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Article

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Three novel species of Bacillariophyta (Diatoms) belonging to *Aulacoseira* and *Lindavia* from the Pliocene Hadar Formation, Afar Depression of Ethiopia

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Abstract

Paleolake Hadar was an expansive lake in the lower Awash Valley of Ethiopia's Afar Depression that existed periodically through the Late Pliocene. The sedimentary deposits from this ancient lake (Hadar Formation) have broad importance because a significant number of hominin fossils have been recovered from the formation. Samples of the Hadar Formation lacustrine sequence were collected from sediment cores extracted as part of the Hominin Sites and Paleolakes Drilling Project (HSPDP). A paleoecological study of the HSPDP Northern Awash (Hadar Formation) material has unearthed three novel species of Bacillariophyta (diatoms) from diatomites that appear periodically in the cores. The Hadar Formation assemblage represents a newly revealed excerpt from the evolutionary history of freshwater diatoms in East Africa during the Piacenzian age (2.59–3.60 Ma). The HSPDP Northern Awash diatom species are compared to previously reported diatoms from Pliocene outcrops, modern and fossil core material from Lake Malawi, and extant species. Here we describe two new species of *Aulacoseira* and one of *Lindavia*. Taxonomic treatment of two diatom varieties reported by previous researchers as *Melosira* are transferred into *Aulacoseira* herein.

Introduction

The Hominin Sites and Paleolakes Drilling Project (HSPDP) is an interdisciplinary investigation aimed at understanding the paleoecology and paleoenvironmental context of major hominin fossil sites in East Africa. Drill cores were taken at five sites in close proximity to prominent hominin fossil localities in Kenya and Ethiopia. This strategy targeted critical intervals in human evolutionary history from the Pliocene (~3.6 Ma) (Cohen *et al*. 2009, 2016). This investigation focuses on novel diatom species revealed from the Pliocene Hadar Formation (2.9–3.8 Ma) Afar Region, Ethiopia (Campisano & Feibel 2007). The Hadar Formation and temporal equivalent sediments are preserved across multiple important paleoanthropological sites in the lower Awash valley (e.g., Hadar, Dikika, Gona, Woranso-Mille, Ledi-Geraru) and contain a rich paleontological record including that of early hominins, particularly *Australopithecus afarensis* (Campisano & Feibel 2008; Dupont-Nivet *et al*. 2008; Kimbel & Delezene 2009; Quade *et al*. 2008; Saylor *et al*. 2016; Wynn *et al*. 2008).

Diatom taxonomy requires careful evaluation to ensure accuracy and complete exploitation of all paleolimnological information available (Flower *et al*. 2013). The literature regarding the taxonomy of East African diatoms is generally sparse and outmoded, particularly with respect to Pliocene material. Previous researchers have reported *Aulacoseira* Thwaites (1848: 167) and *Stephanodiscus* Ehrenberg (1845: 20) in outcrops of Plio-Pleistocene diatomite from the East African Rift (*e.g.*,Trauth *et al*. 2005, 2007) and specifically from the Hadar Formation (Campisano & Feibel 2008; Tiercelin 1986). Gasse (1980, 1986) has also reported several similar species, varieties, and forms of taxa in the genus *Melosira* from Pliocene outcrops in East Africa, two of which are herein transferred to *Aulacoseira*. In this study we provide a modern taxonomic treatment of diatoms from the Pliocene Hadar Formation found in the HSPDP Northern Awash cores.

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Materials and Methods

Site description:—A component of the Hominin Sites and Paleolakes Drilling Project (HSPDP), the Northern Awash coring sites targeted both exposed and buried sediments of a Late Pliocene lake (Paleolake Hadar) in the lower Awash Valley of Ethiopia's Afar Depression (Campisano *et al.* in review, Cohen *et al.* 2016). The modern landscape is dominated by aeolian and alluvial floodplain silts unconformably overlying Plio-Pleistocene sediments. Regional geological studies combined with available outcrop, seismic, and core data suggest that the coring sampled near the lacustrine depocenter of the Hadar Basin (>2.9 Ma), linked to well-exposed fluvio-lacustrine deposits of the fossiliferous Hadar Formation nearby (Campisano & Feibel 2008; DiMaggio *et al.* 2008; Dupont-Nivet *et al.* 2008; Wynn *et al.* 2008).

Field sampling:—Three long boreholes were cored at two locations using a track-mounted wireline diamond coring system in February–March 2014. At the first site, Osi-Isi (NAO, 11.31518°N, 40.73689°E), two boreholes were drilled. At the second site, Woranso (NAW, 11.32535°N, 40.76491°E), located ~3 km east of NAO, a single borehole was drilled (Fig. 1). NAO was cored entirely with H diameter drill string (61.1 mm diameter core) and NAW was cored with H diameter to ~170 m below surface (mbs), then finished with N diameter (47.6 mm diameter core).

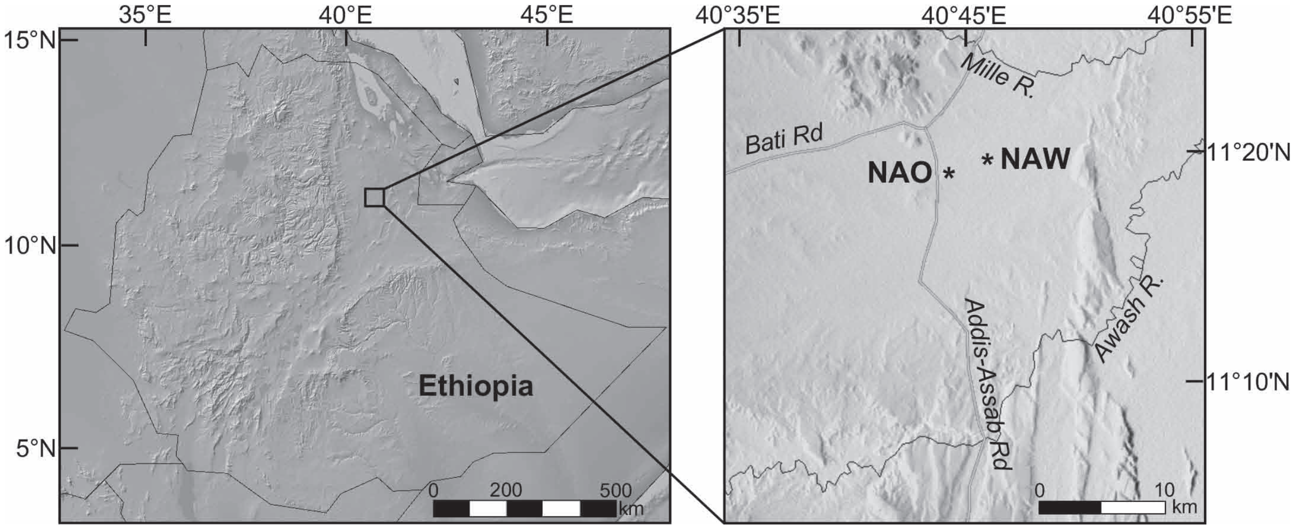

FIGURE 1. Location of the NAO and NAW drill core sites in the Afar Depression of Ethiopia.

Summary descriptions:—The NAO site included twinned boreholes (NAO14-1B and -1D), approximately 5 m apart. NAO14-1B and -1D were cored to a depth of ~187 mbs and ~167 mbs, respectively, including excellent recovery and overlap. NAW14-1A was cored to a depth of ~245 mbs. The cores can be correlated via a tephrostratigraphic tie point at approximately 50 mbs in NAW and 75 mbs in NAO (Garello *et al.* 2015). The sedimentology of the cores is dominated by fine-grained materials, principally massive or laminated clays and silty-clays, but also includes intervals of paleosol development. Three major basalt packages ranging from ~10–65 m thick are also preserved in the Northern Awash core sequence. Coarse-grained material (sand and coarser) is relatively rare in the sequence, and is principally mafic material associated with the upper-most basalt (Cohen *et al.* 2016). Overall, the upper part of the sequence, above the basalts, is interpreted as a fluctuating lake with repeated episodes of subaerial exposure and pedogenesis. The lower part of the sequence represents relatively stable, deep lake conditions (Garello *et al.* 2015). Diatoms are sporadically distributed throughout the length of the cores and are associated with virtually all lithofacies except the basalts (Figure 2). Diatom occurrences in the upper ~20 m of NAO have previously been documented in outcrops and used for regional correlation and reconstructing depositional environments (*e.g.* DiMaggio *et al.* 2008, 2015), but not examined in detail taxonomically. Preliminary ^{40}Ar/^{39}Ar dating of the cores and tephrostratigraphic correlations to outcrops (particularly at NAO) indicate the cores span more than 300,0000 years, from just less than 2.93 Ma to more than 3.22 Ma (Garello *et al.* 2015).

Sample preparations:—All HSPDP cores were shipped to the National Lacustrine Core Facility (LacCore, University of Minnesota) for description and sampling. Sub-samples for preliminary diatom analysis were taken at approximately 32-cm intervals and placed in plastic polycon containers for shipping to Indiana State University.

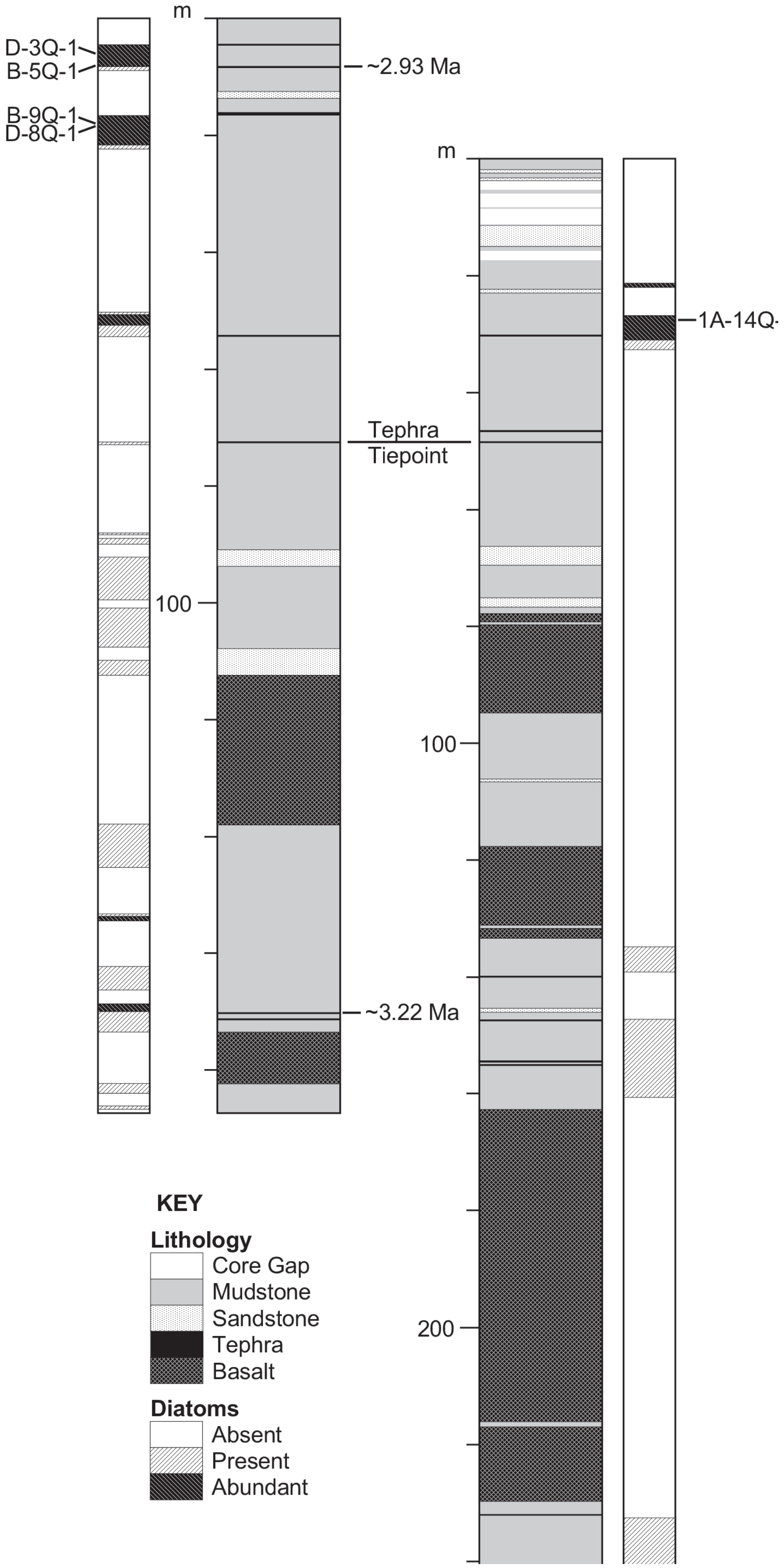

FIGURE 2. Simplified lithology of the NAO and NAW drill cores. NAO14-1B/1D is a composite of NAO14-1B with gaps filled in by NAO14-1D. A tephrostratigraphic tie point correlates NAO with NAW at ~75 mbs and ~50 mbs, respectively. Diatom presence from initial 32 cm sampling

Laboratory Methods:—Initial smear slide observations of the NAW and NAO cores discovered occasional presence of centric diatom forms in both cores. Samples taken throughout each core, were prepared using 30% H_2O_2 in plastic scintillation vials for three weeks to remove organic material. After H_2O_2 processing, samples were rinsed with deionized water. Diatom extracts were then dried on glass cover slips and mounted to slides in Naphrax, a mounting media with a high refractive index. Samples were further analyzed and photographed at 1000× magnification with a Leica DM2500 light microscope. Scanning electron microscope (SEM) images were captured at the University of Arizona's Laserchron Center on a Hitachi 3400N SEM.

Results

Well-preserved diatom valves are abundant in and adjacent to diatomite in the NAW core at the uncorrected depths of 22 m and between 27–31 m below surface (mbs). The NAO core features five intervals of well-preserved diatom valves from 4–8 mbs, 19–22 mbs, 51–52 mbs, 154–155 mbs, and 169–170 mbs in depth (Fig. 2). Identification of well preserved diatoms revealed several species of *Aulacoseira*. One *Aulacoseira* species bears a resemblance to *A*. *muzzanensis* (F.Meister 1912: 41) Krammer (1991: 98) and another *Aulacoseira* species shows similarities to *A*. *granulata* Simonsen (1979: 58). One species of *Lindavia* is present and resembles *L. omarensis* (Kuptsova 1962: 37) Stachura-Suchoples & Khursevich in Kusber & Jahn (2007: 157).

Order **Aulacoseirales**
Family **Aulacoseiraceae**
Genus ***Aulacoseira***

Aulacoseira haruoi (Okuno) **Mohan & Stone, *comb., stat. et nom. nov.***

Basionym: *Melosira granulata* var. *robusta* Okuno in J.G. Helmcke and W. Krieger, *Diatomeenschalen Im Elektronenmikroskopischen Bild*, *Teil V: Fossil Diatoms*. Verlag Von J. Cramer, Weinheim, pl. 415. 1964.

Synonym: *Melosira granulata* var. *valida* f. *robusta* (Gasse 1980).

Type:—JAPAN. Ôita Prefecture: Yagimaki, Yamautsuri, Yabakeimura, Shimoge-gun, Yamautsuri deposite: fresh water; Middle Pleistocene at 340 m above the sea-level. Okuno collection, Prep. no. 1251.

Etymology:—Named in honor of Dr. Haruo Okuno of Kyoto University of Textile Fibers for his contributions to diatom taxonomy, specifically in regards to advancing scanning electron microscopy in fossil sediments.

Aulacoseira gadebensis (Gasse) **Mohan & Stone, *comb., stat. et nom. nov.***

Basionym: *Melosira ambigua* var. *robusta* Gasse in Les diatoméeslacustres Plio-Pléistocénes du Gadeb (Ëthiopie). Sistématique, Paléoécologie, Biostratigraphie. *Revue Algologique*. *Mé-moire hors-série* 3: pl. 7, fig. 3–7. 1980.

Type:—ETHIOPIA. Gadeb. Prepared by F. Gasse, Museum Historiae naturalis, Paris, France.

Etymology:—Named after the Gadeb region of Ethiopia. This is the type locality for the original description by Françoise Gasse (1980).

Aulacoseira helianthus **Mohan & Stone, *spec. nov.* (Figs 3, 4)**

Frustules form filamentous chains and exhibit heterovalvy. Separation valves and linking valves are observed. Valves are cylindrical, 20–43 µm in diameter and 6–12 µm height. The valve face is flat or concentrically undulates to a small degree. Areolae are punctate and large (1.0–1.5 µm in diameter). Areolae commonly blanket the entire valve face, rarely it is largely hyaline and areolae distribution is sporadic. A row of spines projected outward and perpendicular to the valve face encompasses the margin. In girdle view, the spines conjoin from two costae that run the length of the mantel in a straight line. Between each set of costae, striae with 7–9 areolae in 10 µm, run the length of the mantle. With regards to separation valves, every 5th–7th spine there exists an elongated separation spine. Correspondingly, every 5th–7th striae is replaced with a trench that runs the length of the mantle, herein designated as the separation furrow. Separation spines co-occur with the sister-cell's separation furrow. A collum is present at the base of the mantle, the valve however lacks a sulcus. The ringleiste is approximately 1/6 the diameter of the valve diameter, raised toward the center and chamfered. Rimoportulae are not observed.

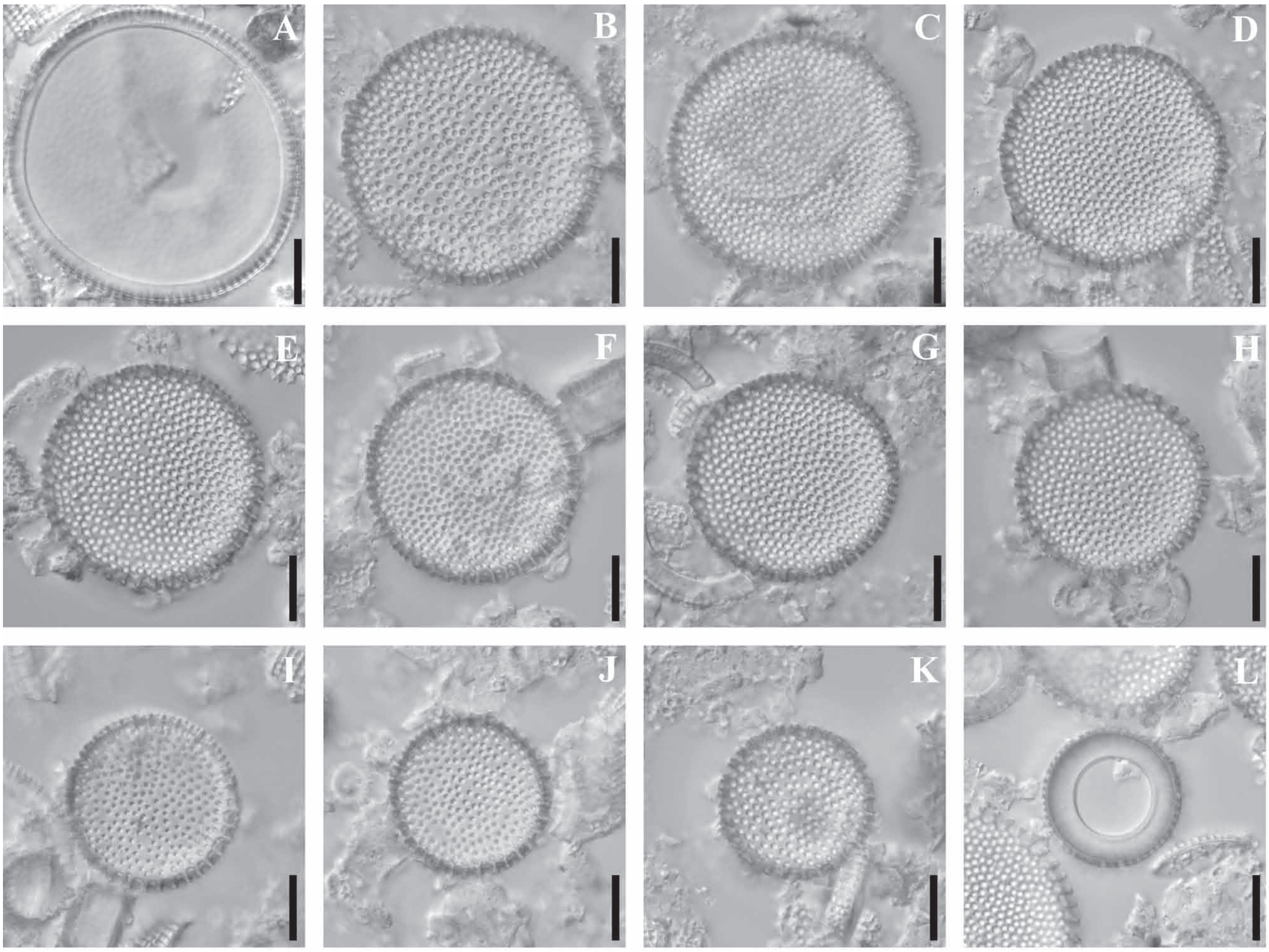

FIGURE 3. Size diminution series of *A. helianthus* (A–L). Holotype shown (B). Ringleiste view (A, L). Scale bars are 10 µm throughout.

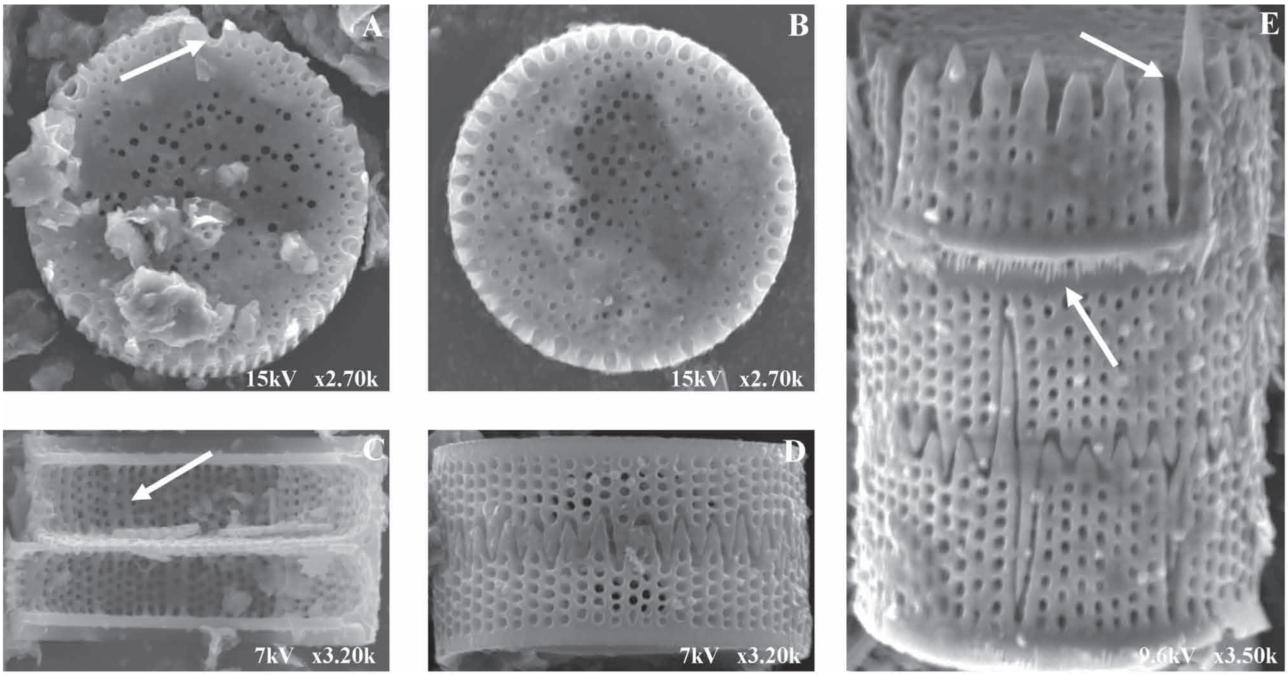

FIGURE 4. Scanning electron micrographs of *A. helianthus*. (A)Valve view of a separation valve. Note the separation furrow (arrowed). A linking valve (B) in valve view lacks separation spines and furrows. Internal view of two separation valves (C) two thickened costae are the internal structure of the separation furrow (arrowed). Two linking valves lacking separation spines (D). A filament of *A. helianthus* with separation furrow arrowed (E). Fimbria attach the two valves of the frustule (E), arrowed.

Type:—ETHIOPIA. Afar Regional State: Osi Isi site, 11.31518° N, 40.73689° E, 514 m a.s.l., late Pliocene lake sediment core (HSPDP-NAO14-1B) material, sediment depth ~19 m below surface, *HSPDP Northern Awash drilling team, February 2014* (holotype ANSP! GC17186, circled specimen on slide HSPDP-NAO14-1B-9Q-1 (91–93 cm), here illustrated as Fig. 3: B).

Etymology:—Named after the plant genus *Helianthus* (sunflower) as *A. helianthus* in valve view exhibits a superficial likeness to the central area of the flower with spines radiating in a way like petals on a flower.

Remarks:—*Aulacoseira helianthus* differs from *A. muzzanensis* (Meister 1912: 41) Krammer (1991: 98) in its full-bodied costae structure, whereas *A. muzzanensis* retains more refined lacy mantle costae. *Aulacoseira muzzanensis* can exhibit slightly twisted striae on the mantle and *A. helianthus* always exhibits straight striae on the mantle. *Aulacoseira helianthus* differs from *A. agassizii* var. *malayensis* (Hustedt 1942: 10) Simonsen (1979: 56) most notably by separation spine concentration. *Aulacoseira helianthus* have separation spines every 3–5 costae while *A. agassizii* var. *malayensis* contains separation spines on every 2–3 costae (Fig. 9). The linking valves of *A. helianthus* have tapered spines whereas *A. agassizii* var. *malayensis* are noted to exhibit cruciform spines on linking valves (Tremarin *et al.* 2012), (Figs 82–83).

Aulacoseira jewsonii Mohan & Stone, *spec. nov.* (Figs 5, 6)

Valves are cylindrical, diameter ranges from 5–16 µm. Mantle height is 6–16µm. The mantle height to diameter ratio is highly variable. The diameter is typically 0.9 of the mantle height and can vary from 0.4–1.9. Frustules form filamentous chains that exhibit heterovalvy. The valve face is flat. On separation valves, acuminate spines surround the face and interlock with a sister cell's spines. Every 3–5 spines there exists an elongated separation spine, projected into the sister cell's separation furrow. Separation valves form costae on the mantle that conjoin to form the spines. Costae alternate with striae composed of 0.6–1.0 µm diameter areolae. Striae are straight, areolae are punctate. Typical areolae density is 8–12 per 10 µm. The collum height varies per valve and a shallow sulcus exists. Linking valve faces are flat with linking spines projected perpendicular to the valve face. Linking spines originate from a single costa and form spatulate ends that interlock with a sister cell's linking spines. Areolae are doubly punctate to form rectangular chambers. Internal valves exhibit doubly punctate areolae and spatulate linking spines. The collum is present at the base of the valve.

Type:—ETHIOPIA. Afar Regional State: Osi Isi site, 11.31518° N, 40.73689° E, 514 m a.s.l., late Pliocene lake sediment core (HSPDP-NAO14-1D) material, sediment depth ~6 m below surface, *HSPDP Northern Awash drilling team, February 2014* (holotype ANSP! GC17185, circled specimen on slide HSPDP-NAO14-1D-3Q-1 (93.5–95.5 cm), here illustrated as Fig. 3:I–L).

Etymology:—Named in honor of Dr. David Jewson for his enormous contributions to the ecological and biological understanding of diatoms, especially *Aulacoseira*.

Remarks:—*Aulacoseira jewsonii* differs from *A. granulata* by possessing rectangular areolae on the internal valves that were likely formed by dissolution of a doubly punctate areola structure and circular areolae on separation valves (Fig. 6: E, F). Whereas *A. granulata* internal valves exhibit singly punctate rounded areola structure commonly covered with a sieve plate and rectangular areolae on separation valves (Siver & Kling 1997), (Figs 23–28). *Aulacoseira jewsonii* also differs from *A. granulata* by possessing a separation spine every 3–5 costae (3–7 per valve) while the latter typically displays 1–3 per valve.

Order **Thalassiosirales**
Family **Stephanodiscaceae**
Genus ***Lindavia*** (Schütt) De Toni & Forti (1900: 553)

Lindavia cohenii Mohan & Stone, *spec. nov.* (Figs 7, 8)

Valve outline is circular, 11–22 µm in diameter. Valve face exhibits transverse undulation. Areola on the valve face are large (0.7–1.1 µm) in diameter and are arranged in a weakly radiate manner. Granules are present between areolae. A single fultoportula is present near the center of the valve. Spinules encompass the margin on well preserved specimens. Areolae are distributed at 6–12 per 10 µm.

Type:—ETHIOPIA. Afar Regional State: Weranso plain, 11.32535° N, 40.76491° E, 493 m a.s.l., late Pliocene lake sediment core (HSPDP- NAW14-1A) material, sediment depth ~28 m below surface, the *HSPDP Northern Awash drilling team, March 2014* (holotype ANSP! GC17187, circled specimen on slide NAW-141A-14Q-1 (51–53 cm), here illustrated as Fig. 7: J–L).

Etymology:—*Lindavia cohenii* is named in honor of Dr. Andrew Cohen, University of Arizona, for his outstanding contributions to the field of paleolimnology, specifically in regards to his extensive studies of African rift lake systems.

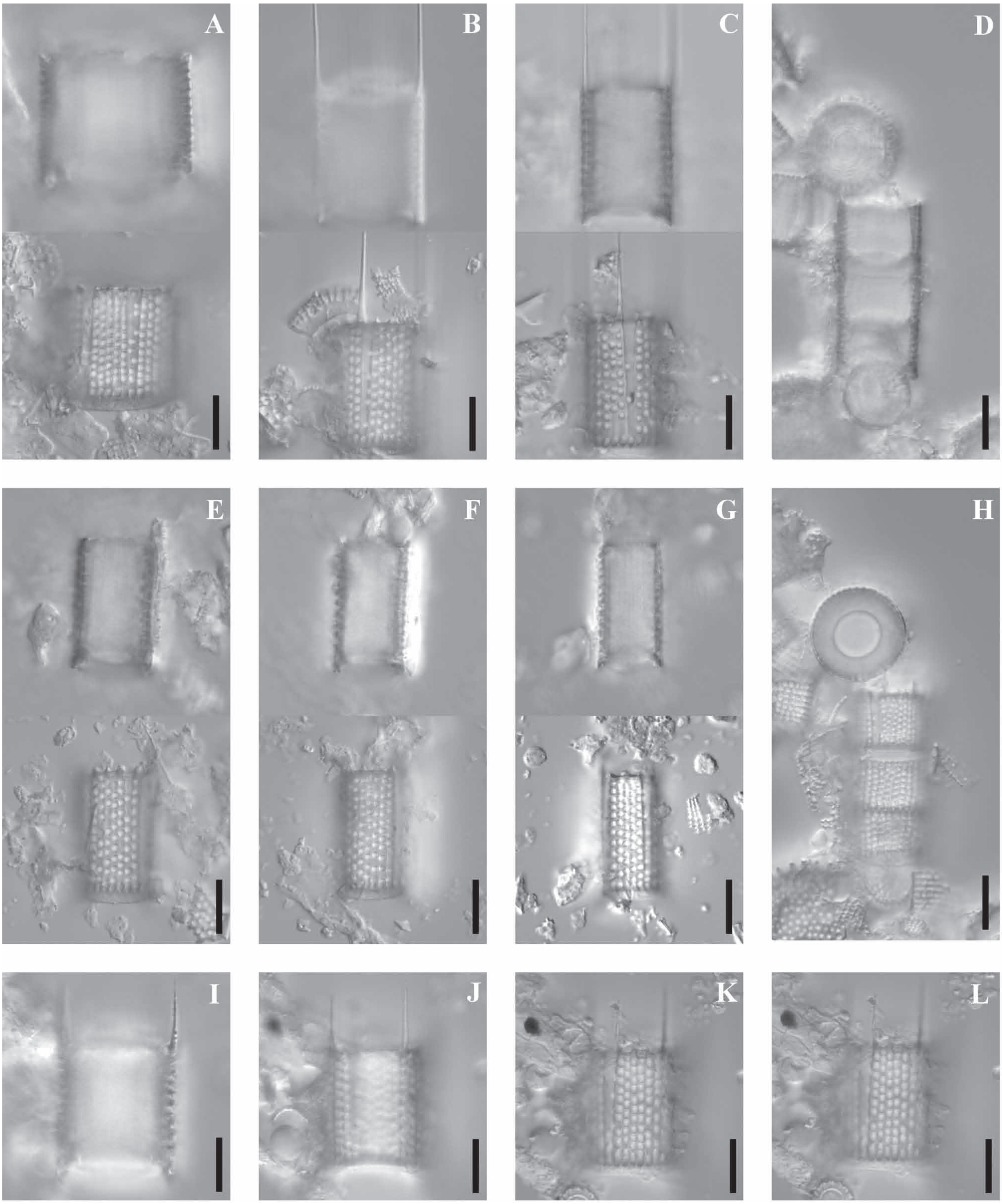

FIGURE 5. Diminution size reduction series pictures of *A. jewsonii* taken at two focal heights to examine the diameter accurately (A–C, E–G). Three valves in a filament (D, H) the top valve is a separation valve while the bottom two are linking valves. The holotype is shown at different focal heights (I–L).

Remarks:—*Lindavia cohenii* differs from *L. omarensis* by having a diminution size range of 11–22 µm whereas *L. omarensis* ranges from 7.5–36.0 µm. Well preserved specimens of *L. cohenii* exhibit spinules near the margin while *L. omarensis* has no spinules. Areolae per 10 µm are 6–12 while *L. omarensis* has 10–16 per 10 µm.

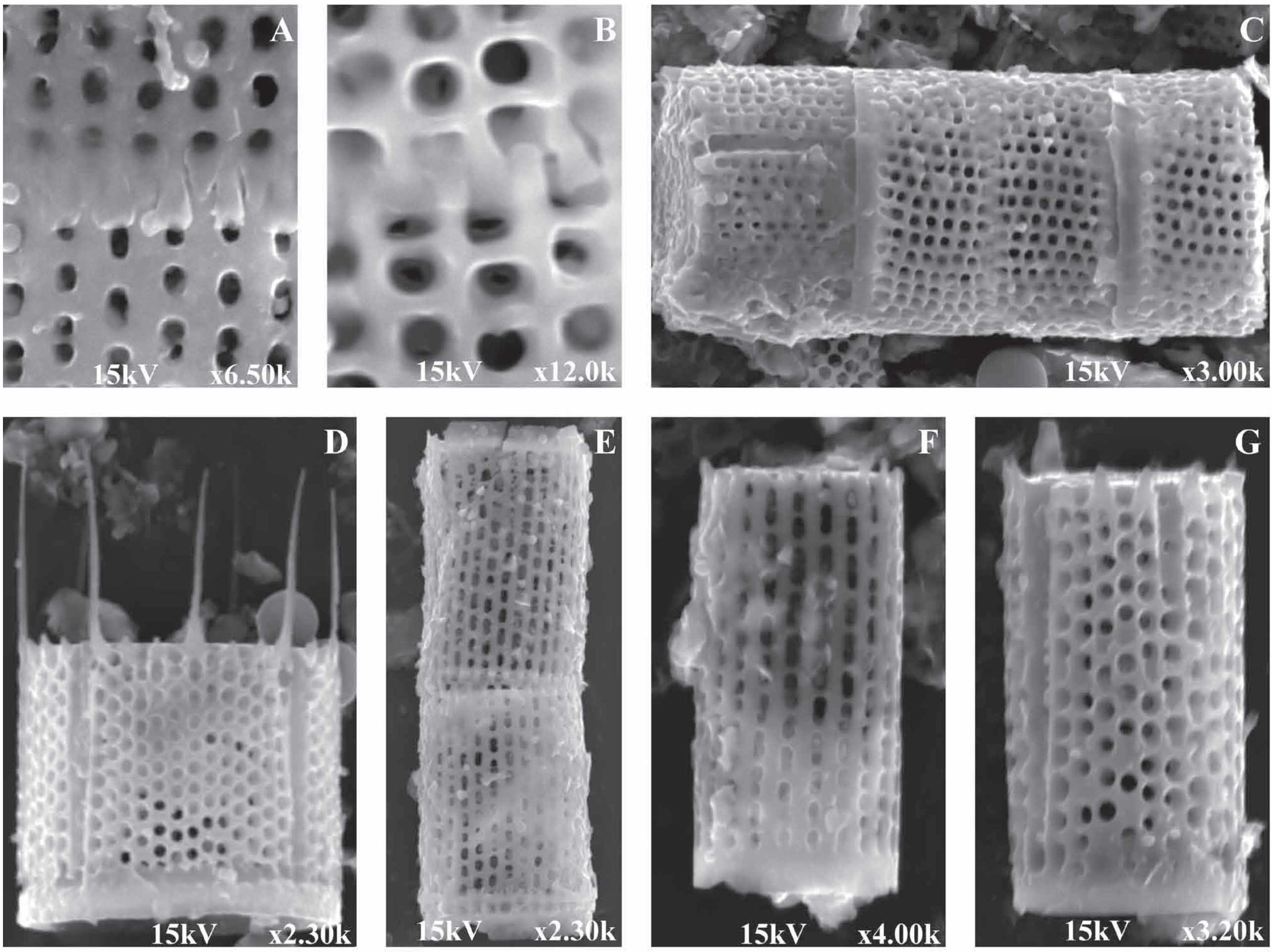

FIGURE 6. Scanning electron micrographs of *A. jewsonii*. Spatulate linking spines of two internal sister valves (A). Note the doubly punctate areolae that is typical of internal valves (E). Spatulate linking spines are also present on linking valves (B) that sometimes exhibit twisting costae (C). A filament of two frustules, one contains a separation valve (C) (far left), and a linking valve (middle left), the frustules on right contains two linking valves. A well preserved separation valve (D). Sister internal valves held together by spatulate linking spines (E). A single internal valve (F). A single separation valve (G).

Discussion

The presence of *Aulacoseira* and *Lindavia* intermittently throughout the NAW and NAO cores indicate that Paleolake Hadar was similar in nature to the Plio-Pleistocene lakes in East Africa that have been previously described (*e.g*. Gasse 1980, 1986). These lakes were oligohaline marked by periods of regressions that resulted in alkalinity shifts. Paleolake Hadar does not exhibit great taxonomic diversity (~6 taxa) in comparison to the rich flora found in Paleolake Gadeb (345 taxa) (Williams *et al*. 1979).

Aulacoseira helianthus resembles *A. agassizii* var. *malayensis* by having similar dimensions, and costae structure. Both species contain spines on separation valves that originate from two mantle costae. Mantle costae are straight and are associated with a single row of areolae. Both species also place the separation furrow beside each separation spine.

The morphological similarities of these two species suggest an ancestor-descendant relationship. *Aulacoseira agassizii* var. *malayensis* is prevalent in many modern East African rift lakes (Gasse & Street 1978; Owen & Crossley 1992; Stone *et al.* 2011). *Aulacoseira helianthus* is present in intermittent paleolake deposits in the Afar from 3.2–2.9 Ma during the Piacenzian age of the Pliocene epoch. A similar species, *A. gadebensis* is reported from the Gadeb Region of Ethiopia from 2.7 Ma and is suggested to be the direct ancestor of *A. agassizii* var. *malayensis* by (Gasse 1980). *Aulacoseira agassizii* var. *malayensis* is reported in the Afar in Late Pleistocene diatomites (Gasse & Street 1978) and has been present in Lake Malawi for at least 120 ka (Stone *et al*. 2011).

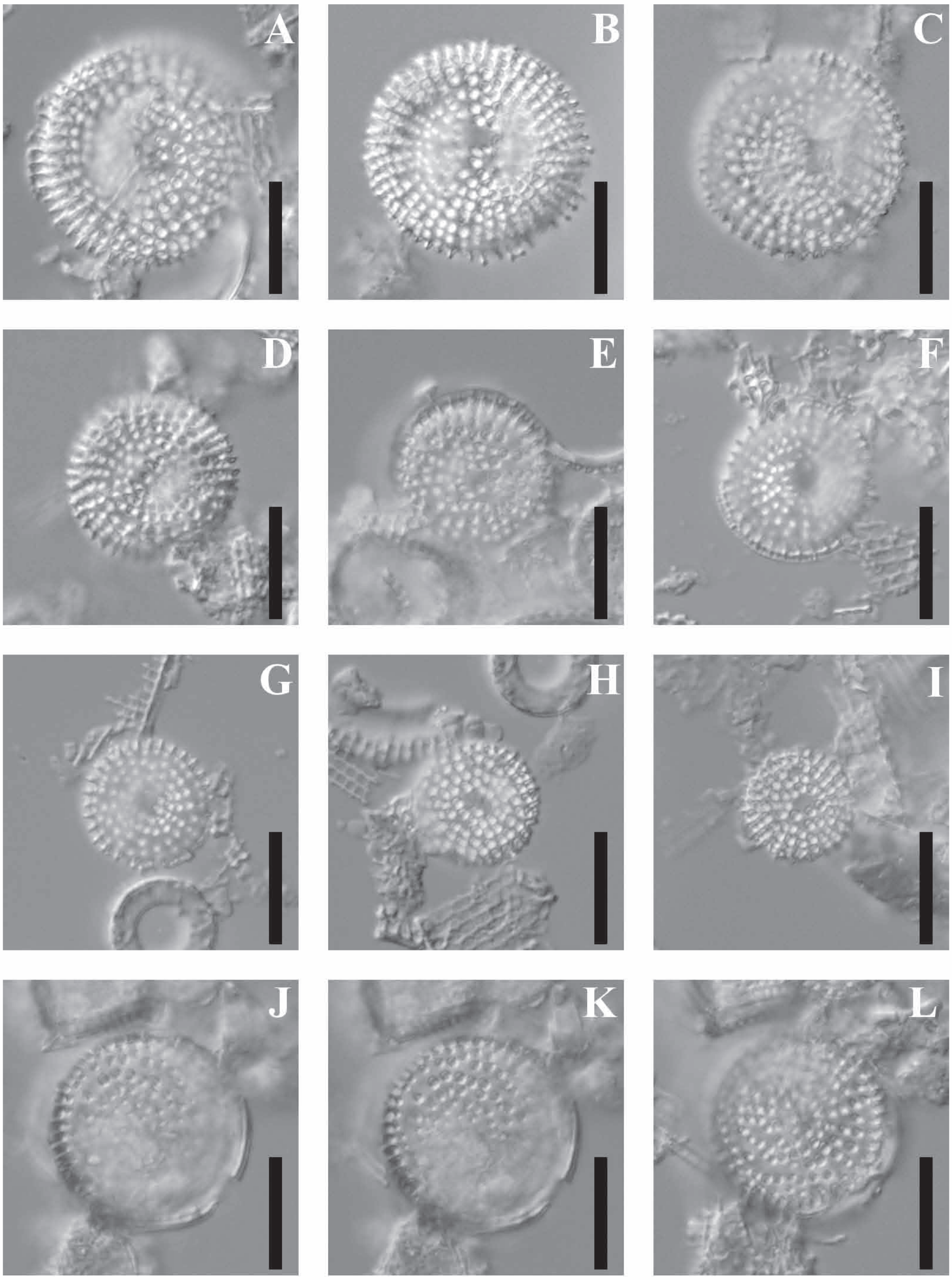

FIGURE 7. Diminution size series of *L*. *cohenii* (A–I). The Holotype at differing focal planes (J–L).

Aulacoseira jewsonii resembles *A*. *granulata* that has been reported in many varieties and forms from diatomite in the Gadeb region of Ethiopia from 2.70–2.34 Ma and reported from the Hadar Formation by Campisano & Feibel (2008), Tiercelin (1986) and Wynn *et al*. (2008). It is likely that previous reports of *A*. *granulata* are actually *A*. *jewsonii* or a close relative. It is possible that *A*. *jewsonii* is the ancestor of the taxa reported by Gasse (1980). Careful morphological analysis and examination of the *A*. *granulata* complex in East Africa is required to firm up this hypothesis. *Aulacoseira jewsonii* is common in the diatom-containing sections of the core and will be useful in paleoecological reconstructions of nutrient contents in Paleolake Hadar.

Lindavia cohenii is similar to *L*. *omarensis* that is reported from the Gadeb region from 2.70–2.34 Ma (Gasse 1980). *Lindavia omarensis* may be a descendent of *L*. *cohenii*. Currently *L*. *cohenii* has only been found in a small portion of the NAW core and thus may prove a valuable biostratigraphic maker in the Hadar Formation.

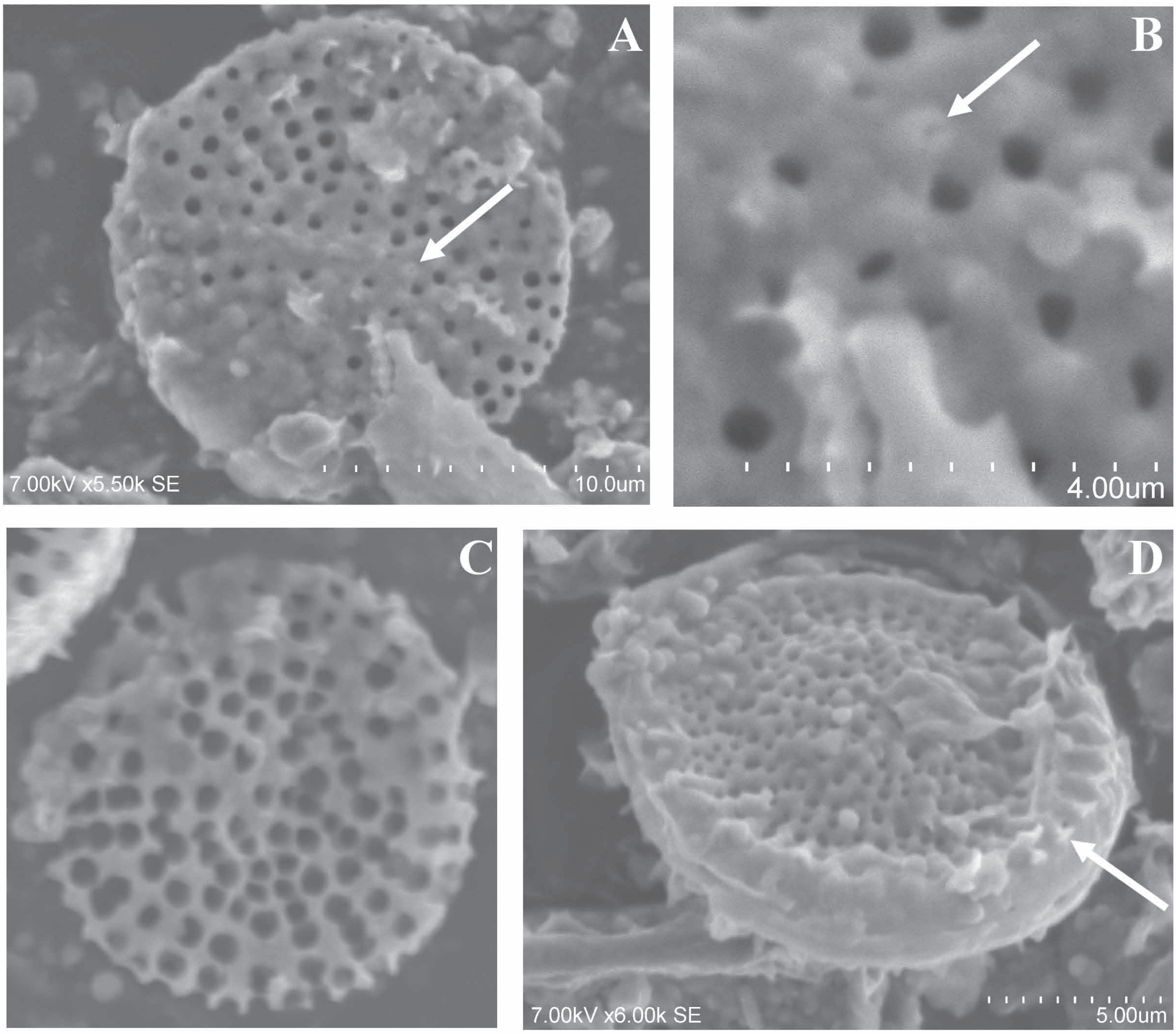

FIGURE 8. Scanning electron micrographs of *L. cohenii*. Central fultoportula arrowed (A, B). A heavily dissolved specimen (C). Isometric view of a well preserved specimen exhibiting transverse undulation, spinules arrowed (D).

Whereas taxonomic treatment of fossil species may be difficult to establish due to preservation issues, it is essential to create a firm taxonomy so species distribution through geologic time and their paleogeographic distribution can be investigated. Both aspects are essential to further paleoecological investigation related to hominin evolution in the Afar region and Paleolake Hadar. Furthermore, species such as *Plioceanicus cohenii* may serve as valuable biostratigraphic markers for the Hadar Formation and may be able to serve as a tie point between the core samples and natural outcrops when volcanic tephra are absent.

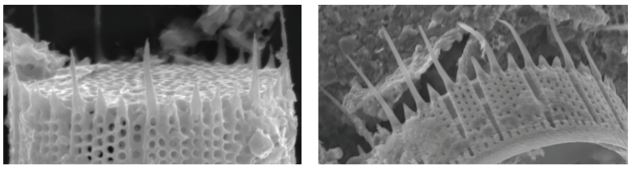

FIGURE 9. Scanning electron micrographs of *Aulacoseira helianthus* (left) and *A. agassizii* var. *malayensis* (right). Note the spine morphology originating from two mantle costae, location of the separation furrow in relation to the separation spine, and spine distribution.

Acknowledgements

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