International Journal of Plant Sciences

FIRST SOUTH AMERICAN RECORD OF WINTEROXYLON, EOCENE OF LAGUNA DEL HUNCO (CHUBUT, PATAGONIA, ARGENTINA): NEW LINK TO AUSTRALASIA AND MALESIA

--Manuscript Draft--

Article Type:	Major Article
Manuscript Number:	44666R1
Full Title:	FIRST SOUTH AMERICAN RECORD OF WINTEROXYLON, EOCENE OF LAGUNA DEL HUNCO (CHUBUT, PATAGONIA, ARGENTINA): NEW LINK TO AUSTRALASIA AND MALESIA
Corresponding Author:	Mariana Brea, PhD ARGENTINA
Corresponding Author's Institution:	
Other Authors:	Ari Iglesias, PhD
	Peter Wilf, PhD
	Eliana Moya, PhD
	María A. Gandolfo, PhD
Abstract:	Premise of research. Winteraceae, a family within the Canellales, is composed of tropical trees and shrubs broadly distributed in the Southern Hemisphere. The family is found today in eastern Australia, New Zealand, Malesia, Oceania, Madagascar, and the Neotropics, across a range of dry to wet tropical to temperate climate regions. The fossil record of woods related to the Winteraceae in the Southern Hemisphere is limited to the Late Cretaceous of the Antarctic Peninsula. Here, we present a detailed anatomical description of the secondary xylem of a well-preserved trunk from the early Eocene Laguna del Hunco site, Huitrera Formation, Patagonia (Chubut Province, Argentina), that is referable to a new species of the genus Winteroxylon (Gottwald) Poole and Francis. Methodology. The wood material is preserved as a siliceous permineralization; it was sectioned using standard petrographic techniques and observed under both light and scanning electron microscopy. The anatomy was compared with extant and fossil species of Winteraceae. Pivotal results. The diagnostic anatomical features of Winteraceae preserved in the fossil include the absence of growth rings; lack of vessels; tracheids rectangular in cross-section with circular bordered pits; diffuse axial parenchyma; rays showing two distinct size ranges (uniseriate-biseriate or multiseriate, 3–15 cells wide); and presence of heterocellular rays containing sclerotic nests, cells with dark contents, and oil cells. The new fossil species most resembles extant genera within the Zygogynum s.l. clade from Australasian and Malesian rainforests; its anatomy is very similar to the extant genus Bubbia. The new Patagonian Winteraceae fossil wood is characterized by the presence of sclerotic nests and oil cells in the rays that differ from previously described species of Winteroxylon. Conclusions. Based on the distinctive characters preserved, we erect Winteroxylon oleiferum sp. nov. The new fossil is the first reliable macrofossil record of Winteraceae from South America, supporting the abundant palynological record of the family from the continent, and it is the oldest record of the Zygogynum s.l. clade, adding to the long list of southern biogeographic connections between South America and Australasia via Antarctica during the warm early Cenozoic.
Author Comments:	
Additional Information:	
Question	**Response**

FIRST SOUTH AMERICAN RECORD OF *WINTEROXYLON*, EOCENE OF LAGUNA DEL HUNCO (CHUBUT, PATAGONIA, ARGENTINA): NEW LINK TO AUSTRALASIA AND MALESIA

Mariana Brea[1,*,**], Ari Iglesias[†], Peter Wilf[‡], Eliana Moya[*], and María A. Gandolfo[§]

[*]Laboratorio de Paleobotánica, Centro de Investigación Científica y de Transferencia Tecnológica a la Producción, Consejo Nacional de Investigaciones Científicas y Técnicas CICYTTP (CONICET-Prov. ER-UADER), España 149, E3105BWA Diamante, Entre Ríos, Argentina and Facultad de Ciencia y Tecnología, Universidad Autónoma de Entre Ríos; [**]Cátedra de Paleobotánica, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata (FCNyM-UNLP), Calle 122 y 60 s/n, 1900, La Plata, Buenos Aires, Argentina; [†]Instituto de Investigaciones en Biodiversidad y Medioambiente, Universidad Nacional del COMAHUE – CONICET, Quintral 1250, 8400 San Carlos de Bariloche, Río Negro, Argentina; [‡]Department of Geosciences and Earth and Environmental Systems Institute, Pennsylvania State University, University Park, PA 16802, USA; and [§]L. H. Bailey Hortorium, Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, NY 14850, USA

[1]Author for correspondence; e-mail: cidmbrea@gmail.com

Premise of research. Winteraceae, a family within the Canellales, is composed of tropical trees and shrubs broadly distributed in the Southern Hemisphere. The family is found today in eastern Australia, New Zealand, Malesia, Oceania, Madagascar, and the Neotropics, across a range of dry to wet tropical to temperate climate regions. The fossil record of woods related to the Winteraceae in the Southern Hemisphere is limited to the Late Cretaceous of the Antarctic Peninsula. Here, we present a detailed anatomical description of the secondary xylem of a well-preserved trunk from the early Eocene Laguna

del Hunco site, Huitrera Formation, Patagonia (Chubut Province, Argentina), that is referable to a new species of the genus *Winteroxylon* (Gottwald) Poole and Francis.

Methodology. The wood material is preserved as a siliceous permineralization; it was sectioned using standard petrographic techniques and observed under both light and scanning electron microscopy. The anatomy was compared with extant and fossil species of Winteraceae.

Pivotal results. The diagnostic anatomical features of Winteraceae preserved in the fossil include the absence of growth rings; lack of vessels; tracheids rectangular in cross-section with circular bordered pits; diffuse axial parenchyma; rays showing two distinct size ranges (uniseriate-biseriate or multiseriate, 3–15 cells wide); and presence of heterocellular rays containing sclerotic nests, cells with dark contents, and oil cells. The new fossil species most resembles extant genera within the *Zygogynum* s.l. clade from Australasian and Malesian rainforests; its anatomy is very similar to the extant genus *Bubbia*. The new Patagonian Winteraceae fossil wood is characterized by the presence of sclerotic nests and oil cells in the rays that differ from previously described species of *Winteroxylon*.

Conclusions. Based on the distinctive characters preserved, we erect *Winteroxylon oleiferum* sp. nov. The new fossil is the first reliable macrofossil record of Winteraceae from South America, supporting the abundant palynological record of the family from the continent, and it is the oldest record of the *Zygogynum* s.l. clade, adding to the long list of southern biogeographic connections between South America and Australasia via Antarctica during the warm early Cenozoic.

Keywords: wood anatomy, early Eocene, Huitrera Formation, Winteraceae, *Winteroxylon*, *Zygogynum* s.l. clade.

Introduction

The early-diverging angiosperm clade Magnoliidae comprises four orders: Magnoliales, Laurales, Canellales, and Piperales (APG IV 2016; Massoni et al. 2014, 2015*a*,*b*). Canellales is the smallest magnoliid order and includes only the Canellaceae and Winteraceae. The sister relationship of Canellaceae and Winteraceae is strongly supported in several molecular analyses (Suh et al. 1993, Qiu et al. 1999, 2005; Zanis et al. 2003; Soltis and Soltis 2004; APG IV 2016; Marquínez et al. 2009; Massoni et al. 2015*a*,*b*; Müller et al. 2015). Both families are comprised of aromatic woody shrubs and small trees with disjunct distributions in the Southern Hemisphere (Marquínez et al. 2009; Thomas et al. 2014).

Today, the Winteraceae include ca. 60–90 species of evergreen trees, shrubs, and rarely epiphytes. Vink (1985) and Marquínez et al. (2009) recognized five extant genera within Winteraceae: *Drimys* J.R. Forst. & G. Forst, *Pseudowintera* Dandy, *Tasmannia* R. Br. ex DC., *Takhtajania* Baranova & J. Leroy, and *Zygogynum* Baill. Vink (1988) later recognized four genera within *Zygogynum* s.l.: *Bubbia* Tiegh., *Belliolum* Tiegh., *Exospermum* Tiegh., and *Zygogynum*. Thomas et al. (2014) also recognized those four genera as a monophyletic group.

Winteraceae and Canellaceae are each monophyletic (Massoni et al. 2014 and references cited therein), and several phylogenetic analyses agree that within the Winteraceae, *Takhtajania* is the earliest-diverging lineage (Marquínez et al. 2009; Massoni et al. 2014; Thomas et al. 2014; Müller et al. 2015; Grímsson et al. 2018), followed by *Tasmannia* and *Drimys*. All the preceding are collectively sister to a clade comprising *Pseudowintera* as sister to *Zygogynum* s.l. (including *Belliolum*, *Bubbia*, *Exospermum*, and *Zygogynum* s.s.; as proposed earlier by Vink 1988). The relationships within *Zygogynum* s.l. are not fully resolved (Grímsson et al. 2018). Marquínez et al. (2009) estimated the divergence of *Takhtajania* from the rest of the family ca. 91.5 (120–74) Ma and indicated that *Tasmannia* may have diverged from other Winteraceae at ca. 69.9 (74.8–66.9) Ma.

The living Winteraceae species are restricted to Australasia, Malesia, Oceania, Madagascar, and South and Central America, primarily in rainforest environments, but including a diverse range of dry

78 to wet tropical to temperate climatic regions (Linsley 1836; Vink 1988, 1993; APG IV 2016). Based on
79 its fossil record, the early history of Winteraceae can be traced back to the Cretaceous to Eocene of
80 both hemispheres, after which the range contracted southwards (Doyle 2000; Grímsson et al. 2018).
81 Several molecular phylogenetic hypotheses based on nuclear and plastid sequence data are generally
82 consistent, indicating that the Winteraceae had a long and complex biogeographic history that is
83 explained by a combination of vicariance, long-distance dispersal, and extinction events (Marquínez et
84 al. 2009; Thomas et al. 2014). The living genera are considered as typical members of the austral flora
85 (Thomas et al. 2014) and have disjunct distributions in Australasia and Malesia (*Tasmannia*,
86 *Pseudowintera*, *Zygogynum*, *Exospermum*, *Bubbia*, *Belliolum*), Madagascar (*Takhtajania*), and the
87 Neotropics (*Drimys*) (Grímsson et al. 2018).

88 This paper reports new fossil material of Winteraceae from South America, consisting of a large
89 stump sampled at the early Eocene Laguna del Hunco fossil site in the Huitrera Formation, Chubut
90 Province, Argentina (fig. 1). The Laguna del Hunco biota was first studied by Berry (1925) and
91 sporadically investigated over ensuing decades (e.g., Frenguelli 1943, Romero et al. 1988). Extensive
92 research during the last twenty years has yielded an extremely diverse flora and fauna from the fossil
93 caldera-lake beds (for summaries see, e.g., Wilf et al. 2013; Barreda et al. 2020; Rossetto-Harris et al.
94 2020) that are highly informative for understanding Southern Hemisphere past and current
95 biogeographical patterns. The extensive biogeographic links of the Laguna del Hunco flora include, via
96 ancient Gondwana, living rainforests of Australasia and Malesia, where the largest number of
97 "survivor" genera are found in Australian and New Guinean lower-montane rainforest floras (e.g.,
98 Zamaloa et al. 2006; Wilf et al. 2009, 2019; Gandolfo et al. 2011; Carvalho et al. 2013; Gandolfo and
99 Hermsen 2017; Andruchow-Colombo et al. 2019).

100 Nearly all reported plant fossils from Laguna del Hunco are compressions (but see Barreda et al.
101 2020 for a diverse palynoflora), although decades ago, Petersen (1946) found fossilized trunks at the
102 top of the main lake-bed sequence that were not further studied. Permineralized material has only
103 recently been described from the area, including a silicified trunk of the fern *Todea* Willd. ex Bernh.

104 (Osmundaceae) with *in-situ* liverworts, fungi, and coprolites from the same source unit (Tufolitas
105 Laguna del Hunco), south of the main Laguna del Hunco exposures (Bomfleur and Escapa 2019;
106 Bippus et al. 2019). Pujana et al. (2020) described a podocarp-dominated conifer wood assemblage
107 from Laguna del Hunco, including *Protophyllocladoxylon francisiae* Pujana, Santillana & Marenssi,
108 *Phyllocladoxylon antarcticum* Gothan, and cf. *Cupressinoxylon* sp.1 and sp. 2.
109 In this paper, we describe the first fossil angiosperm wood from Laguna del Hunco, a new
110 species of Winteraceae based on anatomical study of a silicified stump. Based on anatomical
111 comparisons with extant and fossil specimens, we describe and interpret the significance of the new
112 species with regard to the wood evolution, fossil record, and biogeography of Winteraceae.
113
114 **Material and Methods**
115 The sample studied here was collected at Laguna del Hunco (LH), Huitrera Formation, by AI
116 and PW during the November, 2009 field season at S 42°27'36.26", W 70° 2'17.86", elevation 1109 m
117 (fig. 1). The stump was found lying in horizontal position on an east-facing, steep slope exposure of the
118 fossiliferous LH caldera-lake beds (Tufolitas Laguna del Hunco; fig. 2), at a position above the highest
119 productive levels for compression fossils (i.e., quarry LH6, Wilf et al. 2003). The Tufolitas Laguna del
120 Hunco are well-dated from ^{40}Ar-^{39}Ar analyses of minerals in three different tuffs, all of them below the
121 resting level of the trunk, and the presence of two paleomagnetic reversals (Wilf et al. 2003, 2005). A
122 sanidine ^{40}Ar-^{39}Ar age from one tuff of 52.22 ± 0.22 Ma is considered most reliable (M. Smith in Wilf
123 2012) and provides a minimum age for the wood specimen. In addition, the youngest beds of the
124 underlying local unit, the Ignimbrita Barda Colorada, have recently been ^{40}Ar-^{39}Ar dated as 52.54 ±
125 0.17 Ma (Gosses et al. 2020). The Tufolitas Laguna del Hunco, containing the new fossil, are overlain
126 by the hill-capping (and completely unfossiliferous) Andesitas Huancache unit (Aragón and Mazzoni
127 1997). The Andesitas Huancache have not been dated locally using modern techniques, but potentially
128 correlative strata in the southern caldera exposures have recently been ^{40}Ar-^{39}Ar dated to 49.19 ± 0.24
129 Ma, providing a likely minimum age of the fossil lake beds (Gosses et al. 2020). Thus, the age of the

wood specimen is early Eocene, with a possible age range from ca. 52.2–49.2 Ma. We prefer the older end of this range because of the provenance of the specimen from the Tufolitas Laguna del Hunco (ca. 52.2 Ma radiometric age).

The sampled stump is 150 cm in preserved length and 50 cm in diameter, increasing toward the base to 124 cm, with several woody roots of 4–15 cm diameter that are oriented mostly in axial orientation (fig. 2*B*), although some broad roots are perpendicular to the main stem (fig. 2*B*). Secondary wood from the distal part of the base of the main stem (fig. 2*C*) was sampled, leaving the bulk of the specimen intact at the site. The silicified trunk has well-preserved secondary xylem. Thin sections were made using standard petrographic techniques (transverse, tangential longitudinal, and radial longitudinal). The anatomical terms used in this paper follow the IAWA List of Microscopic Features for Softwood Identification (IAWA Committee 1989). The taxonomic assignment, descriptions, and comparisons with extant and fossil species were performed following the InsideWood website (InsideWood 2004-onwards; Wheeler 2011) and previous descriptions by Bailey and Thompson (1918), Bailey (1944), Bailey and Swamy (1948), Metcalfe and Chalk (1950), Swamy and Bailey (1950); Tortorelli (1956); Patel (1974); Carlquist (1981, 1982, 1983*a*, 1983*b*, 1987, 1988, 1989, 2000, 2001); Scott and Wheeler (1982); Rancusi et al. (1987); Poole and Francis (2000); Carlquist and Schneider (2001), and Schweingruber et al. (2011).

The specimen was studied with a Nikon Eclipse E200 light microscope, and photomicrographs were taken with an attached Nikon Coolpix S4 digital camera. The values in the anatomical description are averages of 25 measurements. In all cases, the average value is cited first, followed by the minimum and maximum values, which are given in parentheses. The material was prepared for scanning electron microscopy (SEM) by cutting 1 cm^3 blocks of fossil wood, mounting them on SEM stubs, and coating them with platinum/palladium; observation and photographs were done using a FEI Nova Nano SEM-230 microscope at the Laboratorio de Microscopía - Caracterización de Materiales - Centro Atómico Bariloche (CAB-CNEA), Argentina. The macrofossil specimens and slides are

deposited at the Museo Paleontológico Egidio Feruglio paleobotanical collection in Trelew, Argentina (acronym MPEF-Pb).

Results

Systematic Paleobotany

Order —Canellales

Family—Winteraceae

Genus—Winteroxylon (*Gottwald) emend Poole & Francis 2000*

Type species. Winteroxylon mundlosi *Gottwald 1992*

Species— Winteroxylon oleiferum *Brea, Iglesias, Wilf, Moya & Gandolfo sp. nov. (fig. 3–6)*

Etymology. The specific name refers to the abundance of oil cells in the wood.

Specific diagnosis. Growth rings indistinct. Tracheids thick-walled with circular bordered pits, mainly in uniseriate, biseriate, and triseriate rows, alternate to opposite. Axial parenchyma either diffuse or in tangentially or radially oriented pairs of parenchyma strands. Rays of two different types (narrow and broad), heterocellular and very tall, 1–2 seriate and multiseriate (3–15 cells wide). Bordered pits in ray cells. Sclerotic nests, oil cells, and dark contents in rays present.

Holotype. MPEF-Pb 3997a–e (one macrofossil and four microscope slides).

Locality. Laguna del Hunco (LH), early Eocene of northwestern Chubut Province, Argentina (S42°27'36.26", W70° 2'17.86"), Huitrera Formation.

Description. The description is based on the mature wood of one stump specimen. In transverse section, the mature wood is vesselless, composed exclusively of imperforate tracheids and parenchyma (fig. 3*A–C*, 4*A*), with indistinct growth rings (fig. 3*A–C*). The tracheids are quadrangular to rectangular (fig. 4*A*, 4*D*, 5*E*) and have a mean tangential diameter of 24 (14–33) µm and a mean radial diameter of 27 (19–31) µm. They are thick-walled (fig. 5*E*), with a wall thickness of 7 (5–9) µm. Middle lamellae and pits are observed on the tracheids (fig. 5*E*). Triangular or quadrangular intercellular spaces (fig. 4*A*, 4*D*) are present between tracheids. The axial parenchyma is diffuse and scarce, presenting as

occasional radially oriented pairs of parenchyma strands (fig. 4*A*, 4*D*). The parenchyma cell pits are small, circular, and simple (fig.4*D*, 4*E*).

In tangential longitudinal section, the tracheid pitting is circular, bordered, and contiguous, with elliptic pit apertures (fig. 5*A–C*). The circular pits have a mean diameter of 8 (7–10) µm and are frequently uniseriate (fig. 5*A*), occasionally biseriate (fig. 5*B*, 6*C*), and rarely triseriate (fig. 5*C*); when bi-triseriate, pits are alternate to opposite. Some tracheids have trabeculae on their walls (fig. 5*D*). The rays are of two distinct types, 1–2 seriate and multiseriate (3–15 cells), and both are heterocellular, composed of predominantly upright cells (fig. 3*I*, 4*G*) and occasionally with procumbent cells (fig. 3*I*, 4*F*).

The sclerotic nests (fig. 3*G*, 4*F*, 5*H*), sclereids (fig. 5*G*), and oil cells (fig. 3*E–F*, 4*H*) are abundant and associated with ray parenchyma. The oil cells are similar in size to parenchyma cells and are found scattered in rays; oil cavities are occasionally present in central portions of multiseriate rays and surrounded by three or more layers of parenchyma cells (fig. 3*E–F*, 4*H*). Sclereid cells are polygonal or hexagonal in outline (fig. 4*F*, 5*G–H*), with a diameter of 99 (43–178) µm and thick-walled with a wall thickness of 34 (8–64) µm (fig. 5*H*). Each sclerotic nest has 3 to 11 sclereid cells. The multiseriate rays have a mean height of 2089 (1035–4105) µm and a mean width of 547 (188–1504) µm. Probable sheath cells occur in the multiseriate rays (fig. 3*D*). The uniseriate (fig. 4*B*) and biseriate (fig. 4*B*) rays are more common (86%) than multiseriate rays (14%) (fig. 3*D–G*, 4*A–C*). The uniseriate rays are heterocellular and have a mean height of 314 (131–655) µm and a mean width of 35 (23–55) µm. In both ray types (narrow and broad), dark amorphous contents are observed inside the ray cells, probably attributable to resins (fig. 3*G*, 4*I*, 5*G*).

In radial longitudinal section, the tracheid pitting is more abundant on the radial compared with the tangential walls (fig. 4*J*). The rays are heterocellular, composed of upright and procumbent cells (fig. 4*G*). The ray cell pits are circular, bordered, and alternate to irregular in arrangement (fig. 4*K*, 5*I*, 6*A*, 6*B*). The procumbent cells are 97 (73–154) µm in height and 26 (16–35) µm in width, and upright cells are 51 (43–58) in height and 32 (22–38) in width.

Discussion

Comparison with extant and fossil taxa

The absence of the typical conifer cross-field pitting, and the presence of heterocellular uni- to multiseriate rays, axial parenchyma, cells with contents (i.e., oil cells, idioblasts), and sclereids, confirm that this fossil corresponds to a vesselless angiosperm. Vesselless woods are present in five early-diverging angiosperm families: Amborellaceae, Tetracentraceae, Trochodendraceae, Chloranthaceae, and Winteraceae (Bailey and Thompson 1918; Bailey 1944; Bailey and Swamy 1948; Metcalfe and Chalk 1950; Swamy and Bailey 1950; Carlquist 1987; Schweingruber et al. 2011). *Amborella trichopoda* Baill. is the only known member of Amborellaceae; it is endemic to New Caledonia, inhabiting the understory of humid forests, where it grows as shrubs or small trees. Its wood is characterized by vesselless xylem with very weakly defined growth rings, bordered circular and scalariform pits on the tracheids, diffuse apotracheal axial parenchyma, dark contents in parenchyma cells, uniseriate and multiseriate (up to 5 cells) rays, and heterocellular rays with >4 marginal upright cells (Carlquist and Schneider, 2001; Schweingruber et al. 2011). This extant species differs from the new fossil specimen in having multiseriate rays of 3–5 cells width, scalariform pits on the tracheids, and rays with >4 marginal upright cells.

Tetracentraceae, native to southern China and the eastern Himalayas, includes the sole extant species *Tetracentron sinense* Oliv. It grows along streams or forest margins in broad-leaved evergreen forests and mixed evergreen-deciduous forests (Suzuki et al. 1991), as trees that can reach up to 40 m tall. The secondary xylem is characterized by having axial parenchyma diffuse and diffuse-in-aggregates, and uniseriate and homocellular multiseriate rays 3–4 cells wide (Poole and Francis 2000; InsideWood 2004-onwards). *Tetracentron* differs from the fossil and extant Winteraceae woods in having rays of 3–4 cells width and exclusively procumbent cells. Also, *Tetracentron* has unusual thin-walled tracheids, arranged in radial files, with crowded, alternate, circular to elliptical bordered pits in

232 the tangential walls and the radial walls without pitting (Suzuki et al. 1991); all of these features unlike
233 those of the new fossil.
234 *Trochodendron aralioides* Sieb. & Zucc. belongs to the monospecific Trochodendraceae. They
235 are evergreen trees or large shrubs growing up to 20 m tall, confined to montane temperate forests in
236 Southeast Asia and Taiwan (APG IV 2016). Its secondary xylem has distinct growth rings, bordered
237 scalariform pit tracheids, axial parenchyma rare or absent, and rays in two types: uniseriate and
238 heterocellular multiseriate with 3–6 cells width. There are large and simple pits in ray cells
239 (Schweingruber et al. 2011). *Trochodendron* differs from the new Patagonian taxon in having distinct
240 growth rings, axial parenchyma absent or extremely rare, bordered scalariform pits in tracheids, simple
241 pits in cell rays, and multiseriate rays with very tall uniseriate extensions (Scott and Wheeler 1982;
242 Richter and Dallwitz 2000).
243 *Sarcandra* Gardner, the only vesselless genus within the Chloranthaceae, includes small shrubs
244 native to Southeast Asia; its wood has distinct growth rings, axial parenchyma absent or rare, tracheids
245 and transitional tracheid-vessel elements present, and heterocellular rays commonly 4–10 seriate
246 (Swamy and Bailey 1950; Carlquist 1987; InsideWood 2004-onwards). *Sarcandra* has fascicular
247 uniseriate rays and interfascicular multiseriate rays. These large multiseriate (up to 5 cells wide)
248 parenchyma rays in *Sarcandra* are derived from a cambial variant that produces axial vascular elements
249 in segments and interfascicular multiseriate rays (Pipo et al. 2020). Cambial variant features are absent
250 in *Winteroxylon oleiferum* sp. nov.
251 Of all these vesselless angiosperms, only Winteraceae have woods with >10-seriate rays, oil
252 cells, and sclerotic nests in heterocellular rays as seen in the fossil. The new fossil species shares
253 additional character states with Winteraceae, including growth rings absent; tracheids rectangular in
254 transverse section with circular bordered pits; diffuse axial parenchyma; rays of two distinct sizes, 1–2
255 seriate and multiseriate (3–15 cells wide) rays; and cells with dark contents.
256 We summarize the anatomical comparison between the new fossil species and the extant species
257 of Winteraceae (table 1). Clearly, the new Patagonian fossil species is most similar to the extant species

in the *Zygogynum* s.l. clade (*Bubbia*, *Belliolum*, *Exospermum*, and *Zygogynum* s.s). The extant genera *Pseudowintera*, *Takhtajania,* and *Belliolum* are different from the new Patagonian species in their absence of oil cells, silica bodies, and sclerotic nests. The American genus *Drimys* does not produce oil cells or sclerotic nests and has smooth and irregular silica bodies, a feature absent in the fossil wood. *Tasmannia* differs in having uniseriate and biseriate radial tracheid pits with helical thickenings and rays that do not have oil cells. *Exospermum* lacks sclerotic nests in rays, and has rectangular tracheids in transverse section and axial parenchyma in bands. *Zygogynum* s.s. differs because it has uniseriate tracheid pitting and absence of trabeculae in tracheids (table 1). On the other hand, *Bubbia* shares with *Winteroxylon oleiferum* sp. nov. the arrangement of tracheid pitting in radial walls that is uniseriate, biseriate, and triseriate; the presence of trabeculae in tracheids; square to irregular tracheid transverse section; and the oil cells associated with the rays.

Winteroxylon oleiferum sp. nov. is placed in *Winteroxylon* based on the presence of indistinct growth rings; axial parenchyma predominantly diffuse; tracheids with circular bordered pits; and rays predominantly multiseriate up to 13 cells or 1-2 seriate, heterocellular, and non-storied (Poole and Francis 2000). All the features of the new fossil fit within *Winteroxylon*, and thus there is no basis for erecting a new genus. Until now, there were only two reliable fossil woods assigned to the Winteraceae, *Winteroxylon jamesrossi* Poole & Francis from the early Campanian Santa Marta Formation, Antarctic Peninsula (Poole and Francis 2000; Olivero 2012; fig. 1) and *Winteroxylon mundlosi* Gottwald from the late Eocene Helmstedt Formation, lignite opencast mine, Lower Saxony, Germany (Gottwald 1992; fig. 1). *Winteroxylon jamesrossi* lacks oil cells and sclerotic cells as seen in the new fossil, whereas *W. mundlosi* differs from the Patagonian fossil in having taller rays and with absence of oil cells (table 2). Also, both of the previously known *Winteroxylon* species have distinct scalariform tracheid pitting not seen in the new species. Page (1979, 1981) described a minute (7 mm in diameter) twig of putative Winteraceae affinity from the Maastrichtian Great Valley Sequence (California, USA, fig. 1) that can be easily distinguished from the new fossil because of its abundant

283 axial parenchyma, absence of bi-triseriate rays, and absence of both oil cells and sclerotic cells (table
284 2).

285 According to Poole and Francis (2000), the anatomical characters of *Winteroxylon jamesrossi*
286 are related to those exhibited in extant *Bubbia*. However, as also noted by those authors, there are many
287 differences between the extant genus and the Antarctic fossil. It seems clear that *W. jamesrossi* matches
288 most closely anatomically with extant *Takhtajania* and *Tasmannia*, especially in ray height, type of
289 tracheid pitting, and absence of both trabeculae and oil cells (table 1).

290 *Winteroxylon mundlosi* has a central pith with sclerotic cells; rays greater than 2 mm in height
291 and up to eight cells wide, and sclerotic cells present (table 2). Although Gottwald (1992) did not
292 identify oil cells in *W. mundlosi*, they were noted as possibly present in this taxon by Poole and Francis
293 (2000). Gottwald (1992) placed *W. mundlosi* as closely related to extant *Drimys* and *Bubbia*. In Table
294 1, the European fossil matches most closely with extant *Takhtajania* and *Tasmannia*. Based on this
295 discussion, *Winteroxylon oleiferum* sp. nov. may represent the sole fossil sharing wood anatomy with
296 the *Zygogynum* s.l. clade (following Thomas et al. 2014).

297 *Sherwinoxylon winteroides* Boura & Saulnier, a vesselless angiosperm of uncertain family from
298 the middle Cenomanian of the Envigne Valley in western France, has exclusively multiseriate rays, up
299 to nine cells wide, heigh 1.03–10.53 mm and composed of square cells, and up to four upright marginal
300 cells. This fossil show similarities with extant and fossil Winteraceae, but the absence of uniseriate rays
301 led Boura et al. (2018) to suggest that it may belong to an extinct group, either unrelated to
302 Winteraceae or belonging to stem Winteraceae. *Sherwinoxylon winteroides* also differs from
303 *Winteroxylon oleiferum* sp. nov. in having tracheids with exclusively uniseriate bordered pits and
304 absence of uniseriate rays, oil cells, and sclerotic cells.

305

306 *Biogeography and phylogenetic relationships of Winteraceae*

307 The living genera of Winteraceae have disjunct distributions in Australasia (*Pseudowintera*,
308 *Zygogynum*, *Exospermum*, *Bubbia*, *Belliolum*, *Tasmannia*), Madagascar (*Takhtajania*), and the

309 Neotropics (*Drimys*) (e.g., Grímsson et al. 2018). The habit and geographical distribution of the extant
310 genera of Winteraceae is shown in Table 3.

311 Winteraceae has fossil records since the Cretaceous in Laurasia and Gondwana, suggesting the
312 group was globally distributed from the Cretaceous until at least the Eocene in the northern
313 hemisphere, subsequently becoming extinct (Grímsson et al. 2018). In the Southern Hemisphere, this
314 family has been a persistent component of rain forests or wet sclerophyll forests (Hill, 1994; Marquínez
315 et al. 2009) with records since the middle Cretaceous (Barreda and Archangelsky 2006; fig. 1).

316 In addition to the Winteraceae fossil wood record (table 2), pollen tetrads of *Walkeripollis*
317 *gabonensis* Doyle, Hotton & Ward were reported from the Barremian-Aptian of Gabon, Africa (Doyle
318 et al. 1990; fig. 1). *Qatanipollis valentini* Schrank is a putative Winteraceae pollen type described from
319 the late Aptian-Albian of Israel (Schrank 2013), originally reported by Walker et al. (1983) and then
320 designated by Doyle et al. (1990) as *Walkeripollis* sp. In Australasia, the fossil record of this family
321 dates from mid-Campanian sediments of the Otway Basin (Dettmann and Jarzen, 1990; Grímsson et al.
322 2018). Grímsson et al. (2018) proposed that Winteraceae pollen fossils recorded in the Paleocene and
323 Eocene of North America and Greenland represent interchange with Europe via the North Atlantic
324 Land Bridge. This hypothesis could also explain the presence of Winteraceae woods in California and
325 Germany (fig. 1, table 2).

326 Reliable leaf fossils of Winteraceae are very rare (fig. 1). *Zygogynum poratus* Liang & Zhou is a
327 leaf compression from the middle Miocene of Yunnan, southwest China that shares cuticular features
328 and morphological characters with *Zygogynum* s.s. (Lian et al. 2018). A leaf impression assigned to
329 *Drimys antarctica* Dusén from the Cross Valley Formation, Seymour Island, Antarctic Peninsula, is
330 poorly preserved and lacks diagnostic features that would provide a reliable taxonomic position within
331 Winteraceae (Dusén 1098; Tosolini et al. 2013). In Patagonia, a leaf impression dubiously assigned to
332 *Drimys*, *D. patagonica* Berry from the middle Eocene Río Pichileufú flora (Berry 1938), Argentina,
333 needs further study to clarify its taxonomic status.

334 The oldest occurrence of Winteraceae pollen in South America was dated to the late Albian-
335 Cenomanian Kachaike Formation (Barreda and Archangelsky 2006; fig. 1). From the Paleogene,
336 *Pseudowinterapollis couperi* (Krutzsch) emend. Mildenhall & Crosbie pollen grains were recovered
337 from Argentine Patagonia in the late Eocene Sloggett Formation (Olivero et al. 1998), late Oligocene?–
338 Miocene Chenque Formation (Barreda 1997*a*), and the Oligocene San Julián Formation (Barreda
339 1997*b*), among others (e.g., Kooyman et al. 2014). According to Doyle (2000), the sculpture and
340 presence of a well-defined annulus in the Oligocene *Pseudowinterapollis couperi*, from the Chenque
341 Formation, could indicate production by plants closely related to *Drimys,* whereas Grímsson et al.
342 (2018) proposed that the South American fossil pollen could be linked to the extant genera *Drimys*,
343 *Tasmannia*, and *Pseudowintera*, along with the Miocene tetrad *Pseudowinterapollis africanensis*
344 Grímsson, Neumann & Zetter of South Africa (Grímsson et al. 2017).
345 As discussed earlier, *Winteroxylon oleiferum* sp. nov. resembles members of the extant
346 *Zygogynum* s.l. clade because it has distinctive sclerotic nests and oil cells. Furthermore, most of its
347 anatomical characters match those of extant *Bubbia* (table 1), including the presence of tracheid pitting
348 uniseriate, biseriate, and triseriate in radial walls; trabeculae in tracheids; square to irregular tracheid
349 transverse section; and oil cells associated with ray cells. Today, the *Zygogynum* s.l. clade is distributed
350 in eastern Australia, New Guinea, the Moluccas, and New Caledonia, and predominantly in tropical
351 premontane and montane cloud forests (table 3), locations and environments that are well identified for
352 having large numbers of "survivor" taxa from the Laguna del Hunco flora and late-Gondwanan fossil
353 floras in general (e.g., Wilf et al. 2009, 2013, 2019; Kooyman et al. 2014, 2019). The only previous
354 fossil record assigned to the *Zygogynum* s.l. clade is Miocene leaves of *Zygogynum poratus* from
355 Southwest China, indicating an additional past distribution of the clade in mainland Asia that is thought
356 to be sourced from Gondwana (Liang et al. 2018).
357 The phylogenetic analyses of Suh (1993), Marquínez et al. (2009), and Thomas et al. (2014)
358 show that the *Zygogynum* s.l. clade can be resolved into two subclades: the (*Zygogynum* + *Belliolum* +
359 *Exospermum*) subclade from New Caledonia, and the other with the *Bubbia* species, distributed in

eastern Australia, New Guinea, the Moluccas, and New Caledonia (table 3). Thus, *Winteroxylon oleiferum* sp. nov. is the oldest reliable macrofossil record of Winteraceae resembling species of the *Zygogynum* s.l. clade ─a derived clade within extant Winteraceae─ that today lives in Australasian and Malesian rainforests. The presence of *Bubbia*-like Winteraceae at middle latitudes of Patagonia during the early Eocene reinforces the evidence for southern biogeographic connections between South America with Australasia via Antarctica during the warm early Cenozoic and subsequent extinction of some Winteraceae clades in South America.

Acknowledgements

For exceptional assistance in the field and laboratory, we are grateful to M. Caffa, L. Canessa, P. Puerta, and E. Ruigomez, and we thank the Nahueltripay family and the Secretaría de Cultura from the Chubut Province Government for land access. We thank Laboratorio de Microscopía – Grupo de Caracterización de Materiales - Centro Atómico Bariloche (CAB-CNEA) for SEM imaging and M. Medina from the LABGEO-Córdoba University (CICTERRA-CONICET) for making the petrographic sections; and two anonymous reviewers and Editor A. Tomescu for helpful comments on the manuscript. We acknowledge financial support from National Science Foundation (NSF) grants DEB-0345750, DEB-0919071, DEB-0918932, DEB-1556666, DEB-1556136, EAR-1925755, and EAR-1925481.

Literature Cited

Andruchow-Colombo A, P Wilf, IH Escapa 2019 A South American fossil relative of *Phyllocladus*: *Huncocladus laubenfelsii* gen. et sp. nov. (Podocarpaceae), from the early Eocene of Laguna del Hunco, Patagonia, Argentina. Aust Syst Bot 32:290–309.

APG IV 2016 An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc 181:1–20.

385 Aragón E, MM Mazzoni 1997 Geología y estratigrafía del complejo volcánico-piroclástico del Río
386 Chubut medio (Eoceno). Rev Asoc Geol Argent 52:243–256.
387 Bailey IW 1944 The comparative morphology of the Winteraceae III. Wood. J Arnold Arbor 25:97–
388 103.
389 Bailey IW, BGL Swamy 1948 *Amborella trichopoda* Baill., a new morphological type of vesselless
390 dicotyledon. J Arnold Arbor 29:245–253
391 Bailey IW, WP Thompson 1918 Additional notes upon the angiosperms *Tetracentron*, *Trochodendron*,
392 and *Drimys*, in which vessels are absent from the wood. Ann Bot 32:503–512.
393 Barreda VD 1997a Palynomorph assemblage of the Chenque Formation, late Oligocene?-Miocene
394 from Golfo San Jorge Basin, Patagonia, Argentina. Ameghiniana 34:145–154.
395 Barreda VD 1997b Palinoestratigrafía de la Formación San Julián en el área de Playa de la Mina
396 (provincia de Santa Cruz), Oligoceno de la Cuenca Austral. Ameghiniana 34:283–294.
397 Barreda VD, S Archangelsky 2006 The southernmost record of tropical pollen grains in the mid-
398 Cretaceous of Patagonia, Argentina. Cretac Res 27:778–787.
399 Barreda VD, MC Zamaloa, MA Gandolfo, C Jaramillo, P Wilf 2020 Early Eocene spore and pollen
400 assemblages from the Laguna del Hunco fossil-lake beds, Patagonia, Argentina. Int J Plant Sci
401 181:594–615.
402 Berry EW 1925 A Miocene flora from Patagonia. Johns Hopkins Univ Stud Geol 6:183–251.
403 Berry EW 1938 Tertiary flora from the Río Pichileufú, Argentina. Geological Survey of America
404 Special Papers 12:1–149.
405 Bippus AC, IH Escapa, P Wilf, AMF Tomescu 2019 Fossil fern rhizomes as a model system for
406 exploring epiphyte community structure across geologic time: evidence from Patagonia. PeerJ
407 7:e8244.
408 Bomfleur B, I Escapa 2019 A silicified *Todea* trunk (Osmundaceae) from the Eocene of Patagonia.
409 Palaontol Z 93:543–548.

Boura A, G Saulnier, D De Franceschi, B Gomez, V Daviero-Gomez, D Pons, G Garcia, N Robin, J-M Boiteau, X Valentin 2019 An early record of a vesselless angiosperm from the middle Cenomanian of the Envigne Valley (Vienne, Western France). IAWA Journal 40:530–550.

Carlquist S 1981 Wood anatomy of *Zygogynum* (Winteraceae); field observations. Adansonia 3:281–292.

Carlquist S 1982 *Exospermum stipitatum* (Winteraceae); observations on wood, leaves, flowers, pollen and fruit. Aliso 10:277–289.

Carlquist S 1983a Wood anatomy of *Belliolum* (Winteraceae) and a note on flowering. J Arnold Arbor 64:161–169.

Carlquist S 1983b Wood anatomy of *Bubbia* (Winteraceae) with comments on origin of vessels in dicotyledons. Am J Bot 70:578–590.

Carlquist S 1987 Presence of vessels in wood of *Sarcandra* (Chloranthaceae); comments on vessel origins in angiosperms. Am J Bot 74:1765–1771.

Carlquist S 1988 Wood anatomy of *Drimys* s.s. (Winteraceae). Aliso 12:81–95.

Carlquist S 1989 Wood anatomy of *Tasmannia*; summary of wood anatomy of Winteraceae. Aliso 12:257–275.

Carlquist S 2000 Wood and bark anatomy of *Takhtajania* (Winteraceae); phylogenetic and ecological implications. Ann Mo Bot Gard 87:317–322.

Carlquist S 2001 Comparative wood anatomy. Systematic, ecological, and evolutionary aspect of dicotyledon wood. Springer Series in Wood Science. Springer, Berlin.

Carlquist S, EL Schneider 2001 Vegetative anatomy of the New Caledonian endemic *Amborella trichopoda*: relationships with the Illiciales and implications for vessels origin. Pacific Sci 55:305–312.

Carvalho MR, P Wilf, MA Gandolfo, EJ Hermsen, KR Johnson, NR Cúneo 2013 First record of *Todea* (Osmundaceae) in South America, from the early Eocene paleorainforests of Laguna del Hunco (Patagonia, Argentina). Am J Bot 100:1831–1848.

436 Dettmann ME, DM Jarzen 1990. The Antarctic/Australian rift valley: Late Cretaceous cradle of
437 northeastern Australasian relicts? Rev Palaeobot Palynol 65:131–144.
438 Doyle JA 2000 Paleobotany, relationships, and geographic history of Winteraceae. Ann Mo Bot Gard
439 87:303–316.
440 Doyle JA, CL Hotton, JV Ward 1990 Early Cretaceous tetrads, zonasulculate pollen, and Winteraceae.
441 I. Taxonomy, morphology, and ultrastructure. Am J Bot 77:1544–1557.
442 Dusén P 1908 Über Die Tertiare Flora der Seymour Insel. In Wissenschaftliche Ergebnisse der
443 Schwedischen Südpolar–Expedition 1901–1903, Geologie und Paläontologie. Nordenskjöld O
444 ed., Norstedt & Söner, Stockholm, 3:1–27.
445 Feild TS, MA Zwieniecki, NH Holbrook 2000 Winteraceae evolution: An ecophysiological
446 perspective. Ann Mo Bot Gard 87:323–334.
447 Frenguelli J 1943 Proteáceas del Cenozoico de Patagonia. Notas Mus La Plata, Bot 8:201–213.
448 Gandolfo MA, EJ Hermsen 2017 *Ceratopetalum* (Cunoniaceae) fruits of Australasian affinity from the
449 early Eocene Laguna del Hunco flora, Patagonia, Argentina. Ann Bot 119:507–516.
450 Gandolfo MA, EJ Hermsen, MC Zamaloa, KC Nixon, CC González, P Wilf, NR Cúneo, KR Johnson
451 2011 Oldest known *Eucalyptus* macrofossils are from South America. PLoS One 6:e21084.
452 Gosses J, AR Carroll, BT Bruck, BS Singer, BR Jicha, E Aragón, AR Walters, P Wilf 2020 Facies
453 interpretation and geochronology of diverse Eocene floras and faunas, northwest Chubut
454 Province, Patagonia, Argentina. Geol Soc Am Bull https://doi.org/10.1130/B35611.1.
455 Gottwald H 1992 Hölzer aus Marinen Sanden des Oberen Eozän von Helmstedt (Niedersachsen).
456 Palaeontographica B 225:27–103.
457 Grímsson F, A Xafis, FH Neumann, R Zetter 2017 Pollen morphology of extant Winteraceae: a study
458 allowing SEM-based affiliation of its fossil representatives. Acta Palaeobot 57:339–396.
459 Grímsson F, GW Grimm, AJ Potts, R Zetter 2018 A Winteraceae pollen tetrad from the early
460 Paleocene of western Greenland, and the fossil record of Winteraceae in Laurasia and
461 Gondwana. J Biogeogr 45:567–581.

462 Hammer Ø, DAT Harper, PD Ryan 2001 PAST: Paleontological statistics software package for
463 education and data analysis. Palaeontol Electronica 4 (1):1–9. doi:10.1007/978-3-319-92735-
464 0_34
465 Hill RS 1994 History of the Australian Vegetation. Cretaceous to Recent. Cambridge Univ. Press,
466 Cambridge, UK.
467 IAWA Committee 1989 IAWA list of microscopic features for hardwood identification. IAWA
468 Bulletin n.s. 10:219–332.
469 InsideWood 2004-onwards Published on the Internet. http://insidewood.lib.ncsu.edu/search [August 7,
470 2020].
471 Kooyman RM, Wilf P, Barreda, VD, Carpenter RJ, Jordan GJ, Sniderman JMK, Allen A, Brodribb TJ,
472 Crayn D, Feild TS, Laffan SW, Lusk CH, Rossetto M, Weston PH 2014 Paleo-Antarctic
473 rainforest into the modern Old World tropics: the rich past and threatened future of the 'southern
474 wet forest survivors.' Am J Bot 101:2121–2135.
475 Krutzsch W 1968 Zur Kenntnis des dispersen Oenotheraceen- (Onagraceen-) pollens, insbesondere aus
476 dem mitteleuropaischen Tertiar. Palaontologische Abhandlungen B 2:765–788.
477 Liang XQ, P Lu, JW Zhang, T Su, ZK Zhou 2018 First fossils of *Zygogynum* from the Middle Miocene
478 of Central Yunnan, Southwest China, and their palaeobiogeographic significance. Palaeoworld
479 27:399–409.
480 Lindley J 1836 Natural System of Botany, second ed. Longmann, Rees, Orme, Brown, Green and
481 Longman, London, UK.
482 Massoni J, F Forest, H Sauquet 2014 Increased sampling of both genes and taxa improves resolution of
483 phylogenetic relationships within Magnoliidae, a large and early-diverging clade of
484 angiosperms. Mol Phylogenet Evol 70:84–93.
485 Massoni J, J Doyle, H Sauquet 2015a Fossil calibration of Magnoliidae, an ancient lineage of
486 angiosperms. Palaeontol Electronica 18.1.2FC:1–25; palaeo-electronica.org/content/fc-2.

Massoni J, TLP Couvreur, H Sauquet 2015b Five major shifts of diversification through the long evolutionary history of Magnoliidae (angiosperms). BMC Evol Biol 15: https://doi.org/10.1186/s12862-015-0320-6.

Marquínez X, LG Lohmann, LF Salatino, A Salatino, F González 2009 Generic relationships and dating of lineages in Winteraceae based on nuclear (ITS) and plastid (rpS16 and psbA-trnH) sequence data. Mol Phylogenet Evol 53:435–449.

Metcalfe CR, L Chalk 1950 Anatomy of the Dicotyledons, volumes I and II. Oxford: Clarendon Press.

Mildenhall DC, YM Crosbie 1979. Some porate pollen from the upper Tertiary of New Zealand. New Zeal J Geol Geophys 22:499–508.

Müller S, K Salomo, J Salazar, J Naumann, MA Jaramillo, C Neinhuis, TS Feild, S Wanke 2015 Intercontinental long-distance dispersal of Canellaceae from the New to the Old World revealed by a nuclear single copy gene and chloroplast loci. Mol Phylogenet Evol 84:205–219.

Olivero EB, V Barreda, SA Marenssi, SN Santillana, DR Martinioni 1998 Estratigrafia, sedimentologia y palinologia de la Formación Sloggett (Paleogeno continental), Tierra del Fuego. Rev Asoc Geol Argent 53:504–516.

Olivero EB 2012 Sedimentary cycles, ammonite diversity and palaeoenvironmental changes in the Upper Cretaceous Marambio Group, Antarctica. Cret Res 34:348–366.

Page VM 1979 Dicotyledonous wood from the Upper Cretaceous of Central California. J Arnold Arbor 60:323–349.

Page VM 1981 Dicotyledonous wood from the Upper Cretaceous of Central California. III. Conclusions. J Arnold Arbor 62:437–455.

Patel RN 1974 Wood anatomy of the dicotyledons indigenous to New Zealand 4. Winteraceae. N Z J Bot 12:19–32.

Petersen CS 1946 Estudios geológicos en la región del río Chubut medio. Secretaría de Industria y Comercio. Dirección General de Minas y Geología Boletín 59:1–137.

512 Pipo ML, A Iglesias, J Bodnar 2020 A new vesselless angiosperm stem with a cambial variant from the
513 Upper Cretaceous of Antarctica. Acta Palaeontol Pol 65:261–272.
514 Poole I, JE Francis 2000 The first record of fossil wood of Winteraceae from the Upper Cretaceous of
515 Antarctica. Ann Bot 85:307–315.
516 Pujana RR, P Wilf, MA Gandolfo 2020 Conifer wood assemblage dominated by Podocarpaceae, early
517 Eocene of Laguna del Hunco, central Argentinean Patagonia. Phytokeys 156:81–102.
518 Rancusi MH, M Nishida, H Nishida 1987 Xylotomy of important Chilean woods. In M Nishida (Ed.),
519 Contributions to the Botany in the Andes II (pp. 68–153). Tokyo: Academic Scientific Book
520 Inc.
521 Richter HG, MJ Dallwitz 2000 onwards. Commercial timbers: descriptions, illustrations, identification,
522 and information retrieval. Version: 9th April 2019 [August 7, 2020].
523 Romero EJ, MC Dibbern, MA Gandolfo 1988 Revisión de *Lomatia bivascularis* (Berry) Frenguelli
524 (Proteaceae) del yacimiento de la Laguna del Hunco (Paleoceno), Pcia. del Chubut. Actas del
525 IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza 3:125–130.
526 Rossetto-Harris G, P Wilf, IH Escapa, A Andruchow-Colombo 2020 Eocene *Araucaria* Sect. Eutacta
527 from Patagonia and floristic turnover during the initial isolation of South America. Am J Bot
528 107:806–832.
529 Qiu Y-L, J Lee, F Bernasconi-Quadroni, DE Soltis, PS Soltis, M Zanis, EA Zimmer, Z Chen, V
530 Savolainen, MW Chase 1999 The earliest angiosperms: evidence from mitochondrial, plastid
531 and nuclear genomes. Nature 402:404–407.
532 Qiu Y-L, O Dombrovska, J Lee, L Li, BA Whitlock, F Bernasconi-Quadroni, JS Rest, CC Davis, T
533 Borsch, KW Hilu, SS Renner, DE Soltis, PS Soltis, MJ Zanis, JJ Cannone, RR Gutell, M
534 Powell, V Savolainen, LW Chatrou, MW Chase 2005 Phylogenetic analyses of basal
535 angiosperms based on nine plastid, mitochondrial, and nuclear genes. Int J Plant Sci 166:815–
536 842.

Sanmartín I, F Ronquist 2004 Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns Syst Biol 53:216–243.

Schrank E 2013 New taxa of winteraceous pollen from the Lower Cretaceous of Israel. Rev Palaeobot Palynol 195:19–25.

Schweingruber FH, A Börner, ED Schulze 2011 Atlas of Stem Anatomy in Herbs, Shrubs and Trees, Volume 1. Springer.

Scott RA, EA Wheeler 1982 Fossil woods from the Eocene Clarno Formation of Oregon. IAWA Bulletin n.s. 3:135–154.

Soltis PS, DE Soltis 2004 The origin and diversification of angiosperms. Am J Bot 91: 1614–1626.

Suh Y, LB Thien, HE Reeve, EA Zimmer 1993 Molecular evolution and phylogenetic implications of internal transcribed spacer sequences of ribosomal DNA in Winteraceae. Am J Bot 80:1042–1055.

Suzuki M, L Joshi, T Fujii, S Noshiro 1991 The anatomy of unusual tracheids in *Tetracentron* wood. IAWA Bulletin n.s. 12:23–33.

Swamy BGL, IW Bailey 1950 *Sarcandra*, a vesselless genus of the Chloranthaceae. J Arnold Arbor 31:117–129.

Thomas N, JJ Bruhl, A Ford, PH Weston 2014 Molecular dating of Winteraceae reveals a complex biogeographical history involving both ancient Gondwanan vicariance and long-distance dispersal. J Biogeogr 41:894–904.

Tortorelli LA 1956 Maderas y Bosques Argentinos. Buenos Aires: Editorial Acme, 910 pp.

Tosolini AM, DJ Cantrill, JE Francis 2013 Paleocene flora from Seymour Island, Antarctica: Revision of Dusén's (1908) angiosperm taxa. Alcheringa 37:366–391.

Vink W 1985 The Winteraceae of the Old World. V. *Exospermum* links *Bubbia* to *Zygogynum*. Blumea 31:39–55.

Vink W 1988 Taxonomy in Winteraceae. Taxon 37:691–698.

562 Vink W 1993 Winteraceae. In: Kubitzki K, Rohwer JG, Bittich V. (Eds.). The Families and Genera of
563 Vascular Plants. Flowering Plants – Dicotyledons, vol. II. Springer-Verlag, Berlin, Germany,
564 pp. 630–638.
565 Walker JW, GJ Brenner, AG Walker 1983 Winteraceous pollen in the Lower Cretaceous of Israel:
566 early evidence of a magnolialean angiosperm family. Science 220:1273–1275.
567 Wheeler EA 2011 InsideWood - a web resource for hardwood anatomy. IAWA Journal 32:199–211.
568 Wilf P 2012 Rainforest conifers of Eocene Patagonia: attached cones and foliage of the extant
569 Southeast Asian and Australasian genus *Dacrycarpus* (Podocarpaceae). Am J Bot 99:562–584.
570 Wilf P, NR Cúneo, KR Johnson, JF Hicks, SL Wing, JD Obradovich 2003 High plant diversity in
571 Eocene South America: evidence from Patagonia. Science 300:122–125.
572 Wilf P, KR Johnson, NR Cúneo, ME Smith, BS Singer, MA Gandolfo 2005 Eocene plant diversity at
573 Laguna del Hunco and Río Pichileufú, Patagonia, Argentina. Am Nat 165:634–650.
574 Wilf P, SA Little, A Iglesias, MC Zamaloa, MA Gandolfo, NR Cúneo, KR Johnson 2009 *Papuacedrus*
575 (Cupressaceae) in Eocene Patagonia: a new fossil link to Australasian rainforests. Am J Bot
576 96:2031–2047.
577 Wilf P, NR Cúneo, IH Escapa, D Pol, MO Woodburne 2013 Splendid and seldom isolated: the
578 paleobiogeography of Patagonia. Annu Rev Earth Planet Sci 41:561–603.
579 Wilf P, KC Nixon, MA Gandolfo, NR Cúneo 2019 Eocene Fagaceae from Patagonia and Gondwanan
580 legacy in Asian rainforests. Science 364 (6444): eaaw5139. DOI: 10.1126/science.aaw5139.
581 Zamaloa MC, MA Gandolfo, CC González, EJ Romero, NR Cúneo, P Wilf 2006 Casuarinaceae from
582 the Eocene of Patagonia, Argentina. Int J Plant Sci 167:1279–1289.
583 Zanis MJ, PS Soltis, Y-L Qiu, EA Zimmer, DE Soltis 2003 Phylogenetic analyses and perianth
584 evolution in basal angiosperms. Ann Mo Bot Gard 90:129–150.

585 Figure captions

586 Figure 1. Distribution of extant (dark gray shading) and fossil (light gray, Cretaceous; black, Cenozoic;
587 star, pollen; circle, wood; rectangle, leaf) Winteraceae. Fossil wood records labeled: *Winteroxylon*
588 *mundlosi* (Helmstedt Formation, late Eocene, Lower Saxony, Germany); *Winteroxylon jamesrossi*
589 (Santa Marta Formation, James Ross Island, early Campanian, Antarctica); *Winteroxylon*? (Great
590 Valley Sequence, Maastrichtian, California, USA); *Winteroxylon oleiferum* sp. nov. (arrow, Laguna del
591 Hunco, Huitrera Formation, early Eocene, Chubut province, Argentina). Modified from Grímsson et al.
592 (2018). References: Doley 2000; Barreda and Archangelsky 2006; Marquínez et al. 2009; Liang et al.
593 2018; Grímsson et al. 2018, and others cited therein.

594

595 Figure 2. *A*, Panoramic view of Eocene strata at Laguna del Hunco (LH), looking southwest from the
596 LH4 fossil locality and showing the positions of selected fossil plant localities. 1. location of the
597 Winteraceae fossil stump sampled here; and 2. fossil locality LH4 (Wilf et al. 2003). *B*, The fossil
598 stump in basal view, showing roots at the base of the stump (black arrow = roots disposed
599 perpendicular to the main stem; white arrow = roots disposed in axial orientation). *C*, Lateral view of
600 the stump, clearly showing the two regions: stump with roots (left) and base of the main stem (right).
601 *D*, View from the apical part of the preserved stem, showing the variation in stump diameter toward the
602 base. Pick for scale = 30 cm length.

603

604 Figure 3. *Winteroxylon oleiferum* sp. nov., MPEF-Pb 3997. *A*, General view in transverse section,
605 showing uniseriate rays (white arrows) and tracheids. *B–C*, General view in transverse section, showing
606 uniseriate (white arrows) and multiseriate rays (black arrows) and tracheids. *D*, General view in
607 tangential longitudinal section, showing uniseriate and multiseriate rays (white arrow) composed of
608 procumbent and upright cells and probable sheath cells (black arrows). *E–F*, General view in tangential
609 longitudinal section, showing oil cavities (white arrows) surrounded by parenchymatic cells inside the
610 multiseriate rays. G, General view in tangential longitudinal section, showing sclerotic nests (white

arrow) and dark amorphous contents (black arrow) in a multiseriate ray. *H–I*, General view in radial longitudinal section, showing heterocellular rays composed of procumbent and upright cells (white arrows). Scale bars = 400 µm.

Figure 4. *Winteroxylon oleiferum* sp. nov., MPEF-Pb 3997. *A*, Detail in transverse section, showing tracheids, axial parenchyma (white arrows), and a multiseriate ray; scale bar = 200 µm. *B*, Detail in tangential longitudinal section, showing multiseriate, biseriate (black arrow) and uniseriate (white arrow) rays; scale bar = 200 µm. *C*, Detail in tangential longitudinal section, showing multiseriate rays up to 15 cells; scale bar = 200 µm. *D*, Detail in transverse section, showing axial parenchyma with pits (white arrows); scale bar = 50 µm. *E*, Detail of a parenchyma pit in transverse section (white arrow); scale bar = 20 µm. *F,* Detail in tangential longitudinal section, showing sclerotic nest; scale bar = 200 µm. *G*, Detail in radial longitudinal section, showing heterocellular ray composed of procumbent and upright cells; scale bar = 200 µm. *H*, Detail in tangential longitudinal section, showing oil canal (white arrow); scale bar = 200 µm. *I*, Detail in tangential longitudinal section, showing dark content in ray cell; scale bar = 50 µm. *J*, General view in radial longitudinal section, showing bordered pits in ray cells (black arrow); scale bar = 200 µm. *K*, Detail in radial longitudinal section, showing bordered pit in ray cell (black arrow); scale bar = 50 µm.

Figure 5. *Winteroxylon oleiferum* sp. nov., MPEF-Pb 3997. *A*, Detail in tangential longitudinal section, showing circular bordered and uniseriate pits; scale bar = 20 µm. *B*, Detail in tangential longitudinal section, showing circular bordered, biseriate and alternate pitting; scale bar = 50 µm. *C*, Detail in tangential longitudinal section, showing circular bordered, triseriate and alternate to opposite pitting; scale bar = 50 µm. *D*, Detail in tangential longitudinal section, showing biseriate ray and trabeculae in tracheids (white arrows); scale bar = 50 µm. *E*, Detail in transverse section, showing three tracheid cells with middle lamellae (white arrow) and pit (black arrow); scale bar = 20 µm. *F*, Detail in radial longitudinal section, showing bordered pits that are alternate to irregular in arrangement (black arrow)

637 in ray cells; scale bar = 50 µm. *G*, Detail in tangential longitudinal section, showing sclerotic cells
638 (white arrow) and dark amorphous accumulations in a cell (black arrow); scale bar = 50 µm. H, Detail
639 in tangential longitudinal section, showing a sclerotic nest; scale bar = 50 µm.
640
641 Figure 6. *Winteroxylon oleiferum* sp. nov., MPEF-Pb 3997, under SEM. *A*, Detail in radial longitudinal
642 section, showing bordered pits in ray cells, alternate to irregular in arrangement; scale bar = 100 µm. *B*,
643 Detail in radial longitudinal section, showing bordered pits; Scale bar = 30 µm. *C*, Detail in tangential
644 longitudinal section, showing biseriate, bordered and alternate to opposite pits in a tracheid; Scale bar =
645 30 µm.
646
647 Table 1. Wood anatomical comparisons of *Winteroxylon oleiferum* sp. nov. with extant and fossil taxa
648 of Winteraceae. *Tracheid diameter measured in tangential section.
649
650 Table 2. Further comparison among fossil wood species of Winteraceae.
651
652 Table 3. Comparison of stem morphology, habit preference, phenology, habit, and geographic
653 distribution of the genera of Winteraceae. References: Tortorelli (1956); Patel (1974); Carlquist (1981,
654 1982, 1983a, 1983b, 1988, 1989, 2000); Feild et al. (2000).
655

Table 1

	taxa	growth rings	tracheid section	radial tracheid pitting	tracheid diameter (µm)*	tracheid pitting	axial parenchyma	ray type and structure	ray height (µm)	ray cell pits	cell contents	oil cells	silica bodies	sclerotic nest	references
	Drimys	indistinct	square to irregular	uniseriate, biseriate, triseriate	25–69	6–16 µm diameter circular, bordered, opposite, alternate, scalariform	scarce or absent, diffuse	uniseriate and multiseriate (4–10 cells) heterocellular	uniseriate (300–3370) multiseriate (1250–4800)	bordered	dark amorphous	absent	present smooth and irregular	absent	Bailey and Thompson 1918 Bailey 1944 Tortorelli 1956 Rancusi et al. 1987 Carlquist 1988
	Takhtajania	absent	quadrangular to rectangular	uniseriate and biseriate, helical thickenings	mean 38	circular, bordered, scalariform	very scarce, diffuse	uniseriate, biseriate and multiseriate (up to 5 cells) heterocellular	uniseriate (mean 1473) multiseriate (mean 4176)	bordered	tannin-like material	absent	absent	absent	Carlquist 2000
	Tasmannia	absent or slightly distinct	quadrangular to rectangular	uniseriate and biseriate, helical thickenings	16–46	circular, bordered, scalariform to transitional	scarce, diffuse occasional tangentially or radially oriented pairs of parenchyma strands	uniseriate, biseriate and multiseriate heterocellular	uniseriate (286–1816) multiseriate (1093–5148)	bordered	------	absent	absent	sclerotic nest	Carlquist 1989
	Pseudowintera	indistinct to slightly distinct	square to irregular	uniseriate, biseriate and trisearíate. Spiral thickenings and trabeculae	13–46	circular, bordered, alternate, opposite and scalariform	scarce, diffuse and diffuse-in-aggregates	uniseriate, biseriate and multiseriate (7–29 cells) heterocellular	uniseriate multiseriate (300–6100)	bordered	absent	absent	absent	absent	Bailey 1944 Patel 1974
Zygogynum s.l. clade	*Belliolum*	absent	quadrangular to rectangular	biseriate and triseriate	42–60	circular, bordered, scalariform to transitional to opossite	scarce, diffuse and in short bands	heterocellular	------	bordered	resin-like material	absent	absent	absent	Carlquist 1983a Bailey 1944
	Bubbia	absent	square to irregular	uniseriate, biseriate, triseriate. Trabeculae common	23–51	7–14 µm diameter, circular, opposite, occasionally elongated and scalariform	diffuse or in bands 1–3 cells thick	uniseriate, biseriate and multiseriate (3–7 cells) heterocellular	600– >1500	circular, bordered	resin-like material	present	absent	absent	Carlquist 1983b
	Exospermum	absent	quadrangular to rectangular	biseriate and triseriate	55 (mean)	circular to elongated, alternate	diffuse or in bands 1–3 cells thick	uniseriate and multiseriate (up to 7 cells)	multiseriate (mean 6812)	bordered	resin-like material	present	absent	absent	Carlquist 1982
	Zygogynum s.s.	absent	square to irregular	uniseriate	------	circular, bordered, scalariform	scarce, diffuse, diffuse-in-aggregates and in bands 2–3 cells thick	uniseriate and multiseriate	------	bordered	------	present	absent	sclereids	Bailey 1944 Carlquist 1981
	Winteroxylon oleiferum n. sp.	Indistinct	quadrangular to rectangular	uniseriate, biseriate, triseriate. Trabeculae common	14–33	7–10 µm diameter, circular, alternate to opposite	scarce, diffuse, occasional tangentially or radially oriented pairs of parenchyma strands	uniseriate, biseriate and multiseriate (3–15 cells) heterocellular	uniseriate (131–665) multiseriate (1035–4105)	circular, bordered	dark amorphous	present	absent	sclerotic nest	this paper
	Winteroxylon mundlosi	Indistinct	------	uniseriate, biseriate, sometimes scalariform	23–36	circular	uniseriate bands	uniseriate and multiseriate (3–7 cells) heterocellular	all rays higher than 2000	circular, bordered	present	absent	absent	present	Gottwald 1992
	Winteroxylon jamesrossi	Indistinct	------	uniseriate, biseriate, elongate to scalariform	30–50	circular to more elongate	diffuse or in radial pairs and short strands of up to *ca.* 4 cells thick	uniseriate, biseriate and multiseriate (3–13 cells) heterocellular	uniseriate (200–1636) multiseriate (500–4300)	circular, bordered	occasional	absent	absent	absent	Poole and Francis 2000

Table 2

		Winteroxylon jamesrossi Poole and Francis 2000	*Winteroxylon mundlosi* Gottwald 1992	*Winteroxylon* ? Page 1979, 1981	*Winteroxylon oleiferum sp. nov.* this contribution
Fossil locality		Lachman Crags James Ross Island Antarctica	Helmstedt area Lower Saxony Germany	Diablo Range Central California USA	Laguna del Hunco Chubut, Argentina
Stratigraphic horizon and age		Santa Marta Fm. early Campanian	Annenberg Fm. late Eocene	Great Valley Sequence Maastrichtian	La Huitrera Fm. early Eocene
Growth rings		indistinct	indistinct	?	indistinct
Axial parenchyma		diffuse or in radial pairs forms short axial strands of up to four cells	uniseriate bands or in tangential apotracheal uniseriate bands	abundant	diffuse, occasional tangentially or radially oriented strand pairs
Tracheids	tangential diameter (µm)	30 (35) 50	23 (29) 36	13 (26) 38	14 (24) 33
	radial diameter (µm)	15 (28) 40	----------	----------	19 (27) 31
	wall thickness (µm)	2.5–10	5 (7) 9	thick-walled	5 (7) 9
	pitting diameter (µm) and shape	2.5–15 µm circular to more elongate	7 (9) 11 µm circular	small, rounded	7 (8) 10 µm circular
	overlapped area	uniseriate, biseriate, elongate to scalariform	uniseriate, biseriate, sometimes scalariform	?	uniseriate, biseriate, triseriate
Rays	structure	heterocellular procumbent cells becoming square to periphery upright cells in uniseriate and multiseriate wings	heterocellular upright cells in uniseriate and multiseriate wings	heterocellular square or upright cells	heterocellular upright and procumbent cells
	height (µm)	uniseriate 200–1636 µm Multiseriate 500–4300	all rays higher than 2000	?	uniseriate 131 (314) 655 Multiseriate 1035 (2089) 4105
	width	uniseriate, biseriate and 4 to 13 cells	uniseriate and 3 to 8 celled	uniseriate and multiseriate 4 to 5 cells	uniseriate, biseriate and 3 to 15 cells
	cell pitting	circular, bordered	circular	minute pits on tangential walls	circular, bordered
Cell content	dark amorphous	occasional	present	absent?	present
	oil cells	absent	absent	absent	present
	sclerotic cells	absent	present	absent	present

Table 3

		Stem diameter (cm)	Stem height (m)	Growth habit	Leaf habit	Habitat	Extant geographic distribution
	Drimys	0.6–10	up to 20	shrub to small trees	evergreen	moist mountain forests (tropical and temperate frost-free) in Neotropics, maritime temperate rainforests and Subantarctic temperate forests	Neotropics (from southern Mexico to southern South America)
	Takhtajania	up to 4.5	up to 5	shrub to small trees	evergreen	sub-humid higher montane forests (~1000 m)	Madagascar
	Tasmannia	4–34	4 or more	small trees	evergreen	moist mountain forests and in wet areas in the drier forests, alpine and lowland temperate rainforests	Australia, New Guinea, Celebes, Borneo, and Philippines
	Pseudowintera	2.5–6.6	1–8	shrub to small trees	evergreen	lowland to higher montane forests (from 35°–42° S)	New Zealand
***Zygogynum* s.l. clade**	***Belliolum***	*c.a.* 10	-----	small trees	evergreen	understory and subcanopy treeless to trees in subtropical lowland rainforests	Solomon Islands and New Caledonia
	Bubbia	-----	15	small to large trees	evergreen	tropical premontane and montane cloud forests	Eastern Australia, New Guinea, New Caledonia, and Moluccas
	Exospermum	*c.a.* 24	-----	large trees	evergreen	subtropical lowland rainforests	Eastern Australia, New Guinea, New Caledonia, and Moluccas
	Zygogynum s.s.	-----	2–3	small trees to shrubs	evergreen	subcanopy trees in subtropical lowland rainforests and montane cloud forests	New Caledonia

Figure 1

Click here to access/download;Figure;Figure 1.tif

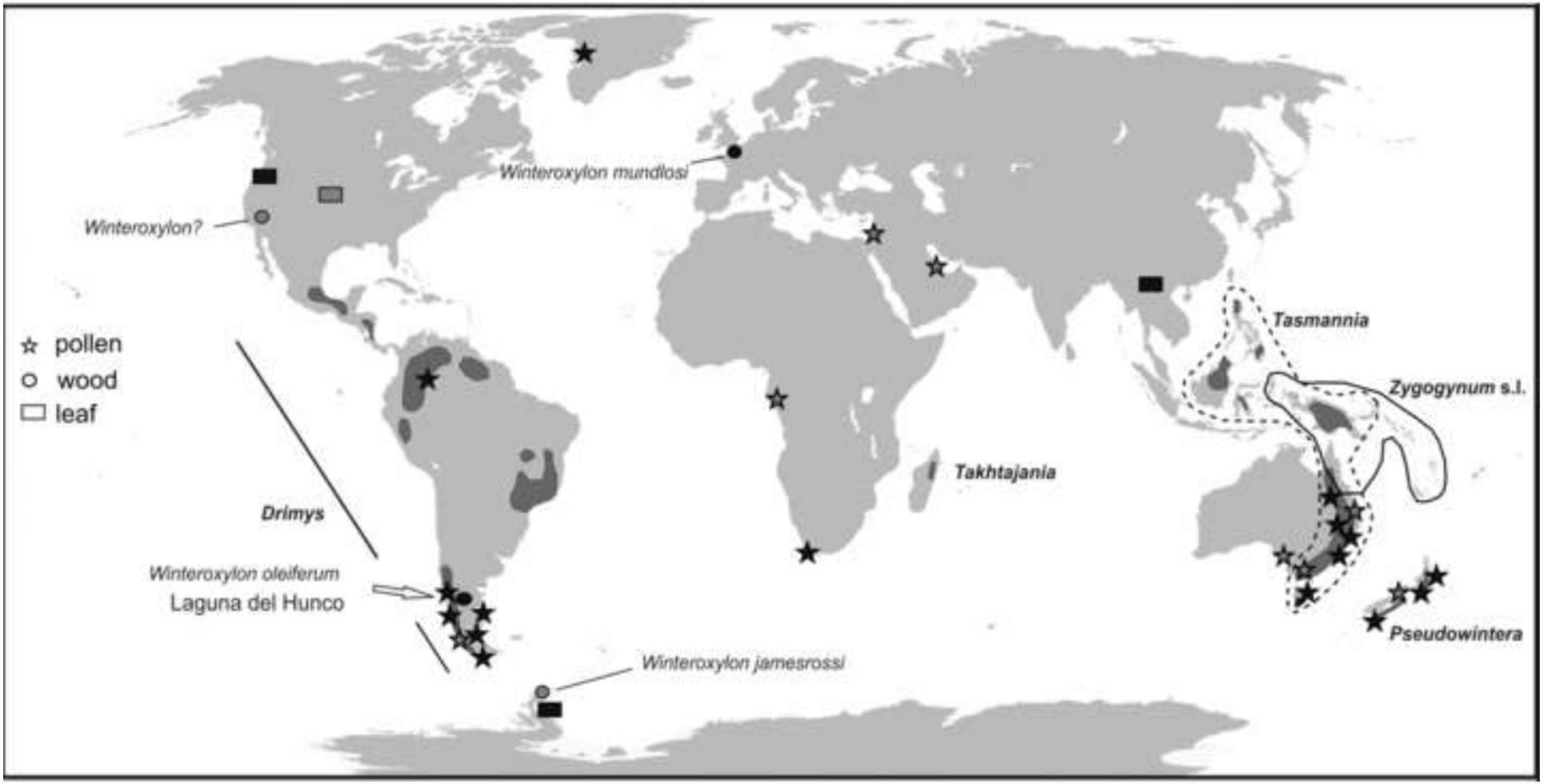

Figure 2 color

Click here to access/download;Figure;Figure 2.tif

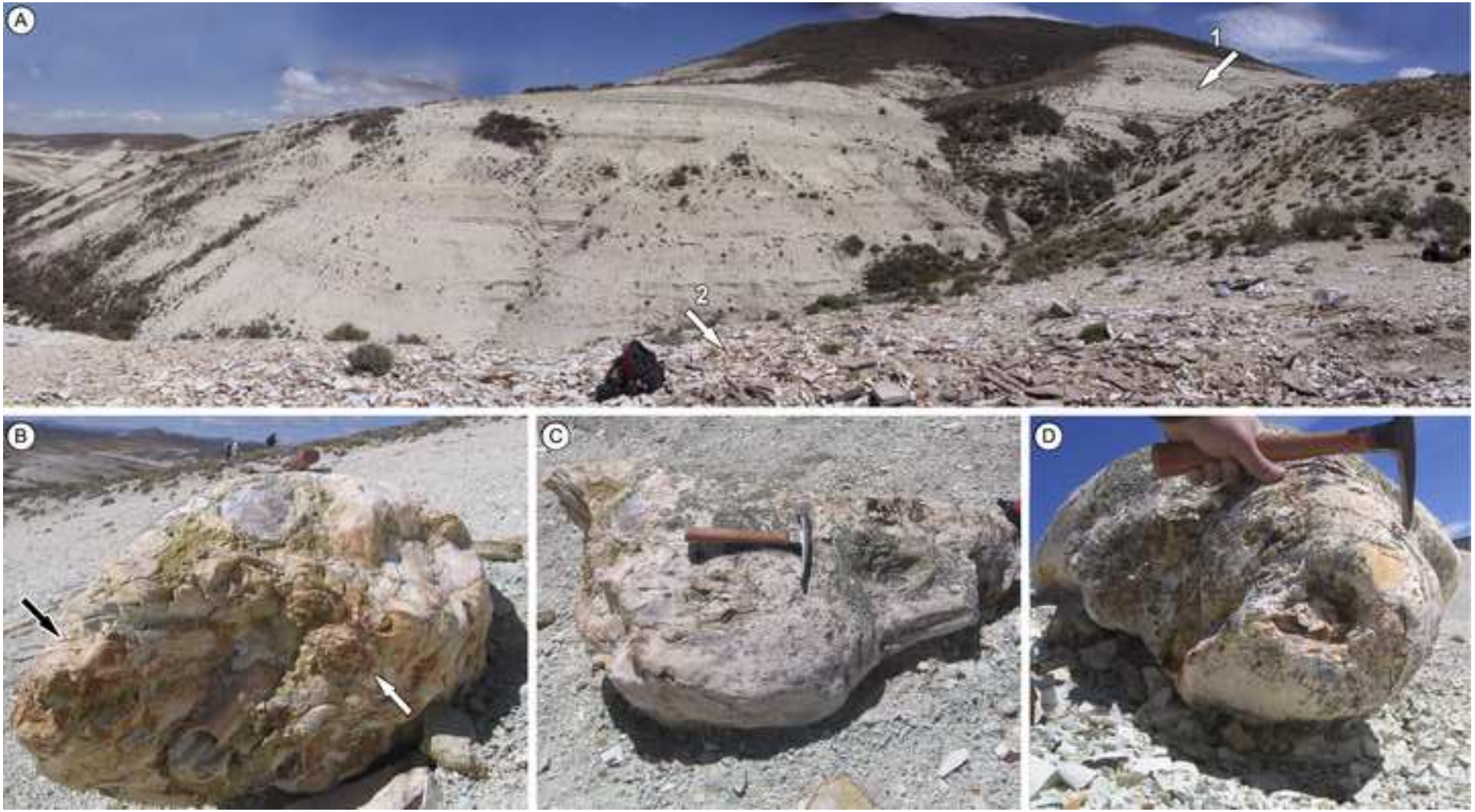

Figure 2 bw

Click here to access/download;Figure;Figure 2 BW.tif

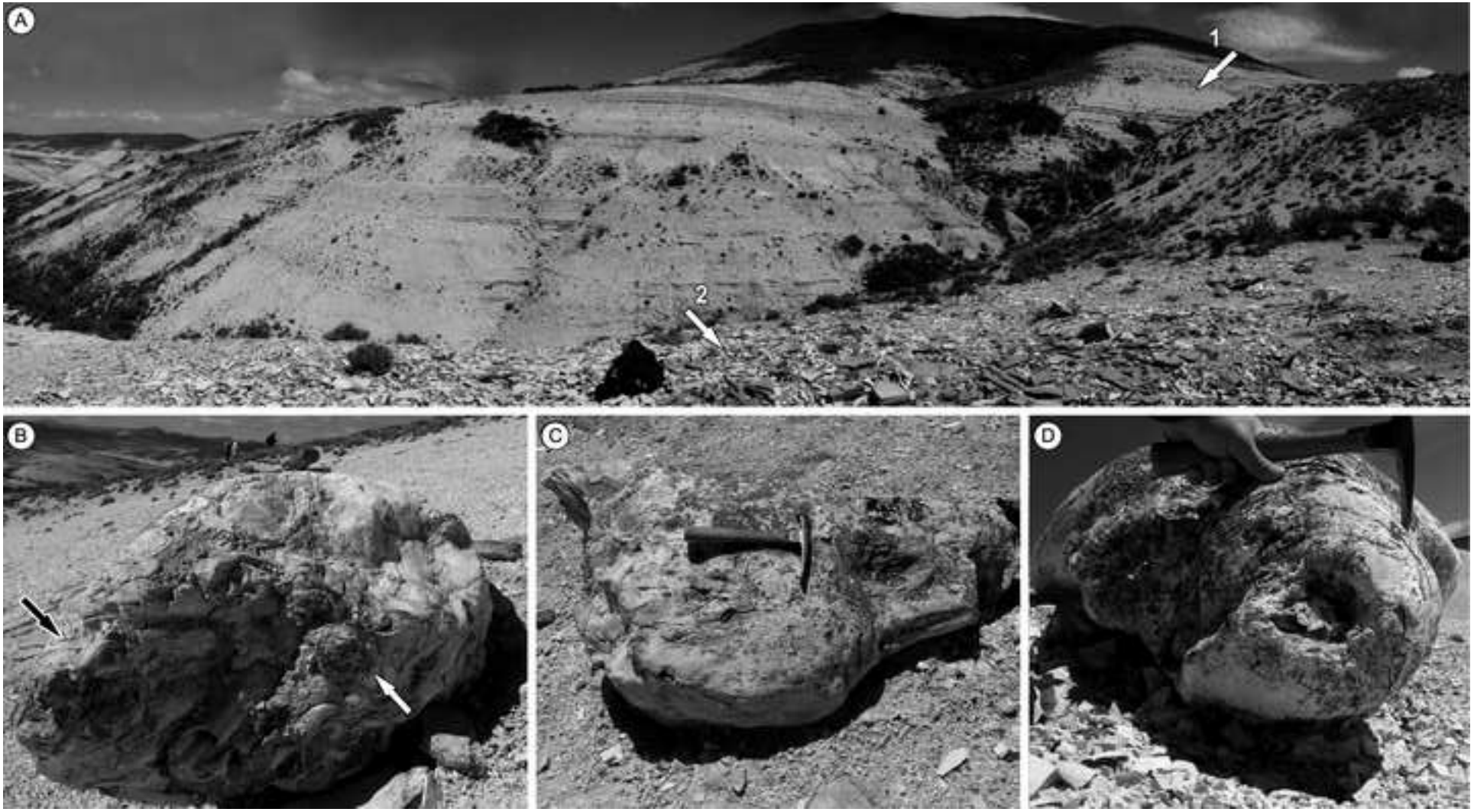

Figure 3 color

Click here to access/download;Figure;Figure 3.tif

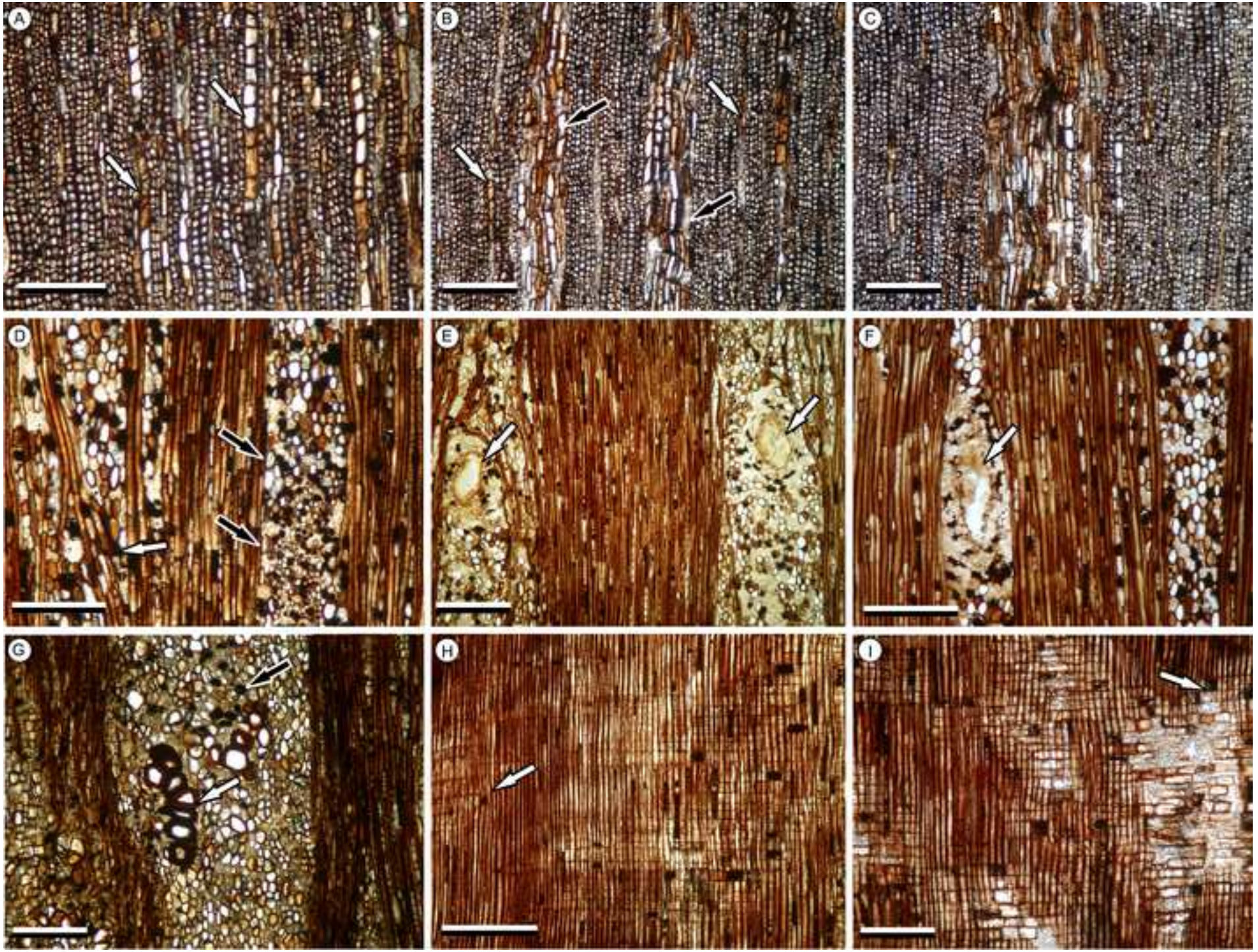

Figure 3 bw

Click here to access/download;Figure;Figure 3 BW.tif

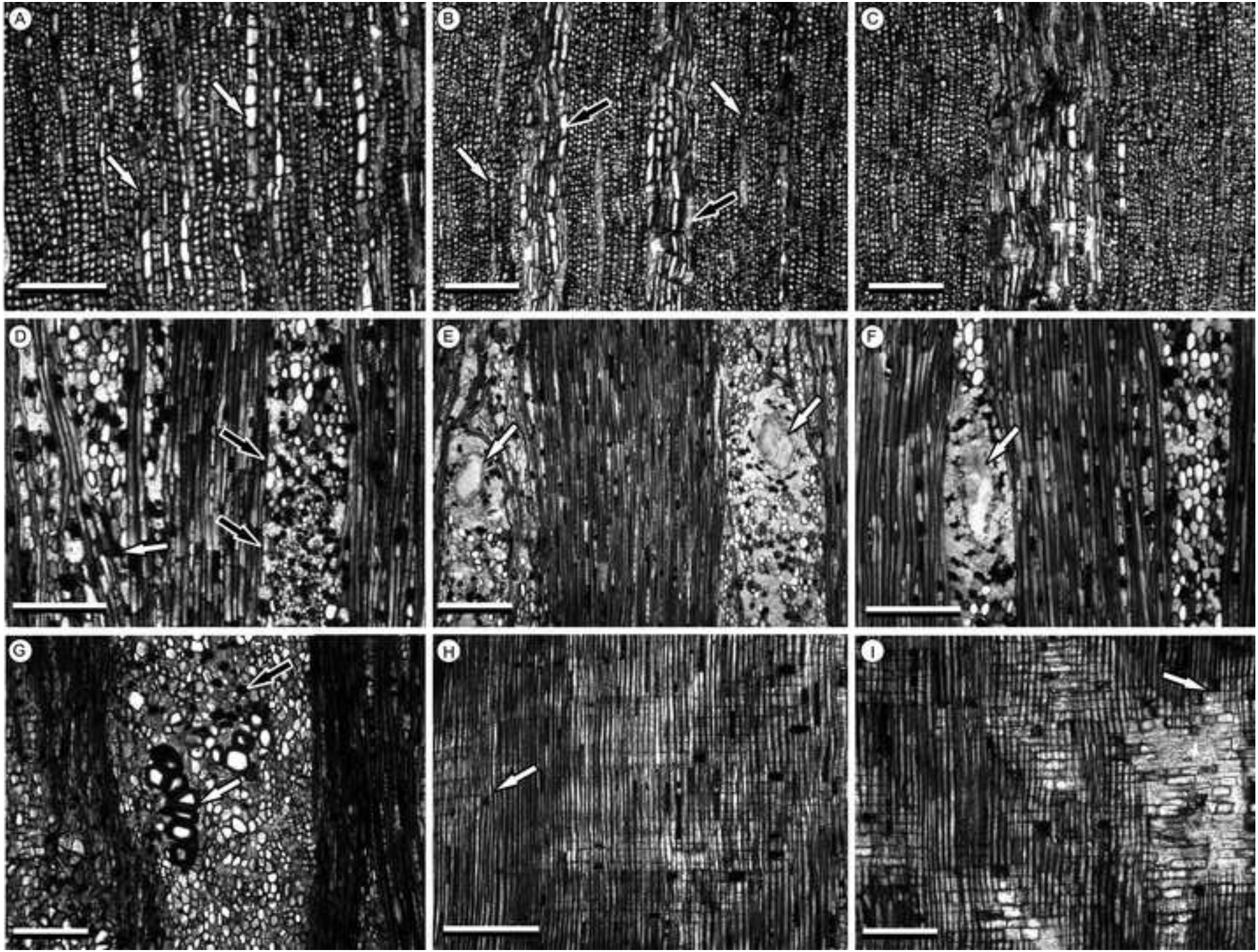

Figure 4 color

Click here to access/download;Figure;Figure 4.tif

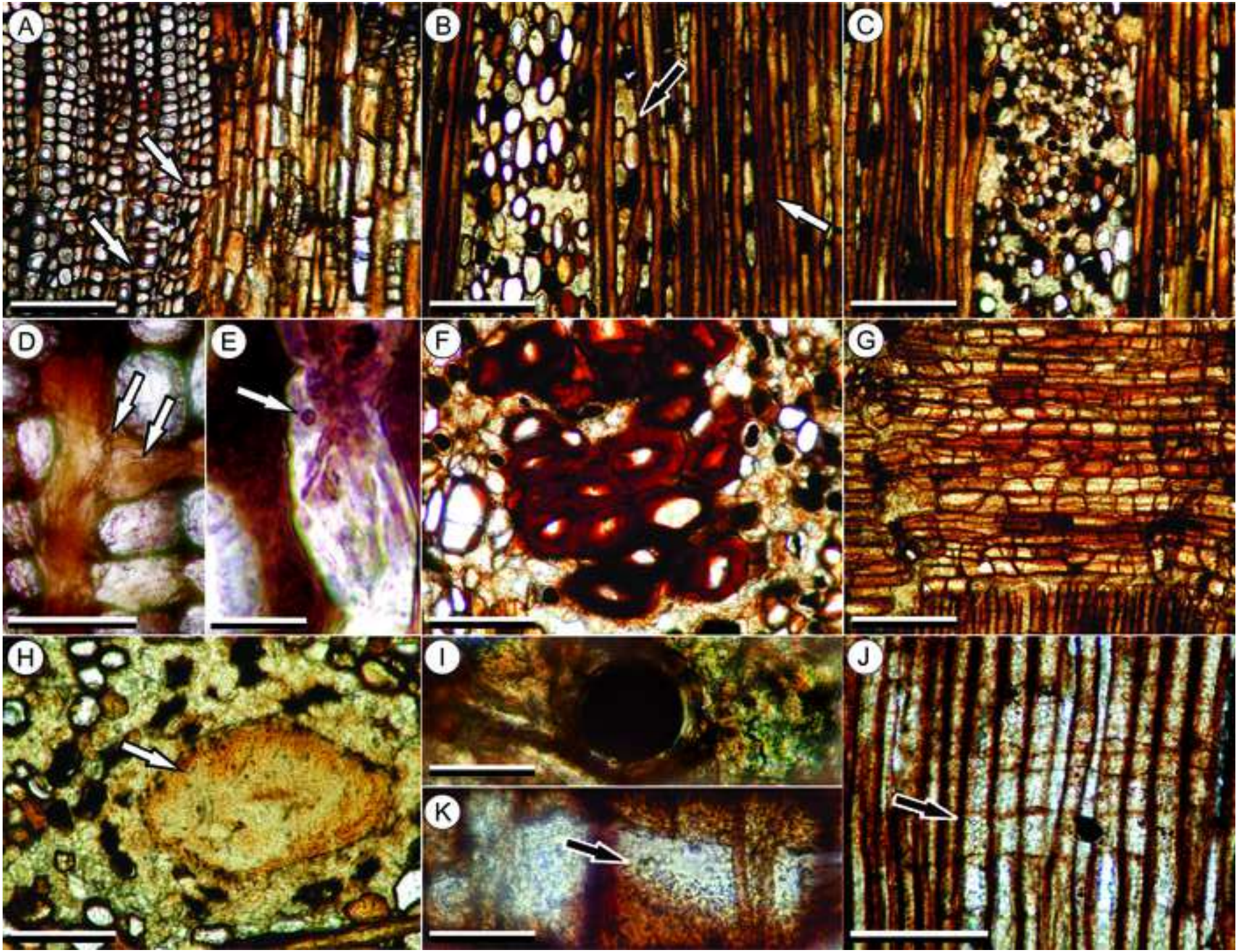

Figure 4 bw

Click here to access/download;Figure;Figure 4 BW.tif

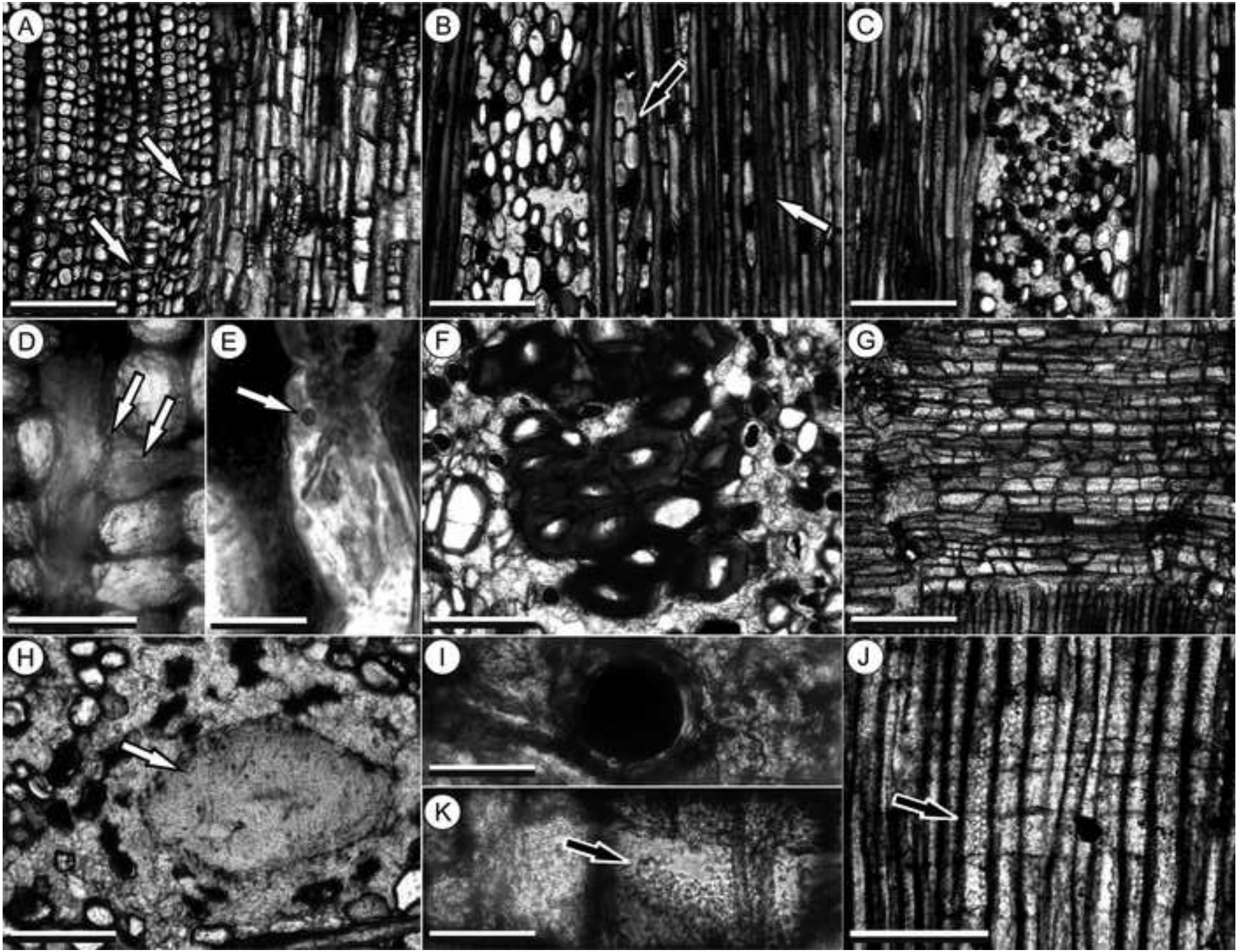

Figure 5 color

Click here to access/download;Figure;Figure 5.tif

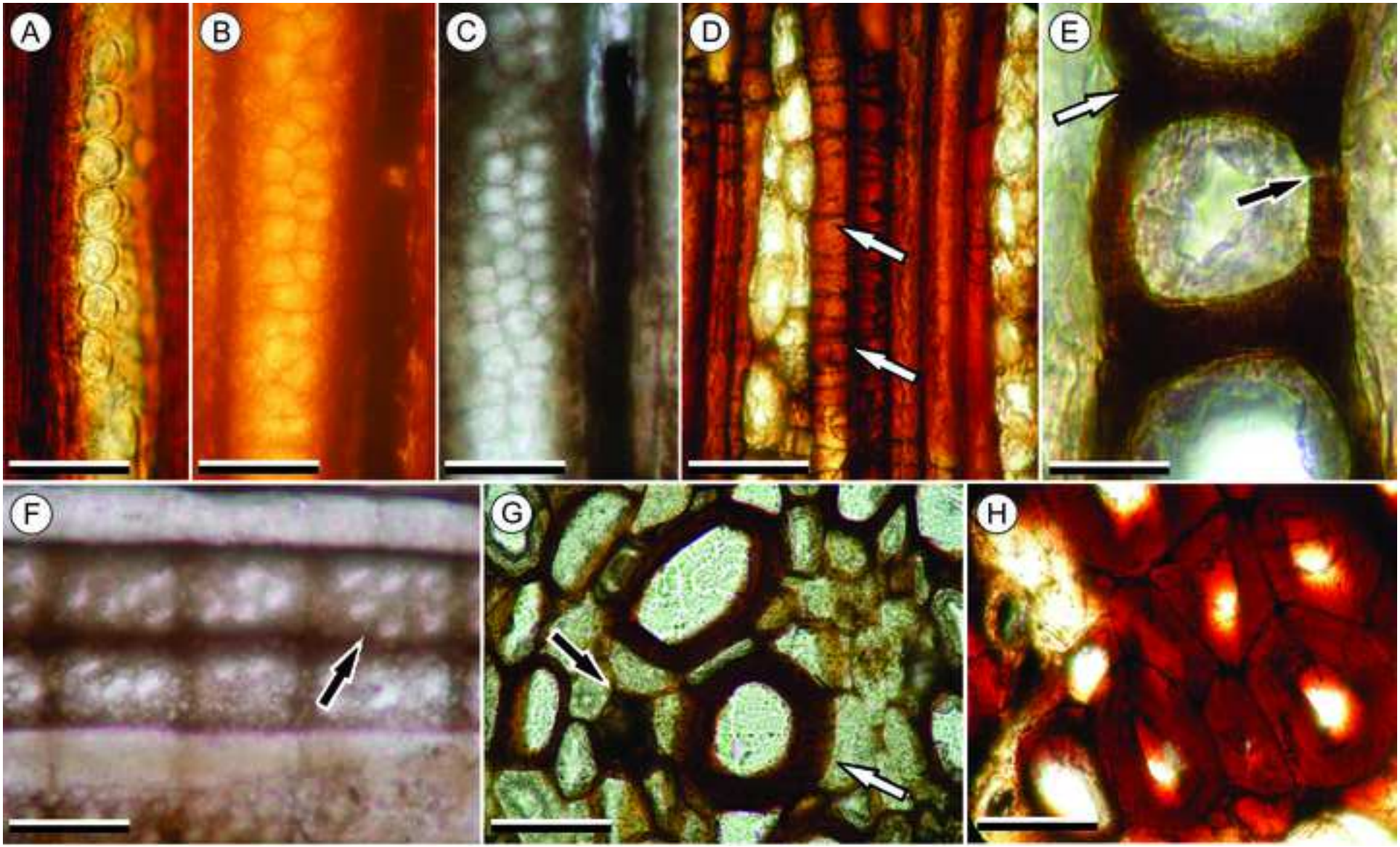

Figure 5 bw

Click here to access/download;Figure;Figure 5 BW.tif

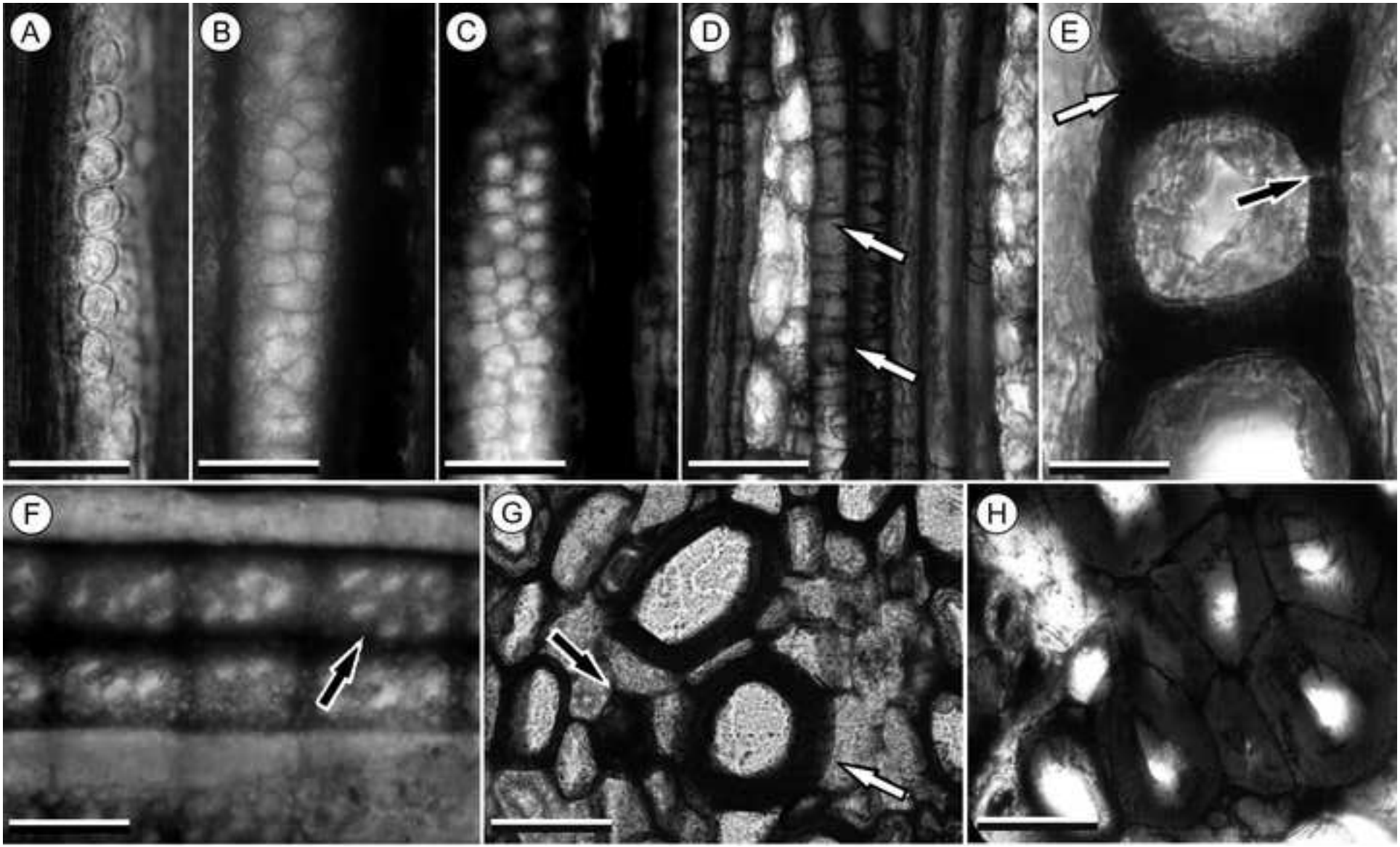

Figure 6