Ben A. LePage[1]: A classification system to separate leaves of the Cephalotaxaceae, Taxaceae, and Taxodiaceae

Abstract　The identification and classification of isolated fossil leaves of the Taxodiaceae is generally difficult when the remains are not associated with reproductive organs. These problems are further exacerbated when more than one genus of the Taxodiaceae and/or genera of the Taxaceae or Cephalotaxaceae are preserved in the same deposits or the quality or mode of preservation precludes confident identification. To help facilitate the identification and separation of isolated taxodiaceous fossil leaves, the leaves of extant representatives of *Cephalotaxus* Siebold et Zuccarini ex Endlicher, *Glyptostrobus* Endlicher, *Metasequoia* Hu et Cheng, *Sequoia* Endlicher, *Taxodium* Richard, *Taxus* L., and *Torreya* Arnott were examined. The results of this investigation provided sufficient data about external morphological features to establish a system of classification for leaves that could be used to assist in the identification and classification of isolated fossil leaves.

Introduction

The identification of the living representatives of the Taxodiaceae (now subsumed within the Cupressaceae) is based on a whole-plant concept, utilizing an approach that recognizes significant morphological features such as the shape, architecture, and age of the tree; leaf arrangement on the leading and lateral branches; leaf morphology; and the size and shape of the seed cones (Silba, 1986; Rushforth, 1987; Wu & Raven, 1999; Farjon, 2005). Regardless of the features used, perhaps the single most useful feature that facilitates species identification, description, and classification among the conifers is seed cone morphology (Matsumoto et al., 1997; Aulenback & LePage, 1998; LePage, 2001, 2003). Whereas leaf morphology alone can sometimes be valuable, the identification and classification of isolated leaves that are preserved as compression fossils is generally difficult in taxa where leaf polymorphism is prevalent. Among the genera of the Taxodiaceae, leaf polymorphism is present in *Glyptostrobus* Endlicher, *Metasequoia* Hu et Cheng, *Sequoiadendron* Buchholz, *Sequoia* Endlicher, *Taiwania* Hayata, and *Taxodium* Richard (Brown, 1936; Bůžek, 1971; Christophel, 1976; Farjon, 2005).

Although this is not necessarily problematic when working with living representatives, variation in leaf morphology together with preservation quality further contribute to the difficulty of correctly identifying fossil leaves that are not associated with reproductive organs. Such difficulties are further amplified when several taxa that are known to produce polymorphic leaves are preserved as part of the same floristic assemblage. As a result, the paleobotanical literature is rife with morphospecies names that are based on isolated leaves that were incorrectly identified (Heer, 1868–1878; Chaney, 1951; LePage et al., 2005; LePage, 2007). This however does not mean that misidentified specimens have no taxonomic and phylogenetic value. On the contrary, the reassessment of fossil leaves and their extant counterparts may often reveal morphological and anatomical features that were previously overlooked as being diagnostic (Matsumoto et al., 1994, 1995; Stockey & Ko, 1986; Stockey & Atkinson, 1993).

The problem of correctly identifying fossil taxodiaceous leaves is not unique to any generation of paleobotanists and the uncertainty of identifying isolated leaves extends to the earliest plant classification systems. Brongniart established the genus *Taxites* Brongniart for fossil leaves that were "analogous in part to the yews and *Podocarpus*, while in other cases they could not be separated from the yews or *Taxodium*" (Brongniart, 1828, p. 101), while Presl created the genus *Taxodites* Presl for "distichous twigs and leaves strongly analogous to those of *Taxodium*" (Presl in Sternberg, 1838, p. 204). Chaney (1951, p. 174) also recognized this problem and stated that "As far back as the middle of the past century, fossil foliage of Sequoia has been confused with that of *Taxodium*. During all

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that time, leafy shoots and cones which we now consider referable to *Metasequoia* have been assigned to *Sequoia*; in many instances foliage specimens identified as *Taxodium* also show *Metasequoia* characters". Thus it is important to recognize that fossil plants have and will continue to be misidentified, and periodically new information comes to light that allows some of the misidentified specimens to be correctly identified and classified.

The creation of the fossil genus *Metasequoia* (Miki, 1941) and the discovery of *Metasequoia glyptostroboides* Hu et Cheng (Hu & Cheng, 1948) in China is one such case in point. Based on these new data Chaney (1951) recognized major differences in leaf morphology and developed a system of classification for separating western North American fossil *Sequoia*, *Taxodium*, and *Metasequoia* leaves from one another. Chaney considered the leaves of *Glyptostrobus* to be more recognizable and less easily confused compared to those of *Sequoia*, *Taxodium*, and *Metasequoia* and did not consider *Glyptostrobus* further in his analysis as he considered Brown's (1936) revision of *Glyptostrobus* satisfactory.

Christophel (1976) later recognized certain limitations with Chaney's approach. His assessment of Chaney's distinguishing characters indicated that many features of the short shoots and leaves are questionable (leaf disposition, leaf dimorphism, stem thickness of the short shoots, and phyllotaxy), not good (persistence of the short shoot), not distinguishing (shape of the leaves—acicular and morphology of the leaf tip), or variable (leaf angle divergence from stem, appearance of the midrib, and basal dark spot). Of the foliar characteristics that were assessed he considered the mode of

leaf attachment to the stem to be very important. His primary criticism however, was the omission of *Glyptostrobus* from the Chaney's identification system given that Christophel did not consider Brown's case for the uniqueness of *Glyptostrobus* foliage to be particularly strong. In fact Brown (1936, p. 354) warned that the "detection and separation of the fossil representatives of *Glyptostrobus* is fraught with considerable uncertainty. This is particularly true when foliage is only available. In the living species this may be of three kinds – cupressoid, taxodioid, and cryptomeroid, in allusion to the typical foliage, respectively, of *Cupressus*, *Taxodium*, and *Cryptomeria*. A given fossil shoot or twig with this range might therefore merit any one of the four interpretations, let alone being confused with other genera such as *Sequoia*, *Cunninghamia*, *Torreya*, *Juniperus*, *Tsuga*, etc. Because of the uncertainty concerning the identity of such twigs as are ordinarily preserved in shale and sandstone, those recorded fossil species of *Glyptostrobus* based on foliage alone will be regarded as doubtful identifications." As such, Christophel expanded on Chaney's system of classification to include *Glyptostrobus* as well as the characters that he deemed to be diagnostic among the four genera that he examined.

In this paper the classification system developed by Chaney (1951) and expanded upon by Christophel (1976) to separate leaves of extant *Glyptostrobus*, *Sequoia*, *Taxodium*, and *Metasequoia* is further expanded to include the leaves of *Taxus* L., *Cephalotaxus* Siebold et Zuccarini ex Endlicher, and *Torreya* Arnott. The intent of this classification system is to help facilitate the identification and separation of isolated fossil leaves, for these latter taxa are also known to coexist

a. Leaves opposite .... *Metasequoia*
a. Leaves alternate .... b
  b. Leaves not petiolate, not narrowed at base c
  b. Leaves petiolate or appearing petiolate, narrowing at base .... d
    c. Decurrent leaf bases prominent, obliquely joined, trending obliquely along stem .... *Sequoia*
    c. Decurrent leaf bases not prominent, squarely joined (perpendicular), trending parallel along stem .... *Glyptostrobus*
      d. Decurrent leaf bases prominent along stem .... e
      d. Decurrent leaf bases not prominent, squarely to obliquely joined, trending parallel along stem .... *Taxodium*
        e. Decurrent leaf base prominent, obliquely joined, trending parallel or slightly obliquely along stem .... f
        e. Decurrent leaf bases prominent, obliquely joined, trending obliquely along stem .... *Metasequoia*
          f. Joint between leaf base and stem narrow, abscission zone not visible,
              leaves generally greater than 2 cm long .... *Cephalotaxus*
          f. Joint between leaf bases and stem narrowed, abscission zone visible .... g
            g. Leaves generally 2-3 cm long .... *Taxus*
            g. Leaves often appearing opposite, 2-8 cm long, leaves sharply acuminate .... *Torreya*

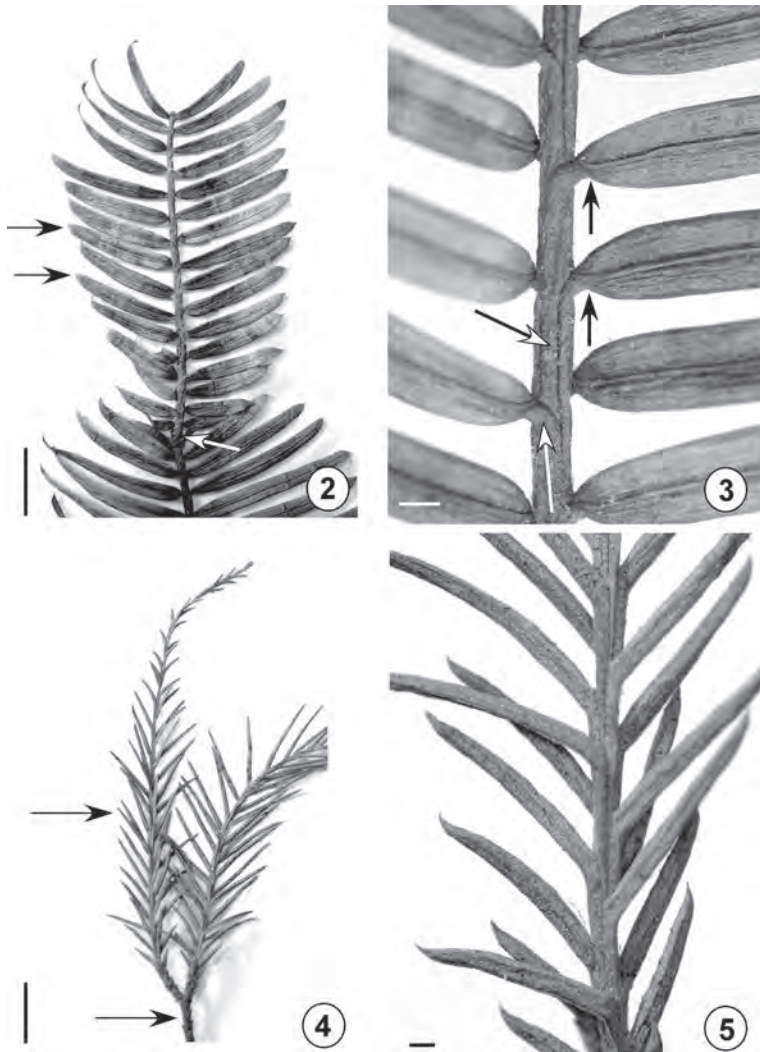**Fig. 1** Extant leaf key of select genera of the Cephalotaxaceae, Taxaceae, and Taxodiaceae.

Fig. 2 Adaxial view of the leaves of *Cephalotaxus harringtonia* var. *drupacea* (Siebold et Zuccarini) Koidzumi. The most recent year's needle-like leaves are borne on a shoot that extends from the apex of the previous year's growth (white arrow). Scale leaves are located at the base of the shoot bearing the most recently produced shoot. Note the mucronate apices (black arrows). Scale bar = 1 cm.

Fig. 3 Closeup of the adaxial surface of *C. harringtonia* var. *drupacea* needle-like leaves showing the short, 1 mm long petiole that is twisted (white arrow) and decurrent leaf bases that trend parallel along the stem (black arrow with white head). Note that the abscission zone where the petiole joins the leaf (black arrows) is not visible as is the case in *Taxus* and *Torreya*. Scale bar = 1 mm.

Fig. 4 Leaves of *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch showing the cupressoid and crypto-cupressoid leaves (basal arrow) that grade into the cryptomeroid and crypto-taxodioid leaves (upper arrow). Scale bar = 1 cm.

Fig. 5 Closeup of the cryptomeroid leaves of *G. pensilis* showing the squarely attached leaves that depart from the stem at an angle of about 40° and the decurrent leaf bases trend parallel along the stem. Note the mucronate leaf apices. Scale bar = 1 mm.

with the representatives of Taxodiaceae throughout the Northern Hemisphere during the Late Mesozoic and Cenozoic fossil record, and as pointed out by Brown (1936), Chaney (1951), Bůžek (1971), and Christophel (1976), isolated fossil leaves can be easily confused with one another.

Description of the Leaves

The information used to derive the leaf key illustrated in Fig. 1 was based in part, on the morphological descriptions provided by Farjon (2005), the features deemed to be diagnostic by Chaney (1951) and Christophel (1976), and personal observations. At this time the information used to expand this classification scheme is limited to external morphological features. Although anatomical features typically provide additional useful classification features, the inability to obtain useful cuticle from many fossils limits the utility of developing a classification scheme based solely on anatomy. Nevertheless, this does not preclude the inclusion of anatomical features being added to this classification scheme in the future. The locations of the living specimens used in this study are provided in Appendix 1.

Cephalotaxus (Figs. 2 and 3) — Leaves dimorphic with the scale leaves borne in a cluster at the base of shoot and needle-like leaves borne along the shoot. The scale leaves are 0.5 to 1 mm long and 0.5 to 1 mm wide, keeled, and with acute apices (Fig. 2). The needle-like leaves are helically arranged along the stem, distichous, linear-lanceolate to broadly acute and may be slightly falcate, and with a prominent midrib adaxially and abaxially. Their apices are bluntly to narrowly acute to acuminate to mucronate. They range in length
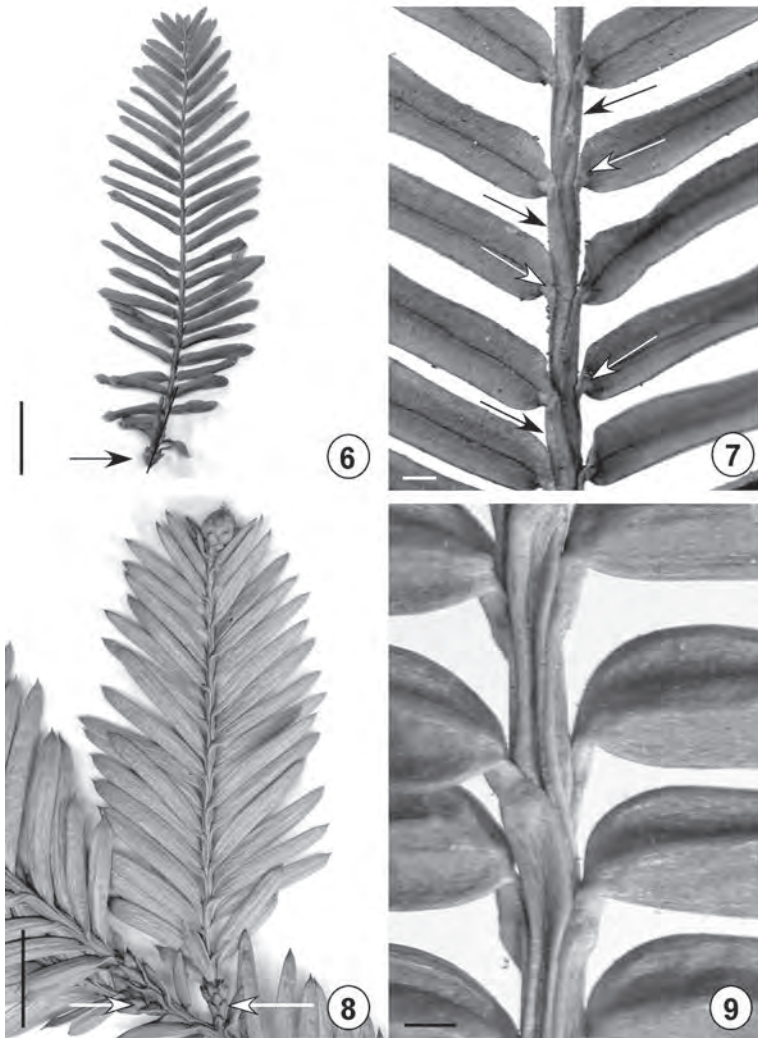
Fig. 6 An adaxial view of a deciduous shoot of *Metasequoia glyptostroboides* Hu et Cheng showing the basal cluster of cupressoid leaves (arrow) and taxodioid leaves. Scale bar = 1 cm.

Fig. 7 Closeup of the abaxial surface of a deciduous shoot of *M. glyptostroboides* showing the bases of the taxodioid leaves attached to the stem. The decurrent leaf bases are oriented obliquely to the long axis of the stem (black arrows). Note the location of the abscission zone (white arrows). Scale bar = 1 mm.

Fig. 8 An adaxial view of the leaves of *Sequoia sempervirens* (D. Don) Endlicher showing the basal cluster of cupressoid leaves (arrow) and taxodioid leaves. Note the mucronate leaf apices. Scale bar = 1 cm.

Fig. 9 Closeup of the adaxial surfaces of the *S. sempervirens* taxodioid leaves showing the leaf bases that are attached obliquely to the stem and the decurrent leaf bases that are oriented obliquely to the long axis of the stem. Scale bar = 1 mm.

from 20 to 130 mm and 2.0 to 4.5 mm in width. Basally the leaves become narrow and appear acute to round. The leaves and are borne on a short, 1 mm long petiole that gives the appearance that the leaves are sessile (Fig. 3). The petiole is joined to the stem obliquely (twisted) and the abscission zone between the petiole and leaf base is not visible. The decurrent portion of the petiole is prominent and trends parallel along the stem. Abscised leaves are acutely rounded basally (no part of the petiole is shed) and the abscission zone is inconspicuous

Glyptostrobus (Figs. 4 and 5) — Leaf morphology ranges from cupressoid, cryptomeroid, to taxodioid types with intermediate forms (crypto-cupressoid and crypto-taxodioid) present. As noted by Christophel (1976) many of the fossil leaves from the Paleocene Smoky Tower locality in Alberta, Canada that he stud-

ied did not fit into the three defined categories (cupressoid, cryptomeroid, to taxodioid), but rather the leaves spanned the continuum of *Glyptostrobus* leaf morphotypes, including the intermediate forms. The leaves examined in this study also span a continuum that includes cupressoid, crypto-cupressoid, cryptomeroid, and crypto-taxodioid. No leaves in the collection could be classified as being exclusively taxodioid. Farjon (2005) notes that the cryptomeroid / crypto-taxodioid leaves are more commonly present than the taxodioid leaves in the extant species, *G. pensilis* (Staunton ex D. Don) K. Koch. The cupressoid and crypto-cupressoid leaves are helically inserted on the stem, 1 to 2 mm long and 0.5 to 1 mm wide, prominently keeled, and with acute apices (Fig. 4). The cupressoid / crypto-cupressoid leaves grade acropetally into cryptomeroid / crypto-taxodioid leaves. The cryptomeroid and crypto-
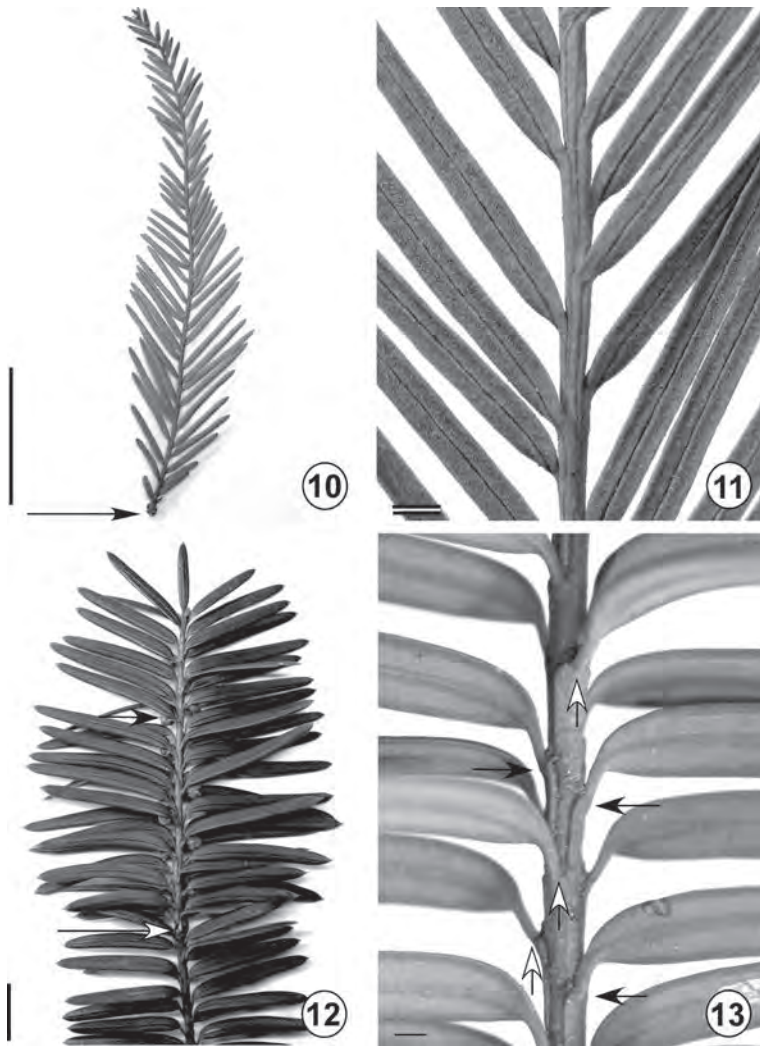
Fig. 10 An adaxial view of the leaves of *Taxodium mucronatum* Tenore showing the basal cluster of cupressoid leaves (arrow) and taxodioid leaves above. Scale bar = 1 cm.

Fig. 11 Closeup of the abaxial leaf surfaces of *T. mucronatum* taxodioid leaves. The leaves are sessile and attached to the stem squarely to slightly oblique. The decurrent leaf bases are parallel to the long axis of the stem. Note that the midrib is sunken producing a groove as opposed to a ridge and that the grove extends into the decurrent part of the leaf. Scale bar = 1 mm.

Fig. 12 An adaxial view of the leaves of *Taxus canadensis* Marsh showing the basal scale leaves and needle-like leaves. The current year's need-like leaves are borne on a shoot that extends from the apex of the previous year's growth (lower white-headed arrow). The scale leaves are located at the base of the shoot bearing the most recently produced shoot. Pollen cones are visible at the base of some of the needle-like leaves (upper black arrow). Scale bar = 1 cm.

Fig. 13 Closeup of the adaxial leaf surfaces of the *T. canadensis* needle-like leaves. Basally the leaves narrow and become petiolate. The petiole is attached to the uppermost part of the decurrent leaf base and the attachment point is bulbous (black arrows). An abscission zone is visible (white-headed arrows). The decurrent part of the leaf bases is distinct with the uppermost portion being widest and narrowing basally. The bases are arranged parallel to the long axis of the shoot. Scale bar = 1 mm.

taxodioid leaves are helically inserted along the stem, sessile, not narrowed at the base, squarely attached to the stem (not twisted) at an angle of about 40°, and with a conspicuous midrib. The leaf apices are acute, obtuse, or mucronate. The decurrent leaf bases are not prominent and trend parallel along the stem (Fig. 5).

Metasequoia (Figs. 6 and 7) — The leaves are dimorphic with taxodioid leaves located along the length of the shoot axis and clusters of cupressoid leaves located at the base of the deciduous shoot (Fig. 6). The cupressoid leaves are 1 to 2 mm long and 0.5 to 1 mm wide, opposite, keeled, and with acute apices. The taxodioid leaves are opposite, sessile, possess a conspicuous midrib, and are narrowed at the base. The leaves are attached to the shoot by a 0.25 to 0.5 mm long petiole that is obliquely attached to the stem. The leaf apices of the leaves are mucronate to obtuse. The decurrent

leaf bases are prominent and trend obliquely along the stem (Fig. 7). Although the tree sheds its leaves as deciduous shoots in the fall with the individual leaves remaining attached to the shoot, an abscission zone at the base of each leaf is present. Isolated leaves are basally rounded (no part of the petiole is shed) and the abscission zone is inconspicuous.

Sequoia (Figs. 8 and 9) — The leaves are dimorphic with the cupressoid leaves borne in clusters near the base of new growth shoots (Fig. 8). The cupressoid leaves are 2 to 8 mm long and 1 mm wide, slightly keeled, and with an acute apex. The taxodioid leaves are helically arranged along the shoot, arranged distichously, and may appear to be sub-opposite. They are sessile, 10 to 25 mm long and 2.0 mm wide, slightly keeled abaxially, and with apices that are obtuse, acuminate, to mucronate. Basally the leaves do not become
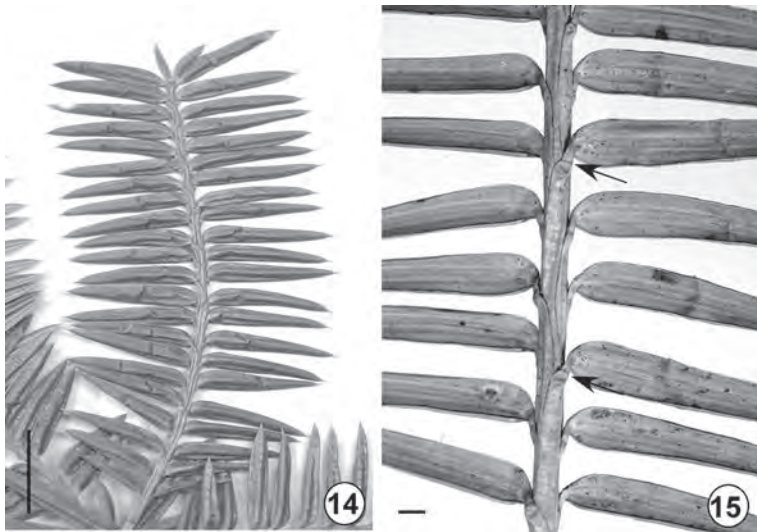
Fig. 14 An adaxial view of the needle-like leaves of *Torreya nucifera* (L.) Siebold et Zuccarini. Note the nearly opposite arrangement of the leaves and sharply acuminate apices. Scale bar = 1 cm.

Fig. 15 Closeup of the adaxial surfaces of the *T. nucifera* needle-like leaves. The leaves narrow basally and are borne on 1 mm long petioles. Note the revolute leaf edges. The petioles are attached to the uppermost part of the decurrent leaf bases. The leaf bases are arranged slightly oblique to parallel to the long axis of the shoot. The point of attachment is bulbous. The abscission zone is clearly visible (arrows). Scale bar = 1 mm.

narrowed and are obliquely attached to the stem (Fig. 9). The decurrent leaf bases are prominent and trend obliquely along the stem.

Taxodium (Figs. 10 and 11) — The leaves are dimorphic with the cupressoid leaves borne in clusters at the base of the deciduous shoots, while the taxodioid leaves are borne helically along the shoot (Fig. 10). The cupressoid leaves are up to 1 mm long and 1 mm wide, slightly keeled, and with acute apices. The cupressoid leaves grade acropetally into taxodioid leaves with the basal three to four transitional leaves increasing in length and appearing spatulate. The taxodioid leaves are 6 to 17 mm long and 1.0 mm wide, and with apices that are acute, acuminate, to mucronate. The leaves are sessile, slightly narrowed at the base, attached squarely to slightly obliquely to the stem, and with a visible midrib (Fig. 11). The midrib however is sunken producing a grove that extends into the decurrent portion of the leaf. The decurrent leaf bases are not prominent and trend parallel along the stem.

Taxus (Figs. 12 and 13) – The leaves are dimorphic with the scale leaves borne in clusters at the base of the current year's growth (Fig. 12). The scale leaves are up to 2 mm long and 2 mm wide, acute, and slightly keeled. The needle-like leaves are 10 to 47 mm long and 1.5 to 3.0 mm wide and helically arranged along the stem. In some cases they may appear to be opposite. The leaves are linear, lanceolate, or narrowly acute to slightly falcate, two-ranked, and with apices that are bluntly acute, acute, or mucronate. The leaves are narrowed at the base, petiolate, and attached squarely to obliquely to the decurrent part of the leaf (Fig. 13).

The decurrent portions are prominent and trend parallel along the stem. The joint between the leaf base and stem is narrowed and bulbous. An abscission zone is present at the base of the bulbous leaf base. Isolated leaves are shed with the petiole attached.

Torreya (Figs. 14 and 15) – The leaves are dimorphic with the scale leaves borne in clusters at the base of the stem (Fig. 14). The scale leaves are up to 2 mm long and 1 mm wide, mucronate, and keeled. The needle-like leaves are helically arranged along the stem and appear oppositely arranged. These leaves are linear to lanceolate to falcate, two-ranked, and broadly keeled adaxially. Abaxially the leaf is not keeled and the leaf edges are revolute. The leaves are 11 to 90 mm long and 2.5 to 5.0 mm wide. The leaf apices are sharply acuminate to spine-tipped. The leaves are narrowed at the base and borne on a 1 mm long petiole. The decurrent bases are prominent, obliquely joined, and trend parallel to slightly oblique along the stem (Fig. 15). The joint between the leaf base and stem is narrow and the point of attachment is bulbous. An abscission zone is visible at the base of the bulb. Isolated leaves are shed with the petiole attached.

Discussion

The leaf key presented in Fig. 1 is based on a suite of morphological characters of extant species that can be used to facilitate the identification and separation of extant and fossil leaves that may either be isolated or attached to pieces of stem. As Brongniart (1828) realized and pointed out, leaf and seed cone morphology can be used to discriminate between extant genera and

following this belief he extended the concept to his system of fossil conifer classification. This premise still holds true today and its use can certainly be extended to assist in the identification and classification of isolated fossil leaves that are either not associated with reproductive material (e.g., Axelrod, 1998), at fossil localities where more than one genus of the Taxodiaceae is represented (e.g., Heer, 1868–1883; Basinger, 1991; Mai, 2004), or at localities that contain a wide variety of conifer genera (e.g., Engelhardt & Kinkelin, 1908; Miki, 1958; Miki & Kokawa, 1962; Momohara, 1992, 1994). However, caution is warranted because the quality and mode of preservation of a fossil may obscure any one of the features that are easily recognizable in a non-compressed state and in some cases the correct identification of an isolated leaf is simply not possible. A couple of points made by Christophel (1976) that are worth remembering are the reliable identification of isolated fossil leaves should be based on a large number of specimens that are exceptionally well preserved and a suite of characteristics, rather than a single feature.

Representatives of the Taxaceae (*Taxus*) and Cephalotaxaceae (*Cephalotaxus* and *Torreya*) were included here because in some instances similarities in leaf morphology and mode of preservation have contributed to incorrect identifications. For example, leaves previously identified as *Taxus* were later reassigned to *Metasequoia* (Chaney, 1927, 1951; Mason, 1927; Meyer & Manchester, 1997). As noted by Brown (1936) any one of the three leaf types of *Glyptostrobus* could easily be confused with those of other conifers including *Sequoia*, *Taxodium,* and *Torreya*. While the fossil record of *Taxus*, *Cephalotaxus* (including *Cephalotaxites* Heer and *Cephalotaxopsis* Fontaine), and *Torreya* is poorly studied and therefore limited, a number of species of these genera have been reported throughout the Northern Hemisphere extending from the Late Mesozoic and to the Late Cenozoic (Dijkstra, 1971–1975). It is therefore important to at least consider these taxa during the process of leaf identification and when compiling a floristic composition of a fossil flora, especially when some of the fossil remains are comprised of isolated leaves.

Appendix 1

Cephalotaxus harringtonia var. *drupacea* (Siebold et Zuccarini) Koidzumi, collected by A. Golinelli, 04/2008, Geneva Botanical Garden, Geneva, Switzerland; *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch, collected by D.R. Vann, 08/1999, Los Angeles County Arboretum, Los Angeles, USA; *Metasequoia*

glyptostroboides, collected by B.A. LePage, 08/2002, Shiziba Valley, Hubei Province, China; *Sequoia sempervirens* (D. Don) Endlicher, collected by B.A. LePage, 06/1998, Humboldt County, California, USA; *Taxodium mucronatum* Tenore, collected by D.R. Vann, 08/1998, Los Angeles County Arboretum, Los Angeles, USA; *Taxus canadensis* Marsh, collected by B.A. LePage, 10/2010, Morris Arboretum, Philadelphia, USA; *Torreya nucifera* (L.) Siebold et Zuccarini, collected by B.A. LePage, 09/1992, Higashiyama Botanical Garden, Nagoya, Japan.

Acknowledgements

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