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SPECIES RICHNESS, ENDEMISM AND BIOGEOGRAPHY OF FRESH WATER DIATOMS (OCHROPHYTA: BACILLARIOPHYCEAE) FROM INDONESIA: A REVIEW

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Abstract
We present the first cumulative list of freshwater diatoms from Indonesia, encompassing literature extending from 1865 until 2023. A total of 1160 names have been published. With a consideration of homotypic synonyms, the total number of different freshwater diatom taxa reported from Indonesia is over 1050. Genera with the largest number of reported species include *Nitzschia* (94), *Cymbella sensu lato* (73), *Eunotia* (72), *Pinnularia* (67), *Surirella* (60), and *Gomphonema* (48). There are two genera endemic to Indonesian freshwaters, namely *Alveocymba* and *Celebesia*, while all but one species of *Tetralunata* are endemic. Over 30% of the reported taxa are endemic to Indonesia. The flora of Indonesia is similar in size to that reported for all of Europe. The reported freshwater diatom flora of Indonesia, with the desmid flora, when combined, surpasses the number of all other algae reported for Indonesia.

***Keywords*:** Bacillariophyceae, endemism, microalgae, species richness, unicellular

Background

Indonesia is one of the largest countries in Southeast Asia. As an archipelagic nation, it consists of over 17,000 islands, over 6,000 of which are inhabited. In total, it has a land area of nearly 2,000,000 $km^{2,}$ making it the third largest country in Southeast Asia after China and India. With a population of over 280 million people, it is the fourth largest country in the world (Vickers 2005). The largest islands of the country include Java, Sumatra, Borneo, the western part of New Guinea, and Sulawesi. It extends east to west from 94^0 45' to 141^0 65' East longitude.

Indonesia is a 'megadiverse' biodiversity hotspot (Myers *et al*. 2000; Mittermeier *et al*. 1997), and some areas have been recognized as evolutionary hotspots (de Bruyn *et al*. 2014). According to the

Convention on Biological Diversity (2016), Indonesia is home to 10% of all flowering plants in the world, more than 50% of which are endemics. In terms of fauna, it houses over 500 species of mammals (second only to Brazil), 16% of the world's reptile species, and 17% of the bird species (ranking 4th and 5th in the world, respectively). It has over 1100 freshwater fish species, of which nearly 450 are endemic. While these records are impressive, like many areas of the world, very little is known about Indonesia's freshwater algal flora, including the diatoms.

Freshwater habitats in Indonesia are quite varied. Indonesia has over 500 lakes (Giesen 1994); well-known among them are the ancient Malili lakes situated on Sulawesi and Lake Toba, a volcanic lake on Sumatra, formed in the crater of a super-volcano. Toba is the largest lake in Southeast Asia and, with a depth of over 500m, one of the deepest lakes in the world. There are many rivers and streams across Indonesia, including the Citarum River, suggested by some to be one of the world's most polluted rivers (Djuangsih 1993), and the freshwater swamp forests of Sumatra have garnered special attention (Posa *et al*. 2011; Biagioni *et al*. 2015). There are many waterfalls and hot springs across Indonesia as well.

Given the high levels of biodiversity reported for Indonesia, the large area it covers, and the diversity of freshwater habitats that support its natural endowment of biological diversity, it seems appropriate to review the current knowledge about the freshwater diatom flora of the country. The purpose of the present report is to summarize our current knowledge on the freshwater diatom flora of Indonesia, documenting the richness of the flora, the number of endemics present, and to assess the biogeography of the species present.

Diatom research in Indonesia

Studies on the freshwater diatom flora of Indonesia began with Grunow's (1865) work on the algae of Banka (=Bangka) Island, from which a total of 25 new taxa (mostly in the genus *Eunotia*) were described. Following Grunow, the works by Hustedt (1935, 1937a-c, 1938a, b, 1939, 1942) are the most extensive, including samples from the largest islands in the country. Cholnoky described 32 new diatom taxa in his 1963 work on New Guinea, though most of them were from marine samples. More recently, Bramburger *et al*. (2004) described 11 new taxa of the genus *Surirella* from Sulawesi. Other new species or new treatments of previously described taxa from Indonesia include the following: Kasputin *et al*. (2021) on the genus *Encyonopsis* Krammer and (2019) on the genus *Cymbella*. Kulikovskiy *et al*. (2019) and Kociolek *et al*. (2018) contributed knowledge and new taxa on the genus *Gomphonema*. Taxonomic revisions of the Indonesian *Denticula* species described by Brun (1891) and Hustedt (1935, 1937) were done by Hamsher *et al*. (2014), who transferred them to the new genus *Tetralunata*. Kasputin *et al*. (2017) described the new genus *Celebesia* and then (2020) transferred *Cymbella mirabilis* Hustedt to the new genus *Alveocymba*.

Other studies have also contributed to the understanding of the freshwater diatom flora of Indonesia. Many of these studies are related to either a survey of freshwater algae or diatoms (e.g., Watanabe & Usman 1987; Hramoko & Krisnawati 2018), the use of diatoms to understand water conditions, both natural (e.g., Sulawesty 2016) or human-induced (e.g., Soeprobowati *et al*. 2022), or for other objectives (e.g., Suartini *et al*. 2022). These types of studies have been more frequent in the past two decades, with over 20 publications on the topic. However, most of these studies have provided only lists of diatom taxa, rarely offering detailed taxonomic accounts or even documentation of taxa with photomicrographs, making it difficult to verify the taxa listed.

In summarizing the current knowledge of diatom research in Indonesia, we surveyed publications to generate a comprehensive list of freshwater diatoms. These papers included reports and descriptions of fossil and recent taxa, from islands currently included within the political boundaries of Indonesia as of 2023. The surveyed publications ranged from Grunow's work in 1865 to those most recently published in 2023. We recorded all names presented in the literature. We included the names of taxa just as they were recorded in the original publication. To get an accurate assessment of the total number of different taxa recorded, we assessed the number of names (and their homotypic synonyms) as a single entry through the use of Catalogue of Diatom Names (Fourtanier & Kociolek 2011) and DiatomBase (Kociolek *et al*. 2024). A list of the diatoms reported from Indonesia is presented in Table 1.

In examining the level of endemicity of the Indonesian freshwater diatom flora, we assumed that species described from Indonesia are endemic. Some of the species described originally from

Indonesia have subsequently been reported elsewhere. An example of this is *Cyclotella atomus* Hustedt. A summary of the literature on its distribution has been compiled by Guiry and Guiry (2025). Based on their summary, it appears that this taxon is distributed globally and can tolerate a wide range of ecological conditions (Arctic to tropical, rivers and lakes, and oligotrophic to eutrophic conditions). There has been no verification process for entries in Algaebase (see Guiry & Guiry 2025). In other examples, taxa first reported from a limited geographic area that were then reported to be cosmopolitan were, after a verification process, shown to be endemic to the area from which they were described. Other reports outside the original distribution area were misidentifications (e.g., Kociolek & Stoermer 1987, 1991), a process of shoehorning of taxon identifications (Tyler 1996). Therefore, until there is a thorough verification of original material as well as subsequent reports, for these original records (of, in the case of *C. atomus*, a species described as 4-5 µm in diameter with few discernible features), we consider the taxa described from Indonesia to be endemics.

A total of 78 diatom genera have been reported from freshwater habitats in Indonesia. Of these three (*Ceratoneis, Diadesmis,* and *Opephora*) are no longer used. *Ceratoneis* is now referred to as *Hannaea*, but that genus is already included on the list. The species in *Diadesmis* are now considered part of *Humidophila*, and the genus *Opephora* is part of the genus *Staurosirella* (Lowe *et al*. 2015; Morales & Manoylov 2006), both of which are currently not reported from Indonesia. Thus, reducing the original genus list by 3, but including *Humidophila* and *Staurosirella*, makes the total number of genera reported from Indonesian freshwaters 77.

However, we can likely add other genera to the comprehensive list for Indonesia. Based on the species identified by Hustedt (1933, 1934a, b, 1935, 1936a, b, 1937a-c, 1938, 1942), and their current taxonomic placement, species assigned to *Navicula* by Hustedt would be placed in *Decussata*, *Geissleria, Pseudofallacia*, *Rexlowea*, *Pseudostaurosira*, and *Strelnikovia*, while some species in *Cymbella* would be assigned to *Cymbopleura* and *Oricymba*. In addition, a species placed in *Gomphonema* would be placed in *Gomphosphenia*, and species placed in *Achnanthes* would be placed in *Platessa*. All of these are missing from the listing in Table 1. This would add 10 genera, making a total of 87 genera in the flora.

Species richness and endemism

The specific number of species and subspecific taxa reported from Indonesia is a bit more difficult to assess. Based on our listing (which does not include obvious typographical errors as separate entities), there are 1199 entries of species, varieties, and forms of reported diatom taxa from Indonesian freshwaters. Of those, approximately 100 are homotypic synonyms, especially for taxa listed in both *Denticula* and *Tetralunata, Surirella* and *Iconella*, and within *Navicula* and the genera *Sellaphora, Craticula,* and several others. So, the number of taxa reported from Indonesia, excluding homotypic synonyms, is approximately 1099. Genera with the greatest number of taxa reported include *Nitzschia* with 96, *Pinnularia* with 84, *Eunotia* with 80, *Cymbella sensu lato* with 76, *Surirella* with 74, and *Gomphonema* with 57 taxa.

With regard to endemism, two genera are exclusively found in Indonesia. These genera are *Celebesia* and *Alveocymba*. A third, *Tetralunata* (Hamsher *et al*. 2014), was previously thought to be only found on Sumatra (and mostly in Lake Toba), but a taxon was recently reported from Africa (Kociolek *et al*. 2024). With regard to species and subspecific taxa, there are currently over 300 presently understood to be endemic to Indonesia. These endemics represent just over 40% of the total taxa reported. We have set aside the genus *Navicula sensu lato*, since species in that genus are now recognized in other genera (e.g., Round *et al*. 1990; Lange-Bertalot 2001). The genus with the largest number of endemic taxa is *Surirella sensu lato,* with 52 taxa (the species were recently transferred to *Iconella,* though they were never analysed with SEM to make sure they possess the diagnostic features of that genus; Kapustin & Kulikovskiy 2018). Other genera with a large number of endemics include *Nitzschia* with 35 and *Cymbella sensu lato* with 33, *Eunotia* with 31, *Pinnularia* with 33 and *Tetralunata* and *Gomphonema* with 18 endemic taxa each. As a percentage of the total, genera with the highest levels of endemism in Indonesia include *Alveocymbula and Celebesia* (100%), *Tetralunata* (95%), *Surirella* (70%), *Stauroneis* (56%,), *Cymbella sensu lato* (43%), *Eunotia* (39%), while *Pinnularia* (39%), *Nitzschia* (37%), and *Gomphonema* (32%) also have high levels of endemism in Indonesia. Areas of endemism include the ancient lakes of the island of Sulewasi (Hustedt 1942), Lake Toba (Hustedt 1935, 1938), and New Guinea (Cholnoky 1963).

Biogeography

Some taxa are not endemic exclusively to Indonesia but are regional endemisms. Hustedt (1942) examined this phenomenon with comparisons of the Indonesian freshwater diatom flora with floras in other parts of Asia Pacific, including North to the Philippines and East to Hawaii. There is almost no overlap between the flora reported from Papua New Guinea and Indonesia. Hustedt (1942, p. 205) reported that only a little over 50% of the flora is shared between Celebes (now Sulawesi) and Java, Bali, and Sumatra, while Sulawesi and the Philippines share only 41% of the flora, and Sulawesi and the Hawaiian Islands share just over 22%. Conversely, Java, Bali, and Sumatra share nearly 77% of their taxa with the Philippines as well as Hawaii. Additionally, some members of the Indonesian flora are shared with areas of Australasia, such as Australia (John 2016, 2018, 2020), New Zealand (Cassie 1989; Foged 1979), Papua New Guinea (Vyverman 1991), and New Caledonia (Manguin 1962; Maillaird 1978; Moser *et al*. 1995, 1998), being the best documented. For example, *Rhopalodia novae-zelandiae* Hustedt was described from New Zealand (Hustedt 1913) and was reported from Sumatra (Hustedt 1938). *Cymbella sumatrensis* Hustedt, described originally from Sumatra, has been reported from Australia (John 1982). There is little overlap between the flora of Indonesia and the flora of Papua New Guinea, since the freshwater diatom flora of Papua New Guinea was identified using names from Europe (see Vyverman 1991, p. 28). Further work is warranted to examine the patterns of endemism and diversity of freshwater diatoms across the Indonesian archipelago and to reveal and describe the patterns of their distributions.

Indonesia has a high degree of biodiversity of freshwater diatoms, evidenced by the high levels of both species richness and endemism. Endemism is currently demonstrated to be nearly 40% and to include 2 endemic genera, *Alveocymba* and *Celebesia*. The nearly 1,100 taxa reported from about 700 samples (Hustedt 1937, 1942) and fewer than 50 publications are higher than reported for all of Central Europe (Krammer & Lange-Bertalot 1986-1991), which has been developed based on thousands of samples and hundreds of publications. In contrast, a mere total of 19 samples were taken for Hustedt's study of the ancient lakes of Celebes. It is also important to note that most of the islands of Indonesia have never been sampled for diatoms, let alone studied in detail. This includes areas such as the Molucca Islands, Timor, and Flores, as well as Irian Jaya, areas noted for their impressive biodiversity of higher plants, mammals, insects, and birds (e.g., Wallace 1869; Millar 1978; Mees 1982; Petocz & de Fretes 1983; Petocz *et al*. 1989; Kottelat & Whitten 1996; Whitten *et al*. 2004), as well as marine species (e.g., Pitriana *et al*. 2020).

The freshwater diatom flora of Indonesia is especially rich in endemic members of the genera *Eunotia, Surirella sensu lato, Nitzschia, Stauroneis, Pinnularia, Gomphonema*, and members of the Cymbellaceae. These genera and groups also rank amongst the highest in terms of overall diversity amongst the freshwater diatoms (e.g., Kociolek *et al*. 2024). High species richness and levels of endemism are evidenced in ancient systems such as the lakes of Sulawesi, particularly expressed in the genus *Surirella* (Hustedt 1942; Bamburger *et al*. 2006), as well as the endemic genera *Celebesia* and *Alveocymba* (Hustedt 1938; Kapustin *et al*. 2017, 2020), but also in very young systems such as Lake Toba, which was formed a mere 75,000 years ago. In this case, the genus *Tetralunata* appears to be a case of a species flock (Hamsher *et al*. 2014; Kociolek *et al*. 2024), where a unique genus and nearly 20 species have been documented (Hustedt 1939; Hamsher *et al*. 2014). There are also many other interesting habitats in Indonesia, such as waterfalls, hot springs, and fossil localities from which diatoms have been documented (Hustedt 1935).

Groups that are not well represented in the diatom flora of Indonesia are members of the Coscinodiscales, Thalassiosirales, Biddulphiales, and Aulacoseirales. A total of 10 genera, represented by less than 40 taxa, have been documented so far from Indonesian lakes and other habitats. These include *Stephanodiscus, Thalassiosira, Melosira, Aulacoseira, Cyclotella, Discostella, Biddulphia, Terpsinoe and Hydrosera,* and *Coscinodiscus*. While some were described as new (e.g., *Cyclotella atomus* Hustedt 1937), most are species that are commonly reported as cosmopolitan.

A comparison of the diatom flora with other microalgal groups from Indonesia is difficult since many of them have not been described in any detail. However, Scott and Prescott (1961) documented the desmids of Indonesia. He found over 550 taxa from less than 50 samples taken from across the largest islands of the country (Java, Sumatra, Sulawesi, and Borneo). Of these, nearly 160 (ca. 30% of the taxa treated) were newly described from Indonesia and are considered endemics there. That

level of endemism almost matches that of the diatoms. The numbers of diatoms and desmids alone surpass the number of algal species reported by the Indonesian government to the Convention on Biological Diversity (Ministry of Environment and Forestry, 2014), which lists only 1500 algal species in the country, all of which appear to represent macroalgal taxa only.

Future work on a greater number of collections, new field collections, and newly evolving techniques will surely add to the already long list of diatom diversity from freshwater habitats in Indonesia.

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Supplemental data
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