

*We dedicate this paper to our friend Harald Walther on the occasion of his 80<sup>th</sup> birthday*

# Inflorescences and compound leaves of the extinct *Platanus neptuni* complex in the Oligocene of Oregon, USA

STEVEN R. MANCHESTER<sup>1</sup> and ZLATKO KVAČEK<sup>2</sup>

<sup>1</sup>Florida Museum of Natural History, University of Florida, Gainesville Florida, USA;  
e-mail: steven@flmnh.ufl.edu

<sup>2</sup>Charles University, Faculty of Science, Institute of Geology and Palaeontology, Albertov 6,  
CZ 128 43 Prague 2, Czech Republic; kvacek@natur.cuni.cz

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**ABSTRACT.** The extinct species *Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček, formerly reported on the basis of infructescences, staminate inflorescences and associated foliage from the Late Eocene to Late Miocene deposits of Europe, is now recognized also in North America, based on a population dominating the Late Oligocene Yaquina flora of coastal Oregon. Staminate inflorescences are of the same morphology as in Europe: globose to ellipsoidal, each borne solitarily on a thick, elongate peduncle. A circumsissle raised scar is visible around the peduncle at the base of inflorescence heads – a feature diagnostic of the extinct *Platanus* subgenus *Glandulosa* Kvaček, Manchester & Guo. Contrary to the European records, which are more variable in foliage (simple to compound tri- and pentafoliolate), the leaves at the Yaquina locality are exclusively trifoliolate, sharing short petioles expanded at the base, as in many European populations of *P. neptuni* morphoforma *fraxinifolia* (Johnson & Gilmore) Kvaček & Manchester. The preservation in coarse deposits precludes anatomical investigation, but the morphology of both leaves and reproductive structures provides evidence for confident assignment to the same species previously recognized only from Europe.

**KEYWORDS:** Platanaceae, Oligocene, Europe-North America disjunction

## INTRODUCTION

Patterns of plant distribution in the northern hemisphere reflect a long history of inter- and intracontinental dispersal, with many examples of genera whose ranges have diminished over time. There are numerous examples of genera known from the early Tertiary of western North America that also occur in Europe and/or Asia (Manchester 1999, Manchester et al. 2009, Hably et al. 2000). In the Platanaceae, some genera are known to have populated both Asia and North America (*Macginitiea*, *Platimeliphyllum*) or both North

America and Europe (*Platanites*), while others were apparently more confined in distribution. The extinct clade of plane trees known as *Platanus* subgenus *Glandulosa* Kvaček, Manchester & Guo, with compound leaves and elliptical to obovate unlobed laminae, was distributed widely during the Palaeocene, with occurrences of *P. bella* in western Greenland, Wyoming in North America, and Xinjiang, north-western China (Kvaček et al. 2001). However, the related species, *P. neptuni*, known from inflorescences, and infructescences as well as

distinctive 3- (sometime 5-) foliolate to simple leaves, has only been recognized from the European Tertiary, where it was a prominent component of vegetation in Late Eocene to Miocene floras. We now report a newly recognized disjunct occurrence of *P. neptuni* from the Oligocene of coastal Oregon, western USA, which is important for its biogeographic implications, as well as providing additional support for the previously hypothesized linkages of foliage and reproductive structures as parts of the same extinct plant (Kvaček & Manchester 2004, Kvaček 2008).

## MATERIAL AND METHODS

Outcrops near Newport, Oregon, USA, were the subject of field work and unpublished studies by James McClammer (1978), yielding several hundred specimens now archived at the US National Museum. An additional smaller collection was made by Manchester in 2004 (deposited at Florida Museum of Natural History-UF), from one of the original sites of McClammer, situated on a steep hill above a road cut of the south Yaquina Bay highway at river marker 25 (GPS: 44°34.95'N; 124°00.76'W), Lincoln County, Oregon. The fossil plants occur in sandstones and siltstones representing a deltaic unit between the lower and upper marine tongues of the Yaquina Formation. No associated radiometric dates are available, but marine biostratigraphy has indicated the formation may range from the uppermost Oligocene to Lower Miocene. According to McClammer's unpublished work, the floral horizon occurs in the upper part of the lower third of the formation, below foramineral assemblages assigned to the Zemorrian foraminiferal stage (a stage spanning from Early Oligocene to earliest Miocene; Prothero 2003), and between thick marine sequences containing molluscan faunas diagnostic of the "Blakely Stage" (Weaver et al. 1944) in the West Coast provincial chronology. On the other hand, molluscan workers placed the entire Yaquina Formation in the Juanian provincial molluscan stage (Addicott 1976, 1981), ranging from Late Oligocene to Early Miocene (ca. 24–29 Ma; Squires 2003)."

Leaves and reproductive structures were obtained by fracturing the fossiliferous sediment along the bedding plane with a hammer and chisel. For the preparation of in situ pollen, small pieces were mechanically removed from a staminate inflorescence with the aid of the collodion-transfer-film technique. The film was cleaned in hydrofluoric acid and after rinsing treated in very dilute KOH, and mounted on glass slides for observation by transmitted light microscopy. In spite of several attempts to remove the leaf cuticles by the same procedure, no cellular structures were obtained. We compared the North American fossils with those from many sites in Europe, housed in various museum collections previously cited in Kvaček and Manchester (2004).

## PLATANACEAE

*Platanus* L., subgenus *Glandulosa* Kvaček, Manchester & Guo

*Platanus neptuni* (Ettingshausen) Bůžek, Holý & Kvaček (Plates 1–3)

### DESCRIPTION OF THE YAQUINA POPULATION

Foliage. Morphoforma *fraxinifolia* (Johnson & Gilmore) Kvaček, Manchester & Guo. Leaves trifoliolate, medial leaflet slender, elongate-lanceolate (?), about 20–27 mm wide. Medial leaflet narrow cuneate, symmetrical, shortly petiolulate with acute lamina base and apex. Lateral leaflets sessile, slightly broader than the medial, arising at angle of 30–45°, at base strongly asymmetric, in rare cases the pair of lateral leaflets connate with the rachis for a short distance, in which cases they appear basally fused by their outer margins (Pl. 1, fig. 2). Leaflet apices acute, margins bluntly dentate, usually in upper parts of leaflets only, teeth small, closely spaced, acute to obtuse, with straight to convex basal side and straight to concave apical side, sinuses shallow, rounded; venation camptodromous to semicraspedodromous, midrib straight in terminal leaflet, and almost straight in lateral leaflets, arising from slightly expanded uppermost part of petiole, secondary veins arched, regularly spaced, arising at wide angles and looping well within the lamina, interspaced with intersecondary and tertiary veins forming a regular reticulum, abmedial side veinlets arising from loops of secondaries either entering teeth or forming a second series of smaller loops, from which veinlets also enter teeth, higher-order veins in  $\pm$  isodiametric meshes.

Staminate inflorescences (Pl. 2, figs 1–4) globular to ellipsoidal (7–10 mm diameter), formed of densely packed stamens on a small central receptacular core, borne on a stout peduncle up to 16 mm long and 2 mm thick. A prominent thickening occurs on peduncle at the junction with the head (Pl. 2, fig. 1). Anthers elongate, 2.0–2.3 mm long, sessile with prominent, apiculate connectives (Pl. 2, fig. 3). Perianth not recognizable. Pollen grains (Pl. 2, figs 5, 6) prolate, 20–22 by 18–20  $\mu$ m;

tricolpate, colpi extending ca 90% of the length of the grain. Sculpture finely reticulate.

Associated pistillate inflorescences not seen but probable infructescences (Pl. 3) are preserved as globose heads bearing numerous stout sessile, narrow-ovate achenes. Achenes often abraded, but sometimes with intact persistent straight styles. Borne singly on stout peduncle (rarely preserved).

Specimens. USNM 508221, 508222, 508228, 508229, 508232, 508233, 508235–508240, 537854, 537855, 537864, UF 19054–46575, 46599, 46603, 46604.

## DISCUSSION

Our assignment of this Oligocene population of *Platanus neptuni* from western Oregon to the same species as the European fossils is supported by distinctive features of both vegetative and reproductive structure. The characters shared with the European populations include: 1) trifoliolate leaves with short, basally expanded petioles, and the same kind of venation and margin (Pl. 1); 2) globose to ellipsoid inflorescences borne singly on stout peduncles with a prominent circular thickening at top of the peduncle (Pl. 2, fig. 1); 3) prolate, tricolpate, reticulate pollen (Pl. 2, figs 5, 6).

The North American population differs from most European occurrences in the uniformly trifoliolate leaf form. Most European occurrences are typically more variable in leaflet number, either with occasional pentafoliolate (Ireland; Klaus, Germany) or prevailing simple leaves, with exceptional apical lobes on simple leaves (most occurrences in the Boreal province). The Yaquina site has not yielded the tubular remains of stipules (known mainly just from the Eocene and Oligocene of north Bohemia), nor young pistillate inflorescences. In both North America and Europe infructescences apparently do not fall into fruitlets in the mature stage, unlike living *Platanus*. The associated female heads from Yaquina are more robust, often with straight remains of styles, while in fully preserved specimens in Europe they are apically slightly curved (Bůžek et al. 1967, pl. 2).

The tendency for the lateral leaflets to be slightly fused together at the extreme base, as observed among some of the Yaquina specimens (Pl. 1, fig. 2), is uncommon in the European

populations. In fact, the only site yielding such foliage with fused leaflets is the Late Oligocene Verőcmaros locality in Hungary (Hably 1982, pl.3, figs 1–2, as *Debeya hungarica*). The usual condition (see Walther 1985, Kvaček & Manchester 2004) is for the leaflets to be completely free, often shortly petiolulate. In a new occurrence at Janda, North Serbia the trifoliolate leaf forms suggest only seemingly fused bases of lateral leaflets, which merely overlap (Djordjević-Milutinović 2009). The shape of the leaflet bases is broad rounded, not cuneate as in other European populations with compound foliage (see Kvaček & Manchester 2004, Fig. 7). In other respects, i.e. short petiole with expanded base, venation, kind and distribution of teeth, the North American population matches the type collection of *P. neptuni* mf. *fraxinifolia* from the Lough Neagh core in Ireland (Johnson & Gilmore 1921) and other occurrences in Europe.

Although no living *Platanus* species has compound leaves nor the unusual surrounding scar at the junction of the peduncle and inflorescence head, placement of *P. neptuni* in the Platanaceae is supported by: 1) the arrangement of the leaflets, which in 5-leafleted forms has a pedate (rather than strictly palmate) arrangement matching the primary venation of a 5-lobed simple leaf of extant *Platanus* species, while 3-leafleted forms show the same arrangement as the lobes of a trilobed simple leaf of extant species. 2) the unusual epidermal structure found both on the leaves and reproductive organs, including anomocytic stomata with thickened periphery, finely undulate anticlinal cell walls and multicellular trichome bases occasionally bearing large disk-shaped glands, 3) stamens with short filaments or sessile, having elongate lateral pollen sacks and domed to apiculate connectives, 4) tricolpate reticulate pollen, 5) fruits bearing a single style and dispersal hairs.

The petiole base in *Platanus neptuni* covers the bud, as in *Platanus* subgen. *Platanus* and contrary to subgen. *Castaneophyllum* Leroy. Although some collections included in the synonymy for this species (Bůžek et al. 1967, Kvaček & Manchester 2004) were previously included in extinct genera of Platanaceae, in particular to *Dewalquea* and *Debeya*, we explained (Kvaček et al. 2001), that these genera were both established on Cretaceous and Palaeocene fossil leaves that appear to be

distinct from *P. neptuni*. We adopted the philosophy that this extinct species can be accommodated in the extant genus, but in the extinct subgenus, *Glandulosa*.

The hypothesized whole plant reconstruction of *Platanus neptuni*, including leaves (compound to simple), dispersed stipules, staminate and pistillate inflorescences, infructescences and fruits is supported by shared epidermal anatomy from the Markvartice and Habartov localities (Bůžek et al. 1967), by the platanaceous characters of the separate organs as judged by comparison with the corresponding organs of extant species of *Platanus*, and by the co-occurrence of these organs at numerous European localities. The additional case of co-occurrences of the same kind of leaves and reproductive structures at the Yaquina locality, far from the type area of the species, further strengthens the basis for regarding these organs as representing the same source plant although they have not been found in physical attachment in the fossil record. It is also noteworthy that the Yaquina population appears to be exclusively trifoliolate, without variation to pentafoliolate or simple as occurs at some other sites in Europe (Klauska, Kučlín, Bílina – see Kvaček and Manchester 2004). European sites with exclusively occurring trifoliolate leaf forms are exceptional, e.g. Janda in North Serbia (Djordjević-Milutinović & Dulić 2009), in a few others trifoliolate form predominates, e.g. Mesta Graben (Palamarev et al. 1999).

We maintain a distinction between the Early Palaeogene *Platanus bella* and the Late Palaeogene to Miocene species, *P. neptuni*. A subtle difference is in the more frequent intersecondaries of the former (Kvaček et al. 2001, Fig. 3E) while in *P. neptuni* the intersecondaries are usually lacking or single, short and incomplete, and widely spaced apart from the secondaries. In addition, we do not have sufficient evidence to merge *P. bella* and *P. neptuni*, because the inflorescences and infructescences of *P. bella* have not been found from any of the Palaeocene sites where the foliage has been found; hence precluding more detailed comparison with the full suite of organs known from *P. neptuni*.

#### ASSOCIATED FLORA

The trifoliolate leaves of *Platanus neptuni* are seen on nearly every slab coming from the McClammer's site 04 in the USNM 14203

collection from Yaquina. Although not as abundant, inflorescences and infructescences were also commonly observed. During our tentative inspection of the collection some other plants associated have been noticed: a fern with goniopterid type of venation, *Metasequoia* and taxodioid foliage, pine twigs with needles in dense fascicles (? *Strobilus* type), a seed cone (*Pinus* type) and male cones, cupressoid twigs with attached seed cones of the *Chamaecyparis* type, *Pseudolarix* (see Gooch 1992), and dicots including *Cornus*-like and lauroid entire leaves, rare lobed to coarsely crenulate leaves with palinactinodromous venation of the *Platanus* type and very common morphotypes with palmate venation of the "*Acer arcticum*" type recalling *Ampelopsis*, betulaceous foliage, *Fagus*, legume leaflets, *Hydrangea* flowers, and some more leaf fragments of dubious affinities, and, among monocots, a leaf resembling *Smilax*. The assemblage seems to be composed prevalently of deciduous arboreal elements including *Platanus neptuni*.

The accompanying vegetation at Yaquina differs greatly compared with that in the floras containing abundant *P. neptuni* in Europe. Plants typically associated with abundant *P. neptuni* in Europe (Kučlín, Markvartice, Suletice, Flörsheim) include thermophilic elements like *Tetraclinis salicornioides*, *Calocedrus*, *Engelhardia*, *Sloanea*, and lauroids and much lower diversity of broad-leaved deciduous elements, such as *Cercidiphyllum*, *Acer*, *Betulaceae*, and *Ulmaceae*.

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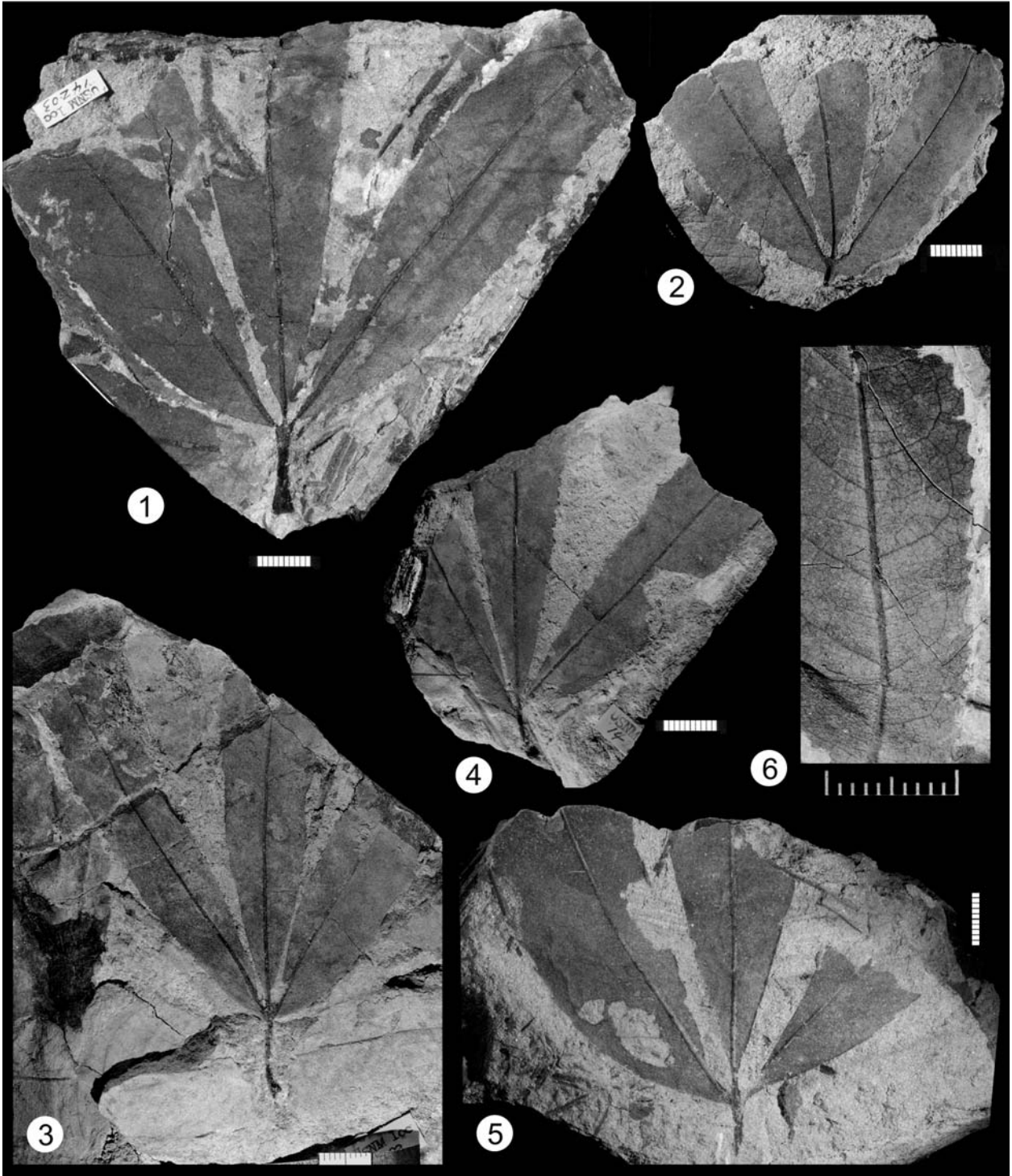
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# PLATES

## Plate 1

Leaves of *Platanus neptuni* from the Yaquina Formation, Oregon, USA. Scale bars 1 cm

1. Leaf showing a medial petiolulate and two lateral sessile leaflets and short, basally expanded petiole, USNM 508228
2. Smaller leaf, showing fusion of lateral leaflets to each other below the terminal leaflet, USNM 508222
3. Leaf with narrow leaflets and complete petiole, USNM 508233
4. Leaf with subsessile narrow leaflets, USNM 508232
5. Leaf showing symmetry of median leaflet, strong asymmetry of lateral leaflets, USNM 508221
6. Well preserved leaflet showing details of higher order venation and serrate margin, USNM 508229



## Plate 2

Staminate inflorescences and *in situ* pollen of *Platanus neptuni* from the Yaquina Formation, Oregon, USA.  
Scale bar in fig. 4 applies also to 1–3

1. Somewhat elongate, ovoid head borne on stout peduncle. Note broadened scar at junction of peduncle and inflorescence, a diagnostic character for the species. USNM 508238
2. Globose inflorescence on stout peduncle, USNM 508236
3. Well preserved globose head, USNM 508235
4. Globose head on stout peduncle, USNM 508240
5. Pollen clump from one of the stamens of the inflorescence in fig. 3. Scale bar – 20  $\mu\text{m}$
6. Detail of tricolpate, reticulate pollen, Scale bar – 10  $\mu\text{m}$



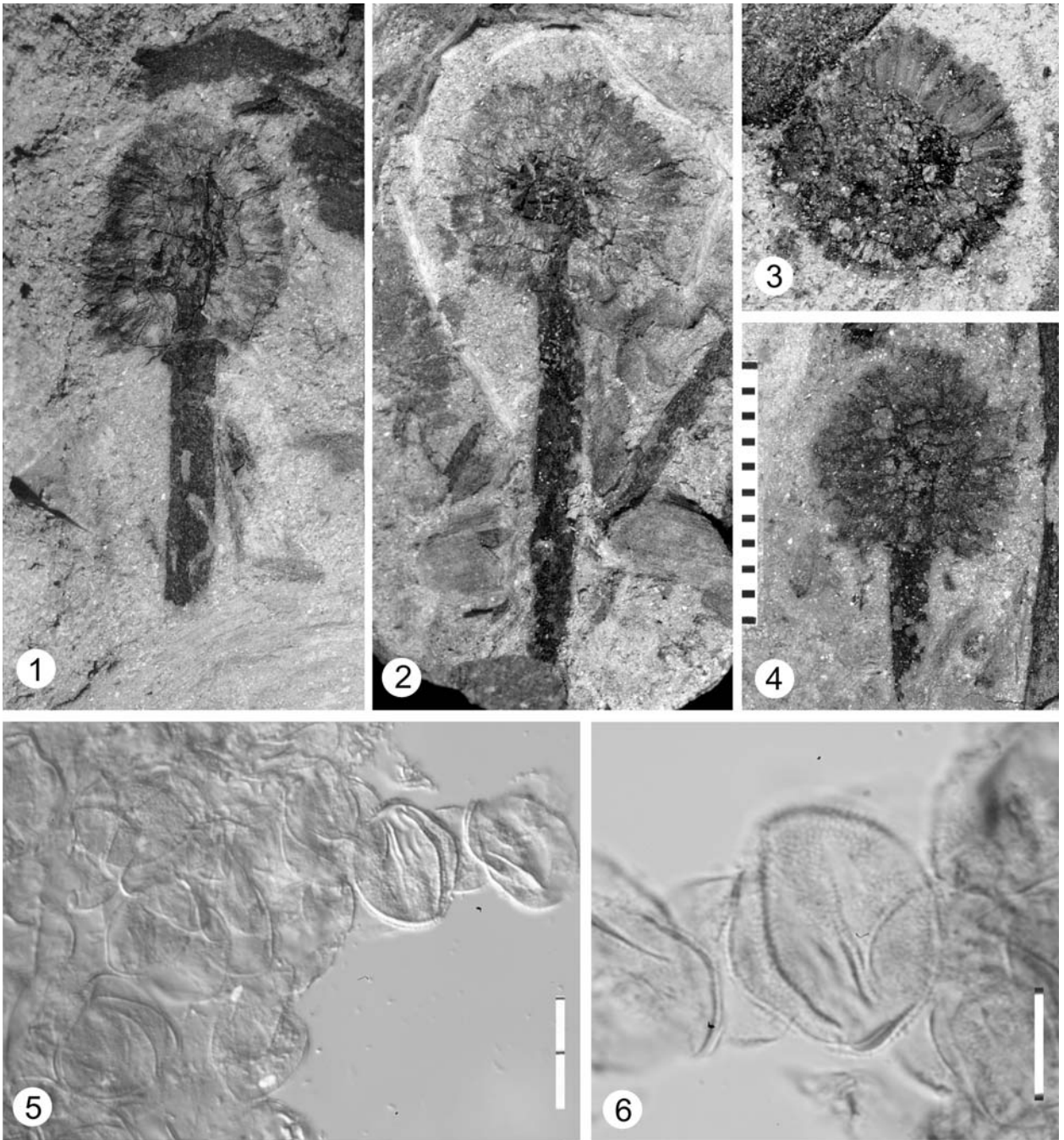


Plate 3

Infructescence found associated with *Platanus neptuni* at the Yaquina flora

1. Pedicellate head, USNM 508237
2. Infructescence with isolated fruitlet at right, USNM 508239
3. Abraded infructescence, USNM 537854
4. Abraded infructescence showing central receptacle, USNM 537864a
5. Slab showing numerous abraded heads of different size, USNM 537855

