A summary of *Synura* taxa in early Cenozoic deposits from Northern Canada

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With 3 figures and 1 table

**Abstract:** Five species of fossil *Synura* are documented from two freshwater Arctic localities, one known as Giraffe that existed during the Eocene, and a second known as Wombat that existed during the Paleocene. The fossils represent the oldest known remains of *Synura* and in each case the specimens were easily assigned to the genus. Two of the taxa, *Synura recurvata* Siver & Wolfe and *S. cronbergiae* Siver, represent species that are presumably extinct, but can still be linked to modern congeners. A third species may represent a new taxon within the *Synura petersenii* complex. The last two taxa have scales that are essentially identical to those produced by the modern species *S. nygaardii* and *S. macracantha*, although fossil scales of the latter species were significantly larger. Based on these findings, the two major sections of the genus, Sectio Synura and Sectio Petersenianae, were well established by the early Cenozoic.

**Key words:** *Synura*, fossils, Cenozoic, Eocene, Paleocene, Giraffe, Wombat

**Introduction**

The genus *Synura* consists of colonial freshwater flagellates within the Class Synurophyceae (Andersen 1987) whose cells are covered with an armour of precisely arranged siliceous scales. Different types of scales are found on the cell, depending on the position of the scale within the cell covering. The majority of scales that cover most of the cell are called body scales. Scales immediately surrounding the emergent flagella, apical scales, are slightly modified relative to body scales, whereas scales covering the posterior portion of the cell, caudal scales, can be shaped quite differently from body scales. Taxa within the genus are defined on the basis of the morphological structure of the siliceous scales, primarily determined using electron microscopy (Siver 2003). Despite the different types of scales that are found on a cell, the basic structure characteristic of the species can be observed on all scales.

*Synura* was originally described by Ehrenberg in 1834, and historically the genus was divided into three sections, Sectio Synura, Petersenianae and Lapponica (Kristiansen & Preisig 2007). Species within the Sectio Synura have scales with a spine projecting from the distal margin.
These spines are hollow and produced by a forward projecting invagination of the silica deposition vesicle (SDV) that occurs during formation of the scale (Mignot & Brugerolle 1982). Within the Sectio Synura, species are further determined based on the extent of development of the upturned margin, details of the spines, and the degree and type of secondary structure developed on the scale surface (Kristiansen & Preisig 2007). Taxa within the Sectio Petersenianae develop a median keel, instead of a forward projecting spine, and the scale margin is upturned only along the posterior portion of the scale (e.g. posterior rim). In this case, the SDV invaginates near the distal margin, but instead of projecting forward bends back onto and comes to rest along the center of the scale eventually forming the median keel. Species within the Sectio Petersenianae are distinguished based on the degree and type of secondary structures developed on the scale surface. Scales of *Synura lapponica*, the sole taxon within the Sectio Lapponica, develop a centrally positioned knob or sphere and lack spines and a median keel.

Scales of *Synura lapponica* bear close resemblance to those of the genus *Tessellaria*. Further, as is true for *Tessellaria*, Wee (2001) confirmed earlier observations that scales of *S. lapponica* are situated on a gelatinous mass that surrounds the entire colony and do not cover individual cells. Based on the similarity in scale morphology, placement of scales around the colony and recent molecular data, Škaloud et al. (in press) transferred *Synura lapponica* to the genus *Tessellaria*.

Given the transfer of *Synura lapponica*, there are currently 41 accepted taxa of *Synura* based on descriptions made with a combination of light and electron microscopy (Škaloud et al. 2012, Siver 2013). Of the 41 taxa, 24 belong to the Sectio Synura and 17 to the Sectio Petersenianae. Two of the species within the Sectio Synura are known only from the fossil record (Siver & Wolfe 2005, Siver 2013).

Except for the recent discovery of the two *Synura* taxa in Paleogene deposits near the Arctic Circle in northern Canada (Siver & Wolfe 2005, Siver 2013), the fossil record for *Synura* is lacking and little is known about the evolutionary history of this important genus. Siver & Wolfe (2005) described *Synura recurvata* from a middle Eocene maar lake contained within a kimberlite deposit known as Giraffe Pipe. Although an extinct species, scales of *S. recurvata* resembled those of the modern congener, *Synura uvella*. More recently, Siver (2013) described a second *Synura* species, *S. cronbergiae*, from the Giraffe Pipe and from a second older deposit from the same region of Canada known as Wombat. The purpose of this paper is to provide a summary of what is known about *Synura* microfossil remains from the Giraffe and Wombat deposits, including descriptions of three additional taxa yielding a total of five species now known from the geologic record. The relationships of the fossil taxa to modern species are discussed.

**Materials and methods**

Preparation and observation of microfossils is as given by Siver & Wolfe (2005) and Siver (2013). Briefly, mudstone or rock chips (0.1–0.5 g) were oxidized using 30% H$_2$O$_2$ under low heat for a minimum of an hour, rinsed with distilled water, and the resulting slurries stored in glass vials. Aliquots of each slurry were then air dried onto pieces of heavy duty aluminum foil. The aluminum foil samples were trimmed, attached to aluminum stubs with Apiezon® wax, coated with a mixture of gold and palladium for 2 min with a Polaron Model E sputter coater, and examined with a Leo 982 field emission scanning electron microscope (SEM). Measurements of specimens were made during examination with SEM or from stored digital images.

As noted by Siver (2013), each sample from the Giraffe and Wombat cores are identified with a three-part number. The first number represents the core box. Deeper sections of the core correspond to larger box numbers. Each box contains three (Giraffe) or four (Wombat) 1.5 m core lengths, identified as channels 1, 2, 3 and 4. The second part of the number represents the
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Table 1. Sections of the Giraffe and Wombat cores containing remains of *Synura*. Samples from the Wombat core are indicated by a “(W).” For the Giraffe core, approximate depth in the maar lake is given. These details have not yet been determined for the Wombat locality.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Section/Depth in Waterbody</th>
<th>Taxon</th>
<th>Section/Depth in Waterbody</th>
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<tbody>
<tr>
<td><em>S. cronbergiae</em></td>
<td></td>
<td><em>S. nygaardii</em></td>
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</tr>
<tr>
<td>13-2-120</td>
<td>8.56 m</td>
<td>14-2-148</td>
<td>12.05 m</td>
</tr>
<tr>
<td>13-1-15</td>
<td>8.89 m</td>
<td>17-3-47</td>
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<td>9.02 m</td>
<td>17-3-125</td>
<td>20.66 m</td>
</tr>
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<td>17-2-94</td>
<td>21.53 m</td>
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<td>9.83 m</td>
<td>17-1-40</td>
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<td>11.20 m</td>
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<td>22.54 m</td>
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<td>12.51 m</td>
<td>18-3-110</td>
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<tr>
<td>15-3-75</td>
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<td>20-2-25</td>
<td>30.90 m</td>
</tr>
<tr>
<td>65-1-45 (W)</td>
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<table>
<thead>
<tr>
<th><em>S. recurvata</em></th>
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<th><em>S. petersenii</em></th>
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</thead>
<tbody>
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<td>13-2-120</td>
<td>8.56 m</td>
<td>64-3-65 (W) NA</td>
</tr>
<tr>
<td>15-3-50</td>
<td>13.46 m</td>
<td>65-1-45 (W) NA</td>
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</table>

channel. The third number represents the length in cm measured down from the top of a core length. Thus, sample 20-2-31 represents a sample taken from 31 cm down along the core length positioned in channel 2 from box 20. The current investigation is based on examination of 26 samples from Giraffe and 6 from Wombat (Table 1).

Details of the Giraffe core are given by Wolfe et al. (2006), Siver & Wolfe (2009) and Doria et al. (2011). Briefly, Giraffe Pipe is a kimberlite diatreme situated in the Lac de Gras region of the Northwest Territories, Canada, that was emplaced into the Slave Craton approximately 47.8 million years ago (Creaser et al. 2004). During emplacement of the kimberlite formation, a volcanic crater formed that subsequently filled with water to form a maar lake. The crater slowly infilled with a sequence of lacustrine, then paludal sediments, and was later capped and entombed by a thick layer of Neogene glacial deposits. A 163 m long drilled core was uncovered from the Giraffe locality in 1999 by BHP Billiton Inc. A total of 113.1 m of the core contained well preserved stratified organic sediment, including 68.3 m of lacustrine lake sediments, overlain with 44.8 m of peaty material. An air-fall tephra bed located near the transition between lake and terrestrial sediments was dated using fission tracking to be 39 Ma (Doria et al. 2011), indicating that all of the lake sediments are Eocene in nature. The Wombat pipe represents an additional kimberlite deposit within the Lac de Gras field that also formed a crater during emplacement. The age of emplaced of the Wombat core has not yet been determined, however, the lake sediments have been dated to the Paleocene based on extensive examination of pollen remains (Hu et al. 2011). A long drilled core, measuring 386.7 m in length, was uncovered from Wombat by BHP Billiton.
Inc. in 1993 that includes approximately 159 m of laminated aquatic sediments (Siver 2013). The sections of the Wombat core examined to date come primarily from boxes 62–66, each of which contain numerous microfossils.

**Results**

A total of five species of *Synura* have been found in the two Paleogene cores, four taxa from the Giraffe Pipe core and two from Wombat (Figs 1–3). Three of the species, *Synura recurvata* Siver & Wolfe, *S. cronbergiae* Siver and *S. nygaardii* (Petersen & Hansen) Kristiansen represent taxa within the Sectio Synura. Two of the species, *Synura macracantha* (Petersen & Hansen) Asmund and *S. petersenii* Korshikov, belong in the Sectio Peterseniana.

*Synura cronbergiae* Siver

This species, recently described by Siver (2013), has long, slender scales with a posterior rim, a short hollow spine and a secondary layer comprised of highly structured hexagonal chambers that covers most of the scale surface (Figs 1C–D). Scales range in size from 6.5–13 μm × 1.75–3.75 μm, and spines from 1.75–3.5 μm. The base plate is perforated with relatively large and evenly-spaced pores. The posterior rim encircles approximately 2/3 of the perimeter, usually extends slightly farther along the left-hand margin, and typically fuses with the secondary layer. The spine is pointed, hollow and originates about 2 μm from the distal margin above the large base plate foram. Each hexagonal chamber encloses a base plate pore and is opened on the dorsal surface via a small surface pore.

Numerous scales of *S. cronbergiae* have been found in both the Giraffe and Wombat cores. This taxon was most abundant in boxes 13–15 in Giraffe Pipe and box 65 in Wombat (Table 1).

*Synura recurvata* Siver & Wolfe

Scales are circular to oval with a base plate perforated with small, randomly-spaced pores of varying diameters, a relatively wide posterior rim encircling half to 2/3 of the perimeter, a stout spine, and a thick secondary layer covering the anterior 1/3 of the scale (Figs 1A–B). A series of short ribs connect the secondary layer to the distal margin forming a row of large openings. The spine is conical with a wide-diameter base tapering to a blunt apex adorned with small teeth that are often recurved. The spine shaft has curved longitudinal thickenings. The secondary layer surrounds the base of the spine and consists of a series of circular to polygonal chambers each opening with a small pore along the dorsal surface.

The largest concentrations of *S. recurvata* specimens were found in boxes 17–20 in Giraffe Pipe core (Table 1) when the depth of the maar lake ranged between 20 and 30 m deep.

*Synura macracantha* (Petersen & Hansen) Asmund

Numerous scales that in many respects resemble those of *S. macracantha* were found in two sections of the Giraffe Pipe core (Table 1). Scales are elongate, with a well formed median keel, a posterior rim encircling about 1/2 of the scale perimeter, and a secondary layer consisting of a reticulation of ribs (Fig. 2). Scales are large and range in size from 4.75–7.75 μm × 1.8–2.5 μm. The base plate consists of large, evenly-spaced pores with thickened rims on the dorsal surface, and a single larger pore, or foram, positioned below the distal portion of the keel (Figs 2E–F). Base plate pores are sometimes lacking around the foram. The median keel extends over 3/4 of the scale, is characteristically curved (Figs 2A–C), and extends past the distal margin forming a pointed spine (Figs 2E–F). Except for part of the dorsal surface, the keel is perforated with pores that are slightly smaller in diameter than those on the base plate. The spine, and at least 1/2 of
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Fig. 1. Scanning electron micrographs of fossil *Synura* species from Paleogene lake deposits. **A–B.** *Synura recurvata.* Note the circular to slightly oval outline, the posterior rim, the thick secondary layer along the distal end of the scale, and the stout conical spine terminating with several small teeth. **C–D.** *Synura cronbergiae.* Scales are long and elongate with evenly-spaced base plate pores, a posterior rim that encircles more than half of the perimeter, a short, pointed spine, and a secondary layer that covers most of the scale surface. **E–F.** *Synura peterseni.* Note the broad posterior rim, prominent median keel, and the series of ribs radiating from the keel onto the scale surface. A series of small ribs attach the distal end of the keel with the base plate on the specimen in F. Specimens A–C and D–F are from the Giraffe and Wombat cores, respectively. Scale bars are 1 μm (E–F), 2 μm (A–B, D) and 5 μm (C).
Fig. 2. Scanning electron micrographs of fossil *Synura macracantha* scales from an Eocene lake deposit. **A–C.** Whole scales viewed from the dorsal surface depicting the long and curved keel with projecting spine, posterior rim and secondary reticulation of ribs. **D.** Portion of the remains of a colony exposed along a fractured piece of mudstone. **E.** Close-up of the undersurface (left) and top surface (right) of the distal portion of the keel denoting the projecting spine and foram. **F.** Undersurface of a scale with an extraordinarily large foram. Note the pores along the sides of the keel, but lacking on the dorsal surface. Scale bars are 1 μm (E–F), 2 μm (A–C) and 5 μm (D).
Fig. 3. Scanning electron micrographs of fossil *Synura nygaardii* scales from an Eocene lake deposit. 
A–C. Whole scales viewed from the dorsal surface depicting the oval shape, broad posterior rim encircling half of the scale, short and stout spine, and extensive secondary layer covering 1/2 to 2/3 of the scale surface. The secondary layer consists of a series of hexagonal-shaped chambers each surrounding a base plate pore and opening along the dorsal surface by a small pore. 
D. Close-up of the distal portion of a scale depicting the spine and secondary layer. 
E–F. Posterior scales denoting the extensive posterior rim, small and reduced spine and secondary layer. Scale bars are 1µm (B–C, E–F), 2µm (A) and 500 nm (D).
the dorsal surface of the keel, lack pores (Fig. 2E). A series of parallel ribs, or struts, originates along the sides of the keel, cross the base plate and terminate at the margin or along the posterior rim (Figs 2A–C). A second series of shorter ribs, more or less aligned with the longitudinal axis of the scale, connect the parallel struts forming a reticulation. Two to five ribs may connect each pair of struts.

*Synura* macracantha has only been found in the Giraffe core, with especially significant concentrations in sample 13-2-120 when the lake was approximately 8.6 m deep (Table 1).

### Synura nygaardii (Petersen & Hansen) Kristiansen

Body scales are oval with a broad posterior rim encircling approximately 1/2 of the perimeter, a short and stout spine, and an extensive secondary layer covering 1/2 to almost the entire scale surface (Fig. 3). Body scales range in size from 3.5–5 μm × 2–3 μm, and spines from 1.5 μm to 2.5 μm. Base plate pores are evenly-spaced and each has a thickened dorsal rim (Fig. 3C). The posterior rim of the scale can be up to 1 μm wide and the margin is often thickened. The secondary layer consists of a series of hexagonal chambers, each of which encloses a base plate pore and contains a small centrally-positioned pore on the dorsal surface (Figs 3A–C). The spine is hollow with a blunt tip that may have from three to five tiny teeth. Transitional scales are slightly smaller than body scales, oval, with a very wide posterior rim and a reduced spine (Figs 3E–F). All scales had spines.

*Synura* nygaardii was found in eight sections of the Giraffe Pipe core, and was most abundant in samples from four consecutive core lengths spanning boxes 17 and 18 and encompassing approximately six meters of mudstone (Table 1).

### Synura petersenii Korshikov

Numerous pieces of, but only a few whole, scales belonging to *Synura* petersenii were uncovered from the Wombat core (Table 1; Figs 1E–F). Most scales were oblong, with a median keel along most of the scale length, a posterior rim encircling 1/2 to 2/3 of the perimeter, and a series of parallel struts connecting the keel with either the posterior rim or scale margin (Fig. 1E). On the majority of specimens, the distal end of the keel is pointed and the dorsal surface is solid and lacks pores. A few specimens had very broad and bluntly rounded keels that were largely devoid of pores as observed with SEM (Fig. 1F). On these specimens, a series of short, closely spaced struts connected the bottom of the keel to the base plate. This species has only been uncovered in the Wombat core (Table 1).

### Discussion

Specimens of *Synura* from the Giraffe and Wombat cores represent the only known remains of the genus in the geologic record. Based on these findings, the genus was well formed by the Paleocene and is at least 60 million years old. It is also clear that the two sections of the genus, Sectio Synura and Sectio Petersenianae, were also well established by the Paleocene.

Two of the five taxa uncovered, *S. recurvata* and *S. cronbergiae*, clearly represent new, and presumably extinct, species (Siver & Wolfe 2005, Siver 2013). However, both of these species can be linked to modern congeners. *Synura recurvata* is most closely related to *Synura uvella*. Both of these species have scales that are almost circular in outline with thick, conical spines terminating in small teeth, a broad posterior rim, and a secondary layer covering only the distal portion of the scale. Scales of *S. recurvata* differ from those of *S. uvella* by having spines with a splayed tip, a thin central portion of the base plate prone to breakage, and lacking struts under the posterior rim (Siver & Wolfe 2005). Although *S. cronbergiae* clearly belongs to the Sectio Synura, its scales closely resemble those of *Synura longisquama* in regards to size, shape and the
structure of the secondary layer, and Siver (2013) hypothesized that both of these taxa may have shared a common ancestor.

Virtually all characters of the *S. macracantha* scales uncovered from the Giraffe core resemble those of modern specimens of this species and it is clear they represent the same lineage. The only difference was that the fossil scale specimens were larger than modern specimens. Otherwise, from a morphospecies point of view, the scales in the Giraffe core represent *S. macracantha*. Likewise, fossil scales of *S. nygaardii* appear to match those on modern specimens. Both the fossil and modern specimens are characterized by a very broad posterior rim, spines that are short, stout and often terminate with a series of teeth, and a secondary layer of hexagonal chambers. In addition, the transitional scales possess spines on both the fossil and modern specimens. Scales of two other modern species, *S. curtispina* and *S. mollispina*, are also similar in structure to those of *S. nygaardii*, but can be distinguished from the latter species as follows. The posterior rim is much broader on *S. nygaardii* scales than on those of either *S. curtispina* and *S. mollispina*. The spine on *S. nygaardii* scales is much thicker than that on *S. mollispina*, and whereas the transitional scales of *S. nygaardii* have spines, those on *S. curtispina* do not. Based on findings from the Giraffe and Wombat cores, both the *S. macracantha* and *S. nygaardii* lineages were present in the Arctic during the early Cenozoic, although at a time when the Earth was much warmer and lacked polar ice (Zachos et al. 2001, 2008). It is interesting to note that today both *S. macracantha* and *S. nygaardii* are rare species, only known from northern temperate to Arctic regions (Kristiansen & Preisig 2007). Perhaps, these two species thrived in Arctic lakes during the Cenozoic hot house, and were subsequently able to adapt and survive the eventual onset of cooler temperatures that began during the Late Eocene and especially marked the transition to the Oligocene (Zachos et al. 2001).

Today, *S. petersenii* is often reported as the most common species found within the genus (e.g. Kristiansen 1975, Wee 1982, Siver 1987, Nicholls & Gerrath 1985) and it is an important component of numerous freshwater ecosystems (Siver 2003). The remains of *S. petersenii* scales in the Wombat core represent the oldest known fossils for this highly successful lineage. The Wombat core contains at least two different scale types for *S. petersenii*, one of which is similar to the type for the species. The second morphotype lacks a definitive modern analog, but bears some resemblance to *S. petersenii* forma *taymyrensis* Kristiansen with its broad median keel (Kristiansen 1995). Interestingly, *S. petersenii* forma *taymyrensis* is also known today only from cold Arctic regions in northern Asia and Greenland (Kristiansen & Preisig 2007).

In summary, five species of *Synura* are now known from freshwater Arctic Paleogene sediments. Characteristics of the scales are similar to those on modern congeners and all taxa are easily assigned to the genus. Given that scale morphology as we know it today was well formed by the Paleogene, it is likely that the genus is older, but how much older remains to be determined.

References


