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FLORISTICS AND TAXONOMY OF THE ENDEMIC DIATOM FLORA OF THE ANCIENT MALILI LAKES, SULAWESI ISLAND, INDONESIA

BY:

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ABSTRACT

The mechanisms regulating the taxonomic composition and relative abundance of taxa within biological systems are poorly understood. The diatoms of the ancient Malili Lakes (Sulawesi Island, Indonesia), however, provide an ideal system to quantify the relative importance of various mechanisms and selective processes, including geographic isolation, competition, selection, and physical limnology on the physical morphology and community characteristics of living organisms. In a quantitative examination of the floristics of the diatoms of the Malili Lakes, I evaluate the influences of geographic isolation and propagule pressure on the development of the diatom floras of the individual lakes. This floristic examination demonstrates that widely accepted stochastic models of diatom dispersal and colonization do not apply to the Malili Lakes and that the diatom floras of these lakes are regulated by mechanisms operating on the lake-to-lake, or within lake scale. In a subsequent taxonomic review of the genus *Surirella*, which contains descriptions of 11 taxa new to science, I demonstrate the morphological cohesiveness of the *Surirella* taxa of the Malili Lakes and evaluate the importance of physical limnology and novel morphological structures in the development and maintenance of highly endemic floras.

DEDICATION

To Gary and Susan Bramburger, for more financial and miscellaneous support than any other granting agency, Adam Bramburger, who needs no peer review, and Laura Pilbeam, for understanding why I'm away so much. Also, to my grandparents, Tom and Kathleen Fowler, who may not understand a word of my thesis, but are the people most likely to read every letter.

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INTRODUCTION

Among the many thousands of lakes in the world, a few are three orders of magnitude older than most lakes (Martens 1997), and are classified as truly ancient systems. These ancient lakes differ vastly in their origin, morphology, limnology, and biology (Martens 1997, Brooks, 1950a, b), yet are all recognized as economically important as sources of fresh water, fisheries resources, avenues for transportation, and destinations for tourism. Biologically, ancient lakes are important reserves for global biodiversity, and many lakes exhibit elevated levels of endemism and species richness (Martens 1997, Brooks 1590a, b, Haffner *et al.* 2001). The factors regulating the species composition and relative abundance in these lakes, however, are poorly understood.

The ancient Malili Lakes of Sulawesi Island, Indonesia (Figure 1.1) are unique among the ancient lakes of the world in that they alone are situated on an island and form a hydrological continuum (Brooks 1950b). The location of the Malili Lakes, along with their unique limnological characteristics, has created a biological system which Brooks (1950b) described as "different from all of the previously discussed old lakes," and the system was recently described by the United Nations Environmental Programme and the World Conservation Monitoring Centre as the "most important single site for biodiversity in Asia," with an estimated 80% endemic taxa.

High levels of endemism on Sulawesi have been well documented. While exploring in the Malay Archipelago, Wallace (1860) noticed that the terrestrial biota in the islands in the northwestern end of the chain bore a striking resemblance to that of mainland Asia, while that of the southeastern islands resembled the biota of Australia.

Upon exploring Sulawesi (then called Celebes), in the geographic centre Indonesia, Wallace had expected to observe a terrestrial biota intermediate to that observed at the ends of the archipelago. Instead, he found a flora and fauna composed almost exclusively of endemic species with little resemblance to the biota of Asia, Australia, or any nearby islands. Following Wallace's observations, Whitten *et al.* (1987) noted that 62 percent of mammals (98% of flightless mammals) and 34 percent of bird species (17 endemic genera) were endemic. Reudi (1995) described six species of shrews (*Crocidura*) all endemic to Sulawesi, pointing out that this is an unusually high number for an island that has never been connected to the mainland. Elevated levels of endemism have also been reported in the birds (White & Bruce 1986), reptiles (Den Bosch 1985), and vascular plants (Whitten *et al.* 2002).

The levels of endemism observed in Sulawesi's aquatic systems in general, and the Malili Lakes, in particular, reflect that observed in terrestrial environments. The Malili Lakes contain the vast majority of Sulawesi's endemic fishes. Kottelat (1990a, b, c) and Larson and Kottelat (1991) described several new species and even some new genera within the families Telmatherinidae (Sailfin silversides), Oryziidae (ricefishes), and Gobiidae (Gobies) within the Malili Lakes. Many of these species are endemic to Lake Matano, the headwater lake of the Malili system, and the Telmatherinids are thought by Kottelat (1990c) to represent a species flock. A sympatric species flock in a lake known to have been isolated since its formation is often suggested by sexual selection for colour morphs (Turner and Burrows 1995) and this would explain the variation in colour of male Telmatherinids in the lake. Naruse *et al.* (1993) used genetic techniques to further explore the ricefishes and their relatives on Sulawesi, reporting that with the exception of *Oryzias celebensis*, each species was endemic to one specific lake. All six species of ricefishes on the island, however, are restricted to the lakes and rivers of Central Sulawesi (Naruse 2001). Additionally, many if the islands aquatic molluscs (Whitten *et al.* 1986) and crustaceans (Victor & Fernnando 1982) are endemic to single lakes.

Perhaps the most striking example of aquatic endemism on Sulawesi Island is provided by the diatom flora of the Malili Lakes. Hustedt (1942) reported many new taxa, almost exclusively endemic to Sulawesi, and remarked that his work had merely "scratched the surface" and that he was certain that there were many taxa yet to be described from the lakes. Hustedt's (1942) findings are somewhat paradoxical when considered in the context of the widely accepted paradigm of cosmopolitan distribution of diatoms. Cleve (1894, 1895) stated that globally, diatom assemblages were dominated by cosmopolitan forms. More recently, Kociolek and Spaulding (2000) postulated that apparent "endemism" among the diatoms was often a result of inaccurate taxonomy and regional differences in nomenclature.

Despite taxonomic difficulties with the diatoms, the diatom flora of the Malili Lakes provides an ideal system in which to quantify the relative importance of various processes that regulate development of species assemblages. While similar to many other ancient tropical lakes in their tectonic origin, and substantial depth, the Malili Lakes are set apart by their island setting, mixing regime, and the fact that they form a hydrological continuum

THE MALILI LAKES: A COMPARISON WITH OTHER ANCIENT LAKES

The morphology of a lake reflects the nature of its original formation and the accumulation of the effects of various processes over time. The ancient lakes of the world were formed by a variety of different processes acting in a variety of background environments. The Caspian Lake (Caspian "Sea") was initially formed some five million years before present (YBP) (Dumont 1998), in a mountainous region of southeastern Europe, near Asia (Kosarev and Yablonskaya 1994). The boundaries of the Caspian catchment basin were defined between 5 and 20 million years ago, when tectonic collision between the Arabian peninsula and western Asia caused the mountain uplift and adjacent sagging that cut the connection between the South Caspian and the Black Sea (Dumont 1998). Subsequent sagging, combined with input from rivers, connections with the Black and Aral Seas, and glacial meltwater from central Asia, gave the lake its present, three-basin shape approximately 100 000 years ago.

The maximum age of Siberia's Lake Baikal has been estimated at between 50 and 75 million years (Brooks 1950a, Zeuner 1946), although it is generally accepted that the entire lake was not formed at the same time. It is only the south basin of the lake that is thought to have held water since the end of the cretaceous (Brooks 1950a). Deepening of the Baikal Basin by the uplift of the Baikal Mountains and the Vitim Plateau did not occur until approximately 1.5 million years ago.

Many of the world's old lakes exist in East Africa. The African Great Lakes were formed over a long time interval. Lakes Tanganyika and Malawi (Nyasa) attained their present form through tectonic uplifting in the East African Rift Valley some 20 million years ago (Lowe-McConnell 1993), but might be much older. Lake Victoria, the largest tropical lake in the world, is another member of this lake chain. It is much younger than Tanganyika and Malawi, with age estimates ranging from the popular 750 000 years (Lowe-McConnell 1993) to 14 000 or 25 000 years (Stager *et al.* 1986). Similarly, in the case of Lake Lanao in the Philippines, there is some dispute over the age of formation. Reid (1980) points out that some authors feel that its relative youth is beyond dispute, yet Brooks (1950b) believes that the lake is truly ancient. Frey (1969) places the lake's formation in the late Tertiary, some 1 million years earlier than the estimates pointed out by Reid (1980).

Like the Great Lakes of the East African Rift Valley, The Malili Lakes of Sulawesi, Indonesia, and Lake Matano in particular, were formed through tectonic collision and mantle uplift during the late Pliocene between 5 and 10 million years ago (Haffner *et al.* 2001). The lakes are located in the centre of the southern arm of the continental island of Sulawesi, and were formed when the eastern half of the island, a fragment of the former Gondwanaland, collided with the western arc, of volcanic origin, traveling in the opposite direction (VanBemmelin 1949). Unlike the African Great Lakes and the Caspian Lake, which were situated on mainlands at the time of their formation, the formation of the Malili Lakes basin was concurrent with the first formation of Sulawesi Island, and this has ensured their geographic isolation since the time of their original formation. The Malili Lakes are also unique among ancient lakes in that they form a hydrological continuum (except Masapi) (Brooks 1950b). This has important consequences for the study of biogeography of aquatic taxa within the region.

While a lake's morphology reflects its formation, it also determines, to a large extent, its limnology. Lakes formed by tectonic folding and faulting, known as graben lakes, are predominantly long and narrow, with steep depth profiles in cross section. Lake Baikal, the world's deepest lake, is 674km in length, yet only 74km wide it its widest point, yet has a maximum depth of 1637m (Microsoft Encarta 2002). Of the African Great Lakes, Tanganyika's proportions are the most similar to Lake Baikal. It has a length of 650km and a maximum depth of 1435m, making it the second deepest freshwater lake in the world. Malawi has approximately the same shape, but on a smaller scale, with a length of 580km and a maximum depth of 706m.

Africa's Lake Victoria has a vastly different morphology from that of its neighbours. It has been described as a "tremendous saucer," (Brooks 1950b) or a "vast evaporation pan astride the equator" (Stager *et al.* 1997). Occupying a surface area of about 69000km^2, Victoria has a maximum depth of only 80m, with much of the lake being shallower than 40m (Kendall 1969). Despite its relatively shallow depth, large surface area, and a high potential for wind-driven vertical mixing, Victoria remains almost permanently stratified, maintaining a slight temperature gradient (Talling 1957).

Beadle (1966) points out that tropical climates are favorable for the stratification of lakes, as the density of water changes rapidly with temperature above 25°C. He observed stratified conditions in the small crater lake, Nkugute, in Uganda, and also in larger Lakes Bunyoni and Edward. Downstream of Lake Edward, the shallow Lake Albert exhibits a weak thermal stratification (Talling 1963), while lakes such as Tanganyika and Kivu are considered meromictic and are permanently and intensely stratified (Baxter *et al.* 1965). Eccles (1974) noted that the thermal profile of Lake

Malawi is similar to that of the offshore areas of Lake Tanganyika, with similar seasonal cycles (Bauchamp 1953). These lakes tend to behave differently than the traditional notion of tropical lakes (Hutchinson and Loffler 1956), and the steep profiles of their basins are thought to enhance the intensity of stratification.

Thermal structuring is often cited as the prerequisite for the deoxygenation of the lower strata or hypolimnion within a lake. Oxygen depletion alters the chemical processes within the hypolimnion of a lake, and thus has profound effects on a system's ecology by altering distribution of habitat types (Nürnberg 1995). Talling (1957) found that dissolved oxygen stratification in Lake Victoria was weak during the mixing season in July and August, but obvious in the rest of the year with a sharp discontinuity between 30 and 60m.

In contrast to most other large tropical lakes, the Malili Lakes exhibit, at best, very mild thermal and density structuring (Haffner *et al.* 2001). Like many other ancient tropical lakes, the headwater, Lake Matano, is long, narrow, and extremely deep. However, unlike many deep tropical lakes, Matano does not stratify strongly and is relatively well mixed (Haffner and Tomczak 1998). Haffner *et al.* (2001) reported a difference of less then 3°C between the surface of the lake and the bottom at 590m. Because of the shape of the basin, it is reasonable to rule out wind action as a source of vertical mixing in the water column. Haffner and Tomczak (1998) suggested density currents and hydrothermal inputs as potential causes of vertical mixing. These density currents, set up by cool dense runoff inputs from the Matano drainage basin, are important events for the primarily benthic diatom flora of the lake.

Lake Towuti, the largest lake in the Malili chain, shows no detectable thermal structure in its 203m depth. The causes of this extraordinary mixing are not understood and the transparency of the lake is exceptionally high. Of all the Malili Lakes, Lake Mahalona is possibly the most similar to lakes on nearby islands. It has a shallow, pan shaped bathymetry, and is also completely mixed. Lakes Wawantoa and Masapi are small headwater lakes adjacent to Towuti, and their bathymetry and limnology are poorly known at this point.

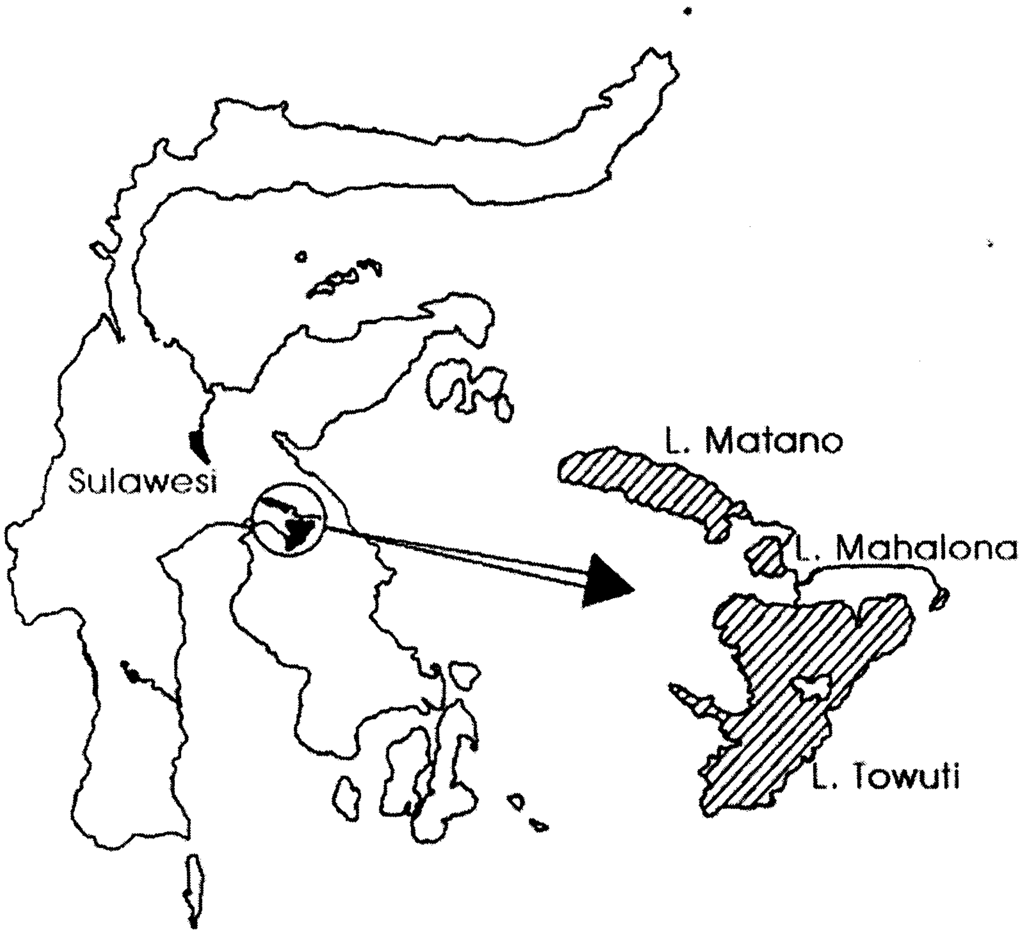

Figure i.1: The Malili Lakes and their Position on Sulawesi Island. Lake Masapi (not shown) lies immediately to the west of Lake Towuti.

DIATOMS

The diatoms (Bacillariophyceae) are unicellular photosynthetic algae that secrete a siliceous shell, known as a frustule (Duke and Reimann 1977). The morphology of diatom frustules varies from taxon to taxon, and forms the primary basis for diatom taxonomy. The uniqueness and permanence of these frustules, along with several other characteristics, have made diatoms a popular choice as indicator organisms in many facets of biology.

Due to their small size and unicellular nature, diatoms are easily dispersed by a variety of passive vectors. Advective transport, wind (both as dust particles and aerosols), animal, and human mediated dispersal have all been implicated as probable means of diatom transport. This ease of dispersal has led to the popular cosmopolitan paradigm of diatom distribution (Cleve 1894, 1895, Kociolek and Spaulding 2000). The global distribution of many taxa, coupled with the incorporation of common diatom frustules into sedimentary rock, has lead many scientists to use diatoms in paleolimnological and paleoclimatic reconstructions (Binford *et al.* 1983, Mannion 1986, Kooistra and Medlin 1996). The order Bacillariophyceae is thought to have diverged some 1.2 billion years ago (Hamilton *pers. comm.*), making diatoms older, by an order of magnitude than even the very oldest of ancient lakes.

Within the global distribution of diatoms in general, various taxa have been reported to respond, often quickly, to changes in chemical conditions, including pH, conductivity, and concentrations of nutrients and metals (Kilham 1976, Kilham *et al.* 1986, Eloranta 1995, Soininen 2002). These responses are usually characterized by changes in relative abundance of taxa, and are thought to be universal. Thus, modern diatom communities have often been used as proxies for historical communities growing under similar conditions (Batarbee *et al.* 1999, Hall and Smol 1999, Bradbury 1999). Similarly, diatom colonization, like that of many other organisms, is thought to be highly conservative and stochastic in nature (Cleve 1894, 1895). As such, colonization by diatom taxa has often been used by forensic scientists as a measure of how long an object has been submerged (Peabody 1999).

Global patterns of dispersal, short generation times, and stochastic colonization patterns have important implications for diatom biogeography. Island biogeography theory (MacArthur and Wilson 1967) states that the species richness of an island or habitat patch decreases with its relative isolation from the mainland. Diamond (1972) demonstrated this "distance effect" with the bird species of the Bismarck Archipelago. According to MacArthur and Wilson (1963), the rate of immigration is decreased and the rate of local extinction of island populations is increased on habitat patches isolated from the mainland, or source patch. For diatom floras in adjacent lakes, there should therefore be a high degree of overlap. The historical data from the Malili Lakes (Hustedt 1942), however, stand in direct contrast to this prediction.

In the first chapter of this thesis, I determine if the historically reported levels of diatom endemism in the Malili Lakes are accurate, and evaluate the range limitation of the Malili Lakes flora. I also evaluate levels of similarity among the diatom floras of the Malili Lakes in order to determine whether the endemism described within a lake can be attributed solely to biogeographical constraints. In the second chapter, I review the taxa within the genus *Surirella* in the Malili Lakes, a genus that exhibits high levels of endemism characteristic of the Malili Lakes flora. In this review, I examine morphological relationships within the genus, and evaluate the possible function and role of novel morphotypes in the ecology and evolution of the Malili Lakes flora.

CHAPTER 1:

EXAMINING THE DISTRIBUTIONAL PATTERNS OF THE DIATOM FLORA OF THE MALILI LAKES, SULAWESI ISLAND, INDONESIA

ABSTRACT

The Malili Lakes are a group of ancient island lakes that, until recently, were relatively free of anthropogenic disturbance. During the 1930s, the diatom community of the lakes was surveyed by Hustedt (1942) who noted that the diatom community was dominated by endemic species. Recent surveys (1997-2002) have revealed little change in the composition of the diatom communities of the lakes, and interesting patterns of distribution within the Malili Lakes and neighboring islands in the Indo-Pacific Region. Each of the Malili Lakes shares a small proportion of its diatom flora with one or two other lakes within the system, and an even smaller proportion with other lakes on the island of Sulawesi and other islands. The abundance of endemic species restricted to single lakes, coupled with the paucity of cosmopolitan species within the system and similarity index values indicating low levels of similarity among lakes suggest that geographic proximity is not governing the similarity of diatom assemblages within this ancient lakes system.

INTRODUCTION

While Charles Darwin (1860) studied the Galapagos Islands, a small island cluster off the coast of Ecuador, Alfred Wallace (1860) examined speciation on the larger and more numerous islands of the Indo-Pacific region. Of particular interest to Wallace was Sulawesi, a tectonically formed island located in the middle of the Indonesian archipelago, almost astride of what became known as Wallace's Line. Upon studying the biota of the island, Wallace was struck by its contrast to his expectations. Where he had expected to see a species assemblage intermediate to those of Australia and Asia, there was instead an assemblage that was completely unique. Those who followed Wallace (1860) made similar observations on mammals (Reudi 1995), birds (White & Bruce 1986), reptiles (den Bosch 1985), fish (Kottelat 1990a,b, c), crustaceans (Victor & Fernando 1982), and vascular plants (Whitten *et al.* 2002). Hustedt (1942) also remarked on the striking uniqueness in the diatom flora of Sulawesi compared to the surrounding islands. Historical data from the Southwest Indo- Pacific region (Hustedt 1939, Vyverman 1991, Moser *et al.* 1998) concurred that endemism is significant in this part of the world. Interestingly, based on the work of Hustedt (1942), the patterns of distribution among the diatoms of Sulawesi do not appear to be constant. Many of the taxa endemic to the island were also restricted to a single lake or lake system.

A chain of five lakes known as the Malili Lakes is located in the mountains of Central Sulawesi. The Malili Lakes system was formed by tectonic displacement and is thought to be as much as 4 million years old (Brooks 1950, Haffner *et al.* 2001). Brooks (1950) pointed out that the Malili Lakes are unique among ancient lakes in that they form a hydrological continuum, with surface water flowing from one lake to the next.. Lake

Matano, the headwater of the system, is the most isolated lake of the group, and drains at 25-30m^3s^{-1} through Lakes Mahalona and Towuti, and then through the Larona River. Lake Masapi drains directly to the Larona River.

The theory of island biogeography (MacArthur & Wilson 1967) predicts that the closer a patch of suitable habitat or "island" is to a mainland, the more likely it is to be successfully colonized by organisms from the mainland. As such, the closer patches of habitat are to one another, the more likely they are to share various species. The main assumption of this theory is that the organisms in question are able to disperse. Diatoms, while not particularly motile, do disperse by a variety of passive means (Mills *et al.* 1994, Denys 1998). The fact that many cosmopolitan species exist attests to this (Cleve 1894,1895). The presence of various cosmopolitan species within the Indo-Pacific region and the apparent paucity of cosmopolitan species within the Malili Lakes raise several questions. Primarily, is the diatom flora of lakes truly as unique as the historical data suggest? Secondarily, does dispersal govern the species compositions of the Malili Lakes and the Indo-Pacific region? If the uniqueness of the diatom flora were purely a function of their relative geographic isolation and distance from other bodies of water, the lakes could be expected to show a high degree of similarity with one another and a less similarity with lakes separated by larger distances. Additionally, the lakes would exhibit lower degrees of similarity with other water bodies farther afield. If this is not the case, then it is unlikely that geographic proximity of water bodies to one another is a good estimate of assemblage similarity in the Indo-Pacific region and determines the species composition of the Malili Lakes.

In this chapter, I to determine the extent of the uniqueness of the flora of the Malili Lakes within the Indo-Pacific region and examine whether the principles of island biogeography can account for this uniqueness by evaluating several null hypotheses.

1. There is no difference in the degree of similarity between assemblages when different assemblages are included in comparison.
2. Species shared among more than one lake in the Malili System are shared among all lakes within the system (cosmopolitan).
3. There is no difference in the mean degree of similarity among lake/lake, lake/other Sulawesi lakes, and lake/lakes from other islands comparisons.
4. There is no difference between the degree of similarity among inter-lake comparisons and inter-island comparisons.

MATERIALS AND METHODS

Sampling and Sample Processing:

The sampling area consisted of a chain of five lakes, known as the Malili Lakes, located in central Sulawesi, Indonesia. The watershed consists of the lakes Matano, Mahalona, Towuti, Masapi, and Wawantoa (Table 1.1).

Sixty samples were collected from Lakes Matano, Mahalona, Towuti, and Masapi between Jan 11 and February 10, 2002. In order to observe a representative number of the taxa from each lake, as many different microhabitat types as possible were sampled within each lake. Sampling techniques included plankton hauls from 20m and 60m, sand and sediment samples, and log, rock and macrophyte scrapes. Organic material was removed from the samples by a 30 minute digestion in boiling concentrated nitric/sulphuric acid. Samples were then rinsed with distilled water and centrifuged at 3000 rpm for 10 minutes to remove excess acid. Rinsing and centrifugation were repeated six times for each sample. Diatom material was subsequently dried onto glass cover slips and mounted onto microscope slides with Naphrax mountant. Smaller cover slips were mounted to aluminum stubs with white glue slurry and sputter coated with gold for 20 seconds at ___kV for SEM examination.

Counting and Statistical Analysis:

Diatom valves were identified and counted on random transects at 1000x using a Leitz Diaplan light microscope under brightfield and phase contrast optics. Valves on each slide were counted until the end of the transect upon which the 100th valve of the dominant taxa was identified. Diatoms were also examined with a Philips XL30 SEM with accelerating voltages between 10kV and 30kV.

In order to determine the point at which a representative number of taxa had been observed, non-linear species accumulation modeling was used to determine a 95% taxa saturation point for each of the four lakes examined. The enumeration of a maximum of any 8 microhabitat samples (Lake Masapi) was sufficient to encompass 95% of the predicted total taxonomic richness of the lake (Fig. 1.1). Inclusion of data from Hustedt (1942) did not affect the position of this saturation point. 10 samples were examined from each lake. Count data was subsequently combined with historical data (Hustedt 1942) to determine species presence/absence within each lake. Presence absence data were used to calculate modified SIMI similarity indices based on SIMI (Hoagland *et al.*1982, Stander 1971) for various species assemblage pairings by the equation below. SIMI was modified to allow for the inclusion of historical data, which included only presence/absence data, rather than relative abundance.

$$\mathrm{SIMI}(a,b) = \frac{\sum_{i=1}^{s} P_{ai} P_{bi}}{\sqrt{\sum_{i=1}^{s} P_{ai}^{2}} \sqrt{\sum_{i=1}^{s} P_{bi}^{2}}}$$

SIMI represents the degree of similarity between assemblages a and b. P_{ai} and P_{bi} are the proportion of the total species assemblage represented by the i^{th} taxon in assemblages a and b. Variable S is the total number of taxa in both assemblages. SIMI has a maximum value of 1 when the two assemblages are identical and a minimum of 0 when they share no species. In this case, SIMI was modified by the removal of the relative abundance term from the calculation of the proportion of the total assemblage represented by a taxon. This Modified SIMI provided a more conservative estimate of differences between assemblages than traditional SIMI (Stander1970). The species assemblage of each of the Malili Lakes was paired with each of the other lakes within the system, composite assemblages of multiple Malili Lakes, and assemblage composed of the species of several other lakes on Sulawesi, and an assemblages composed of the species of lakes on the islands of Java, Bali, Sumatra, and Papua New Guinea (Hustedt 1938, Vyverman 1991). Traditional SIMI (Stander 1970) values were calculated for lake-lake pairings.

One-way ANOVAs with post-hoc Bonferroni tests (SPSS Science 1998) were used to probe for differences in Modified SIMI and mean Modified SIMI among lake/lake pairings, lake/Sulawesi lake outgroup pairings, and lake/other island outgroup pairings. Mean SIMI was calculated for each pairing with the Malili Lakes composite assemblages and plotted against the number of lakes included in the composite assemblage. The resulting relation was analyzed by linear regression analysis. A one-way ANOVA with post-hoc Bonferroni tests was also used to examine differences in mean Modified SIMI among lake/lake, lake/Sulawesi outgroup, and lake/island outgroup pairings. Additionally, a two-sample T-test was used to determine whether mean Modified SIMI for inter-lake comparisons was greater than mean Modified SIMI for inter-island comparisons.

Additionally, relative abundances of diatom taxa were measured and the number of taxa required to account for 95% of the numerical abundance of diatom frustules was calculated for each lake. This measurement provided an estimate of the degree to which a lake's diatom community was dominated by various taxa.

RESULTS

A total of 256 diatom taxa were identified from the littoral habitats of the four lakes examined. The flora was comprised of taxa representing 1 order, 41 genera, and 233 species. Total taxa richness in the Malili Lakes system ranged from 36 taxa in Lake Masapi to 154 in Lake Towuti (Table 1.2). Many of the taxa identified were endemic to Sulawesi Island (245), to the Malili Lakes system, and 83 taxa were restricted to single lakes (Table 1.3).

Modified SIMI values for various assemblage pairings were evaluated to determine patterns of geographic similarity. One-way ANOVA with post-hoc Bonferroni tests indicated that the lakes included in a pairing accounted for a significant amount of variance in Modified SIMI among lake/lake, lake/Sulawesi outgroup, and lake/island outgroup pairings ($p<0.05$, $n=14$). No individual lake, however, accounted for a significant amount of variance in Modified SIMI when included in a pairing (Table 1.4).

Traditional SIMI values for these pairings were lower, but lake had a discernable influence (Appendix 1.) Lakes Matano and Masapi tended to exhibit lower Modified SIMI values in their respective pairings than other lakes in the system. Lake Mahalona exhibited a higher Modified SIMI when compared to the Island outgroup than when compared to the Sulawesi outgroup. When composite assemblage pairings within the Malili Lakes were compared, Modified SIMI values exhibited a positive trend with an increase in the number of lakes included in a composite assemblage (Fig. 1.2). This result, however, was not significant (Linear regression, $p>0.05$, $n=22$).

One-way ANOVA with post-hoc Bonferroni tests also showed that mean Modified SIMI for lake/lake comparisons was significantly higher than mean Modified SIMI for lake/Sulawesi outgroup comparisons and mean Modified SIMI for lake/ island outgroup comparisons ($p<0.05$, $n=14$). Additionally, a Two-sample T-test indicated no significant difference in mean Modified SIMI between interlake comparisons and inter-island comparisons ($p>0.05$, $n=14$).

When relative abundances of diatom taxa were calculated for each lake, it was found that 95% of the numerical abundance of frustules in Lakes Matano, Masapi, Towuti, and Mahalona, were accounted by 11, 17, 18, and 18 taxa, respectively. The diatom community in Lake Matano was represented by significantly fewer taxa than any of the other lakes (ANOVA $p<0.05$, $n=4$).

DISCUSSION

Lake Matano and its neighbours, the other Malili Lakes, on the island of Sulawesi, exemplify the high levels of species diversity and endemism commonly associated with Sulawesi and the Indo-Pacific region. The diatom flora of the Malili Lakes conforms to this trend. Of the 256 taxa observed in this study, 35% are endemic to only one lake.

Similarity indices are widely used to examine the degree of similarity between species assemblages (Truchman & Blinn 1979, Hoagland *et al.* 2002, King *et al.* 2002). SIMI (Hoagland *et al.* 2002) has been used primarily with count and relative abundance data. In this case, presence/absence data has been used in place of relative abundance to allow for inclusion of historical data. Therefore $P_{ai} = P_{bi}$ in each assemblage pairing as the relative abundance of each species present is 1/the total number of species present for both assemblages. Here, Modified SIMI is used as a means to account for differences in species richness when considering the similarity of assemblages. For instance, a lake with an impoverished flora can share its species with a more taxon-rich lake, giving the assemblages a high degree of overlap, but a low degree of similarity. The fact that lake pairing accounts for a significant amount of variance in Modified SIMI, but no individual lake accounts for an inordinately high proportion of this variance suggests that floras of many lakes, including Lake Matano, have evolved independently, and the differences among the lakes are based primarily on the presence of endemic species. Each lake in the Malili Lakes system has a unique and highly endemic flora (Table 1.1). Modified SIMI values for pairings including Lake Masapi are likely artificially reduced, as a result of the relatively impoverished condition of the lake's flora and the lack of historical and modern data. Lake Matano, on the other hand, exhibited a higher percentage of endemic species than the other lakes and its uniqueness is likely real. I predict a further increase in the number of endemic taxa in Lake Matano as further taxonomic work is completed.

Not all species in the Malili Lakes, however, are restricted to single lakes. It is thus important to know if the species shared between two lakes are further shared among all lakes, or if smaller groups of species are shared among subgroups of lakes. If species were shared among all lakes, then the number of shared species would become proportionally smaller as the number of potentially shared species increased. In this study, mean Modified SIMI would be inversely related to the number of lakes included in a composite assemblage. While the relation between the number of lakes included in a composite assemblage and mean Modified SIMI was not significantly positive, a negative trend was clearly not observed, indicating that small groups of species were shared among groups of two or three lakes and very few species are found throughout the entire Malili chain. With a larger sample size, this result would likely have been significant.

While few species within the Malili Lakes flora are found throughout the chain, even fewer are found elsewhere in the Indo-Pacific region. Significantly lower mean Modified SIMI values for lake/lake comparisons than for lake/Sulawesi outgroup comparisons and lake/island outgroup comparisons indicate that although the assemblages of the Malili Lakes exhibit a low degree of similarity with one another, they are more similar to one another than they are to those of other lakes in the Indo-Pacific region. Most of the taxa shared among the Malili Lakes are not shared with lakes outside the system. This result suggests a high degree of endemism, not only at the spatial scale of each individual lake, but at the scale of the watershed itself.

The results so far reflect a system with a high degree of uniqueness and endemism at various spatial scales. Is the level of uniqueness of each individual lake more than what would be expected for lakes so close to one another? A two-sample T-test evaluating the differences between mean Modified SIMI of Malili Lakes assemblage comparisons and comparisons of the assemblages of the islands of Java, Bali, Sumatra, and Papua New Guinea did not produce a significant result. This demonstrates that although the Malili Lakes are geographically very close to one another, they are as dissimilar as islands located hundreds to thousand kilometers apart, often at opposite sides of Wallace's Line. Such dissimilarity among the Malili Lakes suggests that geographic proximity is a poor predictor of species assemblage similarity in the Malili Lakes, and demonstrates that the diatom assemblage of each of the Malili Lakes has evolved individually, and independent of a lake's inclusion in hydrological continuum. Essentially, the processes regulating community composition and relative abundance of taxa function on the lake-to-lake or within lake scale.

The Malili Lakes system may be as much as 4 million years old (Haffner *et al.* 2001). For the lakes to produce and retain unique floras for long periods, some mechanism must effectively keep cosmopolitan species from successfully colonizing the system. The present study indicates that little change in the Malili diatoms has occurred over the last 60 years despite increased anthropogenic activity. In the future fish farming activities in Lake Matano might reveal the importance of local eutrophication and species invasions. This study also demonstrates that geographic proximity is also not likely to influence the diatom distribution of the Malili Lakes.

There are, however, several avenues yet to be explored. Lake morphology and limnology as selective processes seem to be the most promising avenues for future research. The Malili Lakes, with the exception of Lake Mahalona, are all deep for their size, with steep to moderately steep profiles. Steep profiles lead to reduced littoral zone area within a lake. These shallow areas were found to be the most highly productive areas in other deep, ancient tropical lakes. Eccles (1974) noted that fish production was concentrated in the shallow marginal areas of Lake Malawi in the African Rift Valley. Coulter (1963) noted that phytoplankton were most abundant in inshore areas in Lake Tanganyika, whereas the open lake was highly oligotrophic. For primarily benthic diatom communities, such as those found in the Malili Lakes, it follows that the small, productive littoral zone would be most favorable to diatom production. Consequently, decreased diversity of benthic organisms is often reflective of a narrow microhabitat resource gradient, characteristic of graben lakes, and is illustrated, in this case, by the reduced number of taxa that account for 95% of the diatom frustules observed in Lake Matano. The reduced area of the littoral zone could lead to increased competition for suitable microhabitat resources (Zaret and Rand 1971). Moulton (1993) and Moulton and Pimm (1985) showed that communities exhibiting a high degree of competition tend to be more resistant to successful colonization by invasive species.

Perhaps the elevated degree of similarity between Lake Mahalona and lakes on other nearby islands is because of Mahalona's shallower, more sloping profile. The role of the limnology of the Malili Lakes in the shaping of their diatom flora is not clear at this time. However, if Lake Matano is taken as an example, limnology is responsible for preventing a rapid change in the local flora. Colder stormwater (21-22 °C) runoff sinks rapidly down the steep slopes of Lake Matano, setting up density currents and providing vertical mixing. This mixing is sufficient to make temperature and dissolved oxygen (D.O.) profiles relatively constant throughout the water column (Haffner Unpublished. data). This oxygenated water at depth is a rarity among deep tropical lakes. The lakes of the African Rift Valley are essentially anoxic below 250m (Talling 1957, 1963, Hecky *et al.*1994, Eccles 1974). The oxygenation of Matano's deep waters keeps metals in the sediment out of solution. If biochemical oxygen demand (BOD) in the lake were to increase through sediment pollution by organic compounds and enhanced runoff due to deforestation (Cohen *et al.* 1993), these metals would rapidly go into solution. As the diatom community has the potential to react to water quality variables and heavy metal concentrations in a matter of days (Soininen 2002), a rapid and dramatic change in species composition is possible.

The reoccurring documentation of endemism in the Southern and Indo- Pacific regions is striking (Hustedt, 1942, Coste & Ricard 1990, Vyverman 1991, Moser *et al.* 1998). This phenomenon is evident at different spatial scales from adjacent lakes observed in this study to distinct archipelagos (Moser *et al.* 1998). On closer examination, clusters of aligned taxa and genera, across the Southern and Indo- Pacific, may suggest adaptive radiation as postulated by Moser *et al.* (1998). This study further supports this idea, with evidence for adaptive radiation within the *Achnanthes* sensu lato, *Brachysira*, *Cymbella* sensu lato, *Epithemia*, *Gomphonema*, *Mastogloia*, *Navicula* sensu lato, *Nitzschia* and *Surirella* genera. Five of these genera were identified by Moser *et al.* (1998) as possible taxa clusters. The work of Hustedt (1938) would also suggest that *Denticula* is another possible cluster group within the Indo-Pacific.

The Malili Lakes have a unique, highly endemic and potentially sensitive diatom flora, not only as a system, but also on a lake by lake basis. Lake Matano, a deep, ancient lake at the headwaters of the system exemplifies this uniqueness. Many of Matano's species are shared with no, or at best few other lakes, a trend common to all of the Malili

Lakes. In contrast to MacArthur and Wilson's (1967) theory of island biogeography, geographic proximity is likely not determinant of diatom taxa distribution in the Malili Lakes system or the Indo-Pacific Region. The question still remains, how can freshwaters retain unique endemic diatom assemblages throughout the Indo-Pacific.

FIGURE LEGEND

Fig. 1.1. Non linear taxa accumulation model for Lake Masapi.

Fig. 1.2. Mean SIMI values for composite lake assemblages. Error bars = ±1 S.D.

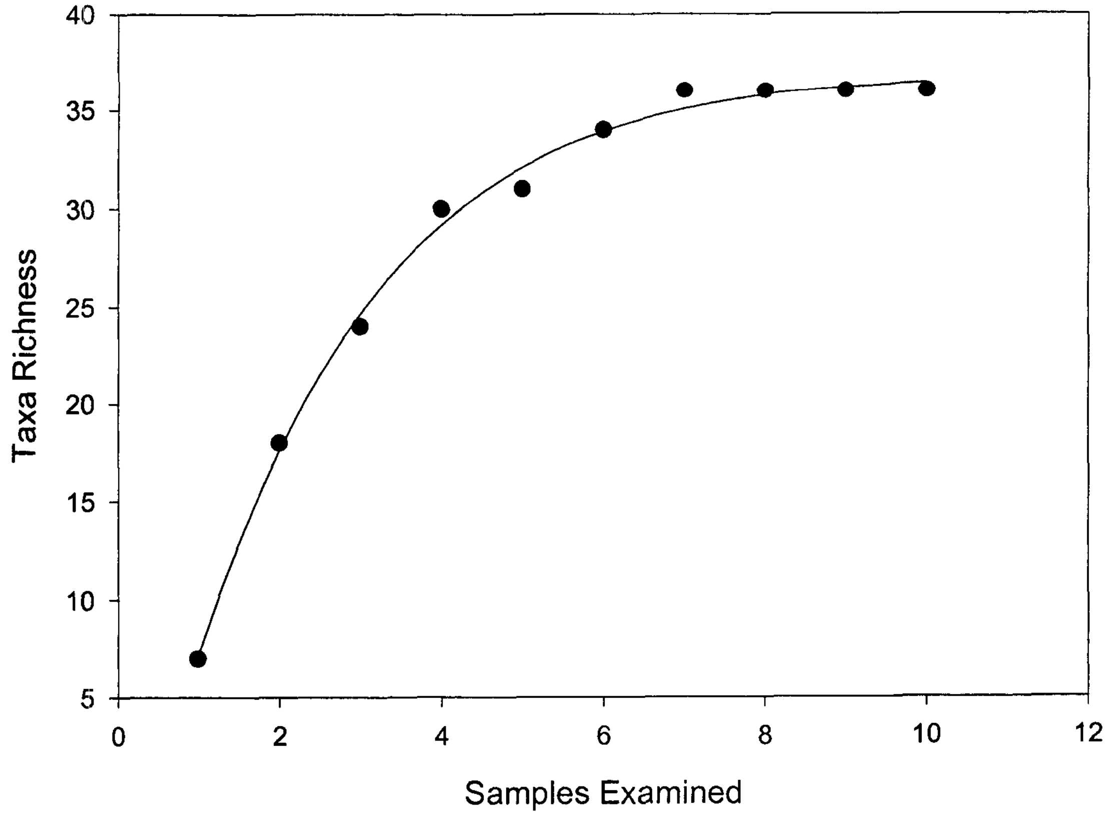
40
35
30
25
20
15
10
5
Taxa Richness
0
2
4
6
8
10
12
Samples Examined

Figure 1.1

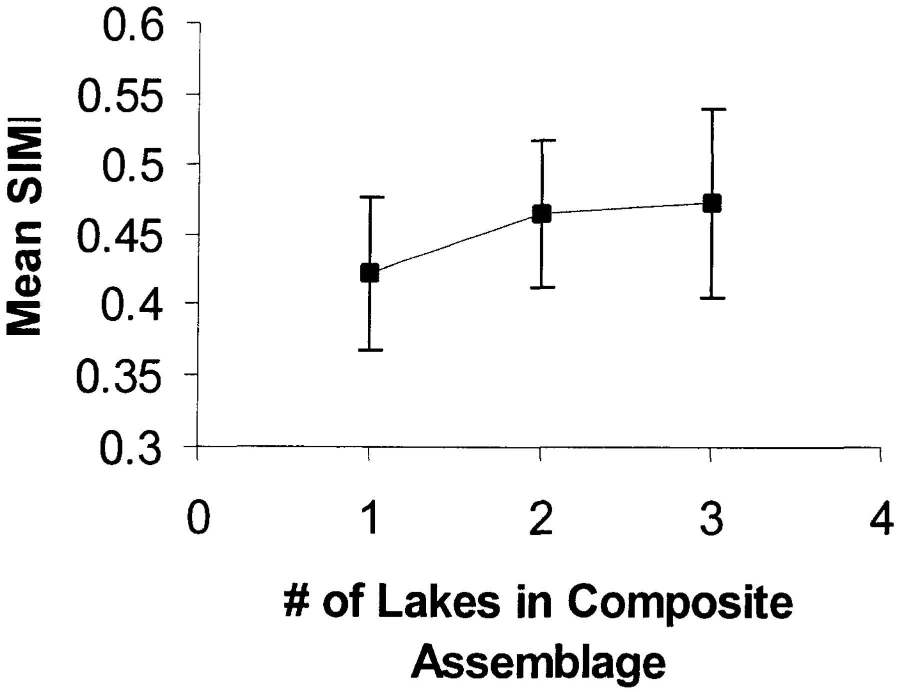
Mean SIMI
0.6
0.55
0.5
0.45
0.4
0.35
0.3
0
1
2
3
4
# of Lakes in Composite Assemblage

Figure 1.2.

Table 1.1: Limnological characteristics of the Malili Lakes

Lake	Surface Area (km^2)	Max. Depth (m)	Elevation (m A.S.L.)	Secchi Disk Depth (m)
Matano	164	590	396	20
Mahalona		60		-
Towuti	560	203	293	22
Masapi	1	<20?		-

Table 1.2. The diatom flora (taxa richness) of the Malili lakes.

Lake	Matano	Mahalona	Towuti	Masapi
Taxa Richness	138	147	154	36
Endemic Taxa	32	12	39	4
Taxa Shared with L, Matano	-	72	74	19

Table 1.3: Diatom taxa of the Malili Lakes. * denotes uncertain taxonomic status.

Taxon
Achnanthes crenulata Grunow in Cleve & Grunow 1880
**Achnanthes exigua* Grunow in Cleve & Grunow 1880
**Achnanthes exigua* f. *elliptica* Hustedt 1937
**Achnanthes hungarica* (Grunow) Grunow in Cleve & Grunow 1880
Achnanthes inflata var. *elata* (Leuduger-Fortmorel) Hustedt 1937
**Achnanthes kryophila* Petersen 1924
**Achnanthes lanceolata* var. *rostrata* (Østrup) Hustedt 1911
Achnanthes lapponica (Hustedt) Hustedt 1933
Achnanthes *lata* Hustedt 1942
**Achnanthes montana* Krasske 1932
Achnanthes oblongella Østrup 1902
**Achnanthes pseudolinearis* Hustedt 1942
Achnanthes subhudsonis Hustedt 1921
Achnanthes tropica Hustedt 1937
Achnanthidium arcus (Hustedt) Lange-Bertalot 1999
Achnanhidium altergracillima (Lange-Bertalot) Round & Bukhtiyarova 1996
Achnanthidium exilis (Kützing) Round & Bukhtiyarova 1996
Achnanthidium microcephalum Kützing 1844
Achnanthidium minutissimum (Kützing) Czarnecki 1994
Achnanthidium woltereckii (Hustedt) Lange-Bertalot 1999
Adlafia bryophila (Petersen) Lange-Bertalot in Moser et al. 1998
Adlafia minuscula (Grunow in Van Heurck) Lange-Bertalot in Lange-Bertalot & Genkal 1999
Amphora ovalis (Kützing) Kützing 1844
Amphora towutensis Hustedt 1942
Aulacoseira ambigua (Grunow in Van Heurck) Simonsen 1979
Aulacoseira granulata (Ehrenberg) Simonsen 1979
Aulacoseira granulata var. *angustissima* (O. Müller) Simonsen 1979
Aulacoseira italica (Ehrenberg) Simonsen 1979
Bacillaria paradoxa Gmelin in Linnaeus 1788
Brachysira longirostris (Hustedt) Mann 1990
Brachysira neoexilis Lange-Bertalot in Lange-Bertalot & Moser 1994
Brachysira procera Lange-Bertalot & Moser 1994
Brachysira rhomboides (Hustedt) Mann 1990
Brachysira styriaca (Grunow in Van Heurck) Ross in Hartley 1986
Caloneis bacillum (Grunow) Cleve 1894
Caloneis incognita Hustedt 1910
Caloneis malayensis Hustedt 1942
Caloneis schumanniana var. *rostrata* Hustedt 1942
Caloneis schumanniana (Grunow in Van Heurck) Cleve 1894
Campylodiscus papillosus Hustedt 1942
Cocconeis brevicostata Hustedt 1937

Cocconeis cingulata Hustedt 1942
Cocconeis placentula Ehrenberg 1838
Cocconeis placentula var. *euglypta* (Ehrenberg) Grunow 1884
Cocconeis placentula var. *klinoraphis* Geitler 1927
Craticula ambigua (Ehrenberg) Mann in Round et al. 1990
Craticula cuspidata (Kützing) Mann in Round et al. 1990
Cyclotella comta (Ehrenberg) Kützing 1849
Cyclotella meneghiniana Kützing 1844
Cymbella affinis Kützing 1844
Cymbella ampullacea Hustedt 1942
Cymbella bengalensis Grunow in A. Schmidt 1874
Cymbella bicapitata Hustedt 1942
Cymbella distinguenda Hustedt 1942
Cymbella gracillima Hustedt 1942
Cymbella lanceolata (Agardh) Agardh 1830
Cymbella leptoceroides Hustedt 1942
Cymbella malayensis Hustedt 1942
Cymbella malayensis var. *rostrata* Hustedt 1942
Cymbella mirabilis Hustedt 1942
Cymbella naviculiformis Auserwald in Rabenhorst 1861-79
Cymbella neocistula Krammer 2002
Cymbella neoleptoceros Krammer 2002
Cymbella pseudodelicatula Hustedt 1942
Cymbella spicula Hustedt 1938
Cymbella subalpina f. *apiculata* Hustedt 1942
Cymbella sumatrensis Hustedt 1938
Cymbella tumida (Brébisson) Van Heurck 1880
Cymbella woltereckii Hustedt 1942
Cymbella woltereckii var. *capitata* Hustedt 1942
Denticula bacillum Hustedt 1942
Denticula linearis Hustedt 1942
Denticula parva Hustedt 1942
Denticula vanheurckii Brun 1891
Diatoma anceps (Ehrenberg) Kirchner 1879
Diploneis elliptica (Kützing) Cleve 1894
Diploneis subovalis Cleve 1894
Encyonema neogracile Krammer 1997
Encyonema neomesianum Krammer 1997
Encyonema prostratum (Berkeley) Kützing 1844
Encyonema subtenuissimum Krammer 1997
Encyonema ventricosum (Agardh) Grunow in A. Schmidt 1885
Encyonema wallaceanum (Hustedt) Krammer 1997
Encyonopsis brevistriata (Hustedt) Krammer 1997
Encyonopsis cesatii (Rabenhorst) Krammer 1997
Encyonopsis cesatii var. *undulata* (Hustedt) Krammer 1997
Encyonopsis cryptocephala (Hustedt) Krammer 1997

Encyonopsis dubitata (Cholnoky) Krammer 1997
Encyonopsis ruttneri (Hustedt) Krammer 1997
Epithemia argus (Ehrenberg) Kützing 1837
Epithemia cistula (Ehrenberg) Ralfs in Pritchard 1861
Epithemia muelleri Frickle in A. Schmidt 1904
Epithemia sorex Kützing 1844
Epithemia zebra (Ehrenberg) Kützing 1844
Epithemia zebra var. *porcellus* (Kützing) Grunow 1862
Eunotia diodon Ehrenberg 1837
Eunotia exigua (Brébisson ex Kützing) Rabenhorst 1864
Eunotia lunaris (Ehrenberg) Brébisson In Rabenhorst 1864
Eunotia monodon Ehrenberg 1843
Eunotia pectinalis var. *minor* (Kützing) Rabenhorst 1864
Eunotia polydentula (Brun) Hustedt 1932
Eunotia pseudoveneris Hustedt 1942
Eunotia tschirchiana O. Müller 1890
Fragilaria capucina var. *lanceolata* Grunow in Van Heurck 1881
Fragilaria lapponica f. *lanceolata* Hustedt 1942
Fragilaria pinnata var. *lancettula* (Schumann) Hustedt 1913
Frustulia rhomboides (Ehrenberg) De Toni 1891
Frustulia rhomboides var. *saxonica* (Rabenhorst) De Toni 1891
Geissleria schoenfeldii (Hustedt) Lange-Bertalot & Metzeltin 1996
Geissleria similis (Krasske) Lange-Bertalot & Metzeltin 1996
Gomphonema angustissimum Hustedt 1942
Gomphonema clevei Frickle in A. Schmidt 1902
Gomphonema dubravicense Pantocsek 1892
Gomphonema gracile Ehrenberg 1838
Gomphonema intricatum Kützing 1844
Gomphonema intricatum var. *pumila* Grunow in Van Heurck 1880
Gomphonema lingulatum Hustedt 1927
Gomphonema longissimum Hustedt 1942
Gomphonema malayense Hustedt 1942
Gomphonema parvulum (Kützing) Kützing 1849
Gomphonema parvulum var. *lagenula* (Kützing) Frenguelli 1923
Gomphonema subtiliforme Hustedt 1942
Gomphonema towutense Hustedt 1942
Gomphonema woltereckii Hustedt 1942
Hannaea arcus (Ehrenberg) Patrick in Patrick & Reimer 1966
Hantzschia amphioxys (Ehrenberg) Grunow 1877
Luticola seposita (Hustedt) Mann in Round et al. 1990
Mastogloia malayensis Hustedt 1942
Mastogloia recta Hustedt 1942
Mastogloia subrobusta Hustedt 1942
**Melosira granulata* var. *angustissima* f. *curvata* Hustedt 1942
Navicula avenacea (Bréb & Godey) Brébisson ex Grunow 1878
**Navicula bacillum* var. *intermedia* Hustedt in A. Schmidt 1934

**Navicula confervacea* (Kützing) Grunow in Van Heurck 1880
Navicula cryptocephala Kützing 1844
**Navicula cymbelloides* Hustedt 1934
**Navicula disparata* Hustedt 1942
**Navicula divaricata* Hustedt 1942
**Navicula exigua* Grunow in Van Heurck 1880
**Navicula exigua* f. *undulata* Hustedt 1942
**Navicula festiva* Krasske 1925
Navicula helvetica var. *woltereckii* (Hustedt in A. Schmidt) Hustedt 1934
Navicula helvetica var. *woltereckii* f. *rostrata* Hustedt 1942
Navicula lagerheimii Cleve 1894
Navicula lanceolata (Agardh) Ehrenberg 1838
**Navicula mediocris* Krasske 1932
**Navicula menisculus* Schumann 1867
**Navicula perventralis* Hustedt in A. Schmidt 1936
**Navicula pupula* f. *capitata* Skvortzow & Meyer 1928
**Navicula pupula* f. *rectangularis* (Gregory) Grunow in Cleve & Grunow 1880
**Navicula pupula* f. *rostrata* Hustedt 1911
Navicula radiosa Kützing 1844
Navicula rhynchocephala Kützing 1844
**Navicula scabellum* Hustedt 1942
**Navicula seminuloides* var. *sumatrana* Hustedt in A. Schmidt 1936
**Navicula septata* Hustedt 1942
**Navicula septata* f. *lancettula* Hustedt 1942
**Navicula subbacillum* Hustedt 1937
**Navicula subcontenta* Hustedt 1942
**Navicula tenera* Hustedt in A. Schmidt 1936
**Navicula tignaria* Hustedt 1942
Neidium iridis (Ehrenberg) Cleve 1894
Neidium productum (W.M. Smith) Cleve 1894
Nitzschia amphibia Grunow 1862
Nitzschia amphibioides Hustedt 1942
Nitzschia denticuloides Hustedt 1942
Nitzschia frustulum (Kützing) Grunow in Cleve & Grunow 1880
Nitzschia interrupta (Reichelt in Kuntze) Hustedt 1927
Nitzschia invisitata Hustedt 1942
Nitzschia irresoluta Hustedt 1942
Nitzschia lacuum Lange-Bertalot 1980
Nitzschia palea (Kützing) W. Smith 1856
Nitzschia palea var. *sumatrana* Hustedt 1938
Nitzschia sigmoidea (Nitzsch) W. Smith 1853
Nitzschia subdenticula Hustedt 1942
Nitzschia subinflata Hustedt in A. Schmidt 1922
Nitzschia towutensis Hustedt 1942
Pinnularia acuminata W. Smith 1853
Pinnularia biceps Gregory 1856

Pinnularia curticostata Krammer & Lange-Bertalot in Lange-Bertalot & Genkal 1999
Pinnularia divergentissima var. *minor* Krammer 1992
Pinnularia lacunarum Hustedt in A. Schmidt 1934
Pinnularia mayeri Krammer 1992
Pinnularia microstauron (Ehrenberg) Cleve 1891
Pinnularia neomajor Krammer 1992
Pinnularia ornata Hustedt in A. Schmidt 1934
Pinnularia pulchella (Boyer) Krammer 2000
Pinnularia sillimanorum Ehrenberg 1841
Pinnularia towutensis Hustedt 1942
Planothidium fragilarioides (Petersen) Round & Bukhtiyarova 1996
Planothidium lanceolatum (Bréb ex Kützing) Round & Bukhtiyarova 1996
Planothidium pseudoswazi (Carter) Bukhtiyarova & Round 1996
Pleurosigma delicatulum W. Smith 1852
Rhoicosphenia curvata (Kützing) Grunow 1860
Rhopalodia gibberula (Ehrenberg) O. Müller 1895
Rhopalodia musculus (Kützing) O. Müller 1899
Rhopalodia novae-zelandiae Hustedt in A. Schmidt 1913
Sellaphora bacilliformis (Grunow in Cleve & Grunow) Mereschkowsky 1902
Sellaphora bacillum (Ehrenberg) Mann 1989
Sellaphora pupula (Kützing) Mereschkowsky 1902
Stauroneis anceps var. *javanica* Hustedt 1935
Stauroneis phoenicenteron (Nitzsch) Ehrenberg 1843
Stauroneis phoenicenteron var. *signata* Meister 1932
Staurosirella lapponica (Grunow in Van Heurck) Williams & Round 1987
Staurosirella pinnata (Ehrenberg) Williams & Round 1987
Stenopterobia intermedia (Lewis) Van Heurck 1896
Stenopterobia intermedia var. *subacuta* Hustedt in A. Schmidt 1912
Stenopterobia pelagica Hustedt 1942
Stenopterobia robusta Hustedt 1942
Surirella alata Hustedt 1942
Surirella angusta Kützing 1844
Surirella angustiformis Hustedt 1942
Surirella bidens Hustedt 1942
Surirella biseriata var. *celebesiana* Hustedt 1942
Surirella biseriata var. *heteropolis* Hustedt 1942
Surirella celebesiana Hustedt 1942
Surirella celebesiana var. *matanensis* Hustedt 1942
Surirella conversa Hustedt 1942
Surirella cuspidata Hustedt 1942
Surirella decipiens Hustedt 1942
Surirella *elegans* Ehrenberg 1841
Surirella *elegans* f. *lata* Hustedt 1942
Surirella elegantula Hustedt 1942
Surirella elegantula f. *cuneata* Hustedt 1942

Surirella excellens Hustedt 1942
Surirella halteriformis Hustedt 1942
Surirella horrida Hustedt 1942
Surirella horrida f. *constricta* Hustedt 1942
Surirella linearis W. Smith 1853
Surirella linearis f. *constricta* (Grunow) Hustedt 1957
Surirella papillifera Hustedt 1942
Surirella pediculata Hustedt 1942
Surirella pseudovalis Hustedt 1942
Surirella robusta f. *lata* Hustedt 1927
Surirella robusta f. *punctata* (Hustedt) Hustedt 1930
Surirella robusta var. *splendida* (Ehrenberg) Van Heurck 1885
Surirella rudis var. *levis* Hustedt 1942
Surirella sublinearis Hustedt 1942
Surirella sulcata Hustedt 1942
Surirella tenera Gregory 1856
Surirella tenuissima Hustedt in A. Schmidt 1913
Surirella thienemannii Hustedt 1935
Surirella ventricosa Hustedt 1942
Surirella woltereckí Hustedt 1942
Synedra robusta Ralfs in Pritchard 1861
Synedra rumpens Kützing 1844
Synedra rumpens var. *neogena* (Grunow) Hustedt 1942
Synedra ulna (Nitzsch) Ehrenberg 1836
Synedra ulna var. *biceps* (Kützing) Schönfeld 1913
Tabellaria flocculosa (Roth) Kützing 1844

Table 1.4. Matrix of SIMI values for assemblage pairings.

Assemblage	Matano	Mahalona	Towuti	Masapi	Sulawesi Outgroup	Island Outgroup
Matano	-	0.5294	0.5262	0.3055	0.2273	0.1909
Mahalona		-	0.5051	0.3312	0.2347	0.2655
Towuti			-	0.3348	0.2529	0.2117
Masapi				-	0.2092	0.0704

CHAPTER 2:

AN EXAMINATION OF TAXA WITHIN THE GENUS *SURIRELLA* FROM THE MALILI LAKES, SULAWESI ISLAND, INDONESIA, WITH DESCRIPTIONS OF 11 NEW TAXA

ABSTRACT

With 35 taxa reported by Hustedt (1942), the genus *Surirella* (Turpin) is one of the most species-rich and important genera in the Malili Lakes, a system of five ancient lakes located in Central Sulawesi Island, Indonesia. In this chapter, I examine in detail the taxonomy of diatoms within the genus *Surirella* from the Malili Lakes. I also statistically evaluate valve morphology and relationships among taxa, and describe 11 new taxa. This study indicates that taxa within the *Surirella* are clustered according to unique combinations of morphological characteristics. Individuals within clusters often shared common valve shape, torsion, and presence of siliceous features including spines, spinules, and novel structures such as siliceous tendrils and tubular processes in the median area. This chapter demonstrates that the siliceous tendrils of *Surirella sublinearis* and its varieties, and *S. tenacis* are used for attachment to substrates and further postulate that the evolutionary development of attachment features contributes to the substantial diversity of *Surirella* taxa in this ancient lake system.

INTRODUCTION

The island of Sulawesi, formerly called Celebes, lies just south of the equator and in the heart of the Indonesian archipelago. The biological uniqueness of Sulawesi was first identified by Alfred Russell Wallace (1860). When Wallace explored the Indonesian archipelago, he noted that the terrestrial biota in the northwestern part of the archipelago bore a striking resemblance to that found on mainland Asia, while the biota of the southeastern islands was similar to that found on Australia. After Wallace's death, this realisation led to the demarcation of the famous line which now bears his name. Sulawesi sits almost astride of Wallacea, and upon exploring it, Wallace had expected to find biota intermediate to those found in either end of the island chain. Instead, he discovered that the flora and fauna on the island's northern peninsula were, in fact, comprised of mostly endemic species that bore no relation to the biota of Asia, Australia, or any surrounding islands.

Sulawesi Island itself was formed though the collision of two island arches, which were fragments of the former Laurasia and Gondwanaland, several million years ago (Van Bemmelin 1970). Consequently, the zone of collision, in north-central Sulawesi, contains many areas of complex folding and faulting, including the one that holds the Larona River Basin and the ancient Malili Lakes system. The Malili Lakes include Lakes Matano, Mahalona, Towuti, Masapi, and Wawantoa. Lake Matano, the headwater of the system, is a deep (600 m) graben lake with an estimated age of 4 million years (Brooks 1950). Lake Mahalona is smaller and shallower, with a dish-like bathymetry, and is directly downstream of Matano. Lake Towuti is the largest lake in the system, with a surface area of 560 km^2 and a maximum depth of 203 m (Haffner *et al.* 2001). Although thoroughly mixed, Towuti maintains a secchi disk depth frequently in excess of 25 m. Lakes Mahalona and Towuti are thought to have been formed approximately one million years ago. The ages of Lakes Masapi, and Wawantoa, two smaller mountain lakes adjacent to Towuti, are not known. It is thought that differences in limnology and littoral microhabitat characteristics in these lakes have contributed significantly to the development and maintenance of a highly endemic diatom community.

Surveys of the diatom assemblages of the Malili Lakes (excepting Lake Wawantoa) in 2002 identified 256 taxa present in the Malili Lakes system (Chapter 1). Species richness was greatest in the genera *Achnanthes* (14 Taxa), *Navicula* sensu lato (30 Taxa), *Nitzschia* (14 Taxa), and *Surirella* (35 Taxa) (Fig 2.1), whereas the most abundant genera (absolute numbers) were *Achnanthes*, *Epithemia*, and *Brachysira*. While most of the Malili Lakes diatom taxa were described by Hustedt (1942) and the type specimens verified by Simonsen (1987), ESEM examination revealed an obvious need for amendments to existing taxa currently observed in the Malili lakes.

The genus *Surirella* (Turpin), with 35 reported species and varieties, is one of the most species-rich genera in the Malili Lakes. Worldwide, approximately 628 taxa (401 species) have been described within the genus (VanLandingham 1978, Vyvermann 1991, Kusber & Jahn 2003). *Surirella* contains three well-defined subgeneric groups (Fastuosae, Pinnatae, Robustae), which are separated by the form of the keel and associated support structures (Paddock 1978, 1985, Krammer & Lange-Bertalot, 1987). The primarily freshwater Robustae have true winged keels connected to the valve by alar canals separated by fenestrae, while the marine and brackish Fastuosae and Pinnatae have keels directly attached to the valve opening internally through portulae. The distribution of the genus is cosmopolitan, the bulk of its diversity occurring in circum-tropical environments. Typically, freshwater *Surirella* taxa (predominantly Robustae) are large in size (40-400 μm), with a variety of ornamentations on the frustule. Recent SEM investigations highlight the diversity of surface ornamentations from small conical spines (*S. pseudospiralis*, Lange-Bertalot & Metzeltin (1996) to crystal-like concretions (*S. elongata*, Vyverman et al. 1995). In the Malili Lakes taxa, the valve face, mantle, and wings, are often covered with siliceous tubules, spines or papillae of various form and size. As a consequence of their large, often heavy frustules, taxa within the *Surirella* typically occupy various littoral habitats. Many are epiphytic, episammic, or epilithic, with few planktonic forms described. In this chapter, I conduct a taxonomic revision of the *Surirella* within the Malili Lakes using light microscopy and SEM techniques. I also describe 11 new taxa and statistically examine the variability in valve morphology and features that are thought to function in littoral zone attachment.

MATERIALS AND METHODS

Diatom material was collected from Lakes Matano, Mahalona, Towuti, and Masapi during the period of Jan 11th to Feb 10th, 2002. Materials collected included scrapes from logs and rocks, macrophyte clippings, sand, sediment, films, and plankton hauls from 20m and 60m. In the field, samples were preserved with Lugol's Iodine. Additional material from Lakes Matano and Towuti were retrieved for SEM examination from the Hustedt Collection (BRM). Photomicrographs of the type specimens from the Hustedt collection were made at BRM using a Zeiss Axioplan, with an AxioCam MRc digital camera.

Diatom valves were cleaned with hot nitric acid / sulphuric acid digestion and subsequently rinsed with distilled water and centrifuged at 3000 rpm for 10 minutes. The rinsing and centrifuging processes were repeated six times. Material for light microscope (LM) examination was dried onto glass cover slips and mounted to microscope slides with Naphrax® mountant. LM examination was conducted on a Leica DMR microscope using brightfield, phase contrast, DIC and RIC optics with a Nikon DXM1200F digital camera. SEM material was filtered through 8 μm nitrocellulose filters and mounted on aluminum stubs using double-sided carbon tape. Stubs were then sputter coated with gold for 20 seconds at ___kV and subsequently examined with a FEI XL30 SEM using accelerating voltages of 10-30 kV.

Measurements were made digitally on scanned electron micrographs utilizing the built-in XL30 software. A definition of valve characters measured is presented in Fig. 2.2.

Discriminant function analysis and hierarchical clustering analysis were performed to examine clustering of taxa based on morphological similarity. Analyses were performed on a set of 17 standardized measurements and scores. Discriminant analysis was performed using the Discriminant Analysis function of SYSTAT 10 (SPSS Science Inc. 2000) and clustering analysis was performed using the Hierarchical Clustering function of SYSTAT 10 (SPSS Science Inc. 2000), following the single linkage (nearest neighbor) method, and using Euclidean distance as the distance metric. *Cymbella woltereckii* Hustedt and *Nitzschia woltereckii* Hustedt, two other diatoms endemic to the Malili Lakes, were used as outgroups.

RESULTS

Taxa Descriptions

Genus. *Surirella* Turpin

***Surirella alata* Hustedt (1942, p. 151, figs 377-378).** Figs 2.3-2.7.

Cells are isopolar, 58-65 µm in length and 20-22 µm wide. Valve outline is linear and constricted with cuneate to rounded apices. Wings are well developed and project almost perpendicular to the valve face near the centre of the valve, although developing a greater lateral slope towards the apices where they terminate. There are 23 alar canals in 100 µm. These canals are somewhat narrower than fenestrae, which are partially occluded by 4-6 thick fenestral bars. The raphe is situated upon a raised ridge on the keel (raphe canal). The keel is also covered, on the inward facing side, with hollow tubes, about 0.65 µm in length, and aligned roughly with the centre of each fenestra. Many smaller spines (0.5 µm) cover the outward-facing side of the keel. The valve face is mildly corrugated on either side of the apical axis, and covered with many small papillae, 0.15µm in length. Striae are uniseriate to biseriate 22-25/10 µm, with nearly circular areolae, 0.1 µm in diameter.

Distribution: *Surirella alata* was reported as very rare from Sulawesi Island by Hustedt (1942), who recorded one specimen. This study confirms the rarity of this taxon, only observed in Lake Towuti.

Similar Taxa: Differs from *S. linearis* f. *constricta* in that the wings are well developed and the alar canals are narrow and widely spaced. *Surirella alata* is also more constricted in shape than *S. linearis* f. *constricta.* This taxon also differs from *S. sublinearis* and *S. sublinearis* var. *suggesta* by the absence of siliceous tendrils. The valve face is more mildly corrugated, and the raphe is on a raised ridge. The presence of small hollow tubes on the keel appears to be characteristic for *S. alata*.

Surirella angusta **Kützing (1844, p. 61, fig. 30)**

Cells are isopolar, becoming weakly heteropolar. Valves linear, sometimes appearing constricted in the mid-region. Apices are cuneate and bluntly rounded. In girdle view frustules are rectangular. According to Krammer & Lange-Bertalot (1988), the length is 18-70 µm and width 6-15 µm. Wing absent, two types of fibular-ribs support the raphe canal (note Krammer 1989, refers to these as transapical costae). In SEM, portulae are easily observed opening into the keel canal. Internally, the longer fibular-ribs 5.5-8 /10 µm extend from high on the mantle to the median line (region) on the valve face. The median line is narrow, sometimes difficult to observe in LM and appears to be a small ridge on the internal valve face. Two to three transapical costae are positioned between the long fibulae. Both the transapical costae and the long fibulae are attached to the median line. Striae 22-28 /10 µm and can be difficult to observe.

LM, specimens from the Type material from Davon, Kützing # 209 are presented in Krammer & Lange-Bertalot (pl. 133, figs 7, 12, 13).

Distribution: Cosmopolitan, reported from waters with good electrolyte levels. In this study, *S. angusta* was commonly observed from Lakes Matano and Mahalona.

Similar Species: *Surirella minuta* Brébisson is similar, only differentiated by heteropolar valve form and rounded, not cuneate-shaped apices. The generally longer *Surirella laponica* A. Cleve is almost identical in the smaller forms, except for frustule depth and striae clarity. For a more detailed discussion on this taxon see Krammer & Lange-Bertalot (1988, p. 187-188).

***Surirella angustiformis* Hustedt (1942, p. 156, figs 389-390)Figs 2.8-2.11.**

Cells isopolar about the apical axis, valves are linear with parallel or slightly concave margins and bluntly cuneate to rounded apices. Length 45-55 µm, width 9-12 µm and 34-40 alar canals/ 100 µm. The lectotype specimen (Figs 8-11) has wing projects almost vertically extending from the valve face and covered by 5-6 striae. The fenestrae are small and no fenestral bars are observed in LM. Valve surface corrugated, the porcae (ridge surfaces) are the same width or slightly wider than the adjacent depressions. A siliceous extension, possible a fin, appears in the depressions between the porcae. The median line is a narrow uneven ridge. The porcae are evenly positioned on either side of the median line, although they can sometimes appear to be forming a zigzag alignment pattern to the median line. Papillae are absent, although there appears to be small spines or tubules present along the median area. This is a rare taxon that we did not observe under SEM.

Distribution: Reported only from Sulawesi. Rare in Lake Towuti, not found in this study.

Similar Species: This taxon is similar in form to *S. angusta* Kützing, but with a distinct wing containing the keel canal. According to Hustedt (1942), the surface depressions (corrugated-valleys) of *S. angusta* are narrow, the ridges wide and flat, which is in contract to the valve surface structure of *S. angustiformis*.

Surirella bidens **Hustedt (1942, p. 168, fig. 420)   Figs 2.16-2.18.**

Cells are heteropolar along the apical axis, valves ovoid to oblong-ovoid, with broadly rounded and narrowly rounded apices. Length 46-160 µm, about 28-70 µm wide. Wings are poorly developed. Alar canals and fenestrae are not visible. The valve surface is weakly corrugated, porcae with the same width as the adjacent depressions. These transapical corrugations extend from the mantle to a linear-elliptical median area. Valves are finely areolate across the complete valve surface with 37-39 striae /10 µm. Striae are uniseriate to biseriate. Two spines are present facing internally at the wide apex.

Distribution: Reported only from Lake Towuti, Sulawesi. Very rare only 2 valves were observed in this study and the study of Hustedt (1942).

Similar Species: The small spines at the wide-apex, along with the heteropolar shape and weak corrugated valve surface easily characterise this taxon. Similar to *Surirella debesii* Hustedt (1922) from Lake Tanganyika as pictured by Cocquyt (1998, Pl. 37:2), although the wing in *S. debesii* is more laterally developed and a spine (fin-spine?) is present at each end of the median line. *Surirella davidsonii* Schmidt 1875 (Pl. 21:7-10) is also similar, but differs by a more developed wing and thickened alar canals (Metzeltin & Lange-Bertalot 1998). Perhaps *S. bidens* is related to *Surirella chinensis* Brun, sensu Hustedt (1939) from Java; however the stronger corrugation and absence of spines at the wide apex separate the two taxa.

Surirella biseriata **var** ***celebesiana*** **Hustedt (1942, p. 146, figs 362-364) Figs 2.19-2.20.**

Cells weakly heteropolar in contrast to var. *heteropolis*. Valves are broad and linear, with a slight central constriction and cuneate bluntly rounded apices. Length ca. 180 µm, width in the mid-region ca. 50 µm. Wings distinctly elevated and horizontally extended from the valve face. The wings terminate at each apex with 15 alar canals at the center to 24 in 100 µm at the apices. The keel in girdle view has a series of spines or papillae above each fenestra. Valve surface corrugated, the porcae narrower than adjacent depressions, which is especially evident towards the median area. The median line is narrow and positioned within a broader media area, which is formed by a mildly uneven alignment of porcae on either side. The median line has randomly distributed fin-like spines on the external face.

Distribution: Sulawesi. Rare, reported from Lakes Matano and Towuti.

Similar Species: This taxon can also be compared with *S. biseriata* var. *robusta* Hustedt (1935, p. 179, Fig. 38) from Lake Toba (Sumatra), but differs with blunt poles and a wider corrugation on the valve face. Although Hustedt (1942) suggests that this could be a new species, we currently continue to recognize this as a variety of *S. biseriata*. *Surirella biseriata* var. *heteropolar* and var. *celebesiana* are separated by shape and size, although both have spines extending along a narrow median line. No intermediate forms of these varieties have been identified.

***Surirella biseriata* var. *heteropolis* Hustedt (1942, p. 146, figs 359-361) Figs 2.21-2.23.**

Cells are slightly heteropolar, long, and linear, sometimes constricted. The smaller pole is slightly more attenuated than the wider pole. Length 200-517 µm, width 35-80 µm and 10-15 alar canals /100 µm. In girdle view, the mantle is strongly curved at the apices. Wings vertically projected but not far removed from the valve face and terminate at the apices. Fenestrae are small and circular, narrower than the alar canals, and not occluded. The valve face is depressed along the apical axis and rises up to meet the wing around the perimeter. The valve surface is corrugated and finely striated (30-35 striae in 10 µm). On the internal valve face, there are numerous fibulae joining the valve and the mantle. These fibulae are located between the alar canal openings (coincide with fenestrae, externally) and extend to a fine linear median line. Fin-like spines appear randomly distributed along the median line. On the interior side of the narrow pole, there are two tooth-like spines, about 1 µm in length curving back towards the head pole. Areolae are 35-50 /10 µm.

Distribution: Sulawesi. Isolated to Lake Matano, where it is common.

Similar Taxa: Differs from *S. biseriata*, which is cosmopolitan and common on the nearby islands of Java and Sumatra, by the longer, slimmer valves and heteropolar apices. The specimens observed in this study were larger and typically had fewer alar canals than the original specimens described by Hustedt (1942).

***Surirella celebesiana* Hustedt (1942, p. 161, figs 403-406) Figs 2.12-2.15.**

Cells slightly heteropolar and linear-elliptical in outline with cuneate narrowly rounded apices. Valves are 70-82 µm long, 22-30 µm wide with ca. 30-35 alar canals in 100 µm. Valves at the apex strongly curved down. The wing is vertically, but not horizontally extended off the valve face, therefore the alar canals and fenestrae are visually obscured. The wings terminate at the apices. Alar canals are much narrower than fenestrae. The raphe canal is also narrow. The valve face is corrugated with transapical porcae extending from the alar canal to a broad linear to linear-elliptical median line. Across these corrugation ridges, the valve surface is covered with many small papillae that terminate at the median area. In the depression zones, papillae are present at the margin. The median area clearly terminates before reach the apices. The median line is a narrow uneven ridge with possible small fin-like spines scattered along the ridge. The valve face is finely striated with uniseriate to biseriate striae, and approximately 55 areolar rows in 10 µm.

Distribution: Reported only from Sulawesi, commonly found in Lakes Matano and Towuti.

Similar Taxa: Differs from *S. leyana* by its greater size, finer papillae, the peaked form of its valve face, and the presence of visible areolae and not papillae in the axial area.

***Surirella celebesiana* var. *matanensis* Hustedt (1942, p. 162, fig. 407) Fig. 2.24**

Cells long and linearly, slightly heteropolar, with bluntly cuneate to rounded apices. Length ca. 130 µm, width 25 µm and 18-20 alar canals /100 µm. Structurally this taxon is identical to *Surirella celebesiana* but with either large spines or possible tubules scattered across the valve face and may not have a ridged median line with fin-like spines.

Distribution: Sulawesi. Very rare in Lake Matano. No specimens observed in this study and only one in Hustedt (1942).

Similar Species: The taxon is larger than the nominate form with fewer alar canals and the presence of spines or tubules. However, as suggested by Hustedt (1942), the morphology of this taxon is similar to *S. celebesiana* and therefore should be maintained as a variety. In his original LM, Hustedt lists the holotype specimen as *Surirella celebesiana* var. ? *matanensis*.

***Surirella conversa* Hustedt (1942, p. 159, figs 397-400)   Figs 2.25-2.31.**

Cells contorted and isopolar, valves elliptical, with narrowly rounded apices. The cell appears slightly heteropolar in outline due to a slight contortion of the valve. Length 50-110 µm, width 35-62 µm and 15-22 alar canals /100 µm. Most specimens are contorted about the apical axis, giving them a saddle-like outline in girdle view. The wings have large keels that extend vertically, but not far from the valve surface and terminate at the apices. Alar canals are typically wider than the fenestrae. The fenestrae are round and partially occluded by 5 or 6 fenestral bars. The keel bears many spines 1-2 µm in length on the valve face side, and a greater number of smaller papillae on the mantle side. The raphe itself sits on a poorly defined ridge. The valve face is deeply corrugated with porcae and depressions. Many spines 1-2 µm long are present upon the valve face, always situated on top of the porcae. In LM, the striae are more easily observed in the depressions due to the absence of spines. Striae are biseriate to sometimes multiseriate, 24-28 striae /10 µm. The median area of the apical axis is slightly depressed. Areolae cover the valve surface.

Distribution: Reported only from Sulawesi Island. Frequent in Lake Towuti.

Similar Species: *Surirella conversa* differs from *S. leyana* through its isopolar apices, contorted valves, more deeply corrugated valve face, and wider alar canals. *Surirella conversa* is also similar to *S. horrida*, but differs in that its valves are more contorted, and there is a more developed wing. This taxon differs from *S. ephippiomorpha* through spine density and morphology, a better-defined wing, and the presence of visible areolae.

***Surirella cuspidata* Hustedt (1942, p. 156, figs 391-393) Figs 2.32-2.35.**

Cells are isopolar, with narrow, linear valves and cuneate developing into subcapitate apices. Valves 35-80 μm long, 5-10 μm wide and 55-60 alar canals /100 μm. In girdle view, the frustule is rectangular with broadly rounded ends. Wings are vertically projected with large rounded keels, making them difficult to observe in LM. The raphe is the only structural feature on the keel and terminal fissures are hooked and deflected down the mantle. Fenestrae are much wider then alar canals and partially occluded by 3-5 thick fenestral bars. The valve face is narrow, and finely striated with >20 striae in 10 μm. The external valve face is weakly corrugated with 9-11 costate-ridges /10 μm separating the striae. These costate ridges are aligned with the fenestral bars and on the alar canals are seen as elevated ridges. The median line is narrow and more or less linear.

Distribution: Sulawesi. Hustedt (1942) reported *S. cuspidata* as very rarely in Lake Wawantoa. The species is also present, but very rare, in Lake Towuti.

Similar Taxa: This taxon is similar to *S. musicola* (Krasske) Lange-Bertalot & Metzeltin 1998 with the linear, slightly constricted valve and well formed laterally expanded wings. *Surirella cuspidata* differs by the absence of a depressed linear median area and small fibular-like support structures on the valve/wing face. *Surirella delicatissima* differs from *S. cuspidata* by a well-defined wing, more closely spaced alar canals, and in the outline of its valves. *Surirella arctissima* Schmidt 1877 is related, but has substantially coarser striae (12 / 10 μm) and *Surirella gotohiana* Moser et al. 1998 is similar in form, but larger, with a wider median area and fewer alar canals.

***Surirella decipiens* Hustedt (1942, p. 161, figs 401-402) Figs 2.36, 2.37.**

Cells are isopolar to slightly heteropolar, the valves are linear centrally constricted with cuneate-rounded or slightly apiculate-rounded apices. However, SEM reveals that cells are in fact, isopolar, slightly constricted, and with rounded apices. The cell appears slightly heteropolar in outline due to a slight contortion of the valve. Length 50-60 μm, width 16-20 μm and 20-30 alar canals /100 μm. Wings are small, projecting horizontally upward from the valve face and terminate at the apices. The keel maintains a raphe sitting atop a wide, flat ridge. Alar canals are narrower then fenestrae, and unevenly spaced. Often there is one extra canal on one side of the valve. Fenestrae vary in width and are partially occluded by 6-11 fenestral bars. The valve face is corrugated with broad undulations extending from the mantle to a narrow zigzag median line. The porcae are sparsely covered by poorly developed tubules or small spines 0.6-1.0 μm in length. The surface is finely striated, with circular areolae on both the porcae and adjacent depressions. Striae are 20-24 /10 μm, uniseriate to biseriate between small ridges that are especially evident in the transapical depressions.

Distribution: Sulawesi. Previously only reported from Lake Towuti (Hustedt 1942), but also present and rare in Lake Matano.

Similar Taxa: Hustedt (1942) places this species close to *S. rudis*. However, SEM reveals that *S. decipiens* is not simply smaller than *S. rudis*, but is isopolar. *S. decipiens* differs from *S. horrida* and *S. horrida* f. *constricta* by its smaller size, as well as the form and density of spines. This taxon could also be compared to *Surirella neocaledonica* f. *punctata* (Maillard) Lange-Bertalot & Steindorf 1995, with the scattered tubules/papillae along the porcae, however it differs in general shape, size of the width of the porcae and presence of only small papillae (Moser et al. 1995).

Surirella elegans **Ehrenberg (1843, p 316. fig. 22)**

Cells slightly heteropolar to isopolar with rounded to somewhat pointed apices. Valves oval to almost linear sometimes with a median concave constriction. Length 110-400 µm, width 35-90 µm and 12-21 alar canals /100 µm. In girdle view frustules are trapezoid. The wings extend vertically from the valve face, appearing small and difficult to discern. Alar canals are narrower than the adjacent fenestrae, which according to Krammer & Lange-Bertalot (1988) gives the appearance of transapical costae (ribs). The transapical corrugations extend from the mantle to a weakly defined median area. The central median-region is lanceolate to elliptical-lanceolate in form and possible raised on the external valve face. As reported in the literature, this taxon is quite variable and commonly misidentified. Further examination of the type material is required.

Distribution: Cosmopolitan. Originally described from North America, but commonly recorded from Europe, Occurs in Lakes Mahalona and Matano.

Similar Species: Other taxa commonly confused with *S. elegans* include, *S. robusta*, *S. splendida* and even variants of *S. biseriata*. Shape, corrugation pattern, vertical wing formation and shape of the median-region in combination best distinguish *S. elegans*.

***Surirella elegans* f. *lata* Hustedt (1942, p. 177, fig. 441) Figs 2.38-2.40.**

Cells are heteropolar, valves ovoid to asymmetrically-elliptical, with rounded apices. Length 230-238 μm, width 120-122 μm and 12-19 alar canals /100 μm. The wings in this isolectotype specimen, extend vertically from the valve face, thus making it difficult to discern wing, alar canal and fenestrae structures. The wings terminate at the apices or at least at one apex. Alar canals are narrower than the adjacent fenestrae. The corrugated valve surface is restricted to the margins with a broad elliptical valve face and no clear median region. The median line is fine and covered with a series of papillae or small spines. Fine papillae appear to be scattered across the valve face.

Distribution: Sulawesi: Observed rarely from Lake Matano.

Similar Species: The larger elongated form, wider corrugated valve face and distinct median area distinguishes *S. elegans* from f. *lata*. Also compare with *Surirella hyppaei* Mölder.

***Surirella elegantula* Hustedt (1942, p. 172, figs 425-427) Figs 2.41-2.43.**

Cells heteropolar, valves linear to linear-ovoid with bluntly rounded or weakly pointed apices. Length 65-122 µm, width 24-30 µm, and 14-20 alar canals /100 µm. Valves at the apex slope down. Wing well developed vertically, therefore appearing narrow and indistinct. Alar canals narrower than the fenestrae. Valve surface weakly corrugated, with porcae narrow and laterally expanding towards the median area. The median area is narrow and linear with fin-like projections evenly distributed along the median line. Papillae or small spines are scattered across the external valve surface.

Distribution: Sulawesi, Currently considered endemic to the Malili lake region. Observed sporadically in Lakes Towuti and Matano.

Similar Species: This taxon is easily identified by the shape, well-developed wing, corrugation pattern, median area and equally spaced fin-link spines along the median line.

Surirella elegantula f. ***cuneata* Hustedt (1942, p. 172, figs 428, 429) Fig. 2.44, 2.45.**

Cells isopolar to heteropolar, valves linear with narrow-cuneate rounded apices. Length 100-110 µm, width 19-21 and 14-17 alar canals /100 µm. The holotype specimen has laterally expanded wings with large round alar canals. Fenestrae with 5-6 fenestral bars which are barely visible in LM. Valve surface weakly corrugated, with narrow and laterally expanded porcae. The median area is linear to linear-lanceolate with uneven margins created by the misalignment of porcae on either side. Two fin-spines are present at each end of the median area and other fin-like projections may also be present along the median line.

Distribution: Reported from Sulawesi, very rare in Lake Matano. Hustedt (1942) reported only a few specimens, and none were observed in this study.

Similar Species: This forma is distinguished from other taxa by wing projection, wing size, poorly defined corrugated valve surface and the spines along the median line.

***Surirella ephippiomorpha* Bramburger & Hamilton sp. nov. Figs 2.46-2.51.**

Cellulae, quarum extrema sunt rotunda, isopolares et ellipticales sunt. Frustula, modice tortuosa, speciem ephippii ferunt. Valvae tendunt 54-57 µm longitudine et latitudine 20-30 µm. Alae, crassae et non recte formatae, proxime valvae frontem adjacent. Spinulae et frontem Valvae et latera Raphis velata, et quoque canales alares tegunt. Canales alares, qui 18-25 intra 100 µm exstant, sunt, ut fieri solet, fenestris latiores. Valvae frons, alte rugosa, porcas latas ad axem apicalem terminatas habet. Porcae spinulis, usque ad -0.5 µm longitudine, acutis et auctis confertim teguntur. Valvae substantiam flexibilem in locis spinosis saepius colligunt.

Cells are isopolar and elliptical in shape, with rounded apices. Frustules are moderately contorted and assume the shape of a saddle. Valves are 54-57 µm long and 20-30 µm wide with 18-25 alar canals /100 µm. The wings are thick, but not well developed, and lie very close to the valve face. The raphe is located on a wide flattened ridge atop the keel with small terminal fissures that deflect slightly down towards the mantle. Both the valve face and mantle sides of the raphe canal, as well as the alar canals, are covered with small spines and a reticulate silica surface. The spines are up to 0.5μm long. The valve surface is broadly corrugated terminating at the apical axis. Valves tend to collect clastic material on the spiny areas. The valve face is finely striated; the striae are uniseriate to biseriate with approximately 30 or more striae in 10 μm.

Type Locality: Lake Towuti. Loeha Island, shoreline sediment. Coll. Date Feb. 26, 2002.
Collector: P.B. Hamilton. S. 02° 45.5, E. 121° 30.9
Holotype: CANA 70137
Isotype: BRM To be acquired

Etymology: *Surirella ephippiomorpha* was named for its saddle-like shape. *Ephippium* is the Latin root for saddle.

Distribution: Reported only from Sulawesi. Not uncommon in Lakes Matano and Towuti; rarely observed in Lake Masapi.

Similar Species: *Surirella ephippiomorpha* differs from *S. conversa* by its rounded apices, thicker silica form, spine-rich raphe canal, the formation of its spines and the fine striae. *Surirella ephippiomorpha* varies from *Surirella horrida* and its varieties in that the raphe is on a ridge; the valve is more highly contorted and not as linear in shape.

***Surirella excellens* Hustedt (1942, p. 174, figs 436, 437) Figs 2.52-2.59.**

Cells heteropolar, the valve is oblong with apiculate to bluntly rounded apices. Length 90-250 µm, width 16-55 µm and 21-32 alar canals in 100 µm. The valve face is depressed (not flat) between mantle and median line with a strong transapically corrugated surface. Wings are prominent, horizontally elevated from the valve face and terminate at the apices. The raphe is situated on an elevated ridge atop the keel and has terminal raphe fissures that hook sharply down at the apex. Alar canals are narrow relative to adjacent fenestrae. The porcae appear parallel at the center of the valve becoming radiate towards the apices. The porcae are also narrower than the adjacent depressions. The median area is linear-lanceolate in shape and elevated, with 9-13 fin-spines located along the median line. These directionally oriented spines or hooks are 0.5-2.5 µm in length. The edges of the median area are wavy in LM indicating large undulations between the porcae and depressions across the valve face. Areolae are circular and about 0.1 µm in diameter. The valve face is uni- or biseriately striated, with 34-47 striae in 10 µm. The valve is very weakly silicified and commonly collapses under SEM observation with accelerating voltages higher than 5 kV. Vyverman (1996, fig. 2:8, 9) presents SEM micrographs for this taxon.

Distribution: Sulawesi, common in the Lakes Matano and Towuti.

Similar Species: Hustedt (1942) separates this taxon from *Surirella robusta* based on the elevated median area with a median ridge on the external valve face. This taxon differs from *Surirella fenestrellata* by its ridged raphe fissure, the presence of spines in the median area, and the lack of spines between corrugated porcae. It also differs from

Surirella pinnigera based on the raphe structure, the lack of small spines on the valve face, and by the more numerous fin-spines on the median area. Also compare with *Surirella splendida* (Ehrenberg) Kützing (1844, p. 62, pl. 7:9) which may have spines along the median line (Sala 1996, fig. 6c).

Surirella fenestrellata **Bramburger & Hamilton sp. nov. Figs 2.60-2.65.**

Cellulae, in extremo lineares-ellipiticae et ovatae lineamento, apices heteropolares tenent. Valvae tendunt 95-135 μm longitudine et latitudine 36-41 μm. Alae, recte formatae, ab valvae fronte paulum ad extremum proiciunt. Canales alares 20-27 intra 100 μm exstant. Fenestrae, canalibus alaribus angustiores, 3-5 claustris fenestrallatis occluduntur. Valvae frons, alte corrugata, multas spinas parvas tenet, longitudine fere 1 μm tendentes, quae in locis inter porcas maxime occurrunt. Praeterea hae spinae in margine canalium alarium exteriore et limbo occurrunt. Striae sunt uniseriate et multiseriatae, quae 38-48 intra 10 μm exstant.

Cells are linear-elliptical to almost ovate in outline with heteropolar apices. Valves are 95-135 μm in length and 36-41 μm wide. Wings are well extended from the valve and project slightly outward. There are 20-27 alar canals /100 μm. Fenestrae are narrower than the alar canals, and partially occluded by 3-5 fenestral bars. The valve face is deeply corrugate, with many small spines approximately 1 μm in length located primarily in the depressed areas. These spines are also located on the outer margin of the alar canals and on the mantle. Striae are uniseriate at the median area becoming biseriate to multiseriate, with 38-48 in 10 μm. The raphe is flat to the keel with strongly deflected terminal raphe fissures down onto the mantle. There are also fine pores scattered on the keel.

Type Locality: Lake Towuti, NW shoreline, east of Desa Pekaloa, sediment. Coll. Date Feb. 18, 2002. Collector: P.B. Hamilton. S. 02° 39, E. 121° 27

Holotype: CANA 70893

Isotype: BRM To be acquired

Etymology: *S. fenestrellata* was named for its small, visible window between the thick alar canals. *Fenestrella* is the Latin root for small window.

Distribution: Reported only from Sulawesi. Common in Lakes Towuti and Matano.

Similar Species: This taxon may be distinguished from *Surirella excellens* based on the absence of a ridge on the keel, the presence of small spines on the corrugated valve face, and the absence of spines or fin-spines on the median area. It also differs from *Surirella pinnigera* by having spinules only between corrugated ridges, its larger, circular areolae, and through the absence of spines or hooks along the median area. It can also be compared to specimens misidentified as *Surirella splendidoides* Hustedt in Metzeltin & Lange-Bertalot (1998, pl. 209:1, 2) with a fine elevated median line within a narrow-lanceolate median area and large laterally developed wing canals. *Surirella subnervosa* is another taxon for comparison in LM based on general shape and the fine median line.

SEM examination of *S. subnervosa* shows a continuos elevated 'siliceous ridge along the median line and not a fine rounded ridge like *S. fenestrellata.*

***Surirella fimbriata* Hustedt (1942, p. 164, figs 409, 410) Figs 2.66-2.69.**

Cells are heteropolar, valves elliptical to ovate in outline, with rounded apices. In girdle view, frustules are trapezoid. Valves 54-58 µm long, 22-25 µm wide and 14-25 alar canals /100 µm. Wings are vertically developed from the valve face and terminate at the apices. Fenestrae are round, wider than the alar canals, and partially occluded by 7-10 thin fenestral bars. The fenestral bars are often damaged or missing. The keel is heavily silicified and bears spines 1-2 µm long on both sides of the keel. The valve face is deeply corrugated and striae are visible (30 /10µm). The corrugated surface extends from the mantle to a thin median area. The valve face also bears spines; both on the porcae and in the depressions, but these spines are much shorter than those on the raphe canal. Areolae and a few spines are also visible on the mantle. The median area is formed by the misalignment of porcae on either side, creating a "zigzag" pattern.

Distribution: Hustedt (1942) reported that *S. fimbriata* was isolated in a pool at Lyon, Luzon. In this study, *S. fimbriata* is also reported in Lake Towuti, where it is very rare.

Similar Species: Hustedt indicates that this species is similar to taxa within the *S. rudis* complex and is separated by the finer striae in the corrugated depressions and the spine along the wing (Simonsen 1987). Also compare with *S. aculeata*, which is more elliptical, has larger spines/tubules (?) and has no spines along the wing (Simonsen 1987, Cocquyt 1995).

Surirella halteriformis **Hustedt (1942, p. 152, figs 379-381) Figs 2.70-2.74.**

Cells are isopolar and near dumbbell-shaped in outline. The middle of the valve is highly constricted, while the apices are broadly rounded. Valves are 68-72 µm in length and 16-20 µm wide at the middle of the valve. In LM, the wings are difficult to see; when observed, the wings are slightly elevated, mainly horizontally, from the valve face with 17-30 alar canals /100µm. Fenestrae and fenestral bars are present but we could not see them clearly in our SEM photomicrographs. The raphe is situated upon a small ridge and the terminal fissures are straight, not deflected, at the apices. The valve face is moderately corrugated, with 20-30 porcae /100µm. The porcae extend from the margin to a fine linear depressed median area. The median area terminates well before the apices. There are many small siliceous "warts" or papillae scattered over the surface, distributed mainly on the porcae. Striae uniseriate, rarely biseriate with 38-40 striae in 10 µm.

Distribution: Sulawesi, uncommon in Lake Matano, and very rare in Lake Towuti.

Similar Taxa: Differs markedly in shape and form from all other taxa within the genus. Compare with *Surirella vasta* Hustedt.

Surirella horrida **Hustedt (1942, p. 157, figs 394, 395) Figs 2.78-2.80.**

Cells are moderately contorted, isopolar to slightly heteropolar; the valves are linear-elliptical with rounded apices, Length 110-150 µm, width 40-50 µm and 13-20 alar canals /100 µm. Wing projections on the lectotype are weakly developed in a vertical direction. At the exposed part of the contorted apex, the wing project is more evident in LM. Alar canals are consistently narrower than adjacent fenestrae. The distinct corrugated valve surface extends from the mantle to a more or less linear median line, as the zigzag formation is poorly developed. The porcae of this corrugation are narrow relative to the associated depressions and contain large numbers of randomly positioned spines. The wing is irregularly frayed along the internal edge and contains spines along the external edge.

Distribution: Sulawesi, Rare in Lake Matano.

Similar Species: Easily identified by the contorted frustule, valve shape and spine orientation. Compare with *Surirella rudis* Hustedt (1922, see Simonsen 1987, pl. 210 figs. 1-3) with a larger wing, flat valve and fewer spines on the porcae. Specimens of similar form have also been reported from Java.

***Surirella horrida* f. *constricta* Hustedt (1942, p. 157, fig. 396) Figs 2.81, 2.82.**

Cells isopolar, sometimes appearing heteropolar. Differs from the nominate taxon by the linear shape with a constriction in middle of the valve and the finer spines on the porcae. Length 122 μm, width at centre 34 μm and 15 alar canals /100 μm. This taxon is almost always observed in valve view.

Distribution: Sulawesi: Like the nominate form, restricted to Lake Matano. *S. horrida* f. *constricta* was not reported from the material in this study.

Similar Species: Similar to *S. vasta*, but differs by the contorted valve, rounded valve shape, higher spine density over the complete porcae, and a more developed median area.

***Surirella leyana* Bramburger & Hamilton sp. nov. Figs 2.75-2.77.**

Valvae, 33 μm longitudine et latitudine 11 μm tendentes, apices heteropolares et formam linearem et ellipticalem tenent. Alae non valde formatae praeter valvae marginem non multo proiciunt. Canales aleares 30 intra 100 μm occurrunt, qui fenestris sunt angustiores, ut fieri solet. Fenestrae latitudine differunt et 2-5 claustris fenestrlibus partim occluduntur. Valvae frons minime corrugata est; sed rugae axem apicalem non transcurrunt. Valvae frons tota spinulis centiplicibus, fere 0.05 μm longitudine, tegitur. Spinulae in diversas lineas, porcarum locis parallelas, disponuntur. Quae spinulae in limbo quoque discernuntur. Raphe lato in dorso educto supra alam iacet et ad apices non deflectitur.

Valves are 33 μm long and 11 μm wide with slightly heteropolar apices and a linear-elliptical profile. The wings are not strongly developed and do not project very far beyond the valve margin. The wings terminate at the apices. There are about 30 alar canals /100 μm and canals are typically narrower than fenestrae. Fenestrae are of varying widths and are partially occluded by 2-5 fenestral bars. The valve surface is mildly corrugated and covered by hundreds of small spinules about 0.05 μm in length. Spinules are arranged in divergent lines, running parallel to the transapical porcae. These spinules are also observed on the mantle. The raphe sits on a broad, raised ridge atop the wing, and is not deflected at the apices. Striae are about 35 or more in 10 μm.

Type Locality: Lake Towuti, North shore, west of Pohontali River, lake sediment. Coll. Date Mar 4, 2002. Collector: P.B. Hamilton. S. 02° 39, E. 121° 27

Holotype: CANA 71251

Isotype: BRM To be acquired

Etymology: Named in honour of Ms. Linda M. Ley, on the occasion of her 35th anniversary in bryological and phycological research at the Canadian Museum of Nature.

Distribution: Reported only from Sulawesi, very rare in Lake Towuti.

Similar Taxa: Differs from *S. celebesiana* in its smaller size, its coarser spinules, and the fine striae along the axial ridge.

Surirella linearis **W. Smith (1853, p. 31, pl. 8: 58a, a').**

Cells isopolar to weakly heteropolar along the apical axis. Frustules rectangular in girdle with curved terminal apices. Valves linear, linear-lanceolate to almost elliptical with rounded apices, which slope down to the mantle (curved terminal apices). According to Hustedt (1930) the measurements are length 20-125 µm and width 9-25 µm with 20-30 alar canals /100 µm. The wing projection is up and horizontally away from the valve face and easily recognizable in LM. The fenestrae are slightly wider than adjacent alar canals. Valve surface is corrugated, extending from the mantle to the median area. Externally, the porcae are equal in width with the adjacent depressions. The median line is quite variable from narrow lanceolate to almost indistinct. Areolae arranged in single or irregular biseriate rows and in LM more apparent in the depression areas adjacent to the porcae. Striae are 38-40 in 10 µm.

Distribution: Cosmopolitan (?) Europe. North America. Scatterd across the Indo-Pacific. Sulawesi, Common in Lakes Mahalona and Towuti.

Similar Species: A taxon identified more by the absence of characters. Elliptical valves, with relatively large wings and a corrugate valve surface that extends from the mantle to a variable median area, more or less identifies this taxon. Further study on wing and keel structure, along with raphe formation should help to further circumscribe this taxon.

Surirella linearis **var.** ***constricta*** **Grunow (1862) sensu Hustedt 1930 fig. 839**

Cells are isopolar, linear in outline and slight to moderately constricted in the middle. Valves 90-95 μm in length, 20-25 μm wide with 16-17 alar canals /100 μm. Wings are distinct and stand vertical to the valve face. Alar canals are about the same width as fenestrae. Fenestrae are rectangular, with rounded edges, and are partially occluded by 6 or 7 fenestral bars. The raphe sits on a ridge atop the keel canal and the valve-face side of the raphe canal is covered with short, poorly developed spines. The valve face is moderately corrugated with porcae becoming wider towards the median line. The median line, and valve face immediately surrounding it, are covered in small spinules (0.2-0.4 μm long) and the area covered by these spinules terminates well before the apices. The valve face is striated, with 18-20 striae in 10 μm. Areolae are small and circular, becoming coarser and diverging towards the apical axis. The epithet constricta has been used by many authors to describe and identify many infraspecific taxa within *Surirella*. To prevent confusion refer to Hustedt's 1930 and 1942 publications for the valve form. It should be noted that the original specimen (Line drawing) referred to by Grunow is from Smith's British Diatomaceae, pl. 8, fig 58a'' which is not the same as Hustedt's specimens.

Distribution: Hustedt (1942) describes this taxon as being circumtropical. In Sulawesi, "*S. sublinearis* f. *constricta*" is found commonly in Lakes Mahalona and Towuti.

Similar Species: *Surirella linearis* f. *constricta* differs from *S. sublinearis* and its varieties through its lack of siliceous tendrils, slimmer form, coarser areolae, and the presence of spinules only in the axial area. *Surirella linearis* differs from *S. tenacis* by the lack of siliceous tendrils, the slimmer form, coarser areolae, and the lack of hollow tubes along the apical axis.

Surirella papillifera **Hustedt (1942, p. 154, figs 382-388) Figs 2.87-2.92.**

Cells are isopolar to slightly heteropolar and linear-elliptical in profile. Valves are typically 80-190 µm long, 30-50 µm width and with 15-20 alar canals /100 µm. Wings are tall and well developed, sloping sharply (terminating) onto the valve face at the apices. The raphe sits on a raised ridge atop the keel. The keel canal also bears many spines ranging in width from 0.5-8 µm, which are positioned along its proximal side where it intersects with the alar canals. Fenestrae are wider than the alar canals and are of constant width. Their outlines are rectangular at the keel becoming rounded on the valve face edge, and are partially occluded by 12-18 fenestral bars. The valve face is moderately corrugated perpendicular to the apical axis, with many papillae and spines 0.2-12 µm in length situated primarily atop the porcae. The median area is occupied by a prominent ridge containing many long broad spines. The valve face slopes away dramatically from this ridge on either side of the apical axis. Spine length and form is highly variable on all areas of the valve. Striae appear to be mainly uniseriate 25-30 in 10 µm.

Distribution: *S. papillifera* has only been reported on Sulawesi, and is frequent in Lake Matano, and Towuti.

Similar Species: *S. papillifera* differs from *S. tubicola* through its fenestrae being broader, the less corrugate valve face, and the presence of spines along the edge of the wing canal, as opposed to tubes on the alar canals, as in *S. tubicola*. *Surirella tubicola* also has tubes, as opposed to spines, along the apical axis. *Surirella papillifera* differs from *S. tenacis* by way of its greater size, the lack of small papillae on the valve face, the presence of spines instead of tubes along the axial area, and the absence of siliceous tendrils at the bases of the alar canals.

***Surirella pediculata* Hustedt (1942, p. 176, fig. 438) Figs 2.85, 2.86.**

Cells are strongly heteropolar, valve asymmetrically ovoid in form with attenuated or apiculate apices, around 80 μm long, 25 μm wide and ca. 20 alar canals /100 μm. On the Holotype specimen the wing is well developed extending vertically from the valve face and terminates around the apices. Alar canals are narrower than the fenestrae, 20 /100 μm at the center, becomes slightly dense towards the apices. Valve face is corrugated from the mantle to a broad lanceolate median line; the porcae somewhat narrow relative to adjacent depressions and have fin-like spines at the junction of the porcae with the median area. Areolae covering the complete valve face, 18 striae /10 μm.

Distribution: Sulawesi, three specimens were found in Lake Matano by Hustedt (1942).

Similar Species: Compare with *Surirella karstenii* Hustedt from Mekong, China which is also heteropolar and similar in form. However, *S. karstenii* is broader, has a distinct median line ridge with fins and smaller papillae scattered over the corrugated valve face.

***Surirella pinnigera* Bramburger & Hamilton sp. nov. Figs 2.93-2.98.**

Cellulae valde heteropolares sunt, et in extremo ellipticales lineamento. Valvae tendunt 94-133 μm longitudine, et latitudine 36-48 μm. Alae, recte formatae, ab valvae fronte directae, 16-25 canalibus alaribus intra 100 μm exstant. Canales alares sunt latiores fenestris, quae 3-5 claustris fenestralibus occluduntur. Raphe non corrugata ab apice adversus valvae frontem deflectit. Valvae frons, cuius porcae fiunt latiores, ut nexum canalium alarium appropinquant, alte corrugatur. Superficies, atque area centralis atque canales alares, papillis paruis teguntur. Dorsum siliceum, quod spina magna (8 μm longa) pinnigera finitur, prope pilleum terminalem, secundum axem apicalem vehitur. Striae sunt biseriatae, quae 45-59 intra 10 μm exstant, et areolae paruae et circulares. Limbus (valvae) papillis quoque tegitur.

Cells are strongly heteropolar and elliptical in outline. Valves are 94-133 μm long and 36-48 μm wide. The wings appear well developed and sit vertical to the valve face, with 16-25 alar canals /100 μm. Alar canals are typically wider than fenestrae, which are shaped as rounded rectangles, and partially occluded by 3-5 fenestral bars. The raphe is not situated on a ridge, and terminal fissures deflect towards the mantle at the apices. The valve face is deeply corrugated, with porcae widening as they approach the junction with the alar canals. The valve surface, including the median area and the alar canals, is covered with small papillae, some of which interconnect. A siliceous ridge runs along the apical axis, terminating in a large (8 μm long), fin-like spine near the broad end of the valve. Striae are fine uniseriate near the median line becoming biseriate towards the margin (45-59 / 10μm). Areolae are small and circular. The mantle and is also covered with papillae (0.5-1.0 μm).

Type locality: Lake Towuti. Timampu town shoreline sediment. Coll. Date: Feb 24, 2002, Collector: P.B. Hamilton. S 02° 39.3, E 121° 25.8

Holotype: CANA 70996

Isotypes: BRM To be acquired

Etymology: Name derived from the Latin *pinnigera*, with fins.

Distribution: Sulawesi. Common in Lake Towuti

Similar Species: This taxon is differentiated from *Surirella excellens* based on the lack of a ridged raphe fissure, the presence of papillae over the entire valve face, and the paucity of directional hooks on the median area. *Surirella pinnigera* differs from *S. fenestrellata* based in its larger fenestrae, the presence of a single large hook on the median line, and the presence of spinules both on and between the corrugated porcae. Based on general shape and formation of the median area, this taxon should be compared with *Surirella splendida* (Ehrenberg) Kützing and *S splendidoides* Hustedt sensu Cocquyt (1998).

Surirella promontorium **Bramburger & Hamilton sp. nov. Figs 2.99-2.104.**

Cellulae sunt isopolares et in extremo lineares lineamento. Valvae 70 μm longitudine et latitudine 21 μm tendunt. Alae, recte formatae, ab valvae fronte fere perpendiculares educuntur. Raphe in dorso non iacet; adversus valvae frontem in extremis deflectit. Canales alares, ut fieri solet, sunt aequales latitudine fenestris; quae 27-35 canales intra 100 μm exstant. Fenestrae, ut fieri solet, forma quadriangulae, 5-10 claustris fenestralibus partim occluduntur. Valvae frons leniter corrugata, maximam aream centralem eductam, quae est multo altiorem sulcis, habet. Valvae frons, praeter dorsum centrale, papillis parvis, aliquando conjunctis, tegitur; hae papillae sunt inter porcas crassiores quam supra porcas. Dorsum centrale, vere sine ornamentis, longe prae cellularum [cellulae] apicem finitur. Praeterea, 1-3, saepius 2, tubulae, breves cavaeque, ad nexum cuiusque canalaris alaris et porcae occurrunt.

Cells isopolar and linear in outline. Valves are about 70 μm long and 21 μm wide. The wings are well developed and project almost vertically from the valve face. The raphe is not on a ridge and terminal fissures are hooked and deflect towards the valve face at the apices. Alar canals are typically the same width as fenestrae, although occasionally, exceptionally wide fenestrae are present. There are 27-35 alar canals /100 μm. Fenestrae are typically rectangular in shape and partially occluded by 5-10 fenestral bars. The valve face is mildly corrugated, and has a very large central elevated median area that is much higher than the corrugated region. The valve face, other than the central ridge, is covered by small, sometimes interconnected papillae, with the papillae denser between porcae in the depressions. The central median ridge is essentially featureless and terminates well before the apices. Also, there are 1-3 short, hollow tubes (usually 2) situated at the junction of each alar canal with a porca. Striae are uniseriate close to the median area becoming biseriate towards the margins with 42 in 10μm.

Type Locality: Lake Towuti. No Name River outflow. Coll. Date: March 4, 2002, Collector: P.B. Hamilton, S 02° 43.8, E 121° 39.3

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Holotype: CANA 71222
Isotypes: BRM To Be Acquired

Etymology: Named for its high ridge. *Promontorium* is derived from the Latin root for promontory, or mountainous ridge.

Distribution: *S. promontorium* has only been reported from Sulawesi, where it is isolated to Lake Towuti and very rare.

Similar Species: *Surirella promontorium* differs from *S. rugosa* primarily through its larger, featureless central ridge, but also by the deflected raphe endings and the presence of 1-3 small tubules at the junctions between the porcae and alar canals. Comparisons can also be made with taxa from the *Surirella biseriata* complex, which have the same elliptical, linear-elliptical valve form, but do not have the prominent promontorium median area and lack tubules on the alar canals. *Surirella bifrons* Ehrenberg 1843 has an elevated median area ridge, small spines on the porcae, not papillae and lacks tubules on the alar canals.

***Surirella pseudovalis* Hustedt (1942, p. 166, figs 412-415) Figs 2.83, 2.84.**

Cells are contorted and heteropolar along the apical axis. Valves ovoid to oblong-ovoid with a somewhat pointed foot-pole. Length 30-95 μm, width 23-40 μm and 20-30 alar canals /100 μm. Wing poorly developed, extending up and horizontally away from the valve face. Alar canals wide relative to the fenestrae, sometimes almost twice the width. Valves face weakly corrugated from the mantle to the proximity of the median line. The median line is narrow and difficult to discern. Areolae cover the complete valve surface. Striae slightly radiate at the center becoming strongly radiate at the apices, about 24 /10 μm.

Distribution: Sulawesi, frequently observed in Lakes Mahalona and Towuti.

Similar Species: *Surirella pseudovalis* could be confused with smaller taxa from the *Surirella ovata* Kützing 1844 and *S. ovalis* Brébisson 1838 complexes. This taxon can be distinguished by partially contorted valve, and the weakly corrugated valve surface. Specimens labeled as *S. pseudovalis* by Vyverman (1996, Fig. 2.6, 7) do not represent this taxon.

***Surirella quadridentis* Bramburger & Hamilton sp. nov. Figs 2.105-2.110.**

Cellulae isopolares sunt et in extremo ellipticales lineamento, 56 μm longitudine et latitudine 27-33 μm, tortae axem apicalem implicant. Ala, minime formata, secundum planitiem valvae frontis occurrit. Canales alares, quorum 14-16 intra 100 μm exstant, sunt ferme aequales latitudine fenestris. Fenestrae, ad valvae frontem rotundae, ad raphis canalem quadriangulae, 4-7 claustris fenestralibus occluduntur. Raphe non in dorso est. Valvae spinas dentatas 2-3 μm longas, quae in valvae fronte supra porcas forma ferme quadriangula disponuntur, tenent. Valvae frons tenuiter striatur; 25-31 striae intra 10 μm exstant. Striae sunt uniseratae aut biseratae, areolae parvae et criculares.

Cells are isopolar and elliptical in outline, 56 μm long, 27-33 μm wide, and contorted about the apical axis. The wing lies along the plane of the valve face and is relatively undeveloped. Alar canals are about the same width as fenestrae, 14-16 /100 μm. Fenestrae are round at the valve face to rectangular at the keel, and are partially occluded by 4-7 fenestral bars. The raphe is not on a ridge on the raphe canal. The valve face is moderately corrugated with porcae alternating and terminating at the median line. Valves have four curved, tooth-like spines (2-3 μm in length) arranged in a rough rectangle on the valve face and situated atop the porcae. The valve face is finely striated (25-31 striae /10 μm). Striae are uniseriate to biseriate and areolae are small and circular.

Type locality: Lake Towuti. Timampu, shoreline sediment. Coll. Date Feb. 24, 2002.

Collector: P.B. Hamilton. S 02° 39.3, E° 121 25.8

Holotype: CANA 70996

Isotypes: BRM To be acquired

Etymology: *Surirella quadridentis* was named for its four large, tooth-like spines. *Quadridentis* is Latin for having four teeth.

Distribution: *S. quadridentis is* reported only on Sulawesi, very rarely in Lake Towuti.

Similar Species: *Surirella quadridentis* differs from *S. coversa* Hustedt through the presence of four large hooked spines instead of many small randomly distributed spines. The wing is better developed in *S. conversa*, and stands roughly perpendicular to the valve face. *Surirella conversa* also has much coarser areolae. *Surirella quadridentis* differs from *S. ephippiomorpha* through its more outwardly projecting wing, the presence of four large spines instead of many small ones, the presence of visible areolae, and the absence of a ridged raphe. Also compare this taxon with the partially contorted *Surirella venusta* Østrup 1910 with clearly defined porcae.

***Surirella robusta* Ehrenberg (1841, p. 215; 1854, pl. 15a: 43).**

Cells are heteropolar, however can on rare occasions appear isopolar. Valves vary from oval to linear-lanceolate with bluntly rounded to cuneate-rounded apices. In girdle view frustules are rectangular with broadly curved apex margins. The wing is easily observed in girdle view. Length 50->400 µm, width 50-150 µm and 7-12 alar canals in /100 µm. Krammer and Lange-Bertalot (1988) indicate that the number of alar canals is usually less than 9. Wing projection is almost vertical from the valve face and by changing the focal-plan in LM can be seen as a round keel. Wings terminate at each apex. The alar canals are broad but slightly smaller than the adjacent fenestrae. Valve face is distinctly corrugated, from the margin to the median area. The porcae are approximately half the width of the adjacent depressions. The corrugated areas are covered by fine striae ranging from 40-50 /10 µm. The striae are biseriate with fine round areolae. The median area is broad varying from lanceolate to linear lanceolate. A fine median line (ridge) is present down the middle of the median area, although at times difficult to observe. Spinules appear randomly on the external valve surface.

Distribution: Cosmopolitan, currently reported from Europe (especially northern Europe), Japan, Java, Sumatra and Sulawesi (Lake Towuti).

Similar Species: This taxon lacks easily identifiable characters and because of its linear-lanceolate shape is commonly misidentified. Indeed, an examination of the type material is required with SEM documentation. The rounded keel on the wing, termination of wings at the apices and the small corrugated ridges extending from the alar canals are the main characters identifying this taxon.

Surirella splendida **(Ehrenberg) Kützing (1844, p. 62, pl. 7 : 9)** ***sensu lato.***

Synonym: *Surirella robusta* var. *splendida* (Ehrenberg) Van Heurck

Cells heteropolar, valves vary from linear-lanceolate to almost ovoid with an apiculate foot-pole. Length 133-195 µm, width 40-56 µm and 14-18 alar canals /100 µm. Wing projection is distinct, almost vertical from the valve and terminate at each apex. The alar canals are broad and equal in size to adjacent fenestrae. The valve face is distinctly corrugated, from the margin to the median area. The porcae are the same width as the adjacent depressions. The median area is narrow and linear-lanceolate. A fine median line (ridge) is present down the middle of the median area.

Distribution: Sulawesi, Lakes Mahalona, Towuti, Poso, and Matano. Although reported by Hustedt from other regions of the Indo-pacific and Casie (1989, SEM, pl. 14, fig. 8) from New Zealand, the variability of this taxon limits our discussion to the Island of Sulawesi.

Similar Species: This taxon is quite variable and could be confused with *S. tenera* Gregory, *S. robusta* Ehrenberg, *S. bifrons* Ehrenberg and possible *S. linearis* W. Smith. A more complete circumscription of this taxon is required. Our specimens are typically smaller than the specimens and description presented in Krammer & Lange-Bertalot (1998).

***Surirella robusta* var. *splendida* f. *punctata* (Hustedt 1942, l.c. p. 173, figs. 434, 435), Fig. 2.128.**

Invalidly published in 1912 and properly emended with a correct neotype by Simonsen (1987). Similar to the teardrop valve form of *S. splendida*. Length 160-161 µm, width 63-66 µm and 14-16 alar canals /100 µm. Wing projection almost vertical from the valve and terminates at each apex. The alar canals are narrower than adjacent fenestrae. The valve is weakly corrugated, from margin to median area. The porcae are the same width as adjacent depressions. The median area is narrow and linear-lanceolate. Spines are present on the porcae, on the median line and scattered in other locations on the valve face. According to Hustedt (1942), the wing projection unanimously agrees with specimens from Northern Germany.

Distribution: Sulawesi isolates from Lake Towuti and Lake Matano. We have not observed this form

Surirella rudis **var.** ***levis*** **Hustedt (1942, p. 164, fig. 408) Fig. 2.125.**

Cells are heteropolar, valves linear to linear-ovoid with a narrow-round foot-pole. Length 153 µm, width, at widest point, 39 µm, and 14 alar canals /100 µm. The holotype specimen has wings that extend vertically and alar canals that are narrower than adjacent fenestrae. Wings appear to terminate at the apices. Corrugations on the valve face are well defined and covered with striae (ca. 30-35/10 µm). The median area is narrow and linear. The median line appears to contain a series of projections, especially large projections towards the apices. Differs from the nominate form by the lack of spines on the valve.

Distribution: Sulawesi: very rarely in the Lake Matano. Hustedt considered this a variety of *S. rudis*, but after our examination of the Holotype, the many differences in valve structure are significant and will justify the transfer to a new species. The nominate taxon was described from LakeTanganyika (S. Atl. T. 356, F. 5, 6), and later identified from Java.

Surirella rugosa **Bramburger & Hamilton sp. nov. Figs 2.111-2.113.**

Cellulae sunt isopolares et lineares, quarum apices extenduntur. Valvae 56 μm longitudine et latitudine 15 μm tendunt. Alae recte formatae a valvae fronte ad extremum proiciunt. Canales alares, ut fieri sit, latitudine aequales fenestris, 30-40 intra 100 μm exstant. Fenestrae quadriangulae 3-5 claustris fenestralibus partim occluduntur. Raphe neque in dorso iacet nec in extremis deflectitur. Valvae frons, minime corrugata, reticulo verrucorum papillarumque tegitur. Area axialis tenet dorsum eminens et educatum quod ante valvae apices multo finitur. Quod dorsum compluribus dorsis conjunctis minoribus tegitur. Striae biseriatae tenuissimae, ex quibus fere 30 intra 10 μm exstant, areolas paruas et circulares tenent. Limbus quoque papillis conjunctis, aliquantum minoribus quam eis, quae in valvae fronte occurrunt, tegitur.

Cells are isopolar and linear, with elongate apices. Valves 56 μm long and 15 μm wide. The wings are well developed and project outwards from the valve face. Alar canals are typically the same width as the fenestrae, 30-40 / 100μm. Fenestrae are rectangular and partially occluded by 3-5 fenestral bars. The raphe does not sit on a ridge, and the terminal fissures are not deflected. Valve face is mildly corrugated, and is covered with a pattern of interconnected warts and papillae, giving it a wrinkled appearance. The median area is occupied by a pronounced, elevated ridge that terminates well before the valve apices. This ridge is covered by a number of smaller, interconnected reticulate projections, most of which run parallel to the larger, underlying elevation. Striae are biseriate and very fine (ca. 30 striae in 10 μm), with small, circular areolae. The mantle is also covered with interconnected papillae, somewhat smaller than those on the valve face.

Type Locality: Lake Towuti. Loeha Island shoreline sediment. Coll. Date Feb. 26, 2002.

Collector: P.B. Hamilton, S. 02° 45.5, E. 121° 30.9

Holotype: CANA 70137

Isotype: BRM To be acquired

Etymology: From the Latin *rugosa*, meaning wrinkled.

Distribution: Sulawesi, very rarely in Lake Towuti.

Similar Species: S*urirella. promontorium* has similar interconnected papillae and a pronounced central ridge, but differs through its more robust outline, the presence of 2 short tubes on each corrugated ridge at the base of the alar canals, the absence of interconnected ridges on the central elevation, and the deflection of the terminal raphe fissures towards the valve face.

***Surirella sublinearis* Hustedt (1942, p. 150, figs 373-376) Figs 2.114, 2.115.**

Cells are isopolar, valves linear in outline, but strongly constricted in the middle. Valve apices are cuneate and rounded. Valves 45-75 µm long, 13-22 µm wide and with 30-40 alar canals /100 µm. Wings are narrow, and stand vertical to the valve face. The alar canals are approximately the same width as fenestrae. Fenestrae are almost fully occluded, with 2-4 fenestral bars. The valve face is moderately corrugated, with a narrow, slightly elevated central area. The surface is covered with small spinules arranged into parallel lines running perpendicular to the apical axis. In the central area, these parallel patterns break down and spinules are coarser and more sparsely and irregularly dispersed. One or two siliceous tendrils project from porcae areas adjacent to alar canals at irregular intervals, more frequently towards the apices. These tendrils are 8-13 μm in length and about 0.5 μm in diameter. These tendrils are frequently attached to substrate particles, including clastic materials and other diatoms, even after cleaning. Striae are about 42 in 10 μm.

Distribution: Reported only from Sulawesi. Common in Lakes Matano and Towuti.

Similar Taxa: *Surirella sublinearis* differs from *S. linearis* and its varieties in its more gibbous form. As well, *S. linearis* has a more deeply corrugated valve face, with coarser areolae, and spinules only along the median area. The presence of siliceous tendrils is also distinct for *S. sublinearis*. This taxon also differs from *S. alata* in the longer, more linear outline, the presence of siliceous tendrils, and the fact that the raphe it not situated upon a ridge. *Surirella tenacis* is very similar to *S. sublinearis* and its varieties, but differs markedly through the presence of 6-15 large hollow tubes along the apical axis of both valves. Also compare with *Surirella heidenii* Hustedt 1922 which has narrow corrugated valve depressions, a very narrow median line and a valve face covered with spines.

***Surirella sublinearis* var. *suggesta* Bramburger & Hamilton var. nov. Figs 2.116-2.118.**

Frustulae sunt breviores et in extremo minus constrictae lineamento, quam sunt cellulae Surirellae sublinearis. Longitudo, ut fieri solet, 48-60 μm; latitudo 13-16 μm.

Valvae frons, modice corrugata, aream centralem eductam et latam, quae supra ceteram eiusdem frontem, habet. Spinulae, ut in Surirella Sublineari, super valvae frontem, non super aream centralem, ordinibus parallelis disponuntur. Spinulae, quae sunt horridae in area centrali, (1 - 2 µm transversim) inaequaliter disponuntur.

Frustules are slightly shorter and less constricted in outline than *S. sublinearis*. Length is typically 40-60 µm, while width is 13-16 µm. The valve face is moderately corrugated and has a wide raised central area which is elevated slightly above the rest of the valve face. As in *S. sublinearis*, spinules are arranged in parallel rows across the valve face, but not the central area. Spinules in the central area are coarse (1-2 µm in diameter) and irregularly dispersed. There are 30-40 siliceous tendrils located on the valve face, typically in groups of 1-3 at the junction between the alar canals and the porcae. These tendrils have been observed attached to substrate particles and other diatom frustules. Striae are 30-44 in 10 µm.

Type Locality: Lake Towuti, Loeha Island shoreline sediment. Coll. Date Feb. 26, 2002.
Collector: P.B. Hamilton. S. 02° 45.5, E. 121° 30.9.
Holotype: CANA 70137
Isotype: BRM To be acquired

Etymology: Name derived from the Latin root *suggestus*, meaning platform or elevated area.

Distribution: Sulawesi, common in Lake Matano.

Surirella sulcata **Hustedt (1942, p. 177, fig. 439) Fig 2.129.**

Cells are heteropolar along the apical axis. Valves are asymmetrically-elliptical to almost ovoid, with bluntly rounded apices, 80 µm long, 30 µm wide and 15 alar canals /100 µm. The holotype specimen has distinct wings, vertically forming from the valvar-plane. Alar canals are typically narrower than fenestrae. Valves with large, oval-lanceolate median areas, surrounded by a distinct corrugated valve surface. Porcae narrower than adjacent depressions. Striae are extremely fine, and scarcely recognizably on the corrugated valve surface. The median area is devoid of structure. According to Hustedt (1942) the wing has distinct fenestrae and the keel is well removed from the valve face.

Distribution: Reported only from Sulawesi. Not common in Lakes Matano and Towuti.

Similar Species: This species is identified by valve shape, the position of the wings, by the deep corrugated valve face and the structure of the median area.

Surirella tenacis **Bramburger & Hamilton sp. nov. Figs 2.89-2.93.**

Cellulae sunt isopolares et in extremo lineares lineamento, autem aliquantum in mediis contrahuntur. Valvae 38-62 µm latitudine et longitudine 12-17 µm tendunt. Ala recte formata et ab valvae fronte perpendicularis, tenens 36-41 canales alares intra 100 µm. Fenestrae, ferme quadratae, 3 - 7 claustris fenestralibus occluduntur. Raphe in dorso parum eminenti. Valvae frons modice corrugatae papillas complures parvas tenet. In area centrali est locus eductus, non porcis; qua papillae paulo majores latius distribuuntur. Area centralis tenetur 6 - 14 tubulis cauis, qui fere 5 µm altitudine et transversim 0.4 tendunt. In quaque porca fundamentum cuiusque canalis alaris attingente, occurrit clavicula silicea longa usque ad 9 µm. Est 1 clavicula cuique porcae, autem prope adversus apices sunt crebriores. Quae claviculae ad aliquem substratum, cum substantia flexibili aut aliis frustulis, etsi purgantur, saepius alligantur.

Cells are isopolar and linear in outline, while often slightly constricted in the middle. Valves are 38-62 µm in length and 12-17 µm wide. The wing is well developed and perpendicular to the valve face, with 36-41 alar canals in 100 µm. Fenestrae are roughly square, and partially occluded by 3-7 wide fenestral bars. The raphe sits on an indistinct ridge. The valve face is moderately corrugated, and has many small papillae dispersed uniformly over most of the surface. In the central area, there is an elevation that is not intersected by porcae, and the papillae are slightly larger and more sparsely distributed. The central area is also occupied by 6-14 tubular processes about 5 µm in height and 0.4 µm in diameter. On each porca, adjacent to the base of each alar canal, there is a siliceous tendril up to 9 µm in length. There is one tendril on each ridge, except near the apices, where they are more frequent. These tendrils are frequently attached to some type of substrate, including clastic material or other diatoms, even after cleaning. Striae are 56-70 in 10µm.

Type Locality: Lake Towuti.

Holotype: BRM AS1323

Isotypes: CANA 70037

Etymology: From the Latin *tenacis*, meaning tenacious. *S. tenacis* is named for the striking tenacity of the bond between its tendrils and substrate particles.

Distribution: *S. tenacis* has been reported only on Sulawesi, where it is not uncommon in Lake Towuti.

Similar Species: *Surirella tenacis* is similar to both *S. sublinearis* and *S. sublinearis* var. *suggesta*. It differs from both of these, most obviously through the presence of large hollow tubes along the apical axis. Furthermore, *S. tenacis* has 1 tendril per porca, as opposed to the usual 2 in *S. sublinearis* and the raphe in *S. tenacis* is situated on an indistinct ridge on the keel. *Surirella tenacis* differs from *S. tubicola* in the number, placement, and morphology of its tubular processes, and through its smaller size.

Surirella tenera* Gregory (1856, p. 11, pl. 1, fig. 38) *sensu lato.

Cell is always heteropolar, valves oblong-ovate to lanceolate with rounded apices. According to Hustedt (1930), the length is 45-170 µm, width 13-40 µm and 20-30 alar canals /100 µm. In girdle view the frustules are trapezoid. Wings distinct, extending outward from the valvar-plane and easily observed in LM. The alar canals are less than half the width of the fenestrae. The valve face is concave on either side of the median line with well-developed transapical corrugations. The porcae are narrow relative to the adjacent depressions and extend to the median area. The median area varies from wide and lanceolate to narrow and linear. Fin-spines are present at the ends of the median line and smaller spines may also be scattered along the median line. Striae can be visible using optimal light conditions.

Distribution: Cosmopolitan (?). Present in the benthos and in the plankton of oligotophic freshwaters with average electrolyte content. Sulawesi, our specimens are similar to *S. tenera* sensu lato are rare in Lake Towuti.

Similar Species: At present this taxon is distinguished by alar canal density, surface structure and the median ridge extending down the middle of the median area. Krammer & Lange-Bertalot (1988) present *S. tenera sensu lato* with and without spines, with large and small median areas and different wing constructions. The historical discussions about the importance of characters such as spines, makes for interesting reading and some confusion. It could be argued that spines appear as a result of environmentally induced phenotypic expression. However, the presence/absence of multiply characters (e.g. papillae, labiate process, spines, thorns, and wing/ keel structures like raphe ridges) does challenge the idea of simple phenotypic expression. With the established significance of endemism within the Indo-Pacific archipelago, it should not be surprising that characters, including spines, appear to be significant and consistent taxonomic features which only appear in selected taxonomic lines. With further, examination, we anticipate this complex will be divided into better consistent taxonomic entities.

***Surirella tenuissima* Hustedt (1913, pl. 299, fig. 15, description Hustedt 1938 p. 504)**

Cells heteropolar, valves oblong-ovate to lanceolate with broadly rounded apices. Length 17-38 µm, width 6-11 µm and 40-79 alar canals /100 µm. In girdle view, frustule rectangular to trapezoid with large distinct wings. In valve view, wings project at an angle away from the valvar plane and terminate at the apices. The keel is round. A poorly developed corrugate valve surface extends almost to the median area. The porcae are narrower than the adjacent depressions. The valve surface appears to be devoid of papillae and spines. Median area is faint and slightly elevated.

Distribution: Tropical, Brazil and Indo-Pacific. Sulawesi, very rare in Lakes Wawantoa, Towuti and Matano.

Similar Species: *Surirella tenera* Gregory and *S. dubraviciensis* Hustedt are comparable in shape and structure but can be separated by size and corrugation development on the valve face.

***Surirella* sp. [*S.* cf. *thienemannii* Hustedt (1935, p. 179, fig. 18)] Figs 2.126, 2.127.**

Cells are isopolar, sometimes appearing heteropolar, valves linear with cuneate to apiculate apices. Length 150-173 µm, 26-29 µm wide and 23-28 alar canals /100 µm. The wing extends almost vertically to the valvar-plane and terminate at the apices. The valve face is corrugate, porcae parallel at the center to strongly radiate at the apices. The median area is relatively wide, linear to linear lanceolate with a depression in the valve surface on either side. Spines are present along the median line. Striae faintly visible under optimum light.

Distribution: Sulawesi, dispersed throughout Lakes Towuti and Matano. Originally described from Lake Toba, Sumatra

The forms observed from Sulawesi, closely follow the isolectotype (Simonsen (1987, pl. 291, Figs 1-4), however, the occurrence of spines along the median line, possible presence of papillae and the transapically asymmetric shape suggest that this may be a new taxon. *Surirella thienemannii* is characterised by valve shape, and the vertical projection of the wing from the valvar-plane which creates a clear wing projection with reduced exposure of the fenestrae. The fenestrae in our specimens are also reduced.

Surirella tortilis **Bramburger & Hamilton sp. nov. Figs 2.131-2.132.**

Cellulae, lineares et ellipticales, apices isopolares tenent. Valvae fere perpendiculares maxime producuntur; quae tendunt 62 μm longitudine et latitudine 26 μm. Alae recte formatae ab valvae fronte proiciunt, et 18 canales alares intra 10 μm exstant. Fenestrae, fere aequales longitudine canalaribus alaribus, 6 aut claustris tenuibus fenestralibus partim occluduntur. Valvae frons, sulco secundum axem apicalem conspicuo, alte corrugatur. Multae spinulae paruae, praecipue in valvae frontis porcis limboque, occurrunt.

Cells linearly elliptical with isopolar apices. Frustules extremely contorted (almost to 90°). Valves 62 μm long and 26 μm wide. Wings are well developed and project outwards from the valve face, with 18 alar canals /100 μm. Fenestrae are approximately the same width as alar canals and are partially occluded by 6 or 7 fine fenestral bars. The valve face is deeply corrugated, with a pronounced furrow along the apical axis. Many small spinules exist primarily on the porcae and on the mantle.

Type locality: Lake Towuti. Timampu, shoreline sediment. Coll. Date Feb. 24, 2002.
Collector: P. B. Hamilton. E 02° 39.3, E 121° 25.8.
Holotype: CANA 70996
Isotypes: BRM To be acquired

Etymology: *S. tortilis* was named for its contorted, highly torsioned form. Tortila is Latin for twisted.

Distribution: Sulawesi, very rare in Lake Towuti.

Similar Species: *Surirella tortilis* can be differentiated from *Surirella conversa* by its more cuneate apices, and a less contorted form. The small spines on *S. tortilis* also lie over the entire valve face, as opposed to mainly on the porcae, as on *S. conversa*. *Surirella tortilis* varies from *Surirella ephippiomorpha* and *Surirella decipiens* in a similar manner.

***Surirella tubicola* Bramburger & Hamilton sp. nov. Figs 2.133-2.138.**

Cellulae sunt isopolares, et extremo lineares in lineamento. Valvae tendunt 84-132 μm longitudine, et latitudine 38-42 μm. Alae, recte formatae, ab valvae fronte ad extremum paulum proiciunt. Canales alares 20-25, angustiores, ut fieri solet, quam fenestris, intra spatium 100 μm, occurrunt. Fenestrae forma quadriangulae claustris fenestralibus occluduntur. Raphe, cuius canalis angustus est et valde siliceus, in dorso prominenti et angusto iacet. 2 - 4 anales alares tubulas, breves cavasque, fere 1 μm longitudine, iuxta valvae frontem occurrentes, tenent. Valvae frons, alte corrugata, secundum axem apicalem educitur. Plurimae tubulae cavae, 0.5 - 0.8 μm longitudine, in valvae fronte supra porcas sparsae, ab altero apice ad alterum directe mittuntur.

Cells are isopolar and linear in outline. Valves 84-132 μm long and 38-42 μm wide. Wings are well developed and project outwards slightly from the valvar plan. There are 20-25 alar canals /100 μm and the canals are typically narrower than fenestrae. Fenestrae are rectangular in shape and are almost completely occluded by 7 or 8 fenestral bars. The raphe sits on a prominent, narrow ridge atop the keel canal that is also narrow and heavily silicified. Alar canals have 2-4 short, tubular processes about 1 μm in length situated on the side of the valve surface. The valve face is deeply corrugated, with an elevated area along the length of the median line. There are many small tubular processes 0.5-0.8 μm in length running in a straight line along the median line. There are also some tubular processes scattered elsewhere on the valve face, always on top of the porcae.

Type Locality: Lake Towuti, Loeha Island, shoreline sediment. Coll. Date Feb. 26, 2002.

Collector: P.B. Hamilton. S. 02° 45.5, E. 121° 30.9

Holotype: CANA 70137

Isotype: BRM To be acquired

Etymology: *Surirella tubicola* was named for its many small hollow tubular processes. The name *tubicola* was derived from the Latin root for having many tubes.

Distribution: Sulawesi. *S. tubicola* is consistently observed in Lake Towuti.

Similar Species: *Surirella tubicola* differs from *S. tenacis* through its isopolar form, its smaller, more numerous tubes, its more deeply corrugated valve face, larger size, and the width and distinctness of the raphe ridge. This taxon is also very similar to *S. elegantula*, but differs by the presence of tubules, not spines along the median line, less developed papillae in the porcae and tubules on the alar canals (Cocquyt (1998).

Surirella ventricosa **Hustedt (1942, p. 168, figs 421-424) Fig. 2.130.**

Cells are small, heteropolar sometimes appearing isopolar, valves narrowly lanceolate, asymmetrically oval to elliptical with apiculate apices. Length 27-37 µm, 11-13 µm wide and 30-40 alar canals /100 µm. The lectotype specimen has poorly developed wings that barely extend off the valvar-plane. Alar canals are much narrower than fenestrae. Valves area with well developed corrugations, porcae narrow almost appearing rib-like. The corrugations extend to a narrow zigzag median line. Valve walls with delicately formed striae.

Distribution: Sulawesi, present but not common in the Lake Towuti.

Similar Species: Similar with many small taxa within the Robustae. Compare with the larger *S. bifrons* Ehrenberg, *S. bohemica* Maly, and *S. tenera* Gregory. Taxa with similar size, *S. roba* Lecercq, *S. linearis* W. Smith and *S. duraviciens* Hustedt, can be separated by different wing structure and form (*S. roba*, *S. linearis*, *S. duraviciens*) and corrugate pattern/size (*S. roba*, *S. duraviciens*). Also compare to *Surirella angustiformis* but is more elliptical, not constricted and generally smaller.

***Surirella woltereckii* Hustedt (1942, p. 166, figs 416-419) Figs 2.139-2.144.**

Cell is contorted and slightly heteropolar, valve rhombic-elliptical in profile. There is a great degree of variability in the contortion of the valve within this species. Many smaller specimens are twisted about the apical axis, causing them to appear as figure-eights or saddles in girdle view. Valves are 40-110 μm long, 35-80 μm wide and with 20-25 alar canals /100 μm. The wings are thick and well developed vertically from the valvar plan. Alar canals are roughly the same width as fenestrae, which are rounded at the edges and partially occluded by 3 or 4 thin fenestral bars. The valve face is flat to mildly corrugated, with a thickening of the silica along the median line. Areolae radiate out from this central thickening. The external valve surface is covered with small, poorly developed papillae that almost reach the alar canals. On the internal surface, areolae extend out from the central thickening to areas between the alar canal openings. Striae are

23-30 in 10 μm. Vyverman (1996, fig. 2.7 [called *S. pseudovalis*], 10) also presents specimens of *S. woltereckii*.

Distribution: Reported only from Sulawesi. Hustedt (1942) reported *S. woltereckii* as a planktonic species in Lakes Matano, Mahalona, Towuti, and Wawantoa. This study found *S. woltereckii* mainly in benthic habitats in Lakes Matano, Mahalona, Masapi, and Towuti, rarely observed in the plankton.

Similar Taxa: *S. woltereckii* is much broader and more coarsely striated than all other contorted taxa.

Numerical Taxonomy:

Sixty-eight individuals representing 28 taxa were included in the analyses. Discriminant function analysis (DFA) was used to identify clusters of individuals. Twenty groups were identified within the study population ($p < 0.05$, $n = 68$). Of these groups, nine contained more than one individual.

Hierarchical clustering analysis (HCA) was also used to determine relationships among clusters of individuals and membership within clusters. The mean Euclidean single linkage distance was 0.441 units ($n = 66$, S.D. = 0.365), while the two outgroup diatoms, *Cymbella woltereckii* and *Nitzschia woltereckii*, were linked to their nearest neighbours at Euclidean distances of 1.780 and 2.004 units, respectively. Like DFA, HCA identified 9 multi-individual groups and 11 single individual groups at Euclidean distances of less than 0.5 units, and group composition was similar between methods.

Linkages between these groups occurred at Euclidean distances of about 0.6 units (Figure 2.145).

DISCUSSION

The striking endemism of biota on Sulawesi Island has been well known for many years (Wallace, 1860). As noted by Hustedt (1942), the diatoms of the island's large lakes truly exemplify this endemism. Recent surveys of the diatom communities from the ancient Malili Lakes in central Sulawesi have identified 256 taxa of diatoms, 245 of which were endemic to Sulawesi (Bramburger *et al.* in press) The diatom genus *Surirella* provides perhaps the best example of the endemism and diversity observed in the Malili Lakes, with 46 taxa identified, many of them endemic. These findings place the Malili Lakes as the world's "hotspots" for diversity among the *Surirella.* Other areas with comparable levels of diversity include the region of Lake Tanganyika (Cocquyt 1998, 36 taxa), tropical South America (Metzeltin & Lange-Bertalot 1998, 14 taxa + many unknowns), and Papua New Guinea (Vyverman 1991, 17 taxa + many unknowns). Foged (1981) identified 37 *Surirella* taxa from 218 localities across Alaska. The Lake Tanganyika region of Africa represents the most similar diversity of *Surirella* forms (See Simonsen 1987, Cocquyt 1998).

The Malili Lakes flora is dominated by rare taxa. Many of Hustedt's (1942) taxa were represented by only one or two specimens, and were not observed in this study. Likewise, several of the new taxa described in this study, and not observed by Hustedt (1942), are represented by few specimens. The fact that this study did not achieve complete overlap with Hustedt's (1942) work, in spite of a rigorous sampling regime, is reflective of the patchiness and small-scale spatial variability of the lakes.

The Malili Lakes *Surirella* are comprised of several sub-genus clades of morphological sister-taxa, grouped together by both traditional taxonomic techniques and quantitative methods (DFA, HCA). These groups of taxa often differ subtly and incrementally in a suite of specific morphological characters. Significant differences among groups identified by DFA can be brought about by either large or highly consistent small differences in morphology. In this study, significant results from DFA have helped us to utilize subtle differences to discriminate amongst morphologically similar taxonomic clusters.

In HCA, the outgroup diatoms, *Cymbella woltereckii* and *Nitzschia woltereckii* were linked to their nearest neighbours at Euclidean distances roughly four times the mean linkage distance (Fig. 2.145). The relatively short Euclidean linkage distances among *Surirella* taxa demonstrate that this genus is largely morphologically cohesive. *Surirella* taxa with unusually long Euclidean distances to their nearest neighbor (>1.0) may be examples of the extremes of typical *Surirella* morphology, as in the cases of *Surirella papillifera* (outside clusters), then *Surirella tubicola* (Cluster 8, separated from clusters 1-7), and *Surirella cuspidata* (separate from clusters 1-7). Conversely, taxa such as *Surirella bidens*, which lacks any evidence of wing or alar canal development, exhibit morphology typical for Pennatae and is clearly separated from the dominant Robustae group found in this mountainous tropical region (outside of clusters 2-7).

The clustering of taxa at Euclidean distances of 0.5 units or less in HCA is reflective of differentiation and specialization among the Malili Lakes taxa. Individual members within these clusters are linked by a unique combination of morphological traits. The clusters are identified by valve morphology (isopolar/heteropolar/flat/twisted), fins, spines, tubules, and tendrils (Table 2.1).

Cluster 1 with *Surirella biseriata* var. *heteropolaris* contains unusually large, slightly heteropolar individuals, lacking external siliceous processes. Individuals in cluster 2 containing *Surirella excellens* possess a series of median area spines and a ridged raphe fissure. Individuals within the group 3(A&B) containing *Surirella quadridentis*, *Surirella conversa*, and *Surirella woltereckii* are bound together by their twisted valve structure, elliptical to ovoid shape and compressed (flattened) frustules. Other torsioned diatoms including *Surirella tortilis* and *Surirella ephippiomorpha* are clustered nearby. *Surirella fenestrellata* and *Surirella pinnigera* (within cluster 4) and allies, *Surirella promontorium*, and *Surirella rugosa* are linked by small spinules on the valve face and mantle, their ridge-less raphe fissures, and their elevated median areas.

Group 6, containing *Surirella sublinearis* and its variety, *S. sublinearis* var. *suggesta*, and *Surirella tenacis* differs from all other groups by the presence of novel structures including siliceous tendrils and axial tubular processes. The appearance of non-derived novel structures within a cluster suggests that speciation and fixation of these new structures within a population may be responsible for the extraordinary diversity of *Surirella* taxa within these lakes. Hustedt (1943) postulated that spines could appear and disappear through time in plastic populations. The structures we propose, however, remained consistent in all specimens within a taxon. Furthermore, differences in a minimum of three characters were required to designate a specimen as a different taxon. Conversely cluster 7 is defined by the absence of prominent or unique characters.

An example of the relationship between structure and function can be seen in the siliceous tendrils of *S. sublinearis* and *S. tenacis*. Both taxa use these tendrils to attach to various hard substrates, including inorganic particulate matter and other diatoms, as demonstrated in Figs. 2.87 and 2.91. The link between structure and function in other features is not as clear, although Krammer (1989) identifies the significance of thinly silicified undulating valves with alar canals, as a selected structural trait. The axial tubular processes of *S. tenacis* may exude mucopolysaccharides for attachment purposes, possibly similar to the function of rimoportulae (Daniels et al. 1987) or b-chitin fibrils for attachment similar to fultoportulae in the centric diatoms (Herth 1978, 1979, Herth & Barthlott 1979). We further anticipate that the hooks and spines observed on many of the Malili Lakes taxa function as clinging devices to secure attachment to littoral zone substrates.

FIGURE LEGEND

Fig. 2.1. Important diatom genera within the Malili Lakes.

Fig. 2.2. Valve characters used in descriptions of *Surirella taxa*. Inset top left: **A**: ridged raphe fissure. **B**: fin spines in median area (hooks). **C**: fenestral bars. Main image: **D**: box encloses section of wing. **E**: fenestrae. **F**: alar canals. **G**: porcae (corrugation ridges). **H**: tubular processes. **I**: raphe canal. The median area lies between the two sets of porcae, and, in this case, contains tubular processes. Inset bottom right: **J**: siliceous tendrils. **K**: circle encloses several spinules on the valve face.

Figs 2.3-2.7. *Surirella alata*. Scale bars = 20 µm (Figs 2.3, 2.4) or 2 µm (Figs 2.5-2.7). **Figs 2.3, 2.4**. LM Holotype, Lake Towuti. BRM #2581, Slide X1/08 (finder 648.5). **Figs 2.5 -2.7**. SEM, Lake Mahalona, CANA# 70881. **Fig. 2.5.** Whole valve. **Fig. 2.6**. Detail of ridged raphe fissure and spines on raphe canal. **Fig. 2.7**. Detail of wing termina and fenestrae.

Figs 2.8-2.15. *Surirella angustiformis* and *S. celebesiana*, LM, Scale bars = 20 µm. **Figs 2.8-2.11**. *S. angustiformis*. **Figs 2.8-2.9**. Whole valve, Lectotype, Lake Towuti, BRM Slide 397/40a (finder 586.3-6). **Fig. 2.10**. Whole valve, Isolectotype, Lake Towuti, BRM Slide x3/81 (finder 611.8). **Fig. 2.11**. Whole valve, Isolectotype Lake Towuti, BRM Slide X1/16 (finder 496.1-2). **Figs 2.12-2.15**. *Surirella celebesiana*. **Fig. 2.12-2.13**. Whole valves, Lectotype, Lake Matano, BRM Slide X1/75 (single mount). **Fig. 2.14**. Whole valve, Isolectotype, Lake Matano, BRM Slide X5/46 (finder 289.6). **Fig. 2.15**. Whole valve, Isolectotype, Lake Matano, BRM Slide 397/39b (finder 585.5).

Figs 2.16-18. *Surirella bidens*. Scale bars = 50 µm (Figs 2.16, 2.17) or 5 µm (Fig. 2.18). **Fig. 2.16**. LM, whole valve, Holotype, Lake Towuti, BRM 2581, Slide #397/42. **Fig. 2.17**. SEM, whole valve, Lake Mahalona, CANA # 70880. **Fig. 2.18**. Detail of striae and raphe fissure, CANA# 70880.

Figs 2.19-2.23. *Surirella biseriata* var. *celebesiana*, *S. biseriata* var. *heteropolis* and *S. celebesiana* var. ? *matanensis*. Scale bars = 50 µm. **Figs. 2.19, 2.20**. *Surirella biseriata* var. *celebesiana*, Whole valve, Lectotype, Lake Matano, BRM Slide X6/99 (single mount). **Figs 2.21-2.23**. *Surirella biseriata* var. *heteropolis*, Holotypes, Lake Matano, BRM Slide X6/100. **Fig. 2.24**. *Surirella celebesiana* var. ? *matanensis*, Holotype, Lake Matano, BRM Slide 397/49 (finder 531.2).

Figs 2.25-2.31. *Surirella conversa*. Scale bars = 50 µm (Figs 2.25-2.27), or 20 µm (Fig 2.29) or 5 µm (Figs 2.28, 2.30, 2.31). **Figs 2.25, 2.26**. LM, whole valve, Lectotype, Lake Towutii, BRM 2580, Slide # 397/35A. **Fig. 2.27**. SEM, Whole valve. Lake Towuti. **Fig. 2.28**. Detail of raphe canal and spines on valve face, CANA# 71037 **Fig. 2.29**. Internal valve view, CANA # 70996. **Fig. 2.30.** Detail of striae and raphe, CANA# 71015. **Fig. 2.31**. Detail of apical area, CANA# 71015.

Figs 2.32-2.37. *Surirella cuspidata* and *S. decipiens*. Scale bars = 50 µm (Figs 2.32-2.34), or 20 µm (Figs 2.36, 2.37) or 10 µm (Fig. 2.35). **Figs 2.32-2.35**. *Surirella cuspidata*. **Fig. 2.32**. LM, Whole valve, girdle view, Paralectotype, Lake Wawantoa, BRM # 2579, Slide 397/46B. **Fig. 2.33**. valve view, Lectotype, BRM Slide Y1/63, (finder 291.4-5). **Fig. 2.34**. SEM, whole valve, Lake Towuti, CANA# 71037. **Fig. 2.35**. Detail of hooked terminal raphe fissures and apical area. **Figs 2.36, 2.37**. *Surirella decipiens*. **Fig. 2.36**. LM. Whole valve, Lectotype, Lake Towuti, BRM #2581, Slide X2/4 (finder 493.4-5). **Fig. 2.37**. SEM. Whole valve, Lake Mahalona, CANA# 70880.

Figs 2.38-2.45. *Surirella elegans* f. *lata* and *S. elegantula*. Scale bars = 20 µm (Figs 2.38-2.45). **Figs 2.38-2.40**. *S elegans* f. *lata*, LM, whole valve, Isolectotype, Lake Matano, BRM Slide 397/49 (finder 585.7). **Figs 2.41-2.43**. *S. elegantula*, LM. **Fig. 2.41.** Whole valve, Lectotype, Lake Towuti, BRM Slide 397/35 (finder 674.6-9). **Figs 2.42**. Whole valve, Isolectotype, Lake Matano, BRM Slide 397/49 (finder 558.6). **Fig. 2.43**.Girdle view, Lectotype, BRM Slide 397/35. **Figs 2.45**. *S. elegantula* f. *cuneata*, whole valve, Holotype, Slide X6/98 (single mount).

Figs 2.46-2.51. *Surirella ephippiomorpha* sp. nov. SEM, Lake Towuti; CANA# 71015. Scale bars = 20 µm (Fig. 2.46) or 10 µm (Fig. 2.47) or 5 µm (Figs 2.48-2.51). **Fig. 2.46**. Whole valve. **Fig. 2.47**. Detail of raphe canal and girdle bands. **Fig. 2.48**. Detail of ridged raphe fissure. **Fig. 2.49**. Detail of spinnules on valve face. **Fig. 2.50**. Detail of terminal raphe fissures. **Fig. 2.51**. Detail of spines on wing and fenestrae.

Figs 2.52-2.59. *Surirella excellens*. Scale bars = 20 μm (Figs 2.52-2.54, 2.56, 2.58, 2.59) or 5 μm (Figs 2.55, 2.57). **Figs 2.52, 2.53.** LM, whole valve, Lake Matano, Lectotype, BRM # 2582, Slide 397/49 (finder 345.8). **Figs 2.54-2.59**. SEM.. **Fig. 2.54**. Whole valve, Lake Towuti, CANA# 70996. **Fig. 2.55**. Detail of ridged raphe fissure, median area spines, and fenestrae. **Fig. 2.56**. Semi-girdle view, Lake Towuti CANA# 71037. **Fig. 2.57**. Detail of terminal raphe ending and intervalve attachment spines. **Fig. 58**. Valve showing broken median area spines, Lake Matano, CANA# 71131. **Fig. 2.59**. Detail of valve broken under SEM beam, Lake Towuti, CANA# 70996.

Figs 2.60-2.65. *Surirella fenestrellata* sp. nov. Lake Towuti, CANA 70893. Scale bars = 20 μm (Figs 2.54, 2.55, 2.57) or 5 μm (Figs 2.56, 2.58, 2.59). **Figs 2.60, 2.61**. LM, Whole valve, Holotype CANA 70893. **Figs 2.62-2.65**. SEM. **Fig. 2.62**. Detail of Mantle area and raphe fissure. **Fig. 2.63**. Whole valve. **Fig. 2.64**. Detail of terminal raphe fissures and valve face. **Fig. 2.65**. Detail of broken raphe canal, Lake Towuti, CANA# 71037.

Figs 2.66-2.69. *Surirella fimbriata*, SEM, Lake Towuti; CANA# 70893. Scale bars =20 μm (Fig. 2.66) or 5 μm (Fig 2.69) or 2 μm (Figs 2.67, 2.68). **Fig. 2.66**. Whole valve. **Fig. 2.67**. Detail of terminal raphe fissures. **Fig. 2.68**. Detail of spines on raphe canal. **Fig. 2.69**. Detail of wing structure including spines and fenestrae.

Figs 2.70-2.74. *Surirella halteriformis*, Lake Matano. Scale bars = 50 μm (Figs 2.72) or 20 μm (Figs 2.70, 2.71, 2.73) or 2 μm (Fig. 2.74). **Figs 70, 71**. LM, Whole valves, Lectotype, Lake Matano, BRM # 2582, Slide# X5/43 (finder 438.4-7). **Figs 72-74**. SEM, Lake Towuti. **Fig. 2.72**. Whole valve, CANA# 71015. **Fig. 2.73**. Internal valve view, CANA# 71037. **Fig. 2.74**. Detail of ridged raphe fissure. Note lack of developed wing structure, CANA# 71015.

Figs 2.75-2.86. *S. horrida*, *S. leyana*, *S. pediculata* and *S. pseudovalis*. Scale bars = 20 µm (Figs 2.75, 2.78-2.82) or 10 µm (Figs 2.83-2.86) or 2 µm (Figs 2.76, 2.77).Figs 2.75-2.77. *Surirella leyana* sp. nov., SEM, Lake Towuti; CANA# 71251. **Fig. 2.75**. Whole valve,. **Fig. 2.76**. Detail of valve face spinules and raphe canal. **Fig. 2.77**. Detail of valve apex. **Figs 2.78-2.80**. *Surirella horrida*, LM. **Fig. 2.78**. Whole valve, Lectotype, Lake Matano BRM Slide X5/52, (single mount). **Fig. 2.79**. Whole valve, Isolectotype, Lake Matano BRM Slide X5/53 (single mount). **Fig. 2.80**. Whole valve, Isolectotype, Lake Matano BRM Slide X5/54 (single mounts). **Figs 2.81, 2.82**. *Surirella horrida* f. *constricta*, LM., Whole valve, Holotype, Lake Matano BRM Slide X5/54. **Fig. 2.83, 2.84**. *Surirella pseudovalis*, LM. **Fig. 83**. Whole valve, Isolectotype, Lake Towuti, BRM Slide X5/16. **Fig. 2.84**. Whole valve, Lectotype, Lake Towuti, BRM Slide X5/15. **Figs 2.85, 2.86**. *Surirella pediculata*, LM, whole valve, Holotype, Lake Matano, BRM Slide X5/45 (finder 313.1).

Figs 2.87-2.92. *Surirella papillifera*. Scale bars = 50 µm (Figs 2.87, 2.91, 2.92) or 10 µm (Fig. 2.88) or 5 µm (Figs 2.89, 2.90). **Figs. 2.87-2.90**. SEM, Lake Towuti, CANA# 71251. **Fig. 2.87**. Whole valve. **Fig. 2.88**. Detail of wing terminus and spines on wing. **Fig. 2.89**. Detail of spine diversity on valve face, wing, and median area; Also detail of fenestrae. **Fig. 2.90**. Detail of spines on valve face. **Figs 2.91, 2.92**. LM. Whole valve, Isolectotype Lake Matano, BRM Slide # X5/42.

Figs 2.93-2.98. *Surirella pinnigera* sp. nov. Scale bars = 20 µm (Figs 2.93, 2.94) or 10 µm (Fig 2.96) or 5 µm (Fig. 2.98) or 2 µm (Figs 2.95, 2.97). **Fig. 2.93**. SEM, Whole valve, Lake Towuti CANA# 70996. **Fig. 2.94**. LM, whole valve, Holotype, Lake Towuti CANA# 71037. **Figs 2.95-2.98**. SEM, Lake Towutii, CANA # 71037. **Fig. 95**. Detail of termina raphe fissures. **Fig. 2.96**. Detail of directional spine on median area. **Fig. 2.97**. Detail of spinnules on valve face and alar canals. **Fig. 2.98**. Detail of directional spine and fenestrae.

Figs 2.99-2.104. *Surirella promontorium* sp. nov., SEM, Lake Towuti, CANA# 71222. Scale bars = 20 µm (Fig. 2.99) or 10 µm (Figs 2.102) or 5 µm (Fig. 2.101, 2.103) or 2 µm (Figs 2.100, 2.104). **Fig. 2.99**. Whole valve. **Fig. 2.100**. Detail of terminal raphe fisures. **Fig. 2.101**. Showing height of elevated median area above valve face. **Fig. 2.102**. Detail of tubes at junction of alar canals and porca. **Fig. 2.103**. Detail of mantle area and raphe fissure. **Fig. 2.104**. Detail of valve face and tubes.

Figs 2.105-2.110. *Surirella quadridentis* sp. nov., Lake Twouti, SEM. Scale bars = 10 µm (Figs 2.105, 2.106) or 5 µm (Fig. 2.107) or 2 µm (Figs 2.108-2.110). **Figs 2.105, 2.106**. Whole valve. **Fig. 2.107**. Detail of raphe fissure and mantle area. **Fig. 2.108**. Detail of areolae and fenestrae, CANA # 70996. **Fig. 2.109**. *Surirella quadridentis,* cross section of raphe canal, CANA# (WP-108). **Fig. 2.110**. Detail of large spines on valve face, CANA # 70996.

Figs 2.111-2.113. *Surirella rugosa* nov. sp., SEM, Lake Towuti, CANA# 71037. Scale bars = 20 μm (Fig. 2.111) or 5 μm (Fig. 2.113) or 2 μm (Fig. 2.112). **Fig. 2.111**. Whole valve. **Fig. 2.112**. Detail of elevated median area and valve face. **Fig. 2.113**. Detail of terminal raphe fissures and wing terminus.

Figs 2.114-2.118. *Surirella sublinearis* and *Surirella sublinearis* var. *suggesta* nov. var., SEM. Scale bars = 20 μm (Figs 2.114, 2.115) or 10 μm (Figs 2.116) or 5 μm (Figs 2.117, 2.118). **Fig. 2.114**. *Surirella sublinearis*, whole valve, Lake Towuti, CANA# 71037. **Fig. 2.115**. LM, whole valve, Lake Matano, Lectotype, BRM Slide 397/38. **Figs 2.116-2.118**. *Surirella sublinearis* var. *suggesta*, Lake Towuti. **Fig. 2.116**. Attached to another diatom frustule. **Fig. 2.117**. Detail of fenestrae amd siliceous tendrils attached to another diatom frustule. **Fig. 2.118**. Detail of wing termina and siliceous tendrils, CANA# 71037.

Figs 2.119-2.124. *Surirella tenacis* nov. sp.. Scale bars = 20 μm (Figs 2.119, 2.120, 2.124) or 5μm (Figs 2.121, 2.122) or 2μm (Figs 2.123). **Figs 2.119-2.123**. SEM, Lake Towuti. **Fig. 2.119**. Whole valve. **Fig. 2.120**. Frustule attached to an inorganic substrate particle. **Fig. 2.121**. Detail of terminal raphe endings and siliceous tendrils. **Fig. 2.122**. Detail of siliceous tendrils attached to an inorganic substrate particle. **Fig. 2.123**. Detail of tubular processes on median area, CANA# 71037. **Fig. 2.124**. LM, whole valve, Lake Matano, BRM # 2582, Slide # 397/48.

Figs 2.125-, 2.132. *Surirella rudis* var. *levis*, *S. robusta* var. *splendida* f. *punctata*, *S. sulcata*, *S. thienemannii*, *Surirella tortilis* and *S. ventricosa*. Scale bars = 50 µm (Figs 2.1125, 2.128) or 20 µm (Figs 2.126, 2.127, 2.129, 2.131) or 10 µm (Figs 2.130, 2.132). **Fig. 2.125**. LM, *Surirella rudis* var. *levis*, Holotype, Lake Matano, BRM Slide X5/42 (finder 497.9). **Figs 2.126, 2.127**. LM, Surirella *thienemannii*, whole valves. **Fig. 2.128**. LM, *Surirella robusta* var. *splendida* f. *punctata*, whole valve, Lake Towuti, Type material. **Fig. 2.129**. LM , *Surirella sulcata*, Holotype, Lake Towuti, BRM Slide X1/76, (finder 405.5-6). **Fig. 2.130**. LM, *Surirella ventricosa*, whole valve, Lectotype, Lake Towuti, BRM Slide 397/35 (finder 585.7). **Figs 2.131-2.132**. SEM, *Surirella tortilis* nov. sp. Lake Towutii; CANA# 70996.

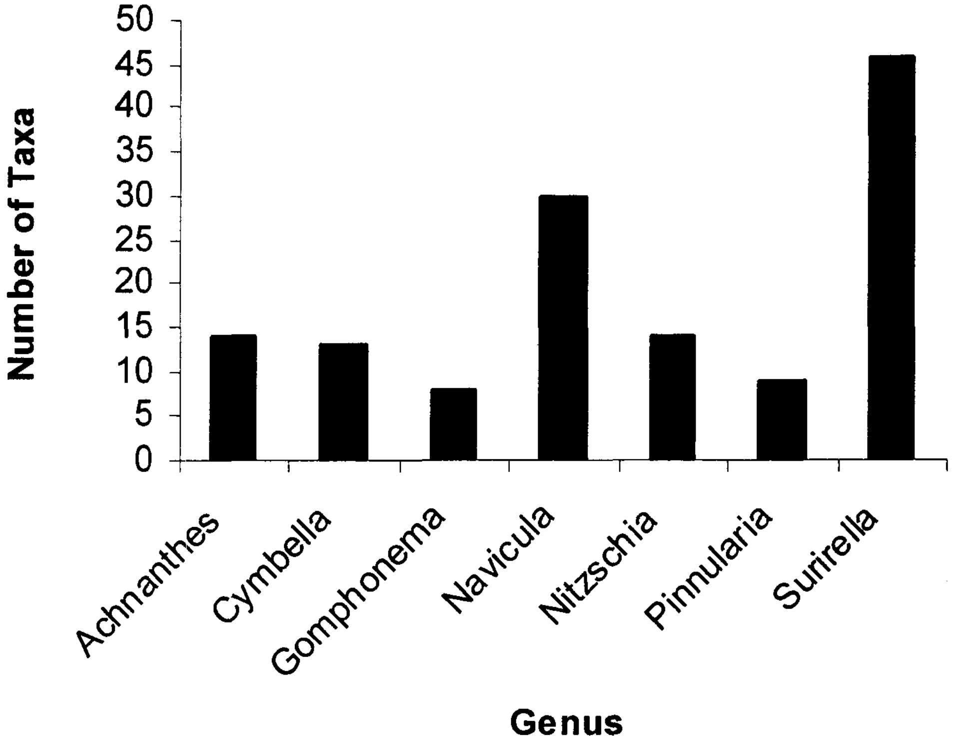
Figs 2.133-2.138. *Surirella tubicola* nov. sp. Scale bars = 50 (Figs 2.133, 2.134) or 20 µm (Figs 2.136, 2.138) or 10 µm (Fig. 2.135) or 2 µm (Fig. 2.137). **Figs 2.133, 2.134**. LM, whole valve, Holotype, Lake Towuti, CANA# 71037. **Figs 2.135-2.138**: SEMs from type material of *Surirella tubicola*. **Fig 2.135**. External view highlighting apex and tubes along median area. **Fig. 2.136**. fractured valve showing valve surface and wing formations. **Fig. 2.137**. Keel on wing with raphe on an extended ridge. Tube-spines on alar canal. **Fig. 2.138**. Whole valve showing girdle bands.

Figs 2.139-2.144. *Surirella woltereckii*. Scale bars = 20 µm (Figs 2.139-2.142) or 10 µm (Fig. 2.144) or 5 µm (Fig. 2.143). **Fig. 2.139**. LM, whole valve, Lectotype, Lake Towuti

BRM # 2581, Slide # X5/18. **Fig. 2.140**. LM, whole valve, Isolectotype, Lake Towuti, BRM Slide X5/19. **Figs 2.141-2.144**. SEM micrographs of *Surirella woltereckii*, CANA # 70852, # 71015. **Fig. 2.141**. Whole valve, external view Lake Matano. **Fig. 2.142**. Whole valve, internal valve view. **Fig. 2.143**. Detail of mantle area, terminal raphe endings, and fenestrae. **Fig. 2.144**. Detail of terminal raphe endings.

Fig. 2.145. Heirarchical clustering tree of 68 individuals representing 26 taxa within the genus *Surirella* and two outgroup taxa, *Cymbella woltereckii* and *Nitzschia woltereckii* from the Malili Lakes. Major groups of individuals are demarcated by numbers between horizontal bars. Group 1 contains individuals sharing a very large valve size and an absence of spines, spicules, or tubular processes. Taxa within group 2 have several median area fin-spines and the raphe fissure lies on an elevated ridge. Taxa within group 3 are ovoid to ovoid-elliptical in shape, with torsioned valves. Group 3a contains smaller, more elliptically shaped individuals, often with moderately sized spines on the valve face. Group 3b contains larger, more ovoid individuals with finer valve face ornamentations. Individuals within group 4 are moderately to highly constricted at the centre of the valve. Group 5 contains taxa with a linear-elliptical shape, may have small spinules on the valve face, and a raphe fissure that is not situated upon a ridge. Individuals in group 6 share a linear shape, small spinnules on the valve face, and siliceous tendrils at the base of the alar canals. Individuals in group 7 are similar, but lack tendrils. Group 8 contains only *S. tubicola*, which is characterised by its heteropolar, linear-elliptical shape, ridged raphe fissure, and the presence of many small hollow tubules on the valve face, median area, and alar canals. Group 9 consists of the two outgroup pennate diatoms, *Nitzschia*

woltereckii and *Cymbella woltereckii*



Number of Taxa
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40
35
30
25
20
15
10
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Cymbella
Gomphonema
Navicula
Nitzschia
Pinnularia
Surirella
Genus

Figure 2.1

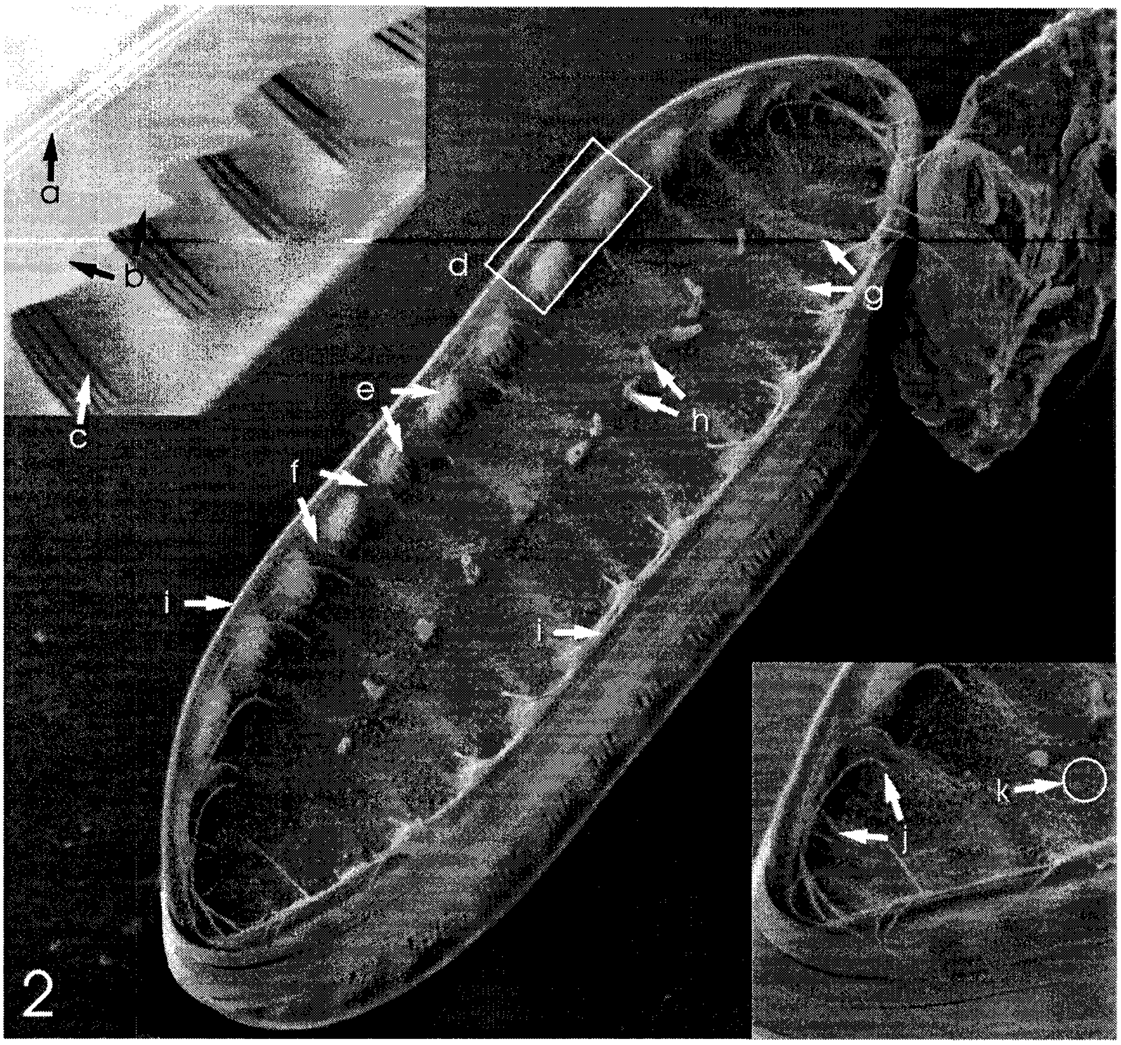
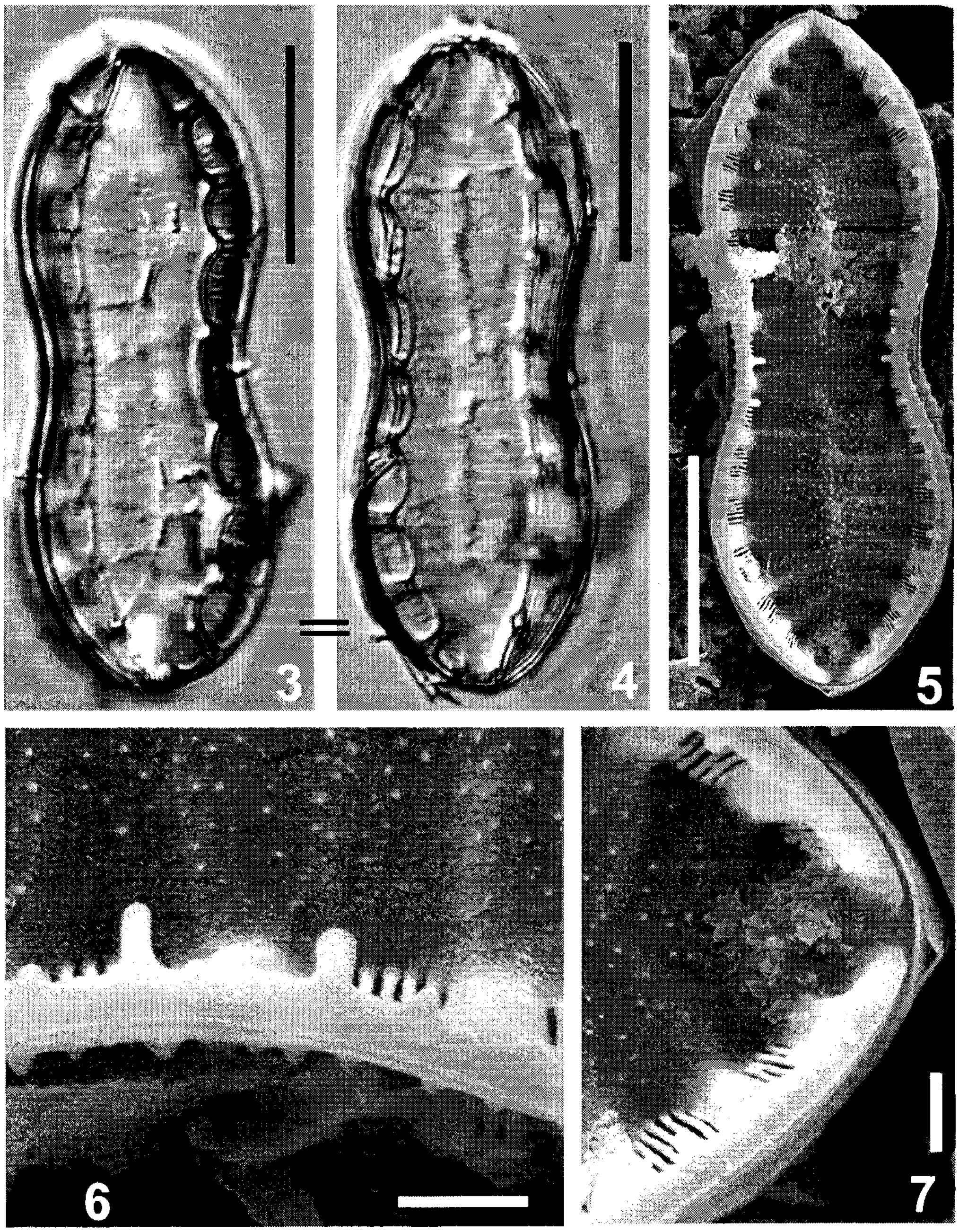
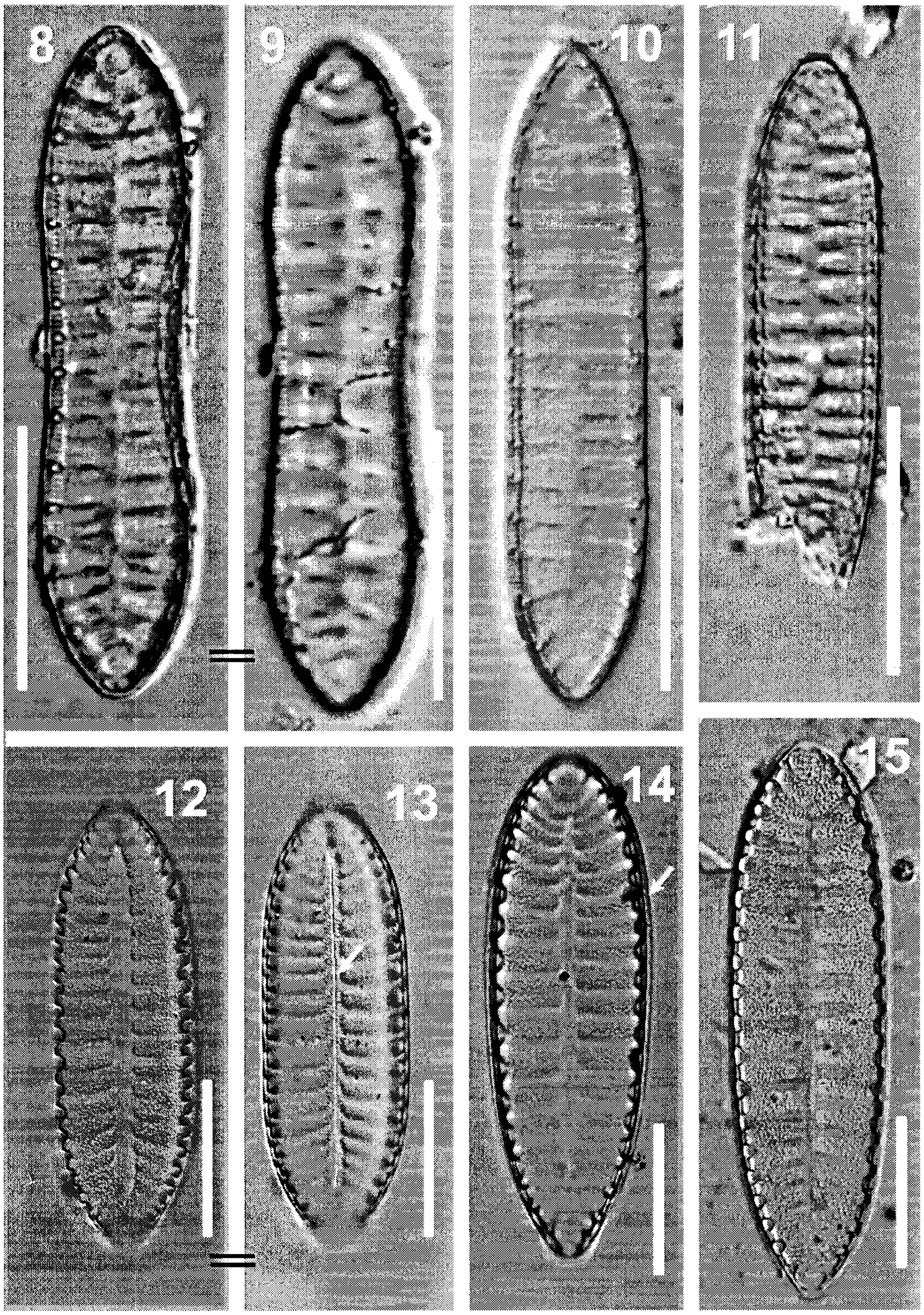


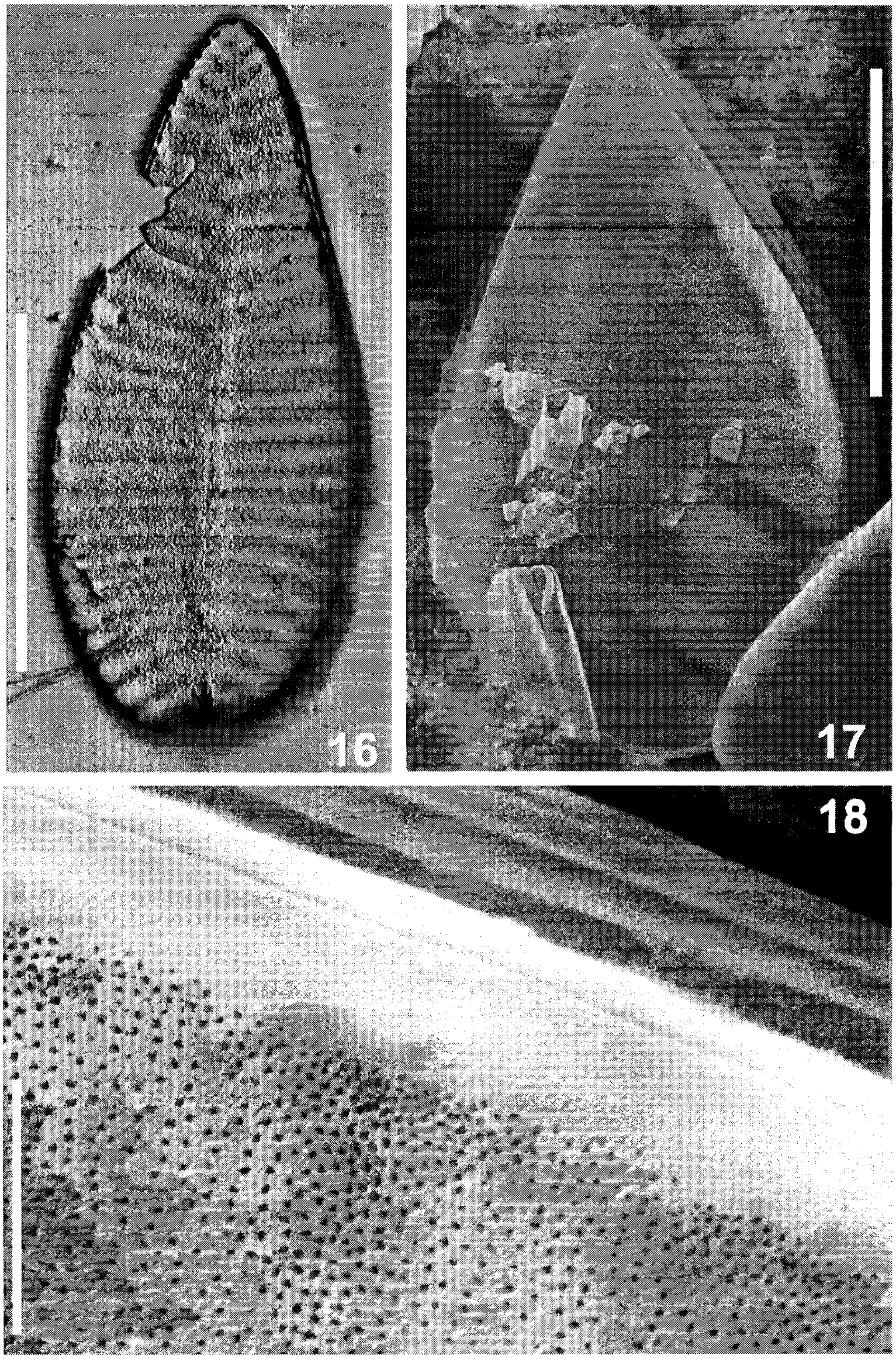
Figure 2.2



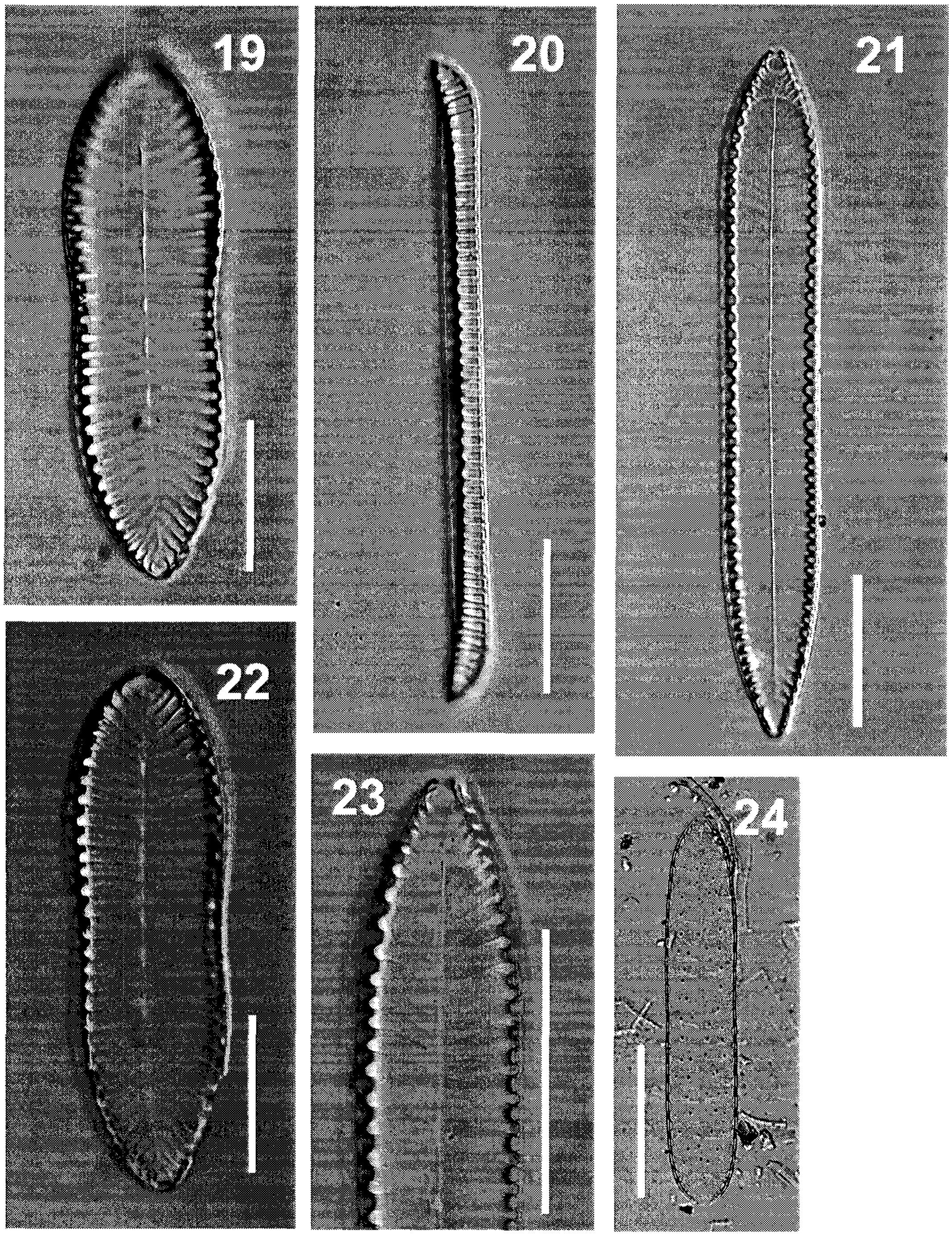
Figures 2.3 – 2.7



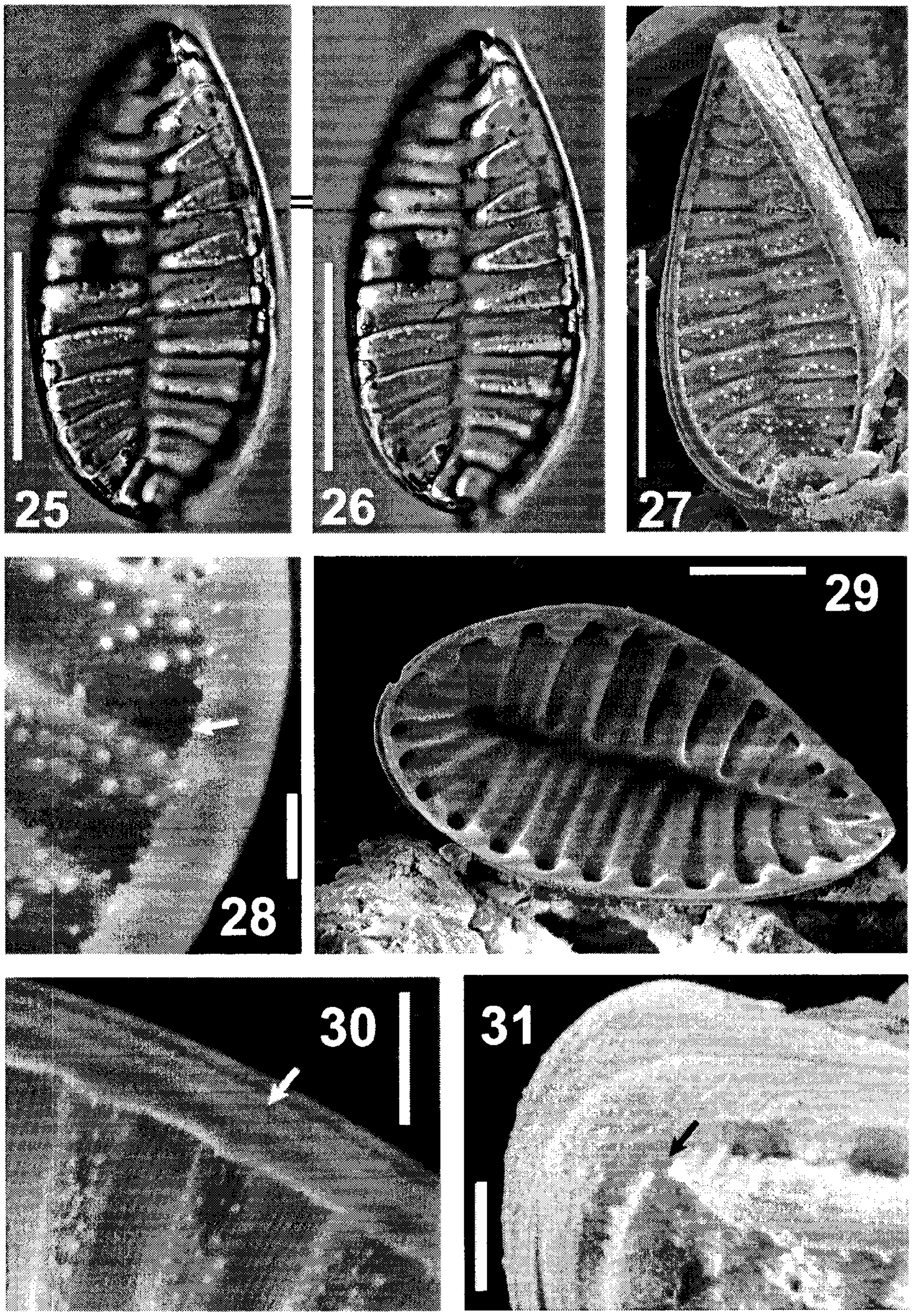
Figures 2.8 – 2.15



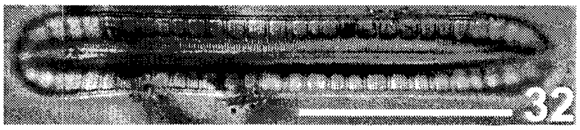
Figures 2.16 – 2.18



Figures 2.19 – 2.24



Figures 2.25 – 2.31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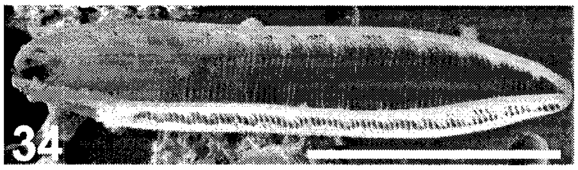
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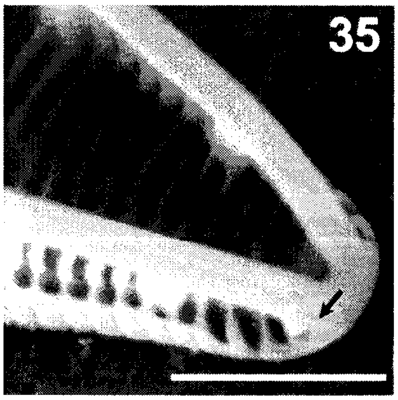
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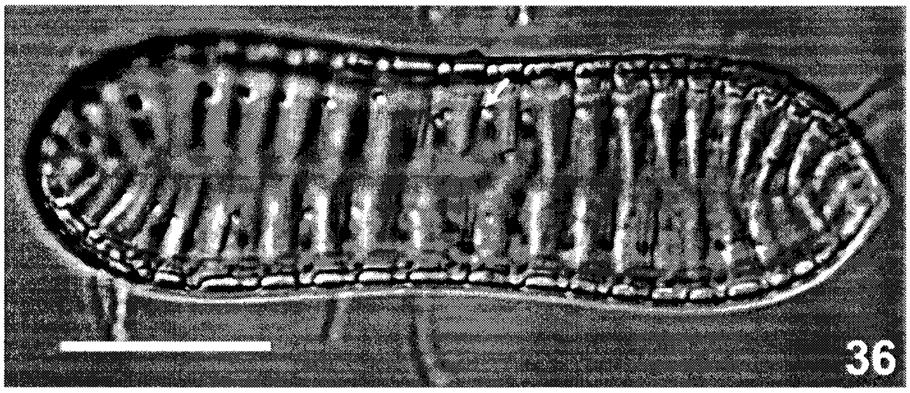
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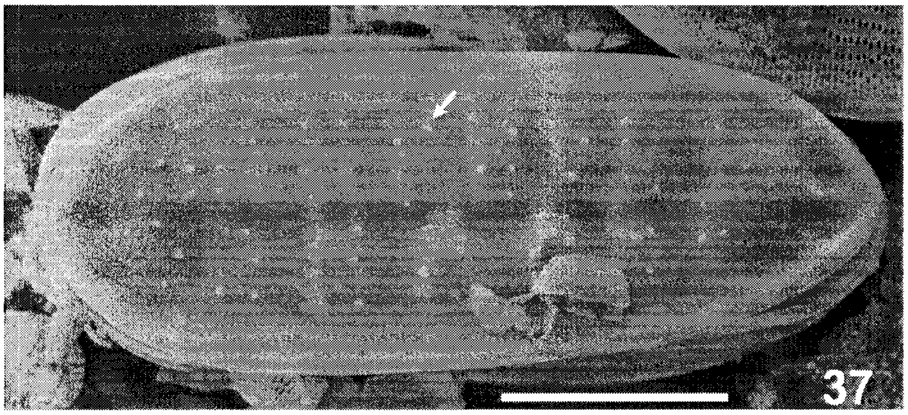
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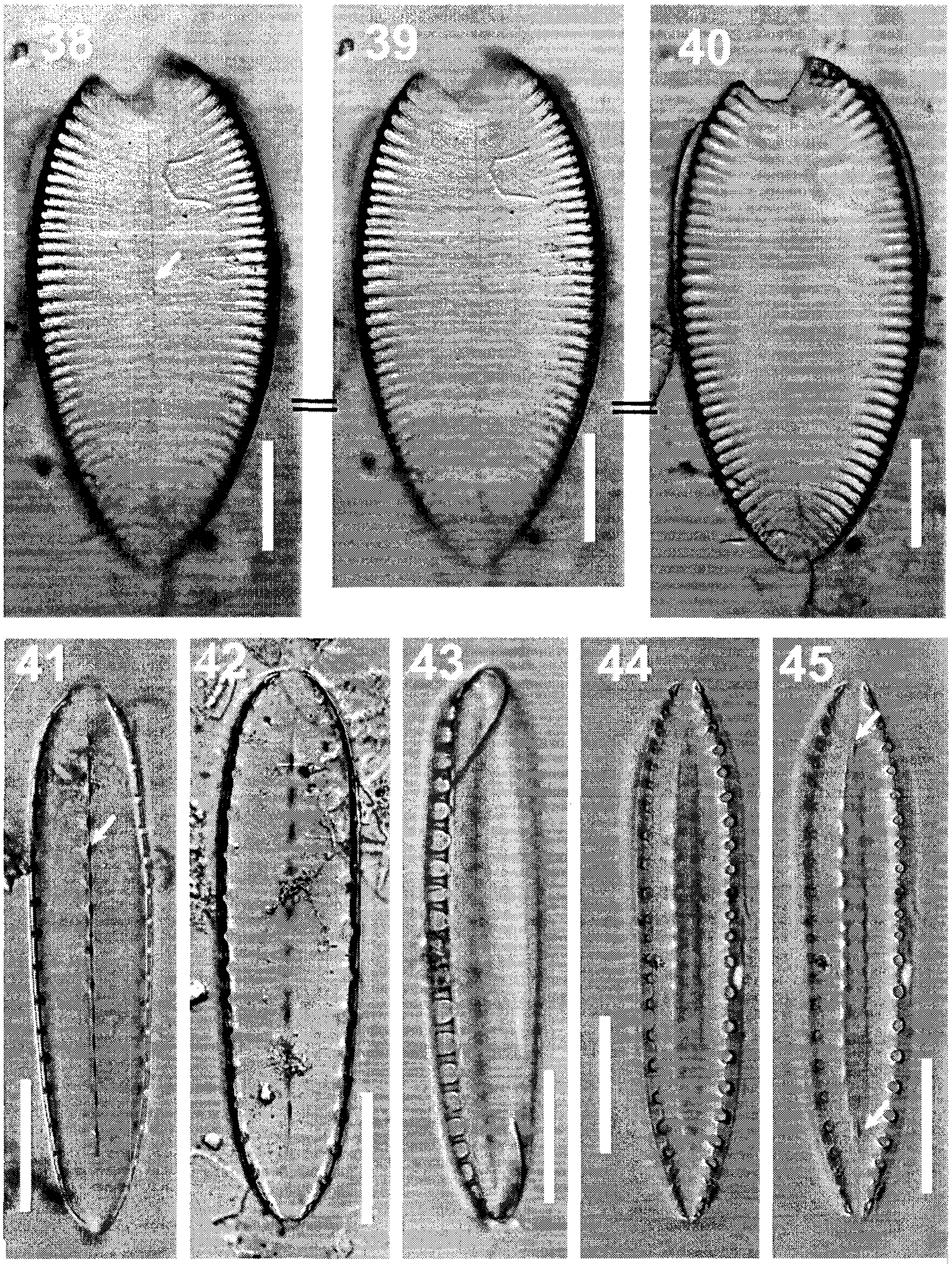
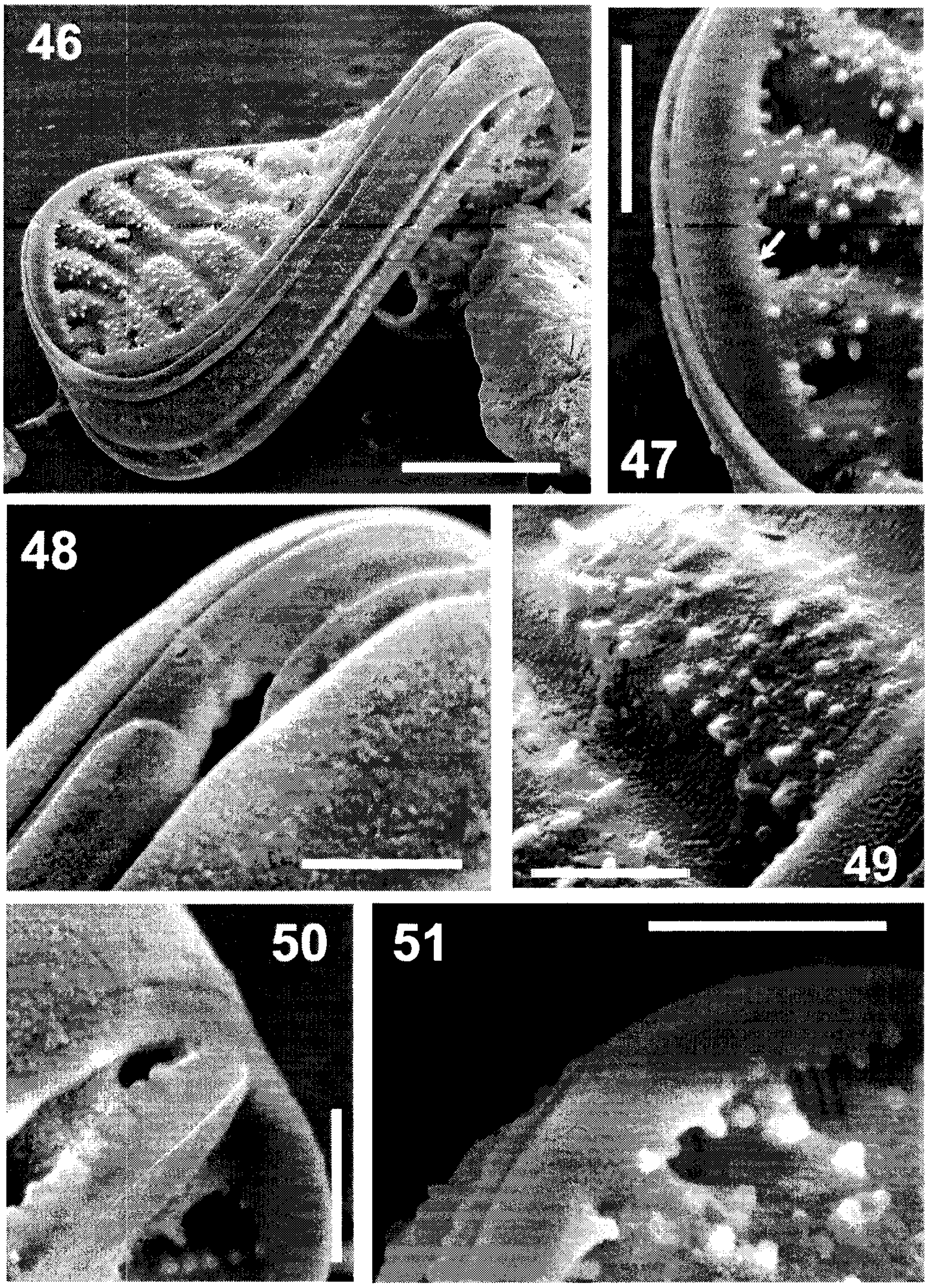
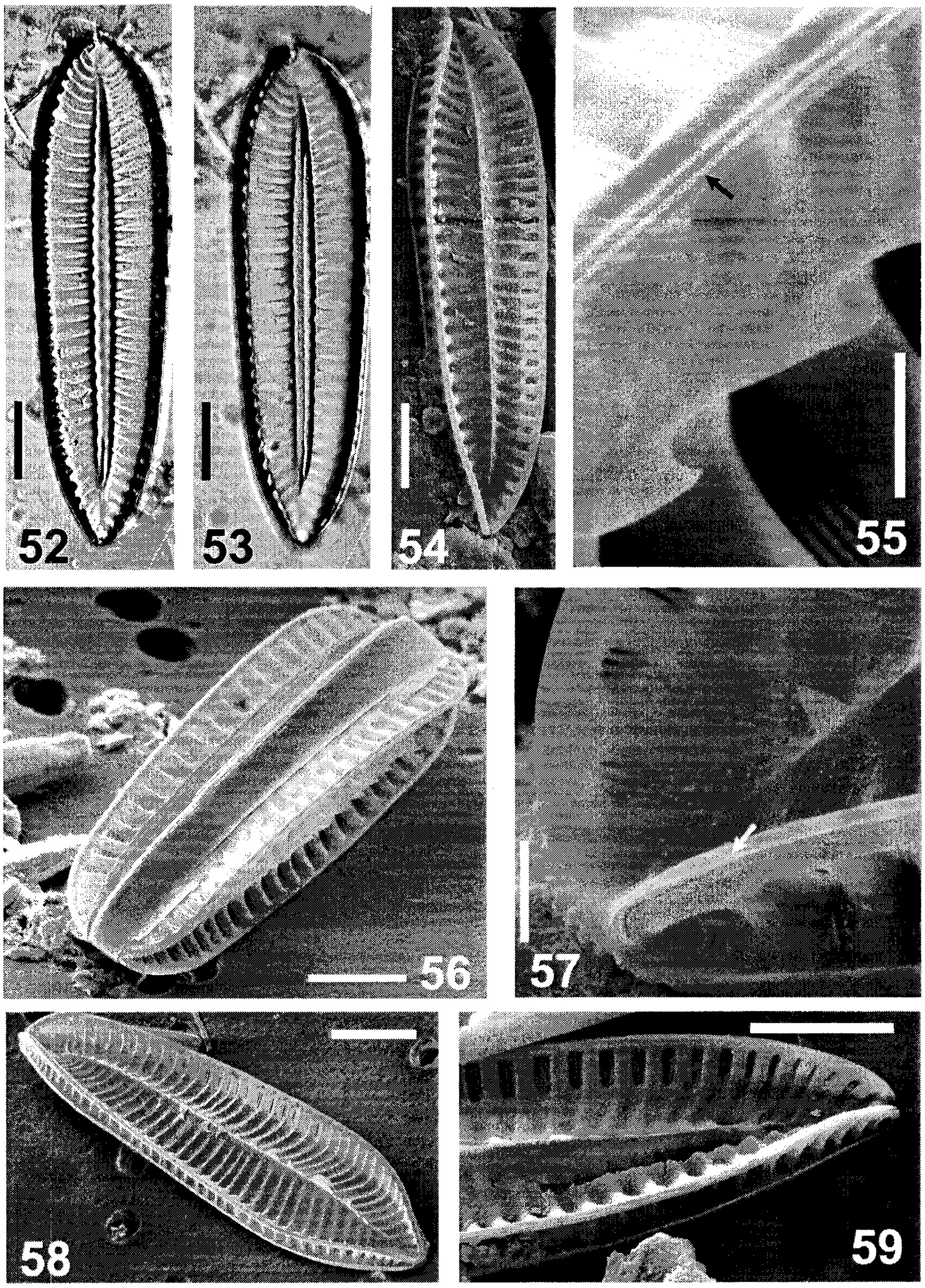


Figures 2.38 – 2.45



Figures 2.46 – 2.51



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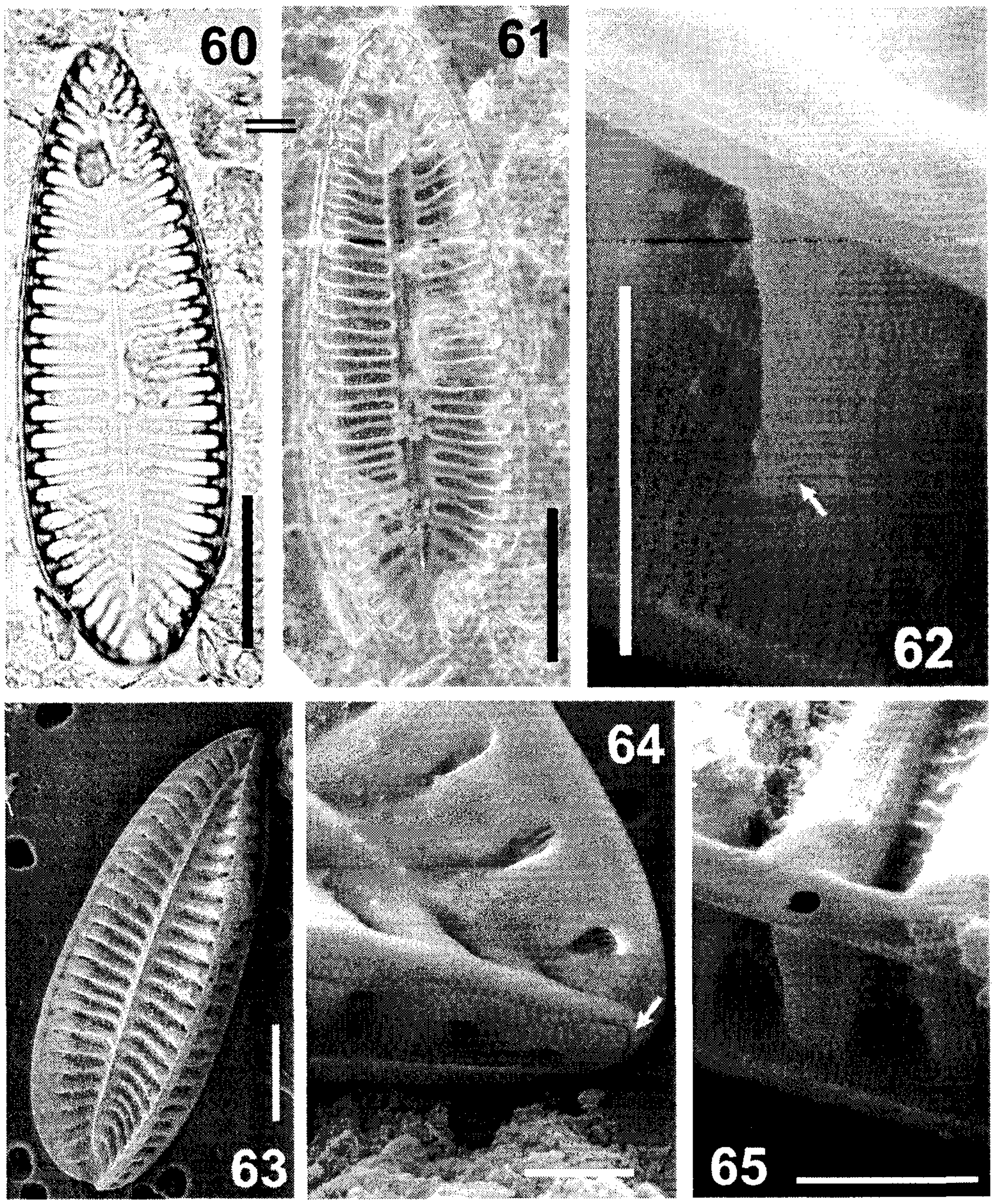

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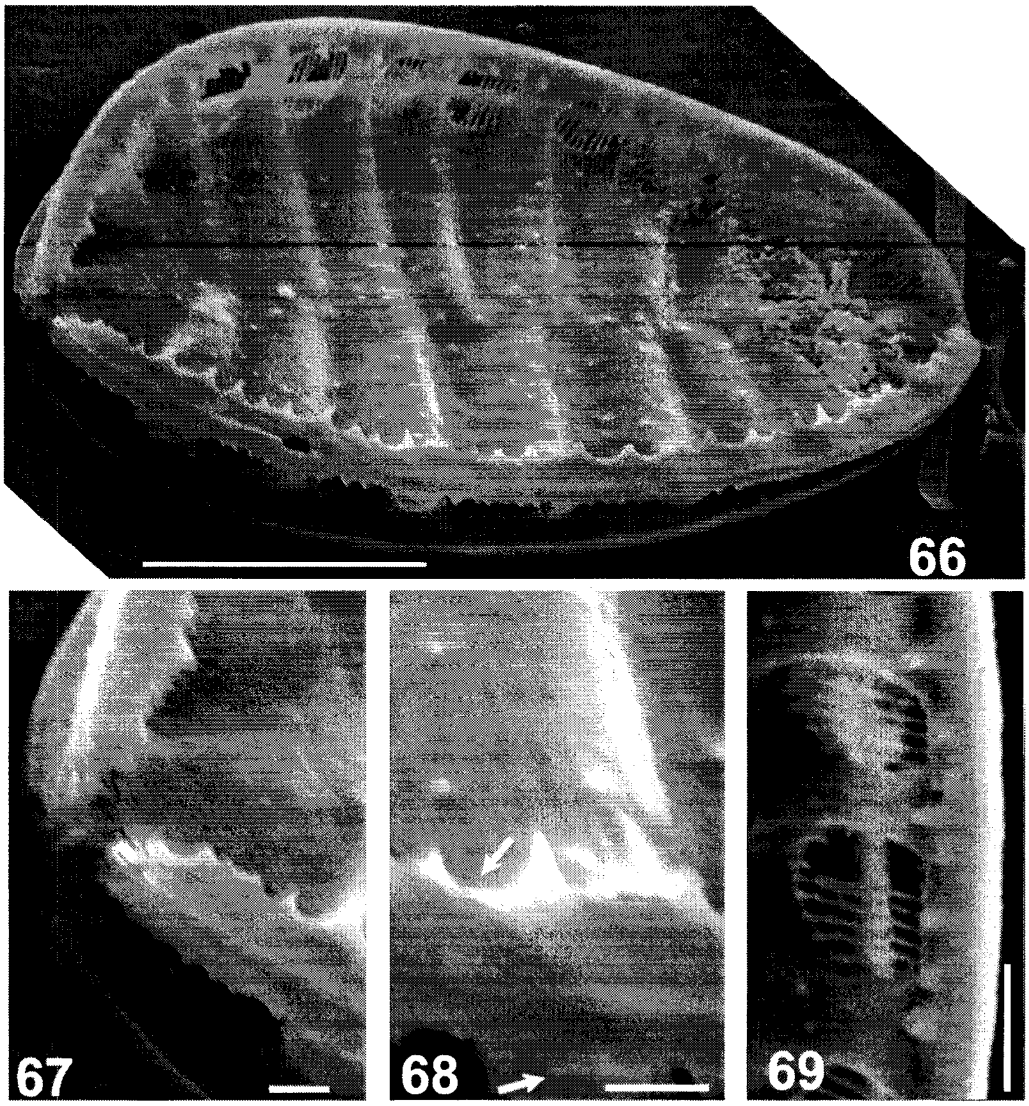

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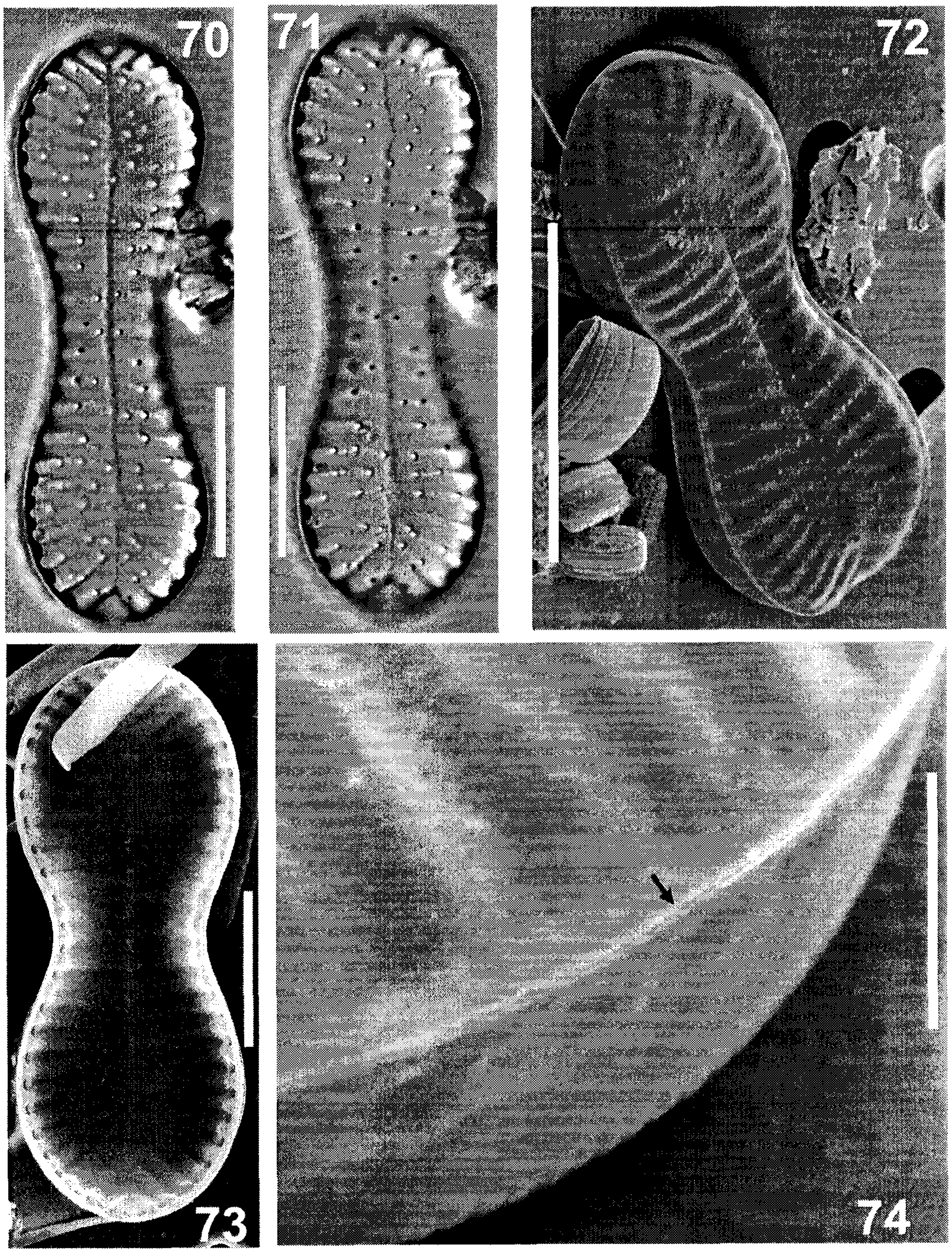

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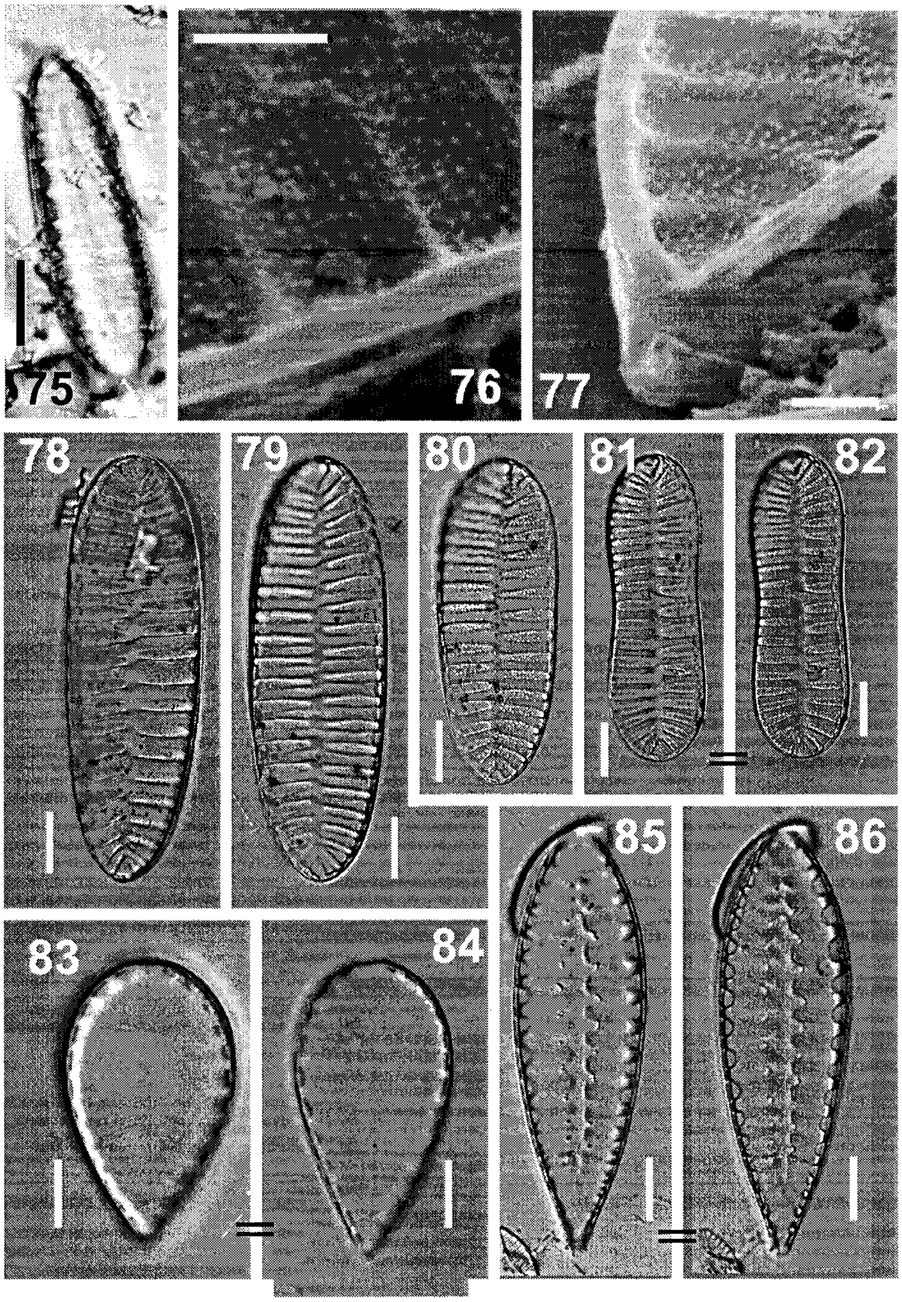

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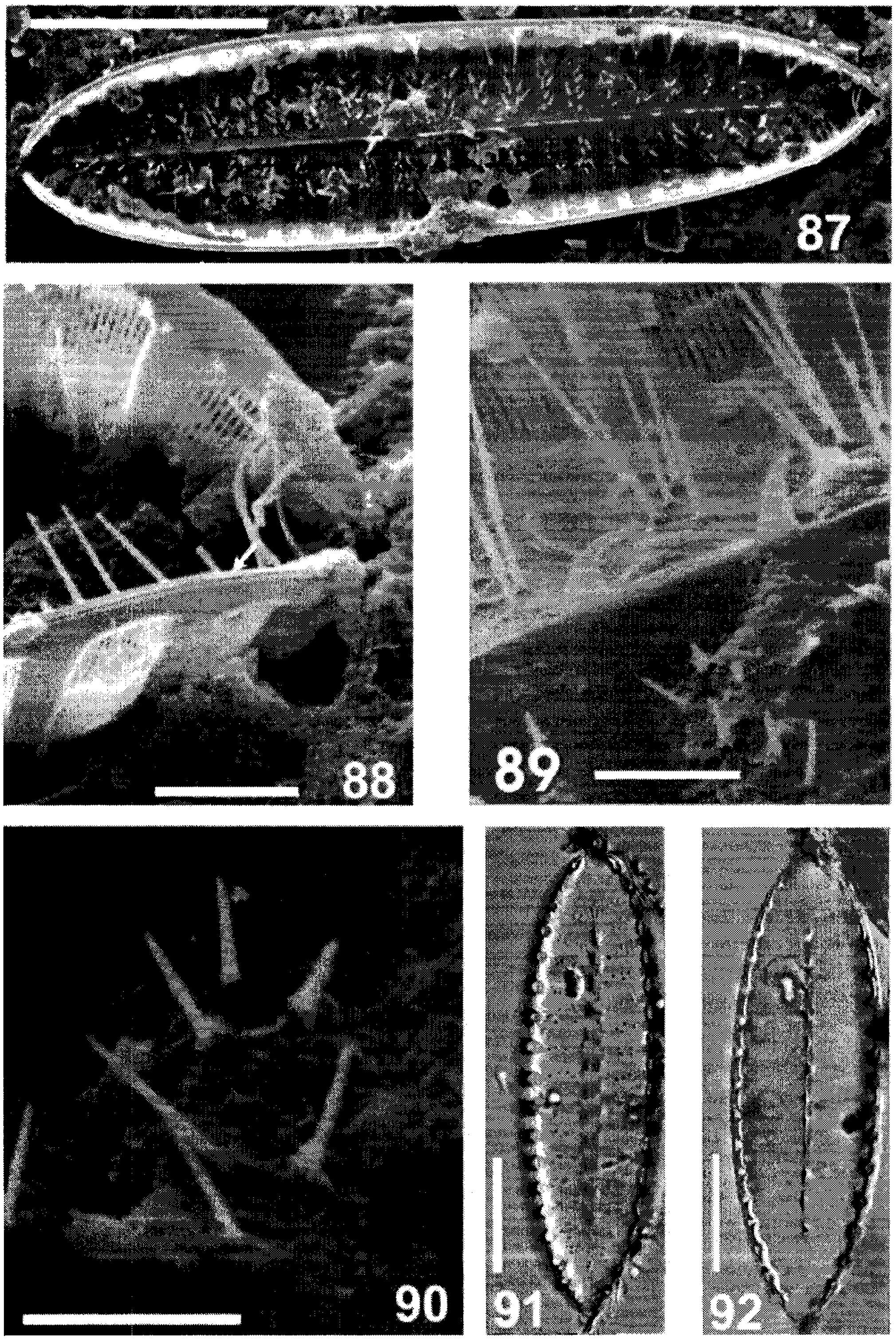

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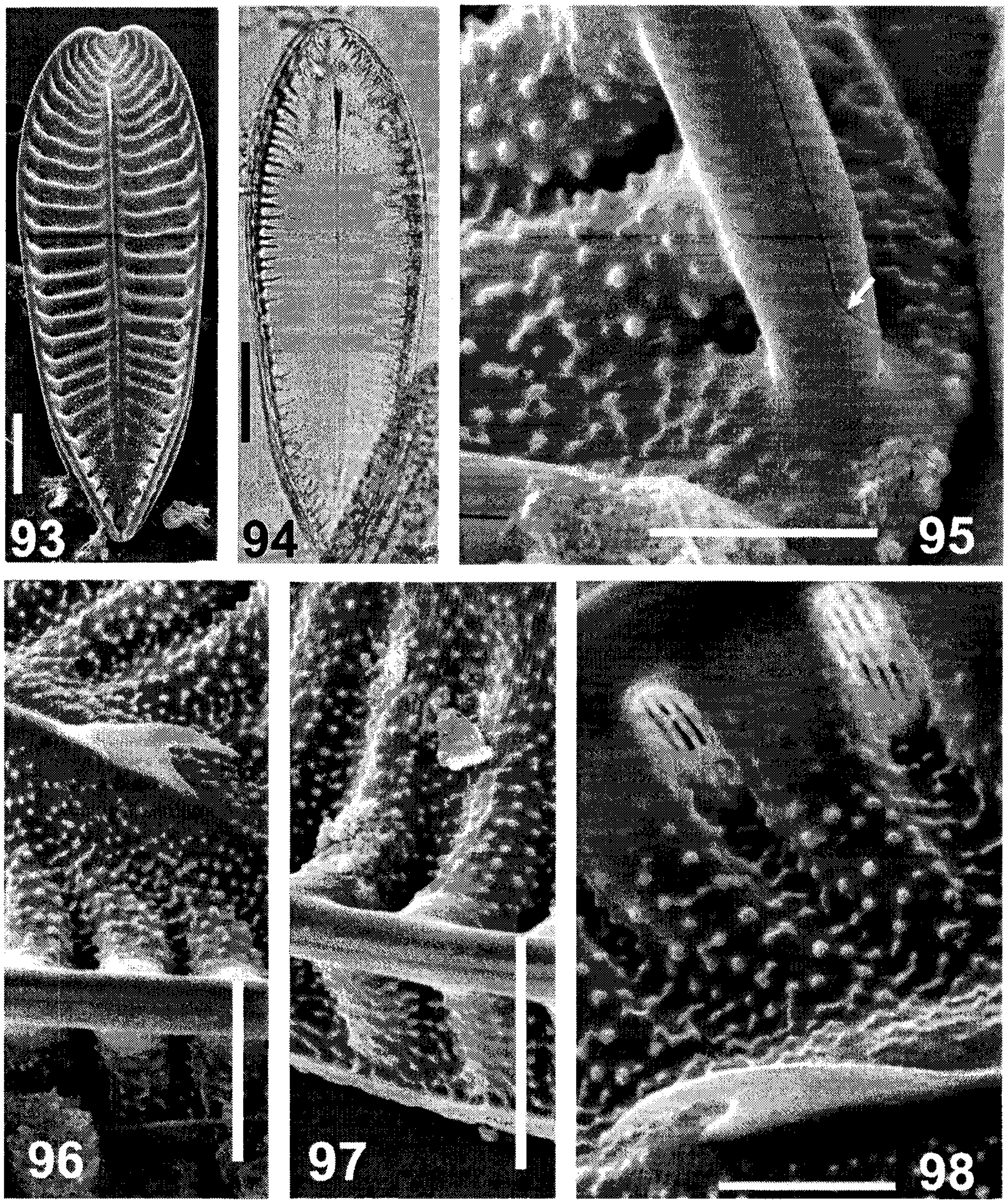

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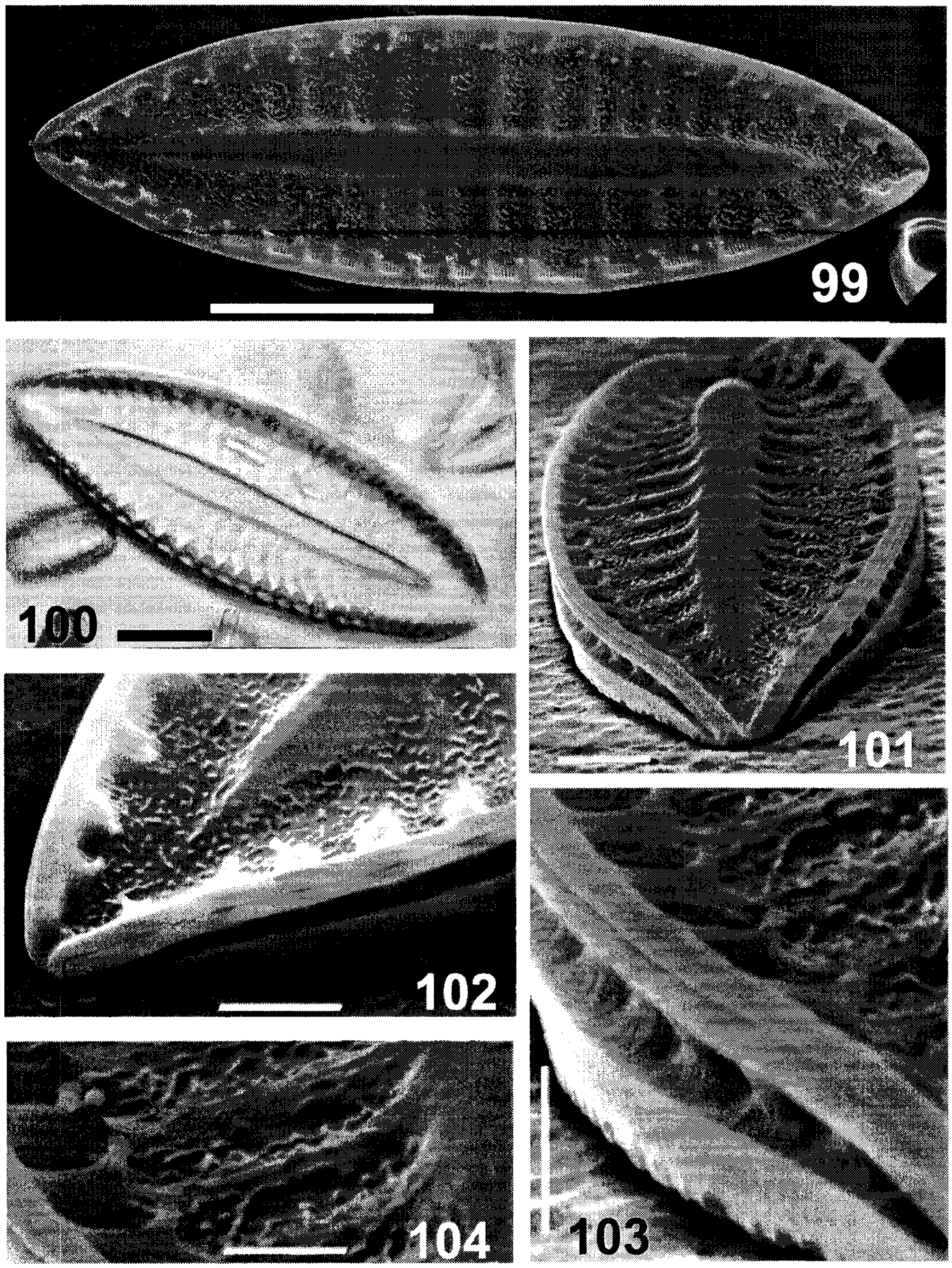

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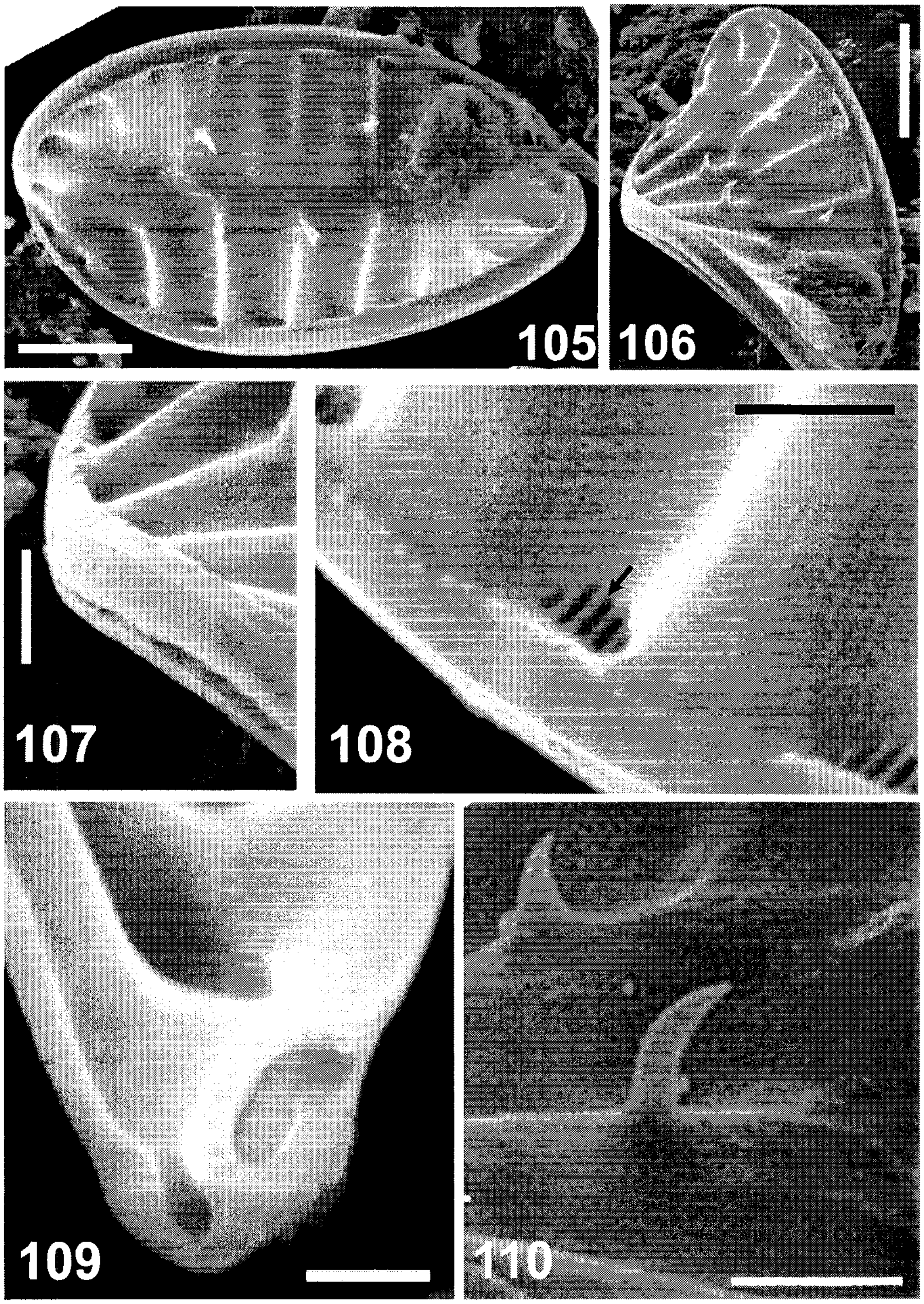

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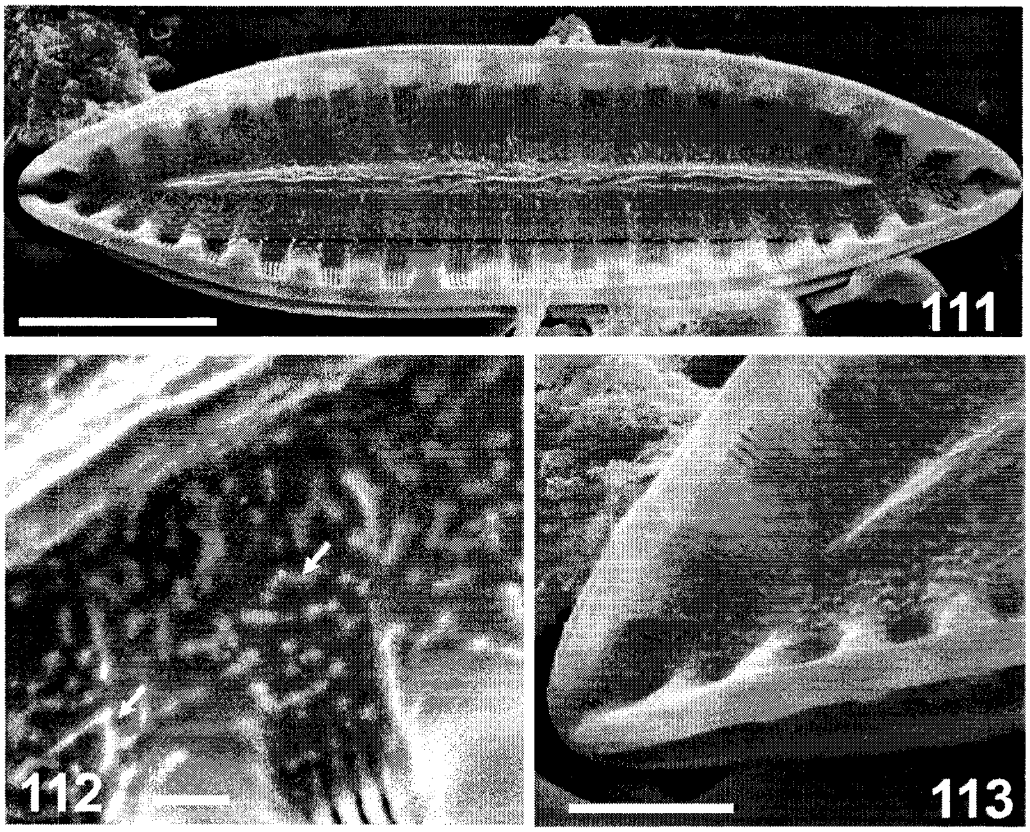

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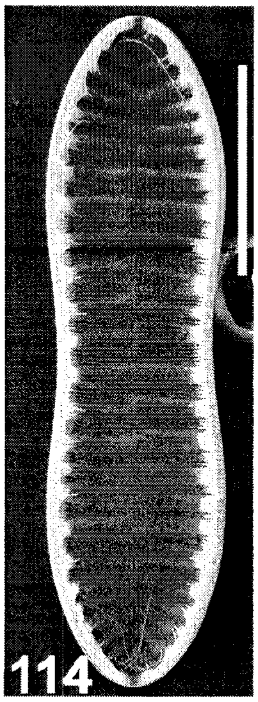
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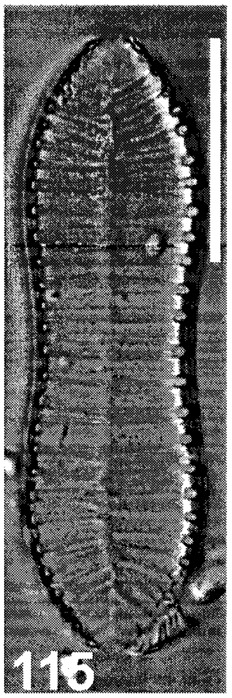
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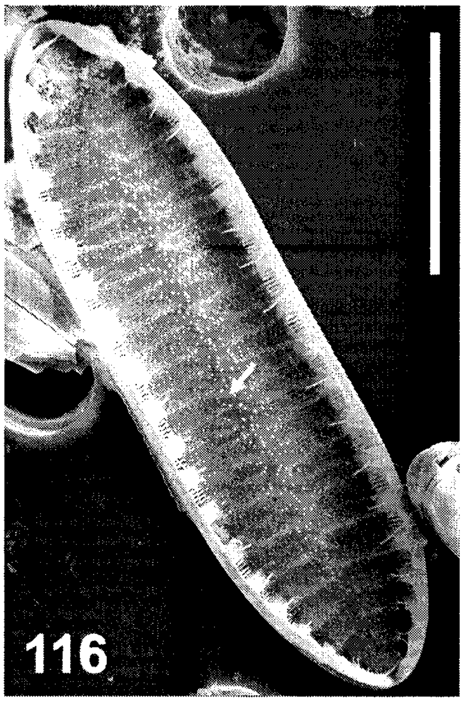
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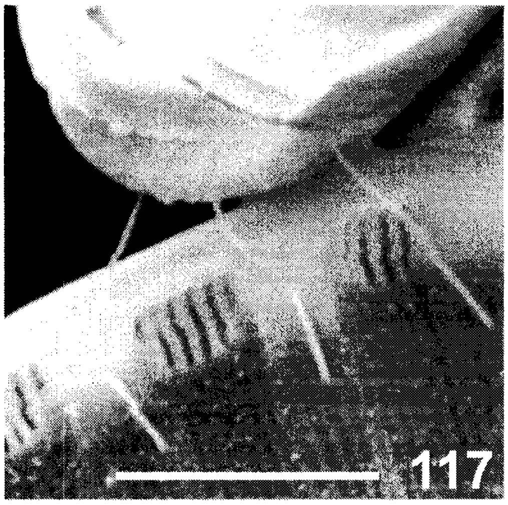
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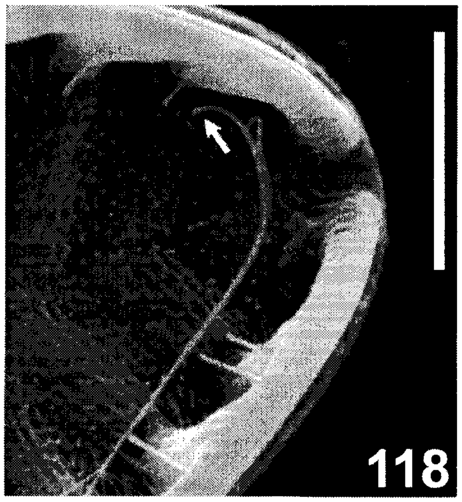
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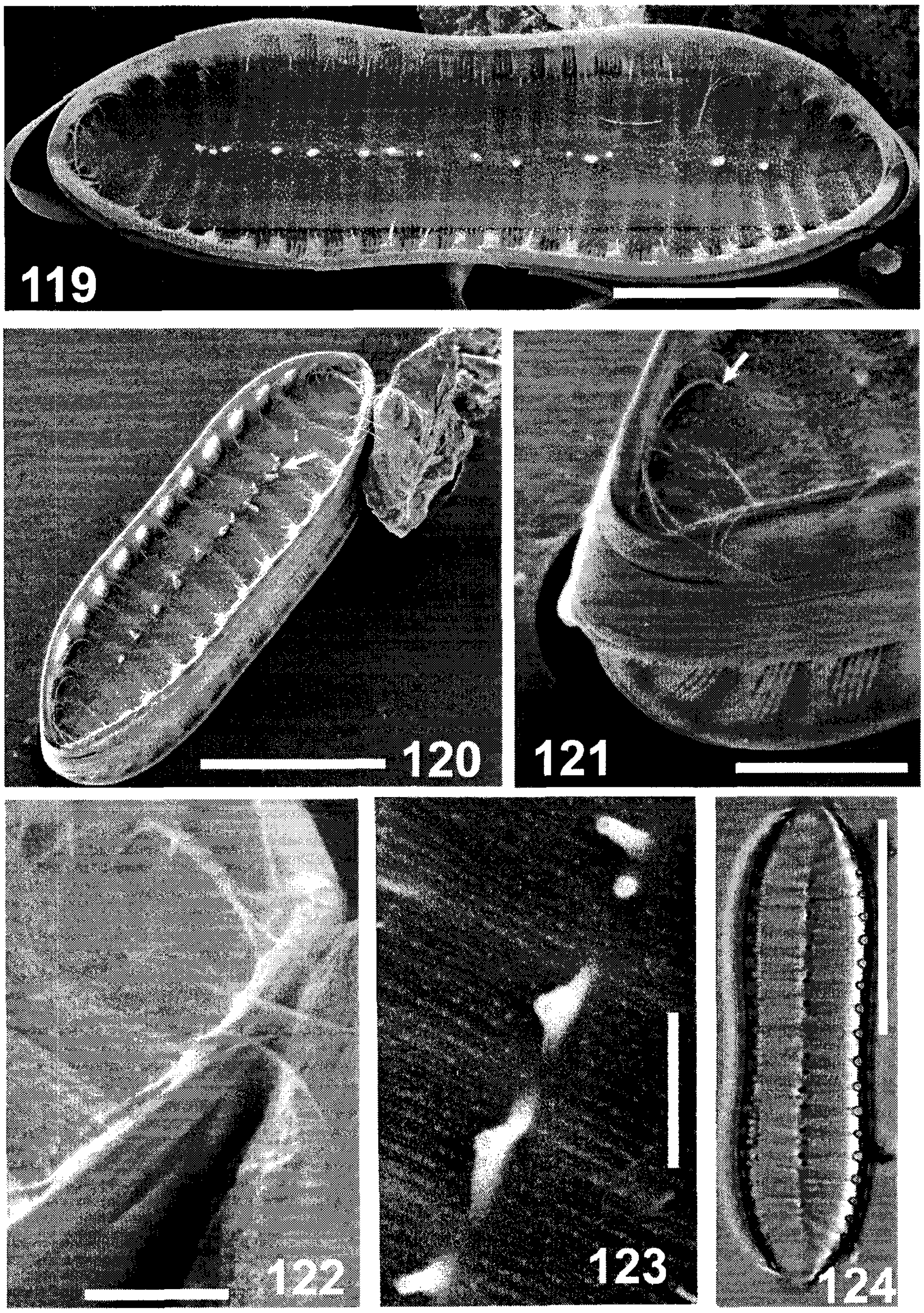
Figures 2.114 – 2.118



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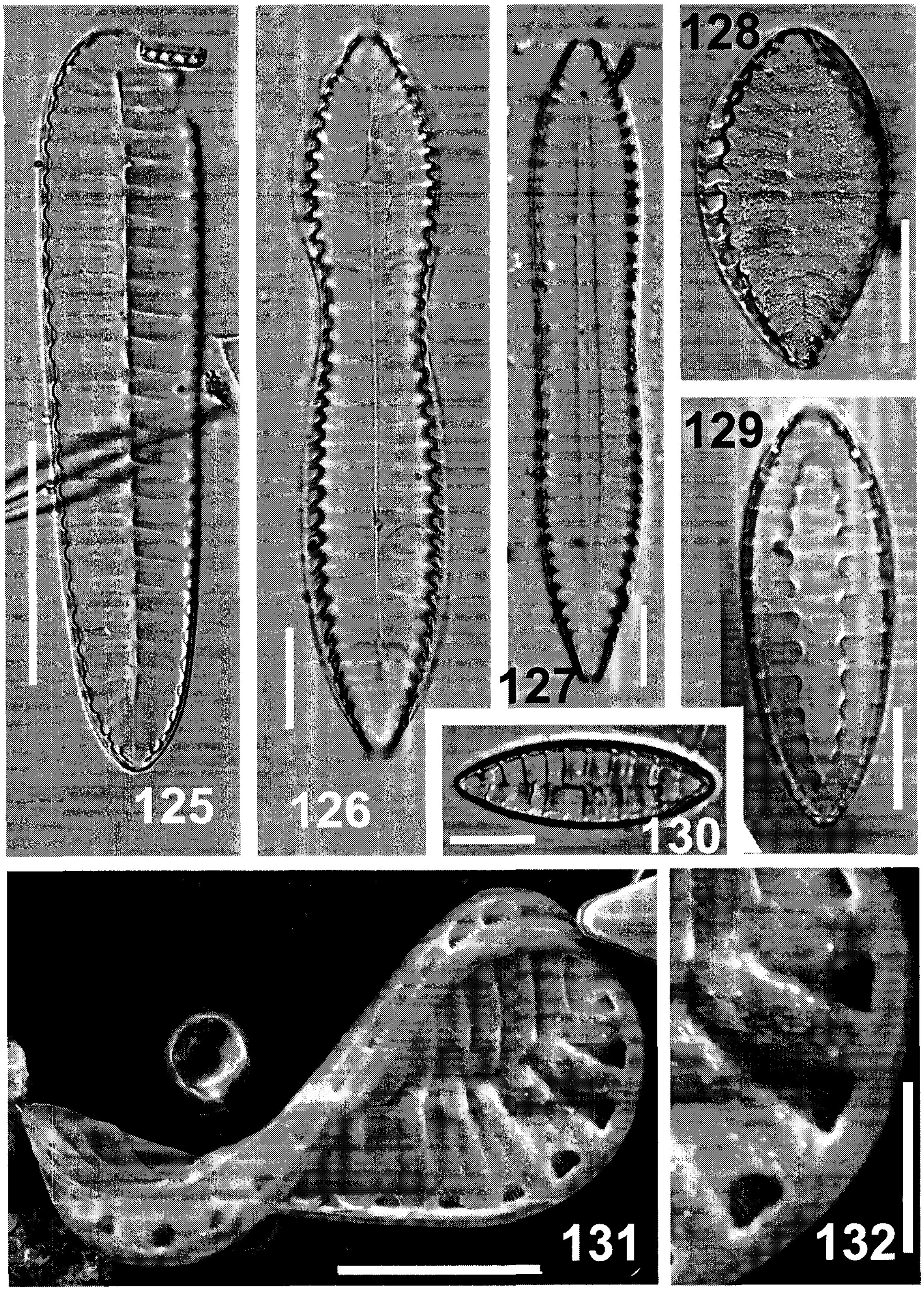

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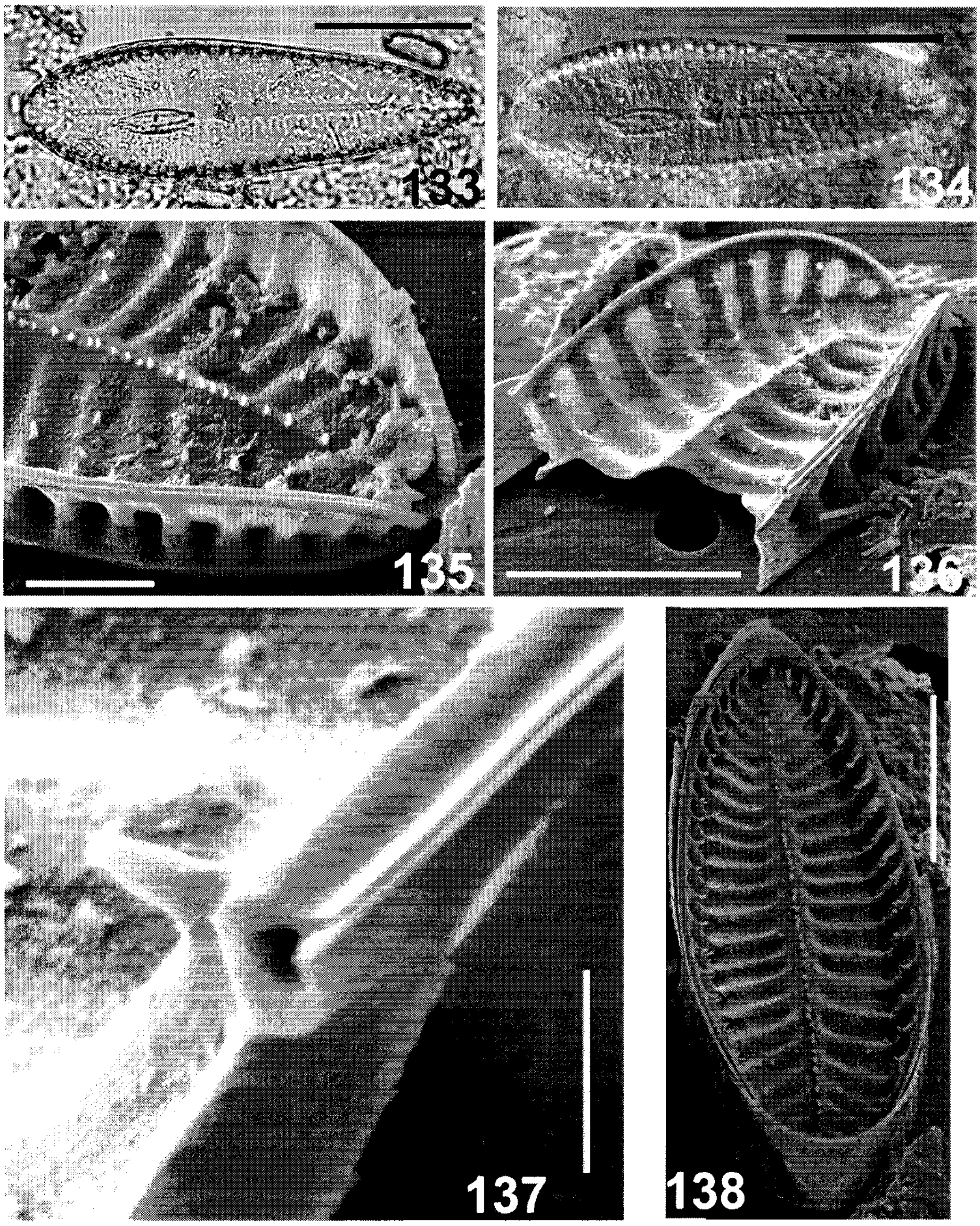

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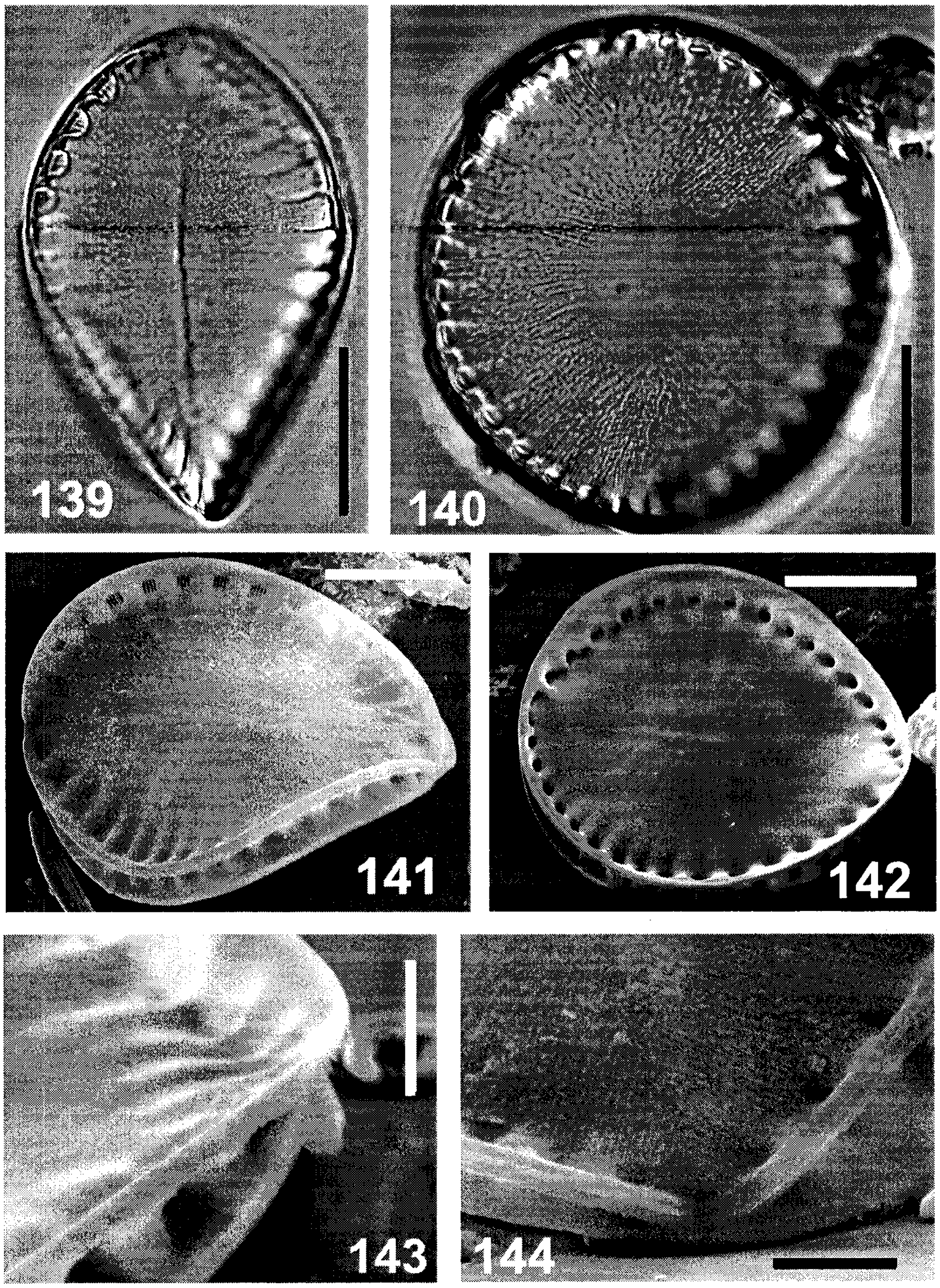

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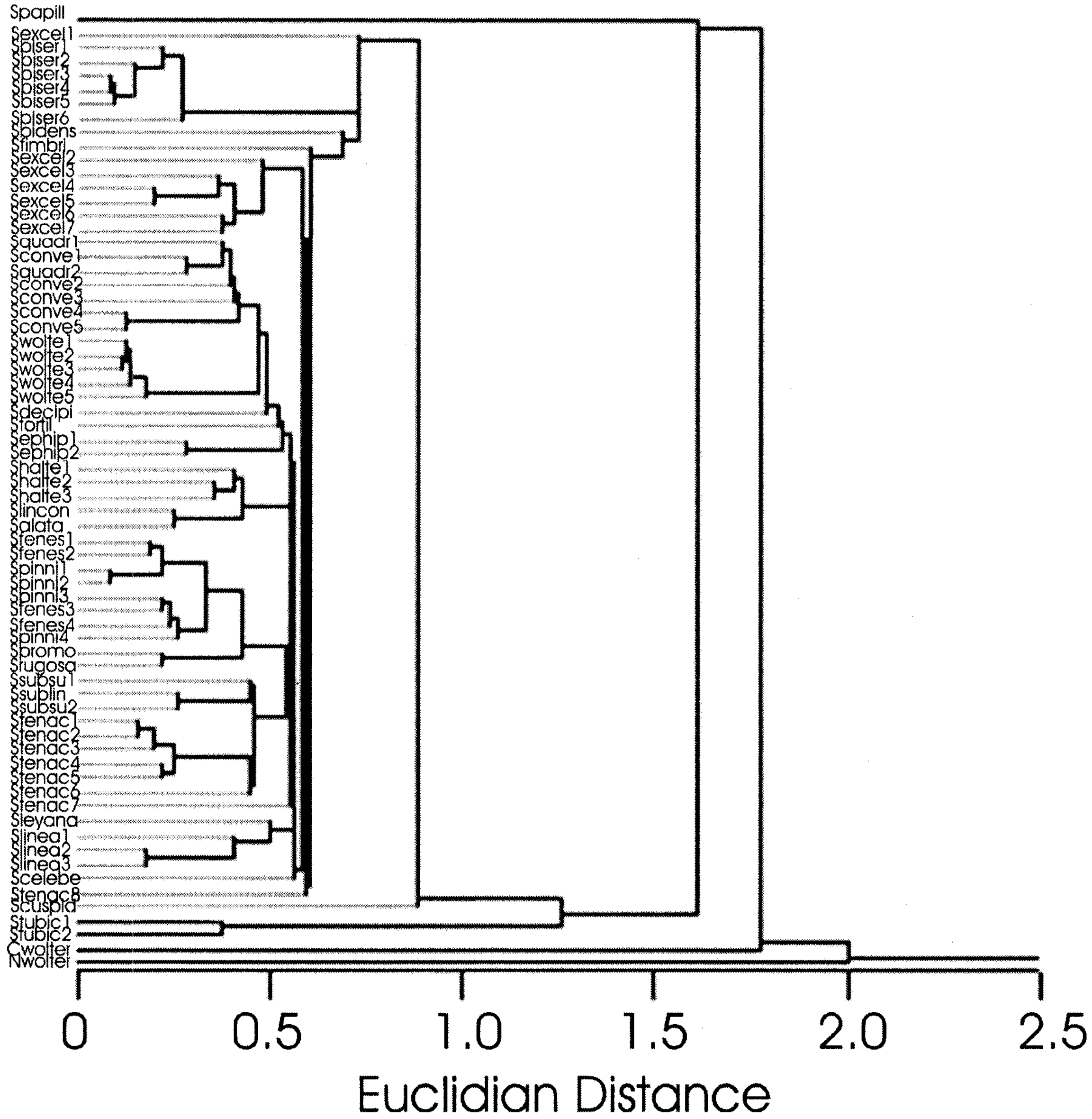
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Slincon
Salata
Sfenes1
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Spromo
Srugosa
Ssubsu1
Ssublin
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Stenac4
Stenac5
Stenac6
Stenac7
Sleyana
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Slinea2
Slinea3
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Scuspid
Stubic1
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Figure 2.145

Table 2.1: Summary of Characteristics of the Malili Lakes *Surirella* taxa.

Taxon	Length	Width	Alar canals/ 100μm	Straie/10μm	Shape	Polarity	Hooks	Spines	Tubes	Tendrils
S. alata	58-65	20-22	22-23	23-25	Linear constricted	Iso		x		
S. bidens	46-160	28-70	0	37-39	Teardrop	Hetero	x			
S. biseriata var. heteropolis	200-517	35-80	10--15	35-50	Linear	Hetero				
S. celebesiana	70-82	22-30	30-35	55	Linear elliptical	Hetero		x		
S. conversa	50-110	35-62	15-22	24-28	Elliptical contorted	Iso		x		
S. cuspidate	35-80	5--10	55-60	>60	Linear	Iso				
S. decipiens	50-60	16-20	20-30	20-24	Linear elliptical	Iso		x		
S. ephippiomorpha	54-57	20-30	18-25	>60	Elliptical contorted	Iso		x		
S. excellens	90-250	16-55	21-32	34-47	Linear elliptical	Hetero	x			
S. fenestrellata	95-135	36-41	20-27	38-48	Linear elliptical	Hetero		x		
S. fimbriata	54-58	22-25	14-25	30	Elliptical	Hetero		x		
S. halteriformis	68-72	16-20	17-30	38-40	Dumbell	Iso		x		
S. leyana	33	11	38	35	Linear elliptical	Hetero		x		
S. linearis	20-125	9-25	20-30	38-40	Linear	Iso		x		
S. linearis constricta	90-95	20-25	16-17	18-20	Linear constricted	Iso		x		
S. papillifera	80-190	30-50	15-20	25-30	Linear elliptical	Iso	x	x		
S. pinnigera	94-133	36-48	16-25	45-59	Linear elliptical	Hetero	x	x		
S. promontorium	70	21	27-35	42	Elliptical	Iso		x		
S. quadridentis	56	27-33	14-16	25-31	Elliptical	Iso	x			
S. rugosa	56	15	31	30-40	Elliptical	Iso		x		

S. sublinearis	45-75	13-22	30-40	42	Linear constricted	Iso	x		x
S. sublinearis var suggesta	40-60	13-16	30-40	30-44	Linear constricted	Iso	x		x
S. tenacis	38-62	12--17	36-41	56-70	Linear constricted	Iso	x	x	x
S. tortilis	62	25	20		Contorted	Iso	x		
S. tubicola	84-132	48-42	20-25	35-40	Linear elliptical	Hetero		x	
S. woltereckii	40-110	35-80	15-25	23-30	Ovoid	Iso			
S. angusta	18-70	1-15'		22-28	Linear	Iso			
S. angustiformis	45-55	9-12'			Linear	Iso			
S. biseriata var. celebesiana	180	50	15-24		Linear	Hetero			
S. celebesiana var. matanensis	130	25	18-20		Linear	Hetero	x		
S. elegans	110-400	35-90	12-21.		Elliptical	Hetero			
S. elegans f. lata	230-238	120-122	12-19.		Ovoid	Hetero			
S. elegantula	65-122	24-30	20-Dec		Linear - ovoid	Hetero			
S. elegantula f. cuneata	100-110	19-21	14-17		Linear	Iso			
S. horrida	110-150	40-50	13-20		Linear elliptical	Iso			
S. horrida f. constricta	122	34	15		Linear constricted	Iso			
S. pediculata	80	25	20	18	Ovoid	Hetero			
S. pseudovalis	30-95	23-40	20-30	24	Ovoid	Hetero			
S. robusta	50-400	50-150	12-Jul	40-50	Linear - ovoid	Hetero			
S. rudis var. levis	153	39	14	30-35	Linear	Hetero			
S. sulcata	80	30	15		Elliptical ovoid	Hetero			
S. tenera	45-85	13-45	20-30		Ovoid	Hetero			
S. tenuissima	17-38	6-11.	40-79		Ovoid	Hetero			
S. tienemanii	150-173	26-29	23-2		Linear	Iso			

S. ventricosa	27-37	11-13.	30-40		Linear - ovoid	Hetero

GENERAL DISCUSSION

The mechanisms regulating community composition are a source of substantial debate in the field of ecology. Current ecological and invasion theory dictates that species composition is primarily regulated by stochastic colonization events (Simberloff 1978), such that natural assemblages have little inherent stability or resistance. For easily dispersed organisms such as diatoms, homogenization is predicted on regional or larger scales (Cleve 1894, 1895, Ross 1983), consistent with current models predicting global homogenization of species as a function of increasing propagule pressure (Simberloff & Van Holle 1999, Rahel 2002), particularly in areas of anthropogenic disturbance (Lodge 1993). According to this paradigm, biological communities of ancient lakes, frequently dominated by endemic species, can therefore only be maintained in geographically isolated areas. It is predicted that even these systems will become homogenized given sufficient time, and the rate of homogenization will be accelerated with increasing anthropogenic disturbance in the watershed.

In the Malili Lakes of central Sulawesi Island, Indonesia, however, cosmopolitan diatom taxa are extremely rare, and most taxa are limited in their distribution to only one or two lakes (Figure 3.1). The exclusion of cosmopolitan forms is, in fact, so complete that global "nuisance" species such as *Fragilaria crotonensis*, *Aulacoseira granulata*, and other planktonic centric diatoms are not observed at all in the lakes. The lack of these species has important implications concerning currently accepted paradigms of diatom invasion and colonization. The paucity of taxa known to be successful colonizers within an already impoverished native flora suggests that the community of the Malili Lakes is structured by interspecific competition (Elton 1946) and is limited by morphological similarity among taxa (Lack 1947). These data are in accordance with the general characteristics of invadable communities proposed by Lodge (1993), but in contrast to several others, and demonstrate that biological systems can exhibit resistance to colonization by foreign taxa.

But, in a system structured by competition, such as the Malili Lakes, why wouldn't taxa with more "derived" structures exhibit broadened geographic ranges or dominate local habitats? As well as setting forth the characteristics of invadable communities, Lodge (1993) also described the general characteristics of successful invaders. Among these are a high reproductive rate with a short generation time, clonal reproduction, high dispersal rates, and simple energetic requirements. All of these characteristics are exhibited by diatoms, yet the bulk of the Malili Lakes diatom flora are limited to very few lakes despite potent, long term colonization vectors. This demonstrates that not only are the diatom communities of the Malili Lakes resistant to colonization by cosmopolitan species, but also that the endemic species of the Malili Lakes, while exhibiting high levels of morphological uniqueness, remain poor colonizers of new aquatic habitats.

A simple empirical model can be used to demonstrate that highly specialized endemic taxa like those of the Malili Lakes are unlikely to colonize new systems. In general, in systems dominated by endemic taxa with severely restricted distributions, the probability of a taxon occupying additional habitat patches decreases rapidly as the number of patches occupied by the taxon increases. In contrast, this decrease in the probability of additional patch occupancy is much more gradual in communities comprised largely of cosmopolitan forms, where taxa are likely to occupy many habitat patches.

In building the model, the probability that a hypothetical taxon occupies at least one habitat patch, given that it is present in the system, by definition, is one. The probability of occupation of additional patches within the system can be represented by a simple exponential decay model following the equation

$$p_x = 1 \cdot e^{-k \cdot (x-1)}$$

where p_x is the probability of the occupation of at least x patches, given that x-1 patches are occupied, and k is constant proportional to the "endemicity" of, or proportion of endemic taxa within the community.

For real data, the probability of occupying at least one patch given presence in a system is, again, one. Subsequently, additional patch probability can be predicted from geographic range distributions of taxa within the system. The probability of occupying at least two patches, given occupation of one patch, is given by the equation:

$$p_{\geq 2.1} = 1 = \frac{\# taxa_{1\,patch}}{\# taxa_{total}}$$

where $\# taxa_{1\text{patch}}$ represents the number of taxa restricted to one patch and $\# taxa_{\text{total}}$ represents the total number of taxa in the system. Similarly, the probability of occupation of at least three patches given the occupation of two patches is given by:

$$p_{\geq 3.2} = \frac{\# taxa_{1.2\,patches}}{\# taxa_{total}} \quad .$$

Figure 3.2 illustrates probability of additional patch occupation curves for communities with high and low endemicity, and actual data from the Malili Lakes diatom flora. This model demonstrates that systems dominated by endemic taxa are not likely sources of colonists to other systems, and that highly specialized endemic taxa, exemplified by the diatoms of the Malili Lakes, are poor colonists of new habitat patches. This characteristic of endemic taxa has helped to promote and maintain dissimilarity among the diatom floras of the Malili Lakes.

Diatom taxa, like other algae, respond differentially to various physio-chemical gradients. In his classic paper, the Paradox of the Plankton, Hutchinson (1961) argued that the coexistence of so many taxa of phytoplankton in a homogeneous, well mixed environment was paradoxical given that taxa competing for the same resources cannot coexist. Subsequently, Scheffer *et al.* (2003) reviewed possible solutions to Hutchinson's paradox, and postulated that so many algal taxa could coexist because of the spatial heterogeneity and high degree of temporal variability in the water column. In such a case, it would be predicted that the algal community would be composed primarily of locally rare, regionally common taxa coexisting in low relative abundances. Any one of these taxa could become locally dominant and regionally common when physical and chemical properties in their portion of the water columns were optimal for their growth.

In the Malili Lakes, water chemistry is relatively homogeneous, both within and among lakes, and as with other tropical systems, climatic patterns are relatively stable. Despite this spatial and temporal homogeneity, and the sampling of similar substrates at each site, the diatom assemblage, comprised almost exclusively of rare taxa, differed markedly from site to site. This finding suggests that the benthic diatom taxa of the Malili Lakes are not simply responding to changes in physical and chemical variables, but that they are also regulated by intrisinc taxonomic characteristics, and interspecific interactions.

SIMI values, combined with the high proportion of within-lake endemism as well as relative abundance data, clearly demonstrate that unique diatom assemblages have been maintained in spite of potent, long-term colonization vectors. Mechanisms other than stochastic colonization are determining the diatom community composition and relative abundance within these ancient lakes. These results are in agreement with the diversity observed in diatom herbarium voucher material and challenge the current paradigms of cosmopolitan diatom distributions (Kociolek & Spaulding 2000) and the general application of stochastic colonization mechanisms to various organisms (Simberloff 1978, Simberloff & Van Holle 1999, Rahel 2002).

The speciose nature of the genus *Surirella* in the Malili Lakes, coupled with the relative paucity of *Surirella* in other parts of the world (Foged 1981, Vyvermann 1991, Cocquyt 1998, Metzeltin & Lange-Bertalot 1998), indicates an evolutionary and biogeographic isolation with implications for microhabitat selection and species radiation. The varieties of *Surirella* with unique morphological features including ornate spines, spinules and papillae are striking with only South American assemblages exhibiting a similar, although reduced, range of morphological variation (Metzeltin & Lange-Bertalot 1998). A similar pattern of morphological adaptation was observed among the functional patterns of the raphe slits of the genus *Cymbella* in Lake Matano.

The inordinately large number of *Surirella* taxa exhibiting attachment characteristics (33 of 46), along with the paucity of planktonic forms, illustrate the importance of attachment as a selective pressure in these lakes. In the case of Lake

Matano, a steep profiled graben lake, planktonic diatoms, or unattached benthic diatoms, sink, are subjected to abrasion, dissolution, burial, and extended periods of darkness, and ultimately lost. Similar processes possibly occur in the lower Malili Lakes. Diatoms with attachment structures persist in these lakes, but might not compete successfully in lakes where a planktonic way of life is the norm. These findings suggest a diatom flora that is governed by the physical limnology of the lakes, and shaped by intense competition for limited suitable microhabitat resources. The role of these limnological and biological filters in the development of the individual floras of the lakes is also demonstrated by the fact that the same genera are present in all the lakes examined, yet these genera have differential success in different lakes. Figure 3.3 illustrates that some genera seem to be radiating, or having more success than others in some lakes. Further work must be conducted, however, to determine which of these mechanisms has played the most important role in the development of the Malili Lakes flora.

Simple modeling of colonization potential based on range sizes of endemic taxa has predicted that highly endemic communities are the poor sources of colonists to other systems and that endemic taxa are not likely to be successful colonists in new habitat patches. The poor colonization ability of taxa from communities with high endemicity promotes and maintains high levels of dissimilarity and endemism on the lake-to-lake scale.

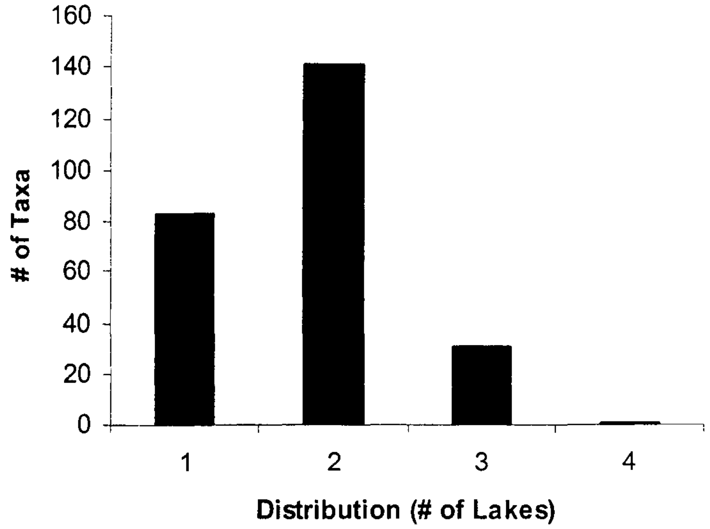

Figure 3.1. Limits to the distribution of Malili Lakes diatom taxa.

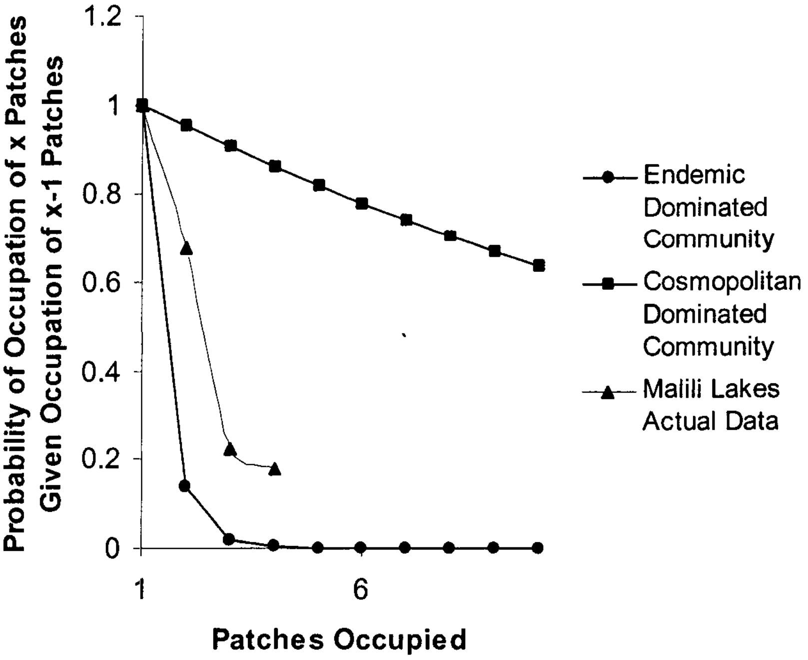

Figure 3.2: Empirical model of probability of additional habitat patch occupancy in hypothetical communities dominated by endemic (k=2) and cosmopolitan taxa (k=0.05), and actual data from the diatom community of the Malili Lakes.

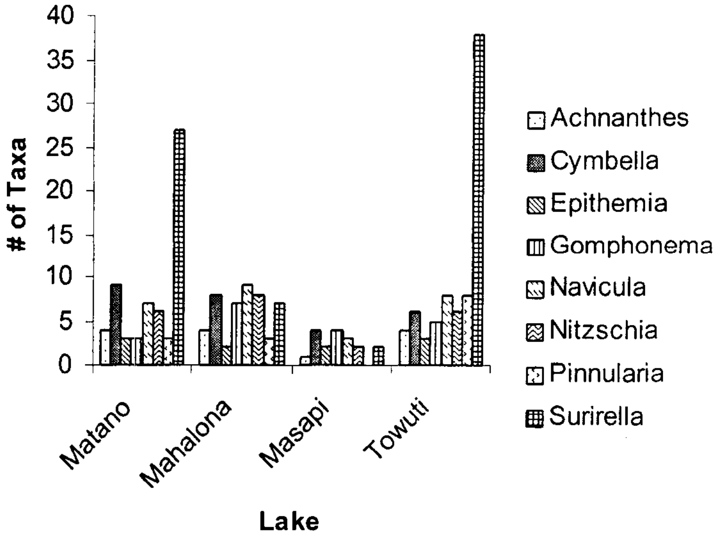

Figure 3.3: The 8 most speciose diatom genera in the Malili Lakes.

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Appendix 1: Traditional SIMI values for Lake-Lake pairings.

	Mahalona	Towuti	Masapi
Matano	0.078	0.314	0.224
Mahalona		0.010	0.213
Towuti			0.218

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