they could be abundant, but the species could be scattered in inland running waters as well. The dominant taxa in the *F. californica* communities were *Nitzschia inconspicua* Grunow, *N. microcephala* Grunow, *Navicula gregaria* Donkin, *Amphora pediculus* (Kütz.) Grunow, and the epiphytic diatoms *Cocconeis placentula* Ehr., *Planothidium lanceolatum* (Bréb. ex Kütz.) Lange-Bert., *P. frequentissimum* (Lange-Betr.) Lange-Bert., *P. delicatulum* (Kütz.) Round & Bukh., and *Rhoicosphenia abbreviata* (C. Ag.) Lange-Bert.

**TABLE 2.** Comparison of size range of *Fallacia californica* Stancheva & Manoylov, *sp. nov.* with similar taxa belonging to *Fallacia tenera* group reported in the literature. NA—not available.

| Taxon | Width (um) | Length (um) | Striae in 10 um | Locality | Reference | SEM Figure | LM figure |
|---|---|---|---|---|---|---|---|
| *Fallacia californica* Stancheva & Manoylov | 4–5.6 | 6–14.5 | 20–23 | Streams in California | This study | Figs. 20–37 | Figs. 1–19 |
| *Navicula tenera* Hust. | 5–6.5 | 12–14 | 16–18 | Ranu Klindungan Lake, Java, Indonesia | Hust. (1937) | NA | Fig. 11 in Shoeman& Archibald (1979) |
| *Navicula auriculata* Hust. | 6 | 16 | 20 | Cameroon lagoon, Cameroon, West Coast of Africa, marine | Hust. (1944) | NA | Hust. Diatom Collection EarthCape Database |
| *Navicula dissipata* Hust. | 6.5 | 24 | 16 | Nordasot, West Coast of Norway | Hust. (1944) | NA | Figs. 13–15 in Shoeman& Archibald (1979) |
| *Navicula dissipata* Hust. | 5–7 | 9–27 | 14–17 | Baltic Sea, Norway, euryhaline, marine | Hust. (1961–1966) | NA | Hust. Diatom Collection EarthCape Database |
| *Fallacia tenera* (Hust.) D.G. Mann (as *Navicula teneroides* Hust.) | 6–6.5 | 11.5–14 | 17–20 | Tidal flat near the entrance of the Yahagi-Furukawa River in Atsumi Bay, Japan | Takano (1990) | 1–6 | NA |
| *Fallacia tenera* (Hust.) D.G. Mann | 5.4–8.6 | 8.5–24.1 | 17–20 | River mouth on Ubara beach, Japan | Li *et al.* (2014) | Figs. 9–30 | Figs. 1–8 |
| *Fallacia tenera* (Hust.) D.G. Mann | 5.7–6.3 | 11–14 | 18–20 | Rivers in France | Ector *et al.* (2015) | NA | Figs. 1–25 |
| *Fallacia tenera* (Hust.) D.G. Mann | 5–5.4 | 9.7–10.6 | 19–21.5 | Westerschelde estuary, The Netherlands | Sabbe *et al.* (1999) | Figs. 75, 78, 82 | Figs. 1–4 |
| *Fallacia tenera* (Hust.) D.G. Mann | 5 | 13 | 13 | Shallow pool in Makauwahi Cave, Kauai, Hawaii, USA | Miscoe *et al.* (2017) | NA | Fig. 104 |
| *Navicula auriculata* Hust. | 5–6 | 13–16 | 16–20 | USA, fresh and brackish water | Patrick & Reimer (1966) | NA | NA |
| *Navicula tenera* Hust. | 5–7 | 11–14 | 16–18 | USA, California, fresh and brackish water | Patrick & Reimer (1966) | NA | NA |
| *Navicula tenera* Hust. | 4–9 | 9–27 | 13–22 | Rivers, streams and lagoons in South Africa | Shoeman& Archibald (1979) | Figs. 29–42 | Figs. 16–28 |
| *Navicula tenera* Hust. | 4–9 | 9–27 | 13–22 | Central Europe, freshwater, euryhaline | Krammer& Lange-Bertalot (1986) | NA | Figs. 19–23 |
| *Fallacia tenera* (Hust.) D.G. Mann | 4–9 | 9–27 | 13–22 | Gulf of Gdansk and Mecklenburg Bay, Baltic Sea, brackish water, occasionally in freshwater | Witkowski *et al.* (2000) | NA | Pl. 71: 52–56 |
| *Pseudofallacia tenera* (Hust.) Liu, Kociolek & Wang | 4–9 | 9–27 | 13–22 | Central Europe, in freshwater with high electrolyte content | Cantonati *et al.* (2017) | NA | Figs. 35–38 |
| *Navicula teneroides* Hust. | 4.5 | 9–12 | 24 | Lago de Maracaibo, Venezuela, brackish water | Hust. (1956) | NA | Hust.. Diatom Collection EarthCape Database |
| *Fallacia* cf.*teneroides* (Hust.) D.G. Mann | 4.4 | 8.7–9.4 | 22–23 | Westerschelde estuary, The Netherlands | Sabbe *et al.* (1999) | Fig. 81 | Fig. 5, 6 |
| *Fallacia* cf. *teneroides* (Hust.) D.G. Mann | 3.5–5 | 9–12 | 24 | Norwegian Sea, Narvik | Witkowski *et al.* (2000) | NA | Pl. 71: 58, 59 |
| *Fallacia arenaria* Sabbe&Vyverrman | 3.9–5 | 6.4–9.8 | 26.5–27.5 | Westerschelde estuary, The Netherlands; Blakeney Point (England); German Wadden Sea | Sabbe *et al.* (1999) | Figs. 76, 77, 79, 80 | Figs.11–18 |
| *Fallacia meridionalis* Metzeltin, Lange-Bert. &García-Rodríguez | 5.5–6.2 | 11.5–15.5 | 19–20 | Several small rivers that flow into coastal lagoons in Uruguay | Metzeltin *et al.* (2005) | Pl. 61: 37 | Pl. 61: 30–36 |

**TABLE 3**. Comparison of *Fallacia californica* Stancheva & Manoylov, *sp. nov.* with similar taxa from *Fallacia tenera* group, based on valve morphology reported in the references listed in Table 2.

| Species | Lyre-shaped marking | Longitudinal hyaline rib crossing the striae | Areolae outside the hyaline rib | Areolae between the hyaline rib and the lyre | Central areolae between the hyaline rib and the lyre | Areolae along the raphe branches | Central area |
|---|---|---|---|---|---|---|---|
| *Fallacia californica* Stancheva & Manoylov | wide; panduriform | parallel to valve margin; slightly enlarged to fan-shaped near the valve center | one transapically elongated areola per stria; gap between central areolae on primary side | one transapically elongated or two small circular areolae per stria; striae variable; areolae irregularly spaced or absent near the center | areolae on primary side fewer or absent; areolae on secondary side small circular, single or double, irregular, situated closer to central area; rarely fewer | one transapically elongated or two small circular areolae per stria on both sides; rows equal in length and nearly symmetrical | small or broad; asymmetrical transapically expanded towards primary side |
| *Fallacia tenera* (Hust.) D.G. Mann | narrow; lanceolate | parallel to valve margin; uniform in size | one transapically elongated areola per stria; striae uniform, equally spaced | one circular or slightly elongated areola per stria; striae uniform, regularly spaced | not differentiated | circular areolae in single row on both sides;row on secondary side shorter withsmaller, fewer or absent areolae | broad; symmetrical |
| *Fallacia auriculata* (Hust.) D.G. Mann (Syn. *N. dissipata* Hust.) | narrow; lanceolate | parallel to valve margin; abruptly enlarged near the valve center on primary side | one transapically elongated areola per stria; striae uniform, equally spaced | one slightly elongated areola per stria;smaller circular weakly developed areolae near the center | areolae on primary side fewer or absent; areolae on secondary side weakly developed | circular areolae in single row on both sides;row on secondary side shorter with fewer areolae | broad;nearly symmetrical; slightly enlarged on primary side |
| *Fallacia teneroides* (Hust.) D.G. Mann | narrow; lanceolate | absent or LM indistinguishable | very small, LM indistinguishable | very small, LM indistinguishable | not differentiated | circular areolae in double row on primary side; single row on secondary side;rows equally long on both sides | broad; symmetrical |
| *Fallacia* cf. *teneroides* (Hust.) D.G. Mann | narrow; lanceolate; slightly constricted | broad; fan-shaped | one transapically elongated areola per stria; striae uniform, equally spaced | one circular areola per stria; striae uniform, equally spaced | circular areolae in a single not interrupted row, slightly curved towards the valve center | circular areolae in single row on both sides;row on secondary side shorter with fewer areolae | absent |
| *Fallacia arenaria* Sabbe & Vyverrman | not visible | parallel to valve margin; uniform in width | one transapically elongated or two small circular areolae per stria; striae uniform, equally spaced | one circular areola per stria; striae uniform, equally spaced | circular areolae in a single not interrupted row, slightly curved towards the valve center | few circular areolae in single unequal rows on both sides | small; symmetrical |
| *Fallacia meridionalis* Metzeltin, Lange-Bert. &García-Rodríguez | narrow; lanceolate | parallel to valve margin; uniform in width | one transapically elongated areola per stria; striae uniform, equally spaced | one slightly elongated areola per stria; striae uniform, equally spaced | not differentiated | elongated areolae in single row on both sides; rows equal in length and nearly symmetrical | broad; symmetrical |

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