

Cenozoic silicoflagellate skeletal morphology: a review and suggested terminology

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Abstract: Silicoflagellate skeletons are made up of siliceous components that interconnect through triple-junctions to form a basket-shaped design made of basal and apical structures. The skeletal framework has a domal shape that can be paired with another to form a double skeleton. For Cenozoic skeletal morphologies, the basal structure consists of a ring of polygonal shape that often includes spines at the basal corners that are directed radially away from the double-skeleton central point, and pikes that point towards the apical axis. The apical structure is made up of elements of less thickness that are connected to the basal ring by struts. The skeletal components of the silicoflagellate conform to a consistently applied set of rules. There is a need to standardize silicoflagellate descriptive terminology in light of recent studies and detailed examination of the elements, spines and pikes that comprise Cenozoic skeletons. Here we review established and recently defined terminology that relates to silicoflagellate skeletons and suggest terminology to standardize future descriptive work.

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Silicoflagellates are a group of single-celled marine heterokont algae that possess a siliceous skeletal latticework, composed of hollow, rod-shaped components, during a portion of their life history. Our knowledge of the fossil record of silicoflagellates begins in the late Early Cretaceous (Albian) with an already diverse assemblage (McCartney *et al.* 2014a), which suggests an earlier period of diversification that is as yet unknown. Late Cretaceous and early Cenozoic silicoflagellate assemblages show a high morphological diversity, which saw a gradual decline over the Neogene. Only three genera, *Dictyocha* Ehrenberg, *Stephanocha* McCartney & Jordan (previously known as *Distephanus* Stöhr, see Jordan & McCartney 2015) and *Octactis* Schiller, are extant (McCartney *et al.* 2014b; Abe *et al.* 2015). Silicoflagellate skeletons also exhibit occasional extreme variability – what Deflandre (1950) called ‘plasticity’ – that often additionally complicates taxonomic interpretations.

Throughout their stratigraphic record, silicoflagellate skeletons display simple geometric patterns, yet descriptive terminology is not standardized and varies between workers. The first illustration of silicoflagellate skeletal terminology was by Lemmermann (1908) and subsequent workers introduced additional terms (Gemeinhardt 1930; Marshall 1934; Deflandre 1950; Gleser 1966; Ling 1972; Poelchau 1976; Bukry 1976a; McCartney 1988; Onodera & Takahashi 2009), with specific terms introduced by these workers listed in the glossary at the end of this paper. Mathematical models of silicoflagellate skeletons (McCartney & Loper 1989; Tsutsui *et al.* 2009) identify a need for terms for specific skeletal components and the locations where these connect. Further, studies of Cretaceous morphologies (McCartney *et al.* 2011, 2014a) and of double skeletons (McCartney *et al.* 2014b, 2015a) have expanded this terminology and demonstrate a need for more consistent application across disparate groups. Finally, a general study of silicoflagellate skeletal structure also shows an almost universal application of simple geometric rules (McCartney & Loper 1989) which provide context for discussion of phylogenetic

history and aberrant and unusual skeletal morphologies (McCartney & Wise 1990).

The purpose of this paper is to propose a standard terminology to describe silicoflagellate skeletons, following a review of established and recently defined descriptive terms and present some new ones. All terms shown in boldface are included in the glossary and generally in the figures. For convenience and comparison of relative length and thickness of each structural component discussed here, Figures 1–4 provide scanning electron microscope (SEM) images at the same magnification (except Figs 3:5, 4:6 and 4:7). Emphasis in this paper is on major Cenozoic genera that have a dome-shaped (apical) structure attached to a basal ring. This is a companion paper to McCartney *et al.* (2014a) which describes Cretaceous silicoflagellate morphology.

Orientation of the silicoflagellate skeleton

Silicoflagellate skeletons may be depicted as a shallow inverted basket-like design. In this analogy, the rim of the basket would be the **basal ring** composed of a series of linear to curved elements, known as **basal sides** that connect to form a circular to elongate structure that often has a polygonal design. The **basal corners** of the polygon lie within a **basal plane**. The basket body, known as the **apical structure**, is formed of a system of elements that meet at triple junctions and compose a dome-shaped design whose apex is above the middle of the basal ring.

The terms **apical** and **abapical** (Fig. 1) are used by convention to orientate the skeleton, although these do not relate to orientation of the living organism (Moestrup & Thomsen 1990). **Apical view** looks down on the top of the apical structure (i.e. towards the bottom of the basket) whereas **abapical view** (sometimes called basal view) looks through the basal ring into the basket. **Lateral view** is a perspective from the side, within the basal plane. Perspectives that are tilted with respect to each of these views are known as **oblique apical view**, **oblique abapical view** and **oblique lateral view**,

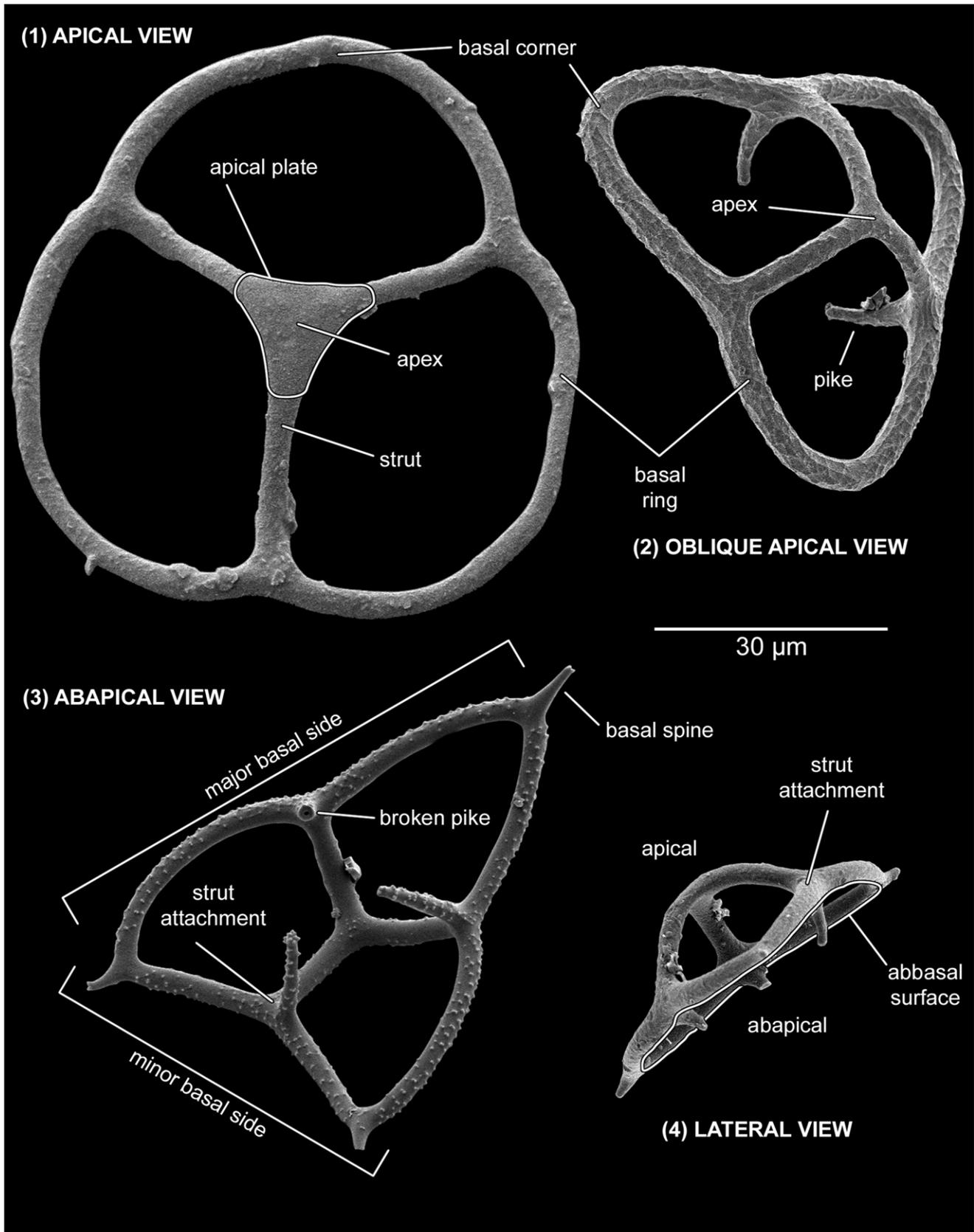


Fig. 1. SEM micrographs of *Corbisema* spp. to show skeleton orientation terminology. **1.** Apical view, *C. geometrica* Hanna, Horton River, Northwest Territories, Canada, Late Cretaceous. **2.** Oblique apical view, *C. archangelskiana* (Schulz) Frenguelli, Urals, Russia, Late Cretaceous. **3.** Abapical view, *C. hastata* (Lemmermann) Bukry, Fur Formation, Mors, Denmark, early Eocene. **4.** Lateral view, DSDP Site 275, Campbell Plateau, SW Pacific Ocean, Late Cretaceous.

respectively. The term **abbasal** is used to refer to locations beyond the basal ring and **abbasal surface** is used for the abapical underside of the ring (Fig. 1:4).

Double skeletons, also known as **paired skeletons** or doublets (Figs 2:1–2:3), are two skeletons that remain attached at the abbasal surfaces as part of silicoflagellate cellular division and

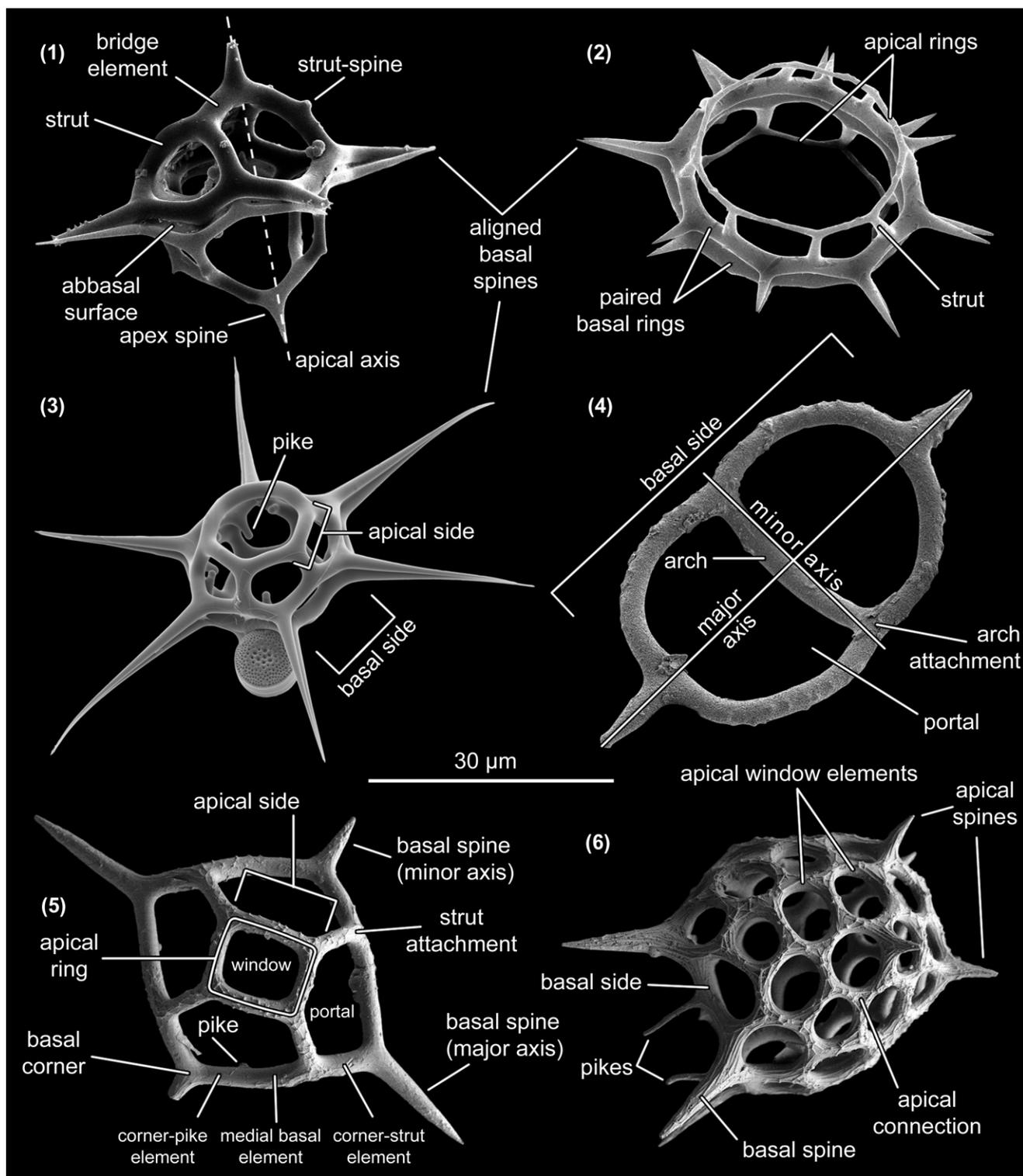


Fig. 2. SEM micrographs of double and single skeletons. **1.** Double skeleton of *Dictyochoa stapedia* Haeckel, Seto Inland Sea, Japan, Recent, lateral view. **2.** Double skeleton of *Octactis pulchra* var. *pulchra* Schiller, Seto Inland Sea, Japan, Recent, oblique apical axis view. **3.** Double skeleton of *Stephanocha speculum* (Ehrenberg) McCartney & Jordan, Southern Ocean near Australia, Recent, oblique apical axis view. **4.** *Naviculopsis lata* (Deflandre) Frenguelli, Hata Formation, Bōsō Peninsula, Japan, Miocene, abapical view. **5.** *Distephanopsis crux* (Ehrenberg) Dumitrică, Tilvici Valley, Romania, middle Miocene, apical view. **6.** *Cannopilus* sp., Tilvici Valley, Romania, middle Miocene, lateral view.

are important to the interpretation of single-skeleton structure (Dumitrică 2014; McCartney *et al.* 2014b, 2015a). The abbasal surface where paired skeletons attach may or may not be planar as some components of the basal sides can be angled slightly in an apical and abapical direction. The **apical axis** is a line perpendicular to the basal plane that runs through the centre of the apical structure and basal ring, and through the

corresponding structures of the paired skeleton (Fig. 2:1). The intersection of this apical axis and the basal plane(s) is considered to be the centre of each individual skeleton and the dividing cell bearing a double skeleton. In most cases, the radial orientation of all spines is with respect to this central point. Since doublets have two skeletons, one often in apical and the other in abapical view, the term **apical axis view** is used, or, **oblique apical axis**

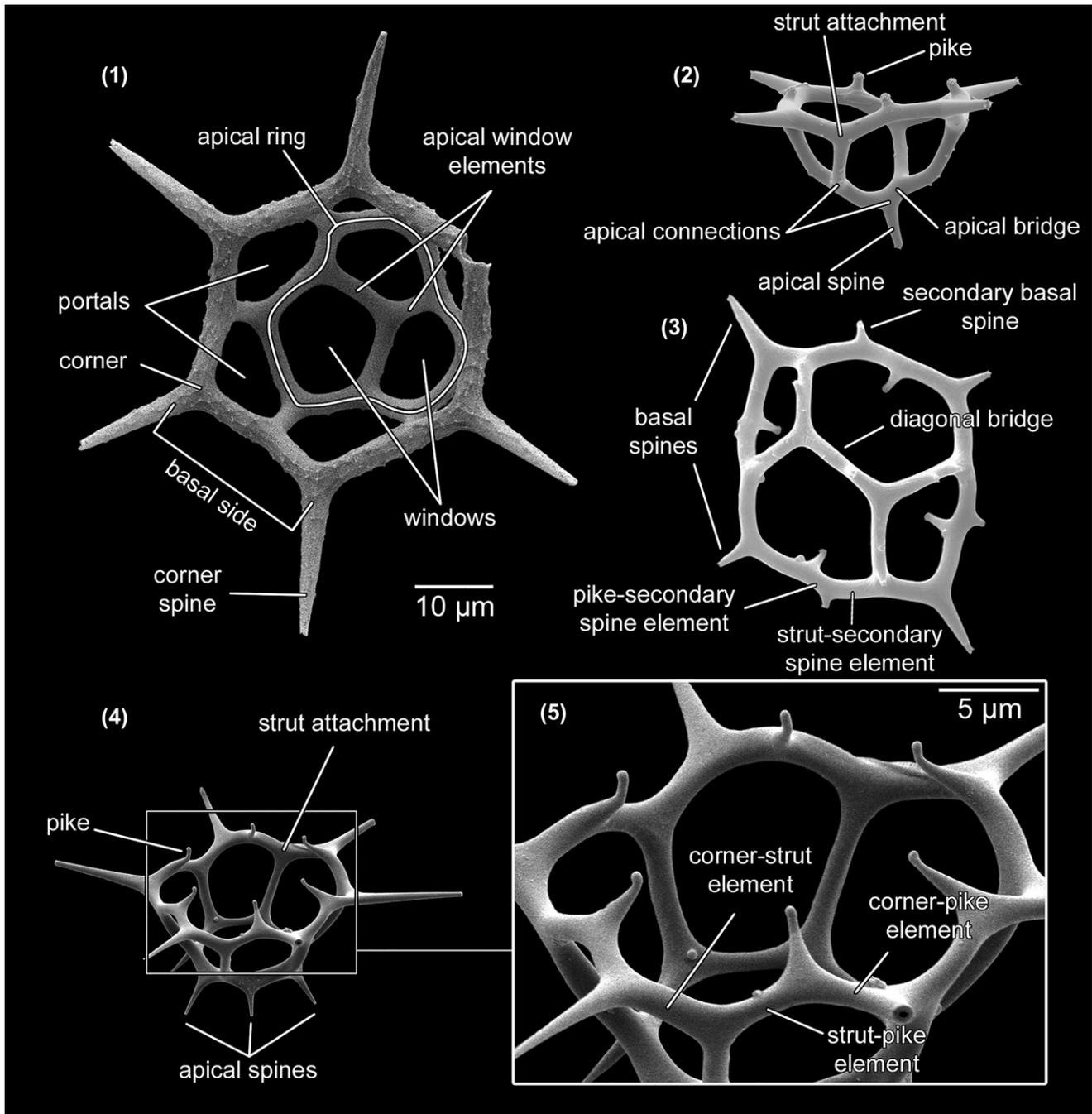


Fig. 3. SEM micrographs showing general terminology for Cenozoic silicoflagellates. **1.** *Stephanocha* sp., Kamyshlov, Russia, early Eocene, abapical view. Note the absence of pikes on the underside of the basal ring. **2.** *Dictyocha* sp., central Pacific Ocean near Hawaii, Recent, lateral view. **3.** *Dictyocha* sp. cf. *D. aculeata* (Lemmermann) Bukry, Recent, apical view. **4, 5.** *Stephanocha speculum* var. *coronata* (Schulz) McCartney & Jordan, SW Pacific, Recent, oblique abapical view.

view where the specimen is somewhat tilted (see McCartney *et al.* 2014b, 2015a).

General terminology

Any integral rod- or plate-shaped piece of a silicoflagellate skeleton can be called a **component**. Rod-shaped components have an external **thickness** that is much less than the length. Essentially all silicoflagellate components are hollow over at least some portion of their extent. Rod-shaped components are of two basic descriptions: those that are connected at both ends, here termed **elements**, and those that are terminated distally. Elements form the basal and apical structures and are connected either to two additional elements or an element and a terminated component. Short elements tend to have

linear or gently curved shapes, but longer elements may have a pronounced convex curve away from the centre of the basal plane (Fig. 2:4). Distally terminated components are known as **spines** or **pikes**, based on location and orientation. Spines most often occur at the corners of the basal ring (Fig. 1:3), known as **corner spines**, but **apical spines** may be present on the apical structure. Spines are nearly always linear, oriented radially with the distal end directed away from the cell centre and connected to two elements as part of a triple junction. Pikes differ from spines in shape, location and purpose. Flat to curved components known as **plates** (Fig. 1:1) occur occasionally on the apical structure.

While all silicoflagellate skeletal morphologies discussed in this paper have a basal ring, the term **basal structure** is also widely used. The basal structure has particular utility among Cretaceous

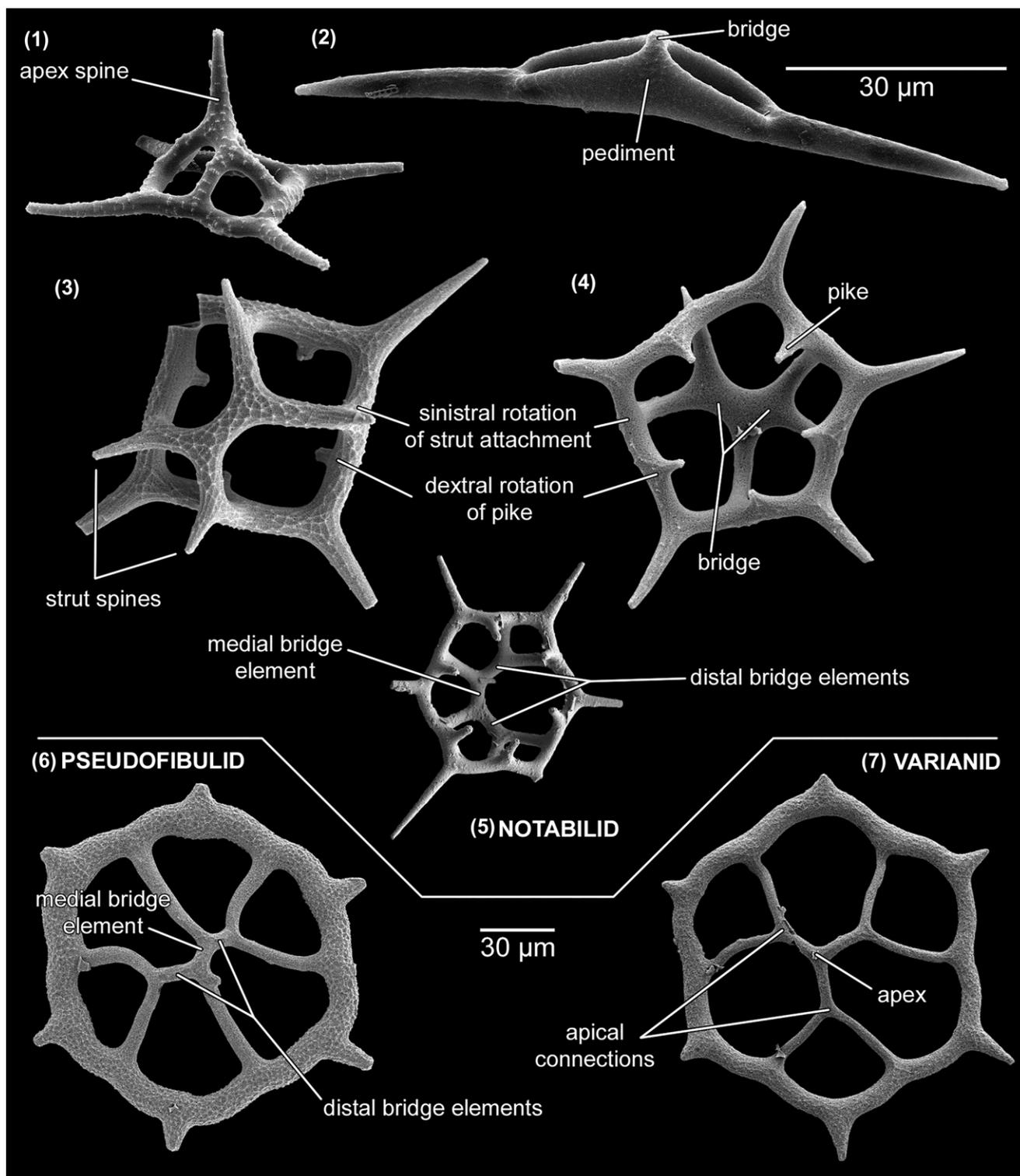


Fig. 4. SEM micrographs showing general terminology for Cenozoic silicoflagellates. 1. *Dictyocha arctios* Ling, Fur Formation, Mors, Denmark, early Eocene, oblique lateral view. 2. *Naviculopsis constricta* (Schulz) Frenguelli, Fur Formation, Mors, Denmark, early Eocene, oblique lateral view. 3. *Dictyocha frenguelli* Deflandre, Kamyshev, Russia, early Eocene, apical view. 4. *Dictyocha pentagona* (Schulz) Bukry & Foster, Kamyshev, Russia, early Eocene, abapical view. 5. *Stephanocha speculum* var. *notabilis* (Gran & Braarud) McCartney & Jordan, ODP Site 693, Weddell Sea, Miocene, abapical view. 6. *Dictyocha grandis* Ciesielski & Shaw, pseudofibulid morphotype, ODP Site 748, Southern Kerguelen Plateau, Southern Ocean, middle Eocene, apical view. 7. *Dictyocha grandis* Ciesielski & Shaw, varianid morphotype, ODP Site 748, Southern Kerguelen Plateau, Southern Ocean, middle Eocene, abapical view.

morphologies that lack a ring design, and is sometimes used here where the application is also to non-ringed morphologies (McCartney *et al.* 2014a). These evolutionarily primitive morphologies include terminated components – segments, sabatons and pike-and-spines – that are not observed in the Cenozoic, except on aberrant or teratoid specimens (Guex 2006). Some Cretaceous

morphologies require other terms, such as ‘limb’, that are not used in regard to Cenozoic silicoflagellates and thus not further discussed in this paper. The general rules and terminology reviewed and presented here, however, also apply to the Cretaceous forms.

The basal ring usually has a polygonal shape that can be elongated with a **major axis** and **minor axis**. The term **diameter** is

applied to the size of the basal or apical ring, measured across opposite corners (we measure across the triple-junction midpoints). Between adjacent basal corners is a basal side composed of a series of one or more elements that includes a single location where the apical structure **attaches** to the basal ring. Thus, the basal sides of all silicoflagellate skeletons that have a basal ring and apical structure have at least two elements, separated by an **attachment**. All other locations where skeletal components adjoin are known as **connections**.

For silicoflagellate skeletons with three or more basal sides, the apical element that attaches to the basal ring and supports any additional elements or spines that compose the apical structure is known as the **strut**, with the location where the apical and basal structure adjoin being the **strut attachment**. The number of basal sides, corners and struts are equivalent except for unusual morphologies. Apical structures exhibit a wide range of designs, from simple (Fig. 1:2 and 2:4) to more complicated (Figs 2:5 and 2:6).

Descriptive terminology

Skeletal taxonomy

Silicoflagellate taxonomy at both genus and species level is based on skeletal morphology, particularly the number of basal sides and complexity of the apical structure. Simple geometries divide the silicoflagellates into separate morphogroups that are interpreted as distinct genera. Nevertheless, taxonomic interpretation varies considerably, particularly among biologists who recognize as few as one, or as many as three, extant genera (e.g. Moestrup & Thomsen 1990; Martínez-López *et al.* 2012). While naked silicoflagellates have been described, such as *Vicicitus* of Chang *et al.* (2012), it is uncertain whether this and other taxa lack a skeleton throughout their life cycle, which, although incompletely understood, is known to include multiple naked and skeleton-bearing stages (Henriksen *et al.* 1993; Chang 2015).

In the Cenozoic, there are six diverse genera with long geological histories, listed here in the order of appearance in the stratigraphic record: three-sided *Corbisema* Hanna (Figs 1:1–1:4), elongate *Naviculopsis* Frenguelli (Figs 2:4 and 4:2), apically bridged *Dictyochoa* Ehrenberg (Figs 2:1, 3:2, 3:3, 4:1, 4:3, 4:4, 4:6 and 4:7), apically ringed *Distephanopsis* Dumitrică with four basal and apical sides (Fig. 2:5), apically ringed *Stephanocha* McCartney & Jordan with more than four sides (Figs 2:3, 3:1, 3:4 and 3:5) and *Cannopilus* Haeckel (Fig. 2:6) with complicated apical structures of more spherical shape. There are cases in which a skeletal morphology has the general appearance of one genus but actually belongs in another; an example is a group of bridged morphologies associated with *Stephanocha speculum* (Ehrenberg) McCartney & Jordan (Fig. 4:5). Not figured in this paper are skeletal morphologies that consist of a basal ring without apical structure that are commonly grouped into *Bachmannocena* Locker (see Bukry 1987: synonyms for this genus include *Mesocena* Ehrenberg, *Paradictyochoa* Frenguelli and *Septamesocena* Bachmann). Of the Cenozoic genera listed above, only *Corbisema* occurs also in the Cretaceous.

Minor Cenozoic genera include *Crassicorbisema* Ling, *Deflandryocha* Jerković, *Eunaviculopsis* Ling, *Hannaites* Mandra, *Neonaviculopsis* Locker & Martini and *Octactis* Schiller. These occur over shorter stratigraphic intervals, have uncertain taxonomic uniqueness and, except for the eight-sided *Octactis* (Fig. 2:2), are not discussed in this paper, although the morphological terms presented here also apply to these genera.

Rules of silicoflagellate skeletal design

The structural design of silicoflagellate skeletons abides by a simple set of 'rules' (McCartney & Loper 1989; McCartney & Wise 1990).

These are summarized as follows and will be applied in the following sections.

- (1) Skeletal components connect at triple junctions, with apical angles generally close to 120°.
- (2) The basal ring has thicker elements than those of the apical structure and a radial, rotational or bilateral symmetry.
- (3) One strut occurs for each basal side and the numbers of strut attachments, sides and corners are equivalent.
- (4) Basal and apical rings are complete and have the same number of sides, with the planes of both rings being parallel.
- (5) Any curvature of elements is away from the middle of the cell.
- (6) Spines are oriented radially away from the middle of the cell.
- (7) Spine lengths are proportional to major and minor axes of the basal ring and often proportional to the acuteness of the angle between the two adjoining elements.
- (8) Completely formed members of a double-skeleton pair have essentially identical features, which would include any rotation of the apical structure in relation to the basal structure.

Silicoflagellate skeletons that violate any of the above rules are generally considered to be teratoid specimens. Due to their extraordinary variability, aberrant silicoflagellate skeletons are not discussed here in the context of terminology (but see McCartney & Wise 1990). However, since the occurrences of aberrant morphologies may be of high significance in palaeoenvironmental reconstructions, we recommend that the number of aberrant specimens be included in formal counts (e.g. McCartney & Harwood 1992; Tsutsui & Takahashi 2009).

The basal ring

The basal ring occurs on all normal (i.e. non-teratoid) Cenozoic silicoflagellate skeletons, and has a polygonal to near-polygonal design with corners and sides that surround an open region known as the **basal window**. The basal plane is defined as including the basal corners, but other components of the basal sides are proximal to this. Seen from apical view, the sides can be linear or bowed convexly away from the cell centre and may be inflected inwards at the strut attachments (Figs 1:1–1:3). From lateral view, strut attachments are slightly above (i.e. in apical direction, see Fig. 1:4) and pikes slightly below (i.e. in abapical direction, Fig. 3:5) the basal plane. Corner spines are usually present and lie within or near the basal plane. Spines may not be present where basal corners are well rounded as occurs with some Cretaceous and Palaeogene *Corbisema* (Figs 1:1 and 1:2). In general, corner and other spines are longer when the angle between the two connecting elements is more acute.

Pikes are curved, trend in an abbasal direction and usually point towards the apical axis (Figs 1:2–1:4). The pike location on the basal side appears to be independent of the rule of triple junctions, as pikes may occur on the abbasal surface immediately beneath the strut attachment (Fig. 1:2). A recent paper (McCartney *et al.* 2015b) offers a terminology for diverse pike morphologies in the Eocene. Pikes appear to serve some function in holding paired skeletons together (Moestrup & Thomsen 1990) and, for some species, may support the outer cell boundary of the paired skeleton (McCartney *et al.* 2015a). However, some species of *Corbisema*, *Dictyochoa*, *Distephanopsis* and *Stephanocha* – and all non-aberrant *Naviculopsis* and *Octactis* – lack pikes (Figs 1:1, 2:2, 2:4, 3:1, 4:1, 4:2, 4:6 and 4:7).

The location of the strut attachments and associated apical structure may be rotated towards a set of basal corners. The direction of rotation is presented in relation to apical view, looking down the apical axis, unless otherwise noted. While Palaeogene silicoflagellates often have strut attachments and pikes in close proximity,

Neogene *Dictyocha*, *Distephanopsis* and *Stephanocha* often have strut attachments rotated towards the sinistral corner, whereas the pike is closer to the dextral corner (Figs 2:1, 2:5, 3:3–3:5, 4:3–4:5). Due to this rotation, the perceived skeletal design can differ according to direction of perspective (see Figs 2:1, 2:3, 2:5, 3:2–3:5 and 4:3–4:5), so apical, abapical or lateral view need to be specified for all specimens.

Where the strut attachment and pike do not occur in close proximity, the separation creates a third basal element that, together with the elements that connect to the corners, can cause the basal side to take a pronounced zig-zag shape in lateral view (Figs 2:1, 3:4 and 3:5), as elements undulate apically towards the strut attachment and abapically towards the pike. We identify the basal elements that connect to the corners as the **corner elements**, or when reference to a specific portion of the basal side is required, the **corner-strut element** and **corner-pike element**, with the element between these being the **medial basal element** (Fig. 2:5). The rotated apical structure does not occur on modern *Oectactis* (Fig. 2:2) and in various fossil specimens (e.g. Fig. 3:1), particularly where there are no pikes.

Fossil specimens of *Corbisema*, *Naviculopsis* and some *Dictyocha* have basal elements that curve away from the centre of the basal ring, but modern species tend to have more linear elements, with flexure of the basal sides accommodated by angular junctures where basal elements adjoin the struts and pikes (Figs 2:1, 3:2, 3:5 and 4:5). For some morphologies, such as the Pleistocene *Dictyocha aculeata* (Lemmermann) Dumitrică (Fig. 3:3), a portion of the basal side may be divided by a triple junction that includes a **secondary spine**, which can break the basal side into four elements. The secondary spine between the strut and pike junctures establishes the **strut-secondary spine element** and **pike-secondary spine element** (Fig. 3:3). For Eocene *Corbisema hexacantha* (Schulz) Perch-Nielsen and Miocene *Distephanopsis stauracantha* (Ehrenberg) Dumitrică, the secondary spines may be of lengths equivalent to corner spines.

The basal sides are usually of equivalent lengths, with the angles at the basal corners also being equivalent. Thus, the basal rings of many *Corbisema* species have an isosceles shape; however, *C. hastata* (Lemmermann) Frenguelli and other species have two longer **major basal sides** and a short **minor basal side** (Fig. 1:3). The minor axis corner spines are in some subspecies not oriented radially, and rare doublets show each skeleton to be flipped 180° with respect to the other (McCartney *et al.* 2015c).

The apical structure

The apical structure comprises a system of skeletal elements that construct a dome-shaped latticework of triple junctions. The interconnected elements enclose openings in the latticework known as **portals** when these abut the basal ring and **windows** when they are surrounded by apical elements (Fig. 3:1). The triple junctions formed by these elements have angles that are more equivalent, and generally near 120°, where the thickness of the components is equivalent near the juncture (e.g. Fig. 3:1). The angles are less equivalent when the thicknesses are unequal, as often occurs where the strut and pikes adjoin the basal ring (Figs 2:5, 3:1 and 3:3).

The simplest apical structure is the arch-shaped component that extends across the minor axis of the spindle-shaped *Naviculopsis* (Figs 2:4 and 4:2). There has, however, not been any detailed morphological study of the group and we find the term most often applied to this structure, the **band** (Bukry 1976a), to inadequately communicate the range of common morphologies. We suggest the new term **arch** for a thin element that connects across the minor axis, with the juncture of the arch and basal ring being the **arch attachment** (Fig. 2:4). We use the term **pediment** for a broad base

that supports an arch (Fig. 4:2). The term **band** would be applied to a curved plate that is more expanded along the major axis, such as occurs with *N. constricta* (Schulz), *N. foliacea* Deflandre or *N. nordica* Bukry (see Bukry 1976b, pl. 2; McCartney & Wise 1987, pl. 5; Ciesielski 1991, pls 9, 10). The midpoint of the arch, which is also the highest point above the basal plane, is the **apex**. An **apex spine** occurs on some *Naviculopsis* species, with an extreme example being *N. trispinosa* (Schulz) (see Perch-Nielsen 1975, pl. 13), which has an apex spine of length equivalent to the corner spines. It is worth noting that *Naviculopsis* includes a wide range of unusual apical structures (e.g. Ciesielski 1991).

Corbisema, *Dictyocha*, *Distephanopsis*, *Stephanocha* and *Cannopilus* consistently have struts that attach to the basal ring and on the apical ends can either: (1) meet at an apex (*Corbisema*), (2) meet to support a bridge (typically, *Dictyocha*), (3) meet two elements that are part of an apical ring (*Distephanopsis*, most *Stephanocha*) or (4) form a more complicated structure (*Cannopilus*). Of these, the three-sided *Corbisema* has the simplest apical structure as the three struts meet at an apex that does not include a spine, although there may be an apical plate (Fig. 1:1). A **bridge** is a series of one or more apical elements that connect the struts and extend across the central region of the skeleton. Among the four-sided *Dictyocha*, the bridge has a linear shape when observed from apical view that is always located immediately above the centre of the basal plane. From lateral view the bridge may take the shape of a single, rather flat-lying element, or can consist of two elements that are inclined apically to meet at an apex where an apex spine completes a triple junction (Fig. 4:1). A spine can also occur on the strut, known as a **strut spine** (Fig. 4:3), although such spines are unusual. The basal ring often has a rhomb-shape in apical view, with a major and minor axis, and the bridge can have various orientations, as will be presented below. For five-sided morphologies, two bridge elements often form a triple junction with a strut (Fig. 4:4). There is a particularly wide range of bridge morphologies that can include considerable variation within a species, among silicoflagellates that have more than five basal sides.

The terms ‘asperid’ and ‘fibulid’ have been applied to describe the orientation of the bridge of four-sided *Dictyocha*, but have become ambiguous and should no longer be used. Asperid (named after *D. aspera* Lemmermann), as originally used, has a bridge aligned with the basal ring minor axis. Fibulid (named after *D. fibula* Ehrenberg), as originally used, has a bridge aligned with the basal ring major axis. ‘Aculeatid’ (named after *D. aculeata* Lemmermann) has been used for bridges diagonal to both axes (Fig. 3:3). However, based on a study of Ehrenberg materials, Locker (1974) assigned an asperid lectotype to *D. fibula*. Some workers have followed this change (e.g. Locker & Martini 1986; McCartney *et al.* 1995), while others have not. Also, there is no consistent use of *D. aculeata* as some workers use *D. mandrai* Ling for what may be the same species. For four-sided *Dictyocha* with bridges parallel to the minor, major or diagonal to both axes, we suggest descriptive reference to **minor-axis-bridged**, **major-axis-bridged** and **diagonally-bridged** morphologies.

Variant apical bridges are also known. For six-sided varieties of *Stephanocha speculum* that make up the late Miocene *pseudofibula* plexus (McCartney & Wise 1990), bridges can consist of three elements. These morphologies, which we now refer to as ‘plexids’, are also commonly observed for *Dictyocha grandis* in the middle Eocene (Witkowski *et al.* 2012) and occur elsewhere as well. The three distinct morphotypes ‘pseudofibulid’, ‘notabilid’ and ‘varianid’ (Figs 4:5–4:7) make up most of the plexid variability. The bridge of the pseudofibulid morphotype has a series of three elements of which the middle element, here termed the medial bridge element, goes over the mid-point of the basal ring and is thus on the apical axis with the connecting struts attaching to opposite sides of the basal ring (Fig. 4:6). Notabilid morphotypes (Fig. 4:5)

have the medial bridge element not centred over the middle of the basal plane and connecting struts attach to adjacent sides (Fig. 4:5). The varianid morphotype has three bridge elements that meet at an apex (Fig. 4:7) immediately above the centre of the basal ring and is the only apical structure that includes a triple junction made exclusively of bridge elements.

Species of *Distephanopsis*, *Octactis* and *Stephanocha* are generally characterized by a series of elements that form an **apical ring**. The ring has a polygonal shape similar to the basal ring that is made of **apical sides** that meet at **apical corners**. The corners lie within an **apical plane** that is parallel to the basal plane. An apical side can have a single **apical ring element** or two elements that form a triple junction with an apical spine. For most *Distephanopsis* and *Stephanocha*, the elements that compose the apical structure are of generally equivalent thicknesses and the struts are inclined towards the apical axis to support an apical ring that is smaller than the basal. *Octactis* has an unusual skeletal morphology in which the struts are nearly perpendicular to the basal plane, and have a thickness that decreases towards the apical ring, which is thus of relatively large diameter but made of thin elements.

The terminology presented thus far for elements of the apical structure includes struts and those elements that compose the bridge or apical ring. Some *Stephanocha* morphologies have an apical ring that is subdivided into two or more windows; this group is commonly called ‘cannopilid’ (Fig. 3:1, see also Bachmann 1970, pls 6, 7; McCartney & Wise 1990, pl. 4). To accommodate these more complicated apical structures, elements that subdivide the apical structure into multiple windows are here presented as **apical window elements**. We offer no more specialized terminology for these elements, but for subdivided apical rings on *Stephanocha*, the terms ‘apex’ and ‘bridge’ can be used; the term ‘strut’ cannot be used as this applies exclusively to elements that attach to the basal structure.

Cannopilus (Fig. 2:6; also called *Caryocha*, see Bukry & Monechi 1985) has a considerably more complex apical structure composed of many elements. The overall shape of the skeleton is often more spheroidal, with an apical diameter that can be larger than that of the basal ring. Unlike multi-windowed skeletons of *Stephanocha* (see Bachmann 1970, pls 6, 7; McCartney & Wise 1990, pl. 4), *Cannopilus* does not have a system of elements that form a distinct apical ring; instead there is a single ring of portals adjacent to the basal ring, and numerous, often undifferentiated windows in the apical structure (Fig. 2:6). Here, all elements that compose the apical structure except the struts can be identified as apical window elements.

Double skeletons

Recent work on double skeletons (McCartney *et al.* 2014b, 2015a) identified the need for additional terminology. Double skeletons develop sequentially and thus consist of a **mother** and **daughter** skeleton. While these are oftentimes indistinguishable, in some cases one skeleton has thicker elements or basal spines and is interpreted as being the older (mother). For the *Dictyochoa* double skeleton illustrated here (Fig. 2:1), the skeleton with thicker skeletal elements (top part of illustration) may be interpreted as the mother and the lower skeleton as the daughter. While the terms ‘sibling’ (McCartney *et al.* 2014b) and ‘partner’ (Boney 1981) have been previously used, we now recommend reference to the **paired skeleton** where the mother and daughter cannot be interpreted.

Fossil double skeletons with basal rings are now known to occur in two distinct configurations. Skeletons that have basal rings of similar orientations that are more or less connected at the corners, which includes all modern silicoflagellates, are referred to as the corner-aligned configuration (McCartney *et al.* 2014b; Figs 2:1–2:3). In contrast, the Star-of-David configuration (McCartney *et al.*

2010) has the basal corners of each skeleton rotated to be midway between the corners of the paired skeleton and represents a group of silicoflagellates that is believed to have become extinct in the Oligocene (McCartney *et al.* 2015a).

Discussion

The past few years witnessed a considerable revival in silicoflagellate studies: a wealth of new data from fossil deposits of various ages has been made available (McCartney *et al.* 2011, 2014a; Witkowski *et al.* 2012) and long-standing taxonomic issues have been successfully resolved (Jordan & McCartney 2015). New insights have provided improved understanding into the cell structure and biology of modern silicoflagellates and closely related taxa (Chang *et al.* 2012; Chang 2015) and double skeletons (McCartney *et al.* 2010, 2014b, 2015a, c; Dumitrica 2014; Abe *et al.* 2015). Even a superficial reading of this new literature demonstrates the need for a consistent and updated terminology for the description of silicoflagellate skeletons, which can be applied to both fossil and living taxa.

The purpose of this work is to review the existing silicoflagellate descriptive terminology, make the necessary amendments and propose new terms either for specific elements previously not identified, or that we found were dealt with in a manner that lacked precision. Any terminology needs to be communicative, which in turn is a compromise between the level of detail and utility. We see no point in attempting to name every single component of a silicoflagellate skeleton. Especially in the extremely complex morphologies, such as the cannopilids, terms could be multiplied *ad infinitum*; the utility of such terms, however, would be limited.

Whether the terminology reviewed and put forward here becomes successful will need to be verified by future studies; we realize some of the terms proposed here, especially the very specialized ones differentiating the basal ring into elements located between struts and pike attachments, etc., will likely remain restricted to highly specialized studies, e.g. mathematical modelling of silicoflagellate skeletons. It is our sincere hope, however, that these propositions will be worked upon and added to, and in the long perspective will help to improve the sometimes deficient communication between scientists working with silicoflagellates.

Glossary

The original source of a term is listed unless there is a well-established convention; synonymous terms are also provided.

Abapical (Marshall 1934, also known as basal): In a direction away from the apex and towards the basal ring. **Abapical view** is the point of perspective that has the basal structure nearest and the apex furthest from the observer.

Abbasal (McCartney *et al.* 2014b): In the portion of the basal structure furthest from the apex. The **abbasal surface**, for example, occurs at the points of connection or between members of a paired skeleton. Also, in a direction or region abapical of the basal ring.

Apex (McCartney 1988): The point on an element or connection of elements that is located directly above the middle of and furthest from the basal plane. Two elements may connect with an **apex spine** at this location.

Apex spine (McCartney *et al.* 2014b): A spine that occurs at the apex of the apical structure, and is usually aligned with the apical axis. Synonymous terms include ‘accessory spine’ (Gleser 1966) and ‘spire’ (Bukry 1976a).

Apical: Related to a system of elements that form a dome-shaped framework known as the **apical structure** that is attached to the basal ring. Also, in the direction towards the apex, which is the point

on the skeleton furthest from the basal plane. **Apical view** is the point of perspective that has the apex nearest the observer.

Apical axis (McCartney *et al.* 2014a, b): An imaginary line that goes through the middle of both members of a double skeleton, and is perpendicular to the basal plane. **Apical axis view** is the point of perspective that has the two members of a double skeleton, one in apical and the other in abapical view.

Apical ring: System of elements that form a ring and are attached to the basal ring by struts. Associated terms include **apical side**, **apical corner**, **apical plane**, **apical ring element** and **apical ring spine**.

Apical window elements (this paper): Elements that abapically connect to the apical ring. Synonymous term is ‘Apikalstäbe’ (Gemeinhardt 1930). These may meet at an apex, support a bridge or form a complicated design with many windows.

Arch (this paper): An element that extends across the minor axis of the basal ring in *Naviculopsis*. The apex of the arch is above the middle of the basal plane. The arch is equivalent to the strut of other basal-ringed skeletons, but extends across the minor axis corners without required additional apical elements or a triple junction.

Arch attachment (this paper): The location where the *Naviculopsis* arch adjoins the basal ring.

Attach/attachment (McCartney 1988): Applies to the location where the apical and basal structures adjoin (e.g. **strut attachment** or **arch attachment**).

Band (Bukry 1976a): A curved plate that extends across the minor axis of *Naviculopsis*, having an apex that is expanded in the major axis direction to be significantly wider than the basal elements. Synonymous term is ‘apical plate’ (Gleser 1966).

Basal: Related to a system of skeletal components that are furthest from the apex, and part of the basal ring or basal structure. Also, a synonym for abapical, that shows direction or view away from the apex.

Basal corner: Sharp angle or change in curvature that separates a system of elements that make up the side of the basal ring. The basal corner is often a junction of two basal ring elements and a **corner spine**.

Basal plane (McCartney *et al.* 2014b): Plane that connects the corners of the basal ring.

Basal ring: System of elements that form a ring, to which the apical structure is attached, and that provides the surface to which a similar ring of a paired skeleton may be joined. Also known as the **basal structure**.

Basal side: System of one or more elements on the basal ring that connect the basal corners. Synonymous terms include ‘basal rod’ (Gleser 1966) and ‘Basalbögen’ (Stradner 1961). The elements that connect between the corners, struts, pikes, secondary spines and arch can be individually identified as the **corner-strut element**, **corner-pike element**, **medial basal element**, **pike-secondary spine element**, **strut-secondary spine element** and **corner-arch element** (all terms from this paper). In the case of a ‘hastatid’ *Corbisema* skeleton (Fig. 1:3) the basal sides can be differentiated as a **minor basal side** (shorter) and two **major basal sides** (longer).

Basal window (Gleser 1966): The region within the basal ring that lacks skeletal components.

Bridge (Poelchau 1976): Apical element or series of elements that abapically connects to other apical elements and extends across the apex region of the skeleton. Most typically supported by struts but the term can be applied to elements that connect across an apical ring. Synonymous terms include ‘Diagonaler’ (Gemeinhardt 1930), ‘central arch’ (Marshall 1934), ‘apical rod’ (Gleser 1966), ‘apical bar’ (Ling 1972) and ‘bar’ (Bukry 1976a). The bridge can have **major-axis-**, **minor-axis-** or **diagonally-bridged** alignments (all terms, this paper).

Component (McCartney *et al.* 2014a): Any integral portion of the silicoflagellate skeleton, connected to other components.

Connect/connection: Applies to the location where skeletal components of the apical or basal structures adjoin. Locations between apical and basal structures are termed attachments.

Corner: See apical corner, basal corner.

Corner element (this paper): Any element that connects to the corner of a basal or apical ring. The **corner-pike element** and **corner-strut element** are associated with the pike and strut, respectively.

Diameter: Distance across the apical or basal ring, usually measured across the triple-junction midpoints of the major and/or minor axis.

Double skeleton (also known as a doublet or paired skeleton): Two skeletons connected at the abbasal surfaces, in a position prior to cellular division. The first formed skeleton, if this can be interpreted, is the **mother** and the second, the **daughter**. Each is the **paired skeleton** of the other.

Element (McCartney *et al.* 2014a): A component between two triple junctions that makes up a portion of the basal or apical structure.

Lateral view: Perspective where the observer is positioned on or near the basal plane.

Major axis: Where the basal ring has an elongated shape, the line that connects the two opposite basal corners that are furthest apart. For *Corbisema* and other morphologies with an odd number of sides, the longest line that connects a basal corner with the midpoint of an opposite basal side.

Major basal side: For an elongated *Corbisema* basal ring, one of two sides that connect with the major axis. Term can also be applied to any of the four sides that connect to the major axis of *Stephanocha*.

Medial basal element (this paper): The element that is bounded by the locations where the pike and strut adjoin the basal ring.

Minor axis: The line that connects opposite basal corners that are separated by a shorter distance than those that determine the major axis. For *Naviculopsis*, *Distephanopsis* and four-sided *Dictyocha*, the minor axis is perpendicular to the major axis. For six-sided *Stephanocha*, there are two minor axes, each located at about 60° relative to the major axis.

Minor basal side: For *Corbisema* and other odd-sided morphologies, the short basal side that is perpendicular to the major axis. Can also be applied to any of the sides associated with the minor axis of six- and eight-sided morphologies.

Oblique apical view or **oblique abapical view**: Perspective with the apical or basal structure nearer to the observer, respectively, but the apex not being the nearest or furthest. **Oblique apical axis view** is applied to a doublet that is tilted less than 45° with respect to the observer.

Oblique lateral view: Perspective where the basal plane is inclined and elements of the basal ring are nearer than the apex to the observer.

Pediment (this paper): An arch attachment that is expanded near the basal ring (Fig. 4:2).

Pike (Bukry 1976a): Terminated component that points in general direction of paired skeleton of a doublet. Located on abbasal surface of basal element. Synonymous terms include ‘centripetal tooth’ (Haeckel 1887), ‘Stützstachel’ (Lemmermann 1908), ‘subordinate radial spine’ (Poelchau 1976) and ‘basal accessory spine’ (Ling 1972).

Plate (Mandra 1968): Broad continuous surface at the apex; occurs on silicoflagellate skeletons from the Late Cretaceous to Eocene.

Portal (Bukry 1976a): The space between the basal ring and elements of the apical structure, bounded in part by basal elements and struts. Synonymous terms include ‘Basalfenster’ (Lemmermann 1908) and ‘lateral window’ (Ling 1972).

Secondary spine (this paper): Spine that occurs along a basal side (Fig. 3:3), usually between the strut attachment and major axis corner and associated with morphologies that have considerable

rotation of the apical structure (*Dictyocha aculeata* Lemmermann, *Distephanopsis stauracantha* (Ehrenberg) Dumitrică). Synonymous term is 'subordinate radial spine' (Poelchau 1976).

Spine: Terminated component that is usually oriented radially with respect to the centre of the basal plane. Spines are often identified by location such as the **corner** (basal) **spine**, **apical spine**, **strut spine**, **apical ring spine** or **apex spine**. Synonymous terms for corner spine include 'radial Stachel' (Lemmermann 1908) and 'radial horn' (Deflandre 1950); for apical spine synonymous terms include 'accessory spine' (Gleser 1966) and 'apical pike' (Bukry 1976a); for apex spine a synonym is 'spire' (Bukry 1976a).

Strut (Bukry 1976a): Element that joins the apical structure to the basal structure, at strut attachment (McCartney 1988). Synonymous terms include 'Basalstäbe' (Lemmermann 1908), 'supporting bar' (Marshall 1934) and 'lateral rod' (Gleser 1966). The strut can include a **strut spine** (Onodera & Takahashi 2009).

Strut attachment (McCartney 1988): Juncture of a strut to the basal structure.

Thickness: The external diameter of a skeletal component. For an apical plate, the thickness would be measured in the direction of the centre of the basal plane.

Window (Lemmermann 1908, as 'Apicalfenster'): Opening in the apical structure bounded by apical elements, or subdivided portions, but not in contact with the basal ring. Synonymous term is 'apical opening' (Bukry 1976a).

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