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Buckya austroamericana nov. gen. et sp. (Bennettitales) from the Upper Triassic Laguna Colorada Formation (El Tranquilo Group), Santa Cruz province, Argentina

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Abstract: *BUCKYA AUSTROAMERICANA NOV. GEN. ET. SP. (BENNETTITALES) FROM THE UPPER TRIASSIC LAGUNA COLORADA FORMATION (EL TRANQUILO GROUP), SANTA CRUZ PROVINCE, ARGENTINA.* A new genus and species of a bennettitalean trunk from the Upper Triassic of Santa Cruz province, Argentina, is described. *Buckya austroamericana* is based on a specimen with its internal anatomy: monoxylic trunk including pith with secretory, sclerenchymatic and mucilaginous cells; primary xylem endarch with scalariform thickened tracheids; secondary xylem with circular bordered pits, uni- and biseriate rays. Poorly preserved secondary phloem. Cortex with parenchyma cells, abundant secretory cells, mucilagenous sacs and isolated sclerenchyma bands. Externally, leaf bases and/or foliar scars correspond to those of *Bucklandia* Presl (in Sternberg). The validity of this generic name is analyzed for specimens with preserved anatomy, as it was erected for trunks showing only external morphology (branch traces and/or foliar bases). It is concluded that the name should be conserved for the last type of fossils; as a consequence, a new genus is necessary for specimens preserving internal anatomy. For this purpose, the new genus *Buckya* is proposed and several species are transferred to it. *Buckya* nov. gen. is a worldwide known cosmopolitan genus from the Jurassic and Cretaceous but species of *Bucklandia* (*sensu* this work) are also known from the Triassic; fronds usually ascribed to bennettites such as *Pterophyllum* Brongniart, *Pseudoctenis* Seward, *Anomozamites* Schimper, among others are also frequent in the Gondwana Triassic. The closest species to *B. austroamericana* are *Bucklandia kerae* Saiki and Yoshida from the Cretaceous of Japan and *Bucklandia indica* Seward from the Jurassic of India (both here transferred to *Buckya*) but they differ in several aspects, some of them showing primitive features.

Resumen: *BUCKYA AUSTROAMERICANA NOV. GEN. ET. SP. (BENNETTITALES) DEL TRIASICO SUPERIOR DE LA FORMACIÓN LAGUNA COLORADA (GRUPO EL TRANQUILO), PROVINCIA DE SANTA CRUZ, ARGENTINA.* Se describe un nuevo género y especie de tallo de Bennettitales del Triásico Superior de la provincia de Santa Cruz, Argentina. *Buckya austroamericana* está basada en un ejemplar con caracteres anatómicos internos preservados: tronco monoxílico, con médula parenquimática conteniendo células secretoras, esclerenquimáticas y mucilaginosas, xilema primario endarco con traqueidas con engrosamientos escalariformes; xilema secundario con punteaduras areoladas y radios uni- y biseriados. Floema secundario pobremente preservado. Corteza parenquimática con numerosas células secretoras, sacos mucilaginosos y bandas aisladas de esclerénquima. Externamente, sus cicatrices foliares corresponden a las del género *Bucklandia* Presl (in Sternberg). Se analiza la validez de este nombre genérico para ejemplares con su anatomía interna preservada, ya que *Bucklandia* fue erigido para troncos solamente con morfología externa (cicatrices rameales y /o foliares). Se concluye que el nombre *Bucklandia* debe ser conservado para este tipo de ejemplares por lo cual es necesario diferenciar con otro género aquellos materiales con su anatomía interna preservada para lo cual se propone el nombre de *Buckya* y se le transfieren varias especies. *Buckya* es un género ampliamente difundido en el Jurásico y Cretácico de todo el mundo, aunque especies de *Bucklandia* (*sensu* este trabajo) también fueron registradas en el Triásico y frondes, generalmente adjudicadas a las Bennettitales como *Pterophyllum* Brongniart, *Pseudoctenis* Seward, *Anomozamites* Schimper, entre otras, también son bastantes frecuentes en el Triásico gondwánico. Las especies más cercanas a *B. austroamericana* son: *Bucklandia kerae* Saiki y Yoshida del Cretácico del Japón y *Bucklandia indica* Seward del Jurásico de la India (ambas transferidas a *Buckya*) aunque se diferencian de éstas por diversos caracteres, algunos de ellos con rasgos en su mayoría primitivos.

Key words: Bennettitales. Trunks. Anatomy. Upper Triassic. Argentina.

Palabras clave: Bennettitales. Leños. Anatomía. Triásico Superior. Argentina.

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Introduction

Among the many specimens of fossil wood collected several years ago from the El Tranquilo "fossil forest" (Crisafulli and Herbst, 2008, 2011), a specimen of a "cycadophyte" was recovered. This finding is most interesting as there are few species of bennettitalean stems with preserved anatomy and none has been cited from the Triassic of South America. Most of the bennettitalean "cycadophytes", known on the base of their anatomy, have been included in the genera *Bucklandia* Presland/or *Cycadeoidea* Buckland and in *Williamsonia* Carruthers, *Bennetticarpus* Harris and, *Bennettistemon* Harris where their reproductive structures ("flowers" *sensu lato*) are known. Moreover, they are all Jurassic-Cretaceous in age. Delevoryas (1973) and Bose (1974) gave short accounts of Jurassic species from India, England, and Japan but did not mention Triassic species. No Jurassic bennettitalean stems have been found in South America. Instead several true Cycadales have been described from this part of Gondwana: Triassic genera include *Michelilloa* (Archangelsky and Brett, 1963) from the Ischigualasto Formation of San Juan province, *Vladiloxylon* (Lutz *et al.*, 2003) from La Ternera Formation of Chile, and *Antarticycas* (Smoot *et al.*, 1985 *emend.* Hermsen *et al.*, 2006), from the Antarctica. Cretaceous genera of Cycadales from Argentina are *Worsdellia* (Artabe *et al.*, 2004), *Brunoa* (Artabe *et al.*, 2004) and *Wintucycas* (Martinez *et al.*, 2012) whereas Lower Tertiary stems are *Bororoa* (Petriella, 1969) and *Menucoa* (Petriella, 1969). These genera and their species are here compared with species of *Bucklandia* Presland are considered to be distinctive genera.

A short account of these taxa and several others of worldwide distribution, belonging to Cyacadales, Bennettitales and *"vessel-less Angiosperms"* was given by Artabe *et al.* (2009). Martínez *et al.* (2012) carried out a phylogenetic analysis and relationships between fossil and extant stem genera of Cycadales. Also a few "cycadophyte" fronds are known from the Triassic of Argentina and a few more from nearby Chile. Gnaedinger and Herbst (1999) described several species of *Pseudoctenis* Seward (a genus also used for Cyacadales) and *Pterophyllum multilineatum* (Shirley) Du Toit, the latter having been transferred to *Pseudoctenis multilineata* by Herbst and Troncoso (2000). Other genera of Triassic cycadophyte fronds from Argentina are included in *Anomozamites* (Bonetti, 1972) and *Ctenis* (Menéndez, 1951) while in the Triassic of Chile *Pterophyllum* and *Pseudoctenis* are frequent (Herbst and Troncoso, 2000). Other examples are the incomplete "female flowers" cited by Bardola and Guerra Sommer (2011) without a formal name, from the Triassic of Brazil and that of Barboni and Dutra (2013). All these fronds have been assigned or correlated with bennettitales and/or cycads, but none has preserved cuticles and thus it becomes difficult to define their botanical status. As shown by Delevoryas (1973) these leaf genera are not homogeneous and different species have been considered either bennettitalean or cycadalean. An interesting example of a pure "bennettitaleane-flora" has been described by Wade-Murphy and van Konijnenburg van Cittert (2008) from the Jurassic of Indonesia showing the presence of several species of *Pterophyllum* and other genera, putatively belonging to the Bennettitales. The flora includes at least one specimen classified as *Bucklandia* sp. The ordinal and familial assignation of the bennettitalean stems and fronds is another problem as there are different opinions on generic diagnostic features. This will not be discussed in this paper, but a thorough revision was presented by Watson and Sincock (1992) who dealt mainly with the English Cretaceous leaves and stems, but include a historical review of the confusing nomenclature of the trunks. In their opinion, shared by Saiki and Yoshida (1999), there are four genera, described by their anatomy: *Bucklandia* Presl (in Sternberg, 1828), *Cycadeoidea* Buckland, *Monanthesia* Wieland ex Delevoryas and *Cycadeoidella* Ogura. For reasons given in the generic discussion below, it became necessary to create a new genus for the Patagonian specimen and

several of the many described species under the name of *Bucklandia*, as it turned out that the latter cannot be used to include anatomically preserved trunks, as the original diagnosis, with the type-species *Bucklandia anomala* (Stokes and Webb) Presl 1825 (see also Watson and Sincock, 1992) describes only external morphology (leaf bases or foliar scars) and we were unable to find a formal emendation of the genus.

Geological setting

The Triassic Laguna Colorada Formation is the uppermost unit of the El Tranquilo Group (Jalfin and Herbst, 1995) (Fig. 1), which is composed of sandstone, tuffaceous sandstone, siltstone and silicified tuff, mainly of reddish and purple colours, representing fluviale and lacustrine environments. Its age has been established as Norian (Jalfin and Herbst, 1995). This Formation has rendered a substantial amount of anatomically preserved woods such as the pteridosperm *Tranquiloxylon petriellai* (Herbst and Lutz, 1995), and at least one fern *Millerocaulis sanctaecrucis* (Arch. and de la Sota) Tidwell (1994). Crisafulli and Herbst (2011) gave the first descriptions of several pycnoxylic gymnosperms from the "fossil forest" of this Formation, which include: Araucariaceae: *Agathoxylon dallonii* (Boureau) Crisafulli and Herbst, *Agathoxylon lamaimbandianus* Crisafulli and Herbst, *Agathoxylon amraparense* (Sah and Jain) Crisafulli and Herbst, Podocarpaceae: *Podocarpoxylon indicum* (Bardwaj) Bose and Maheshwari, *Podocarpoxylon paralatifolium* Vozenin-Serra and Grant-Mackie, *Protophyllocladoxylon* sp. and a new species of a ginkgoalean, *Ginkgophytoxylon isychozianus* Crisafulli and Herbst. The impression megaflora is composed of several species each of *Neocalamites, Cladophlebis, Dicroidium, Xylopteris, Yabeiella, Ginkgoites, Linguifolium, Heidiphyllum* (Gnaedinger and Herbst, 1998 a, b, 1999; Herbst, 1988) and among the presumed Cycadophyta, as mentioned above, *Pseudoctenis* and *Pterophyllum* (Gnaedinger, 1999). Vertebrates (Baez and Marsicano, 2001; Pol and Powell, 2007) have also been found.

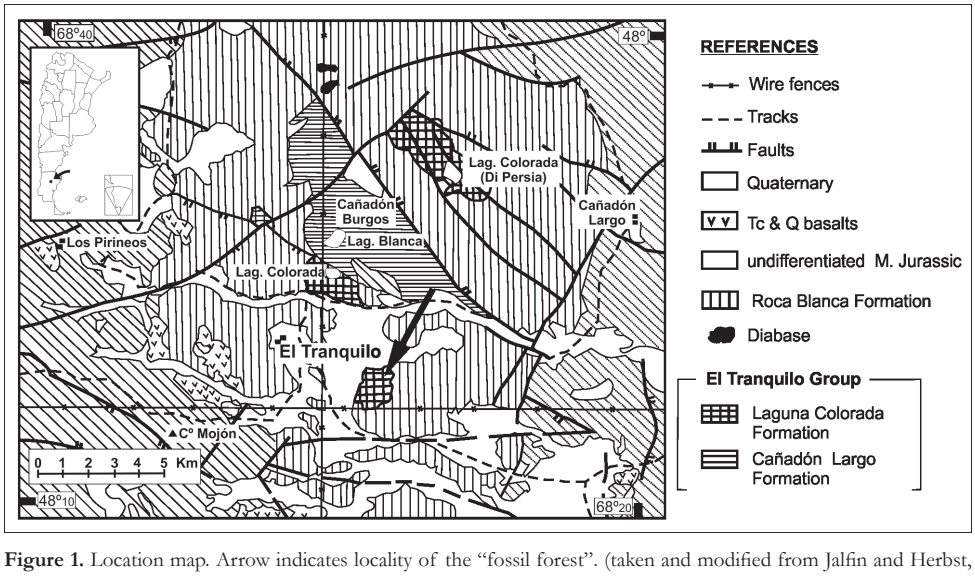

Figure 1. Location map. Arrow indicates locality of the "fossil forest". (taken and modified from Jalfin and Herbst, 1995)./ **Figura 1.** *Mapa de ubicación. La flecha indica el "bosque fósil" (tomado y modificado de Jalfin y Herbst, 1995).*

Material and methods

The studied specimen is silicified; it was cut in half to obtain transverse and longitudinal (radial and tangential) thin sections; observations were also made on the polished surfaces of the remaining half and thin sections. The acetate peels of HF treated surfaces gave poor results. Observations were made with a Leica ICC50 microscope, a Leica M50 stereoscope and the Scanning Electron Microscope of the Universidad Nacional del Nordeste, Corrientes, Argentina. A minimum of 20 measurements were made quoted as: average, minimum and occasional maximum were recorded. Terminology used is from the IAWA Glossary (2004). The specimens belong to Paleontological Collection "Dr. Rafael Herbst" of the Universidad Nacional del Nordeste (Corrientes, Argentina) and are numbered under the acronym CTES-PB and CTES-PMP (thin sections).

Systematic Paleontology

CLASS CYCADOPSIDA *sensu* Sternberg, 1820
ORDEN CYCADEOIDALES (=BENNETTITALES) Meyen, 1984
FAMILY WILLIAMSONIACEAE Nathorst, 1913
GENUS *Buckya* nov. gen.

Synonymy:
Bucklandia Presl, *pro parte* (see Appendix for species list).
Yatesia Carruthers and *Fittonia* Carruthers, which had already been synonymized to *Bucklandia* by Seward (1895).

Derivation of name: a short derivation of *Bucklandia*

Type species: *Buckya austroamericana* Herbst and Crisafulli (this paper)

Included species: see Appendix.

Occurrence: In the sense of this work the genus extends from the Triassic of Argentina through the Jurassic of India, England and Mexico to the Cretaceous of India and Japan.

Diagnosis: Stem mainly oval in outline, monopodial; pith wide, oval in outline, containing either parenchymatic, secretory, mucilaginous, sclerenchymatic, vascular strands, dark cells and mucilaginous sacs, or different associations of these elements. Pith surrounded by one cycle of xylem (monoxylic condition); endarch primary xylem with tracheids with scalariform thickenings, with scarce parenchyma, surrounded by phloem and dense secondary xylem, with variable tracheid pitting types (scalariform and/or uni-multiseriate bordered pits). Growth rings (generally well) distinct. Rays one- to tetraseriate, of variable height. Cortex parenchymatous with mucilaginous elements, dark-content cells and interstitial sclerenchyma, sometimes organized in elongated bands, sporadically with vascular strands and hairy indumentum. In transverse section, leaf and / or branch scars of variable and irregular size and outline, composed of secondary xylem surrounded by a sclerenchyma ring. Externally (laterally) leaf scars also of irregular form and size, not contiguous, helically arranged around the stem (of the *Bucklandia* type).

Discusión: The genus *Bucklandia* was established by Presl (1825) but published by Sternberg (1828) for stems describing only the external morphology of their leaf scars. Several later authors described mainly English specimens but using different names confused the nomenclature. Carruthers (1870) tried to clear this problem and described several stems including genera such as *Yatesia* and *Fittonia* also based on external morphology and some with poorly described and defined internal anatomy, which have since been synonymized (see Watson and Sincock, 1992). Seward (1895) gave a short account of the previous history of *Bucklandia* Presl (originally *Clathraria* Stokes and Webb) establishing tacitly *Bucklandia anomala* (Stokes and Webb) Presl 1825 as the type species but did not describe its anatomy. Seward (1900) and Bancroft (1912) provided short descriptions of part of the anatomy of what was named "Cycadeoidea". Additional historical accounts and discussions were presented by Watson and Sincock (1992), later by Watson and Lydon (2004) and Saiki and Yoshida (1999). In none of these papers and others such as Nishida (1969) and Nishida and Nishida (1983) was the genus *Bucklandia* formally emended in accordance to the ICBN rules. As a result, earlier and later workers included in this genus several other species mainly from the Jurassic and Cretaceous of Europe, India, Japan and Mexico. A second result is that the genus presently includes a variety of taxa, some of them with- and others without the external description. As an example of this situation, Watson and Sincock (1992) described a new species, *Bucklandia florovia*, based on scales helical arranged on a stem; these scales are preserved with their cuticles and should, therefore, be assigned to a different genus. It is thought that to clear the status of these many species and to keep the original sense or meaning of *Bucklandia* Presl and to comply with the rules of the ICBN (2012), a new genus has to be erected. Currently, it is not possible to know whether a certain species of *Bucklandia* (*sensu* Presl) will have the same anatomical construction when found at different localities (and ages) or whether a given anatomically preserved stem will bear the same *Bucklandia*-type of external leaf scars when these are absent. It was also found that among the anatomically preserved species published to date, it is possible to distinguish two "groups": those with the monoxylic and those with polyxylic conditions. This character seems to be rather important and although it could have been possible to include it in the present generic diagnosis, it is believed that it is better to keep the species with either condition separate, eventually considering them distinct genera or subgenera. Future findings might solve this issue. At present 10 species with their anatomical characters preserved are considered, and these have been transferred to the new genus, in Appendix 1. It is possible that eventually some other species might have escaped our attention. The remaining species or records cited as "*Bucklandia* sp." are not dealt with here, as they show only external characters. In several cases, even their inclusion in *Bucklandia* seems doubtful. In some other cases, such as the specimens from the Middle Jurassic described by Wang *et al.* (2005), names are not given but based on the photos and sketches (showing the monoxylic condition) they look very similar to a *Buckya* and it is possible that they might be related to it. Finally, for the inclusion of *Buckya* within the Williamsoniaceae we follow the criteria of Sharma (1991); Banerji (1991); Watson and Sincock (1992); Stewart and Rothwell (1993) and Taylor *et al.* (2009).

For example, a rather incomplete list of species of *Bucklandia* (*sensu* Presl) showing only external morphology is the following:

B. anomala (Stokes and Webb) Presl, 1825
B. mantelli Presl, 1825
B. gracilis Carruthers, 1870
B. milleriana Carruthers, 1870

B. ruffordi Seward, 1900
B. saportana Nathorst, 1902
B. squamosa (Brongniart) Seward, 1917
B. pustulosa Harris, 1969

All these species are from the Northern Hemisphere, but one named as *B. anomala* was also found by Seward (1907) in South Africa.

Buckya austroamericana nov. sp.
Figures 2 - 6

Diagnosis: Stem mainly oval in cross section, monoxylic, compact trunk. Pith consisting of parenchymatic, circular secretory and sclerenchyma cells, and scattered mucilage sacs. Primary xylem endarch. Tracheids with scalariform thickenings. Secondary xylem consisting of tracheids with bordered pits and abundant uni- and biseriate rays. Secondary phloem poorly preserved. Cortex consisting of large parenchyma and secretory cells, numerous mucilage sacs, more abundant than in the pith, sclerenchymatous strands mostly as elongated bands. Several leaf traces arising from the vascular cylinder in association with leaf gaps; trace emission not girdling. In transverse section, leaf and /or branch scars of variable irregular size and outline, composed of secondary xylem surrounded by a sclerenchymatic ring of variable width. Externally, leaf scars are also of irregular form (ovate to circular) and size, not contiguous, helically arranged around the stem.

Holotype: CTES-PB nº 14074, CTES-PMP nº 3055 to 3061.
Geographic occurrence: south western corner of Estancia Cañadón Largo, Santa Cruz province, Argentina, (aprox. 48º 08' S – 68º 29' W).

Stratigraphic occurrence: Laguna Colorada Formation; Norian.

Description: Stem mainly oval in outline, about 22 cm in diameter, composed of pith, a monoxylic vascular system, poorly preserved phloem and cortex (Figs 2.1, 2; 4.1, 3). Pith large, about 4 cm in diameter consisting of parenchyma, circular secretory and sclerenchyma cells and scattered mucilage sacs (Fig. 2.2; 4.3 and 5.3). In transverse section, parenchyma cells circular to oval 80-100 μm in diameter. Circular secretory cells, ca. 60 μm in diameter (Figs 2.2; 5.3).
In transverse section, the scattered mucilage sacs are oval and their density increases towards the peripheral region of the pith, figure 6.3 shows their distribution in longitudinal radial section of the pith. Polygonal sclerenchyma cells averaging 35-40 μm by 20-34 μm are present, not arranged in bundles (Fig. 2.2). The xylem cylinder is 1 cm thick. Primary xylem is endarch with wedge-shaped projections and scarce wood parenchyma (Fig. 5.3). Metaxylem consists of 8 - 10 rows of tracheids with scalariform thickenings in longitudinal radial section (Fig. 6.1). Wood parenchyma cells rectangular in cross section measuring 25 - 33 μm and 30 - 35 μm in radial and tangential diameters. Secondary xylem, dense, consisting of 12 rows of tracheids. The tracheids are square and rectangular in transverse section, and measure 60 - 70 μm and 70 - 85 μm in tan gential and radial diameters respectively. Rays separated by 1-5 rows of tracheids. Growth rings absent, but shearing zones (*sensu* Erasmus, 1976) are present (Fig. 5.3). In longitudinal radial section, circular bordered pits are present on the tracheid walls, usually uniseriate, but in some cases biseriate, contiguous and alternately arranged, 12 - 15 μm in diameter, and with pit apertures 8 μm in diameter (Fig. 6.2, 4). Cross-fields pitting with two or three bordered pits. Rays

short, mostly 4 - 12 cells high, mainly uniseriate, in some cases biseriate. Ray cells oval in tangential section, 29 - 35 μm and 18 - 30 μm in vertical and horizontal diameters, respectively. Transverse end walls of axial parenchyma cells are smooth, irregularly thickened or with nodules (features 76, 77 and 78, IAWA, 2004) (Figs 6, 5.7). Poorly preserved secondary phloem, with rectangular cells in cross section, 12 - 15 μm and 14 - 28 μm in radial and tangential diameters, arranged in radial rows (Fig. 5.5). Cortex consisting of large parenchyma and secretory cells, numerous mucilage sacs, these more abundant than in the pith, sclerenchyma cells appear

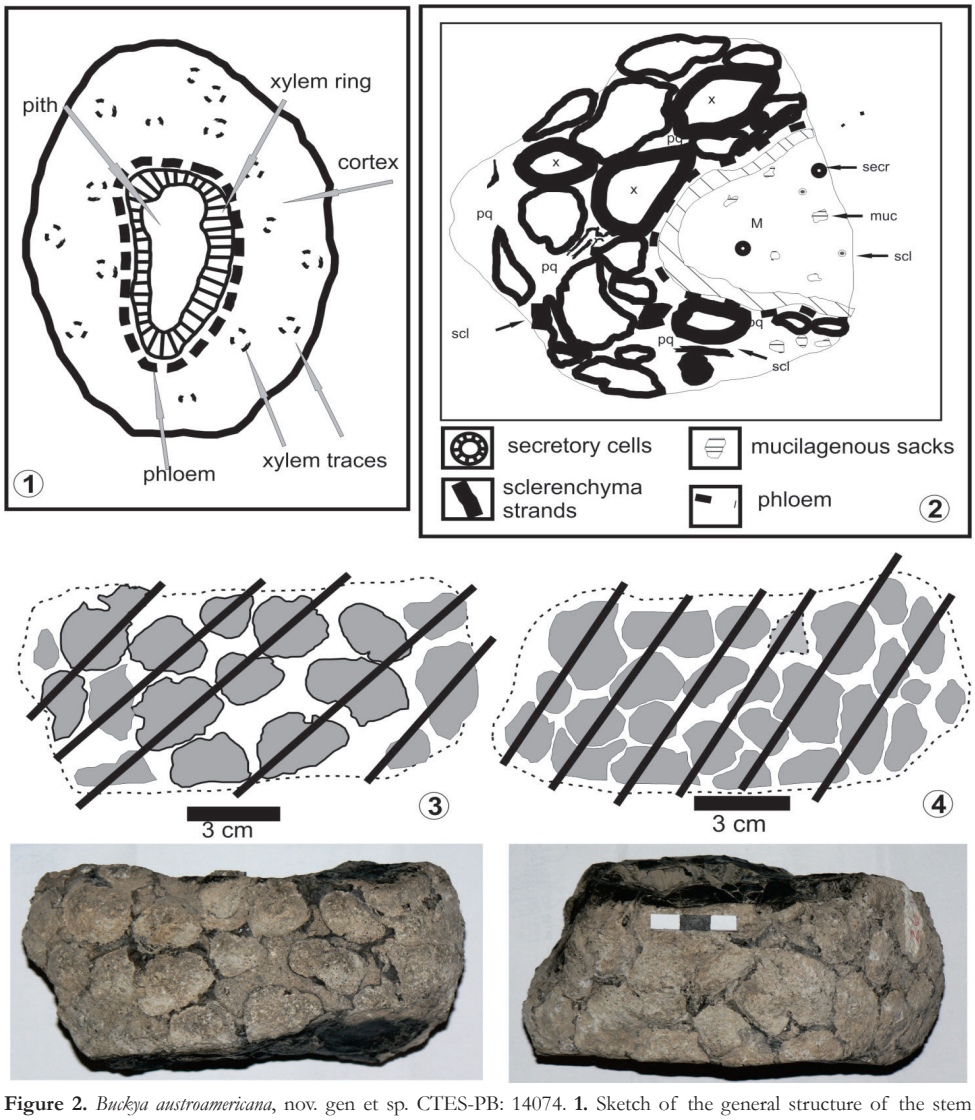

Figure 2. *Buckya austroamericana*, nov. gen et sp. CTES-PB: 14074. **1.** Sketch of the general structure of the stem (transverse section). **2.** Sketch of (half) transverse section. Different thicknesses of sclerenchyma of traces indicate its variability in width. **3-4.** Sketches and photographs of two tangential outer surfaces showing irregular distribution and frequency of traces. / **Figura 2.** Buckya austroamericana*, nov. gen et sp. CTES-PB:14074.* **1.** *Esquema de la estructura general del leño (sección transversal).* **2.** *Esquema de la mitad de la sección transversal. Diferentes grosores en las traza del esclerénquima indican su variabilidad en espesor.* **3-4.** *Esquemas y fotografías de dos superficies tangenciales externas mostrando la distribución irregular y la frecuencia de las trazas.*

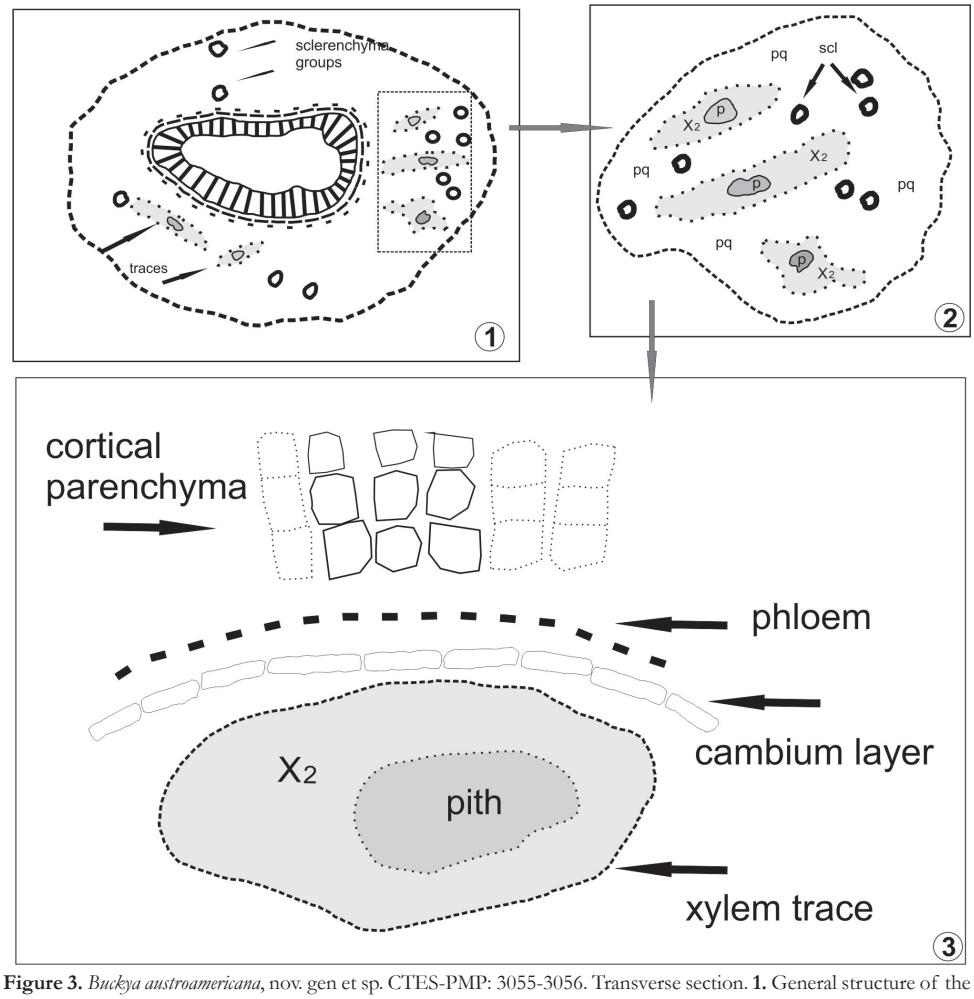

Figure 3. *Buckya austroamericana*, nov. gen et sp. CTES-PMP: 3055-3056. Transverse section. **1.** General structure of the stem showing traces. **2.** Detail of traces; in 1. pq: parenchyma, scl: sclerenchyma, p: pith, x2: secondary xylem. **3.** Detail of a trace and position of adjoining tissues. / **Figure 3.** Buckya austroamericana*, nov. gen et sp. CTES-PMP: 3055-3056. Sección transversal.* **1.** *Estructura general del tallo mostrando las trazas.* **2.** *Detalle de las trazas; en 1: pq: parénquima, scl: esclerénquima, p: médula, x2: xilema secundario.* **3.** *Detalle de una traza y posición de los tejidos adyacentes.*

mostly as elongated bands (Figs 2.1-2; 3.1-3; 4.1, 3; 5.2, 6). Several leaf traces arise from the vascular cylinder in association with leaf gaps; traces are slender and not girdling. Transversally, leaf and /or branch traces are of variable and irregular size, the biggest with their major axes 3 cm average (2-4 cm), minor axes 2 cm average (1-2,5 cm), the smallest with major axes 0,75 cm average (1-0,50) and minor axes 0.50 cm, composed of secondary xylem surrounded by a sclerenchyma ring 3 mm wide (average). The ring is composed of sclerenchyma and parenchyma cells and crystals (Figs 2.1-2; 3.1-3; 4.2-4; 5.1-2, 6). Externally (laterally) leaf scars also of irregular form (oval to circular) and size, measuring average of 1 to 1,5 cm, loosely helically arranged around the stem (Fig. 2.3-4). Reproductive structures are absent.

Discussion (for the species): Only two species of *"Bucklandia"* (now *Buckya*) can be compared closely with *B. austroamericana*, *viz. Bucklandia kerae* Saiki and Yoshida and *Bucklandia indica*

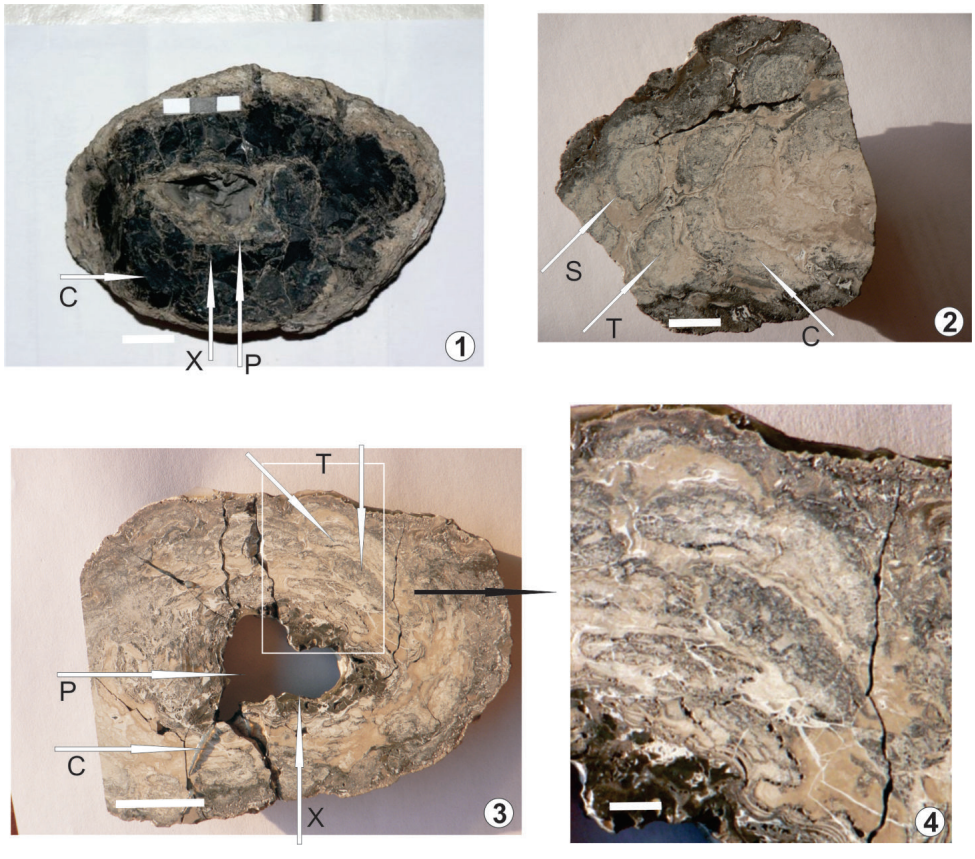

Figure 4. *Buckya austroamericana*, nov. gen et sp. CTES-PB: 14074. **1.** Polished transverse surface. **2.** Longitudinal tangential polished surface. **3.** Specimen after first cutting, transverse section. **4.** Detail of upper right angle of 3 (arrow). / **Figura 4.** Buckya austroamericana*, nov. gen et sp. CTES-PB: 14074.* **1.** *Superficie transversal pulida.* **2.** *Superficie longitudinal tangencial pulida.* **3.** *Sección transversal del ejemplar después del primer corte.* **4.** *Detalle del ángulo superior derecho de 3 (flecha). Scale bars/escalas: 1, 3 =2,75 cm; 2 = 2 cm; 4 = 0,5 cm.c: cortex/corteza; p: pith/médula; s: sclerenchyma/esclerénquima; t: trace/traza; x: xylem/xilema.*

Seward. From the first one *B. austroamericana* differs in not having an indumentum or hairs, lacking vascular strands in the pith, its xylem is not manoxylic, and although not clearly seen, there is not a five-trace nodal structure as described by Saiki and Yoshida (1999); also *Bucklandia kerae* has rhomboidal and circular petioles in cross section, whereas they are irregularly shaped in *B. austroamericana, B. kerae* has areolate hexagonal pits (alternate and circular in *B. austroamericana*) and abundant uni- and biseriate ray sup to 40 cells high (low numbers in *B. austroamericana*) and cross-fields with only one pit (more than one pit in *B. austroamericana*), *B. austroamericana* differs from *B. indica* in not having secretory channels either in the pith nor the cortex; the secondary xylem is monoxylic, lacking multiseriate or hexagonal pits and the rays are not bi-triseriate as in *B. indica*. However, the rays are uniseriate in the specimen described by Seward (1895) from England, and the scalariform pits are absent or very scarce. The Mexican specimen of *B. indica* discovered by Wieland (stated by Seward, 1900) shows these pits. Seward (1895) already suggested to consider all these specimens under the same name.

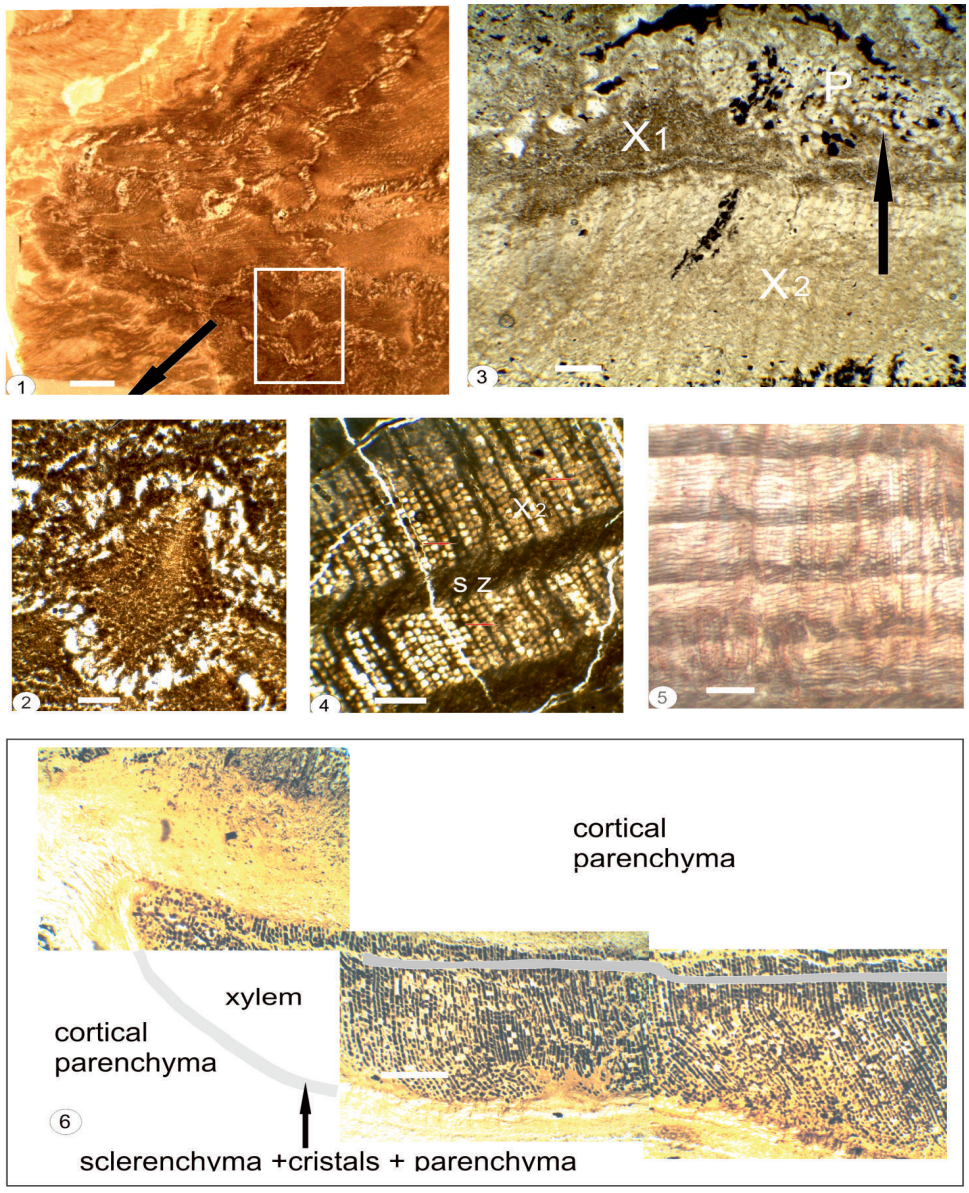

Figure 5. *Buckya austroamericana*, nov. gen et sp. (1-3) CTES-PMP 3056. **1**. Transverse section showing pith, cortex, trace (rectangle) and sclerenchymatic bands. **2**. Detail of a trace (t) in transversal section (of 1, arrow). **3**. Transverse section of wood showing a part of pith (p), primary xylem (x1) with wedge-shaped projection and secondary xylem (x2). (4-6) CTES-PMP 3057. **4**. Transverse section of secondary xylem (x2) showing shearing zones (sz); arrows indicate resin plates in tracheids. **5**. Transverse section showing phloem cells. **6**. Transversal section: reconstruction of a trace showing tissue disposition. / **Figura 5.** Buckya austroamericana, *nov. gen et sp. (1-3) CTES-PMP 3056*. **1**. *Sección transversal mostrando la médula, la corteza, las trazas (rectángulo) y las bandas de esclerénquima.* **2**. *Detalle de una traza (t) en sección transversal (de 1, flecha).* **3**. *Sección transversal del leño mostrando una porción de la médula (p), xilema primario (x1) con proyecciones cuneiformes y xilema secundario (x2). (4-6). CTES-PMP 3057.* **4**. *Sección transversal del xilema secundario (x2) mostrando "shearingzones" (sz); las flechas indican placas de resina en las traqueidas.* **5**. *Sección transversal mostrando las células del floema.* **6**. *Sección transversal: reconstrucción de una traza mostrando la disposición de los tejidos. Scale bars/escalas: 1= 3 cm; 2 = 8 mm; 3 = 200 μm; 4 = 400 μm; 5 = 270 μm; 6 = 18 mm.*

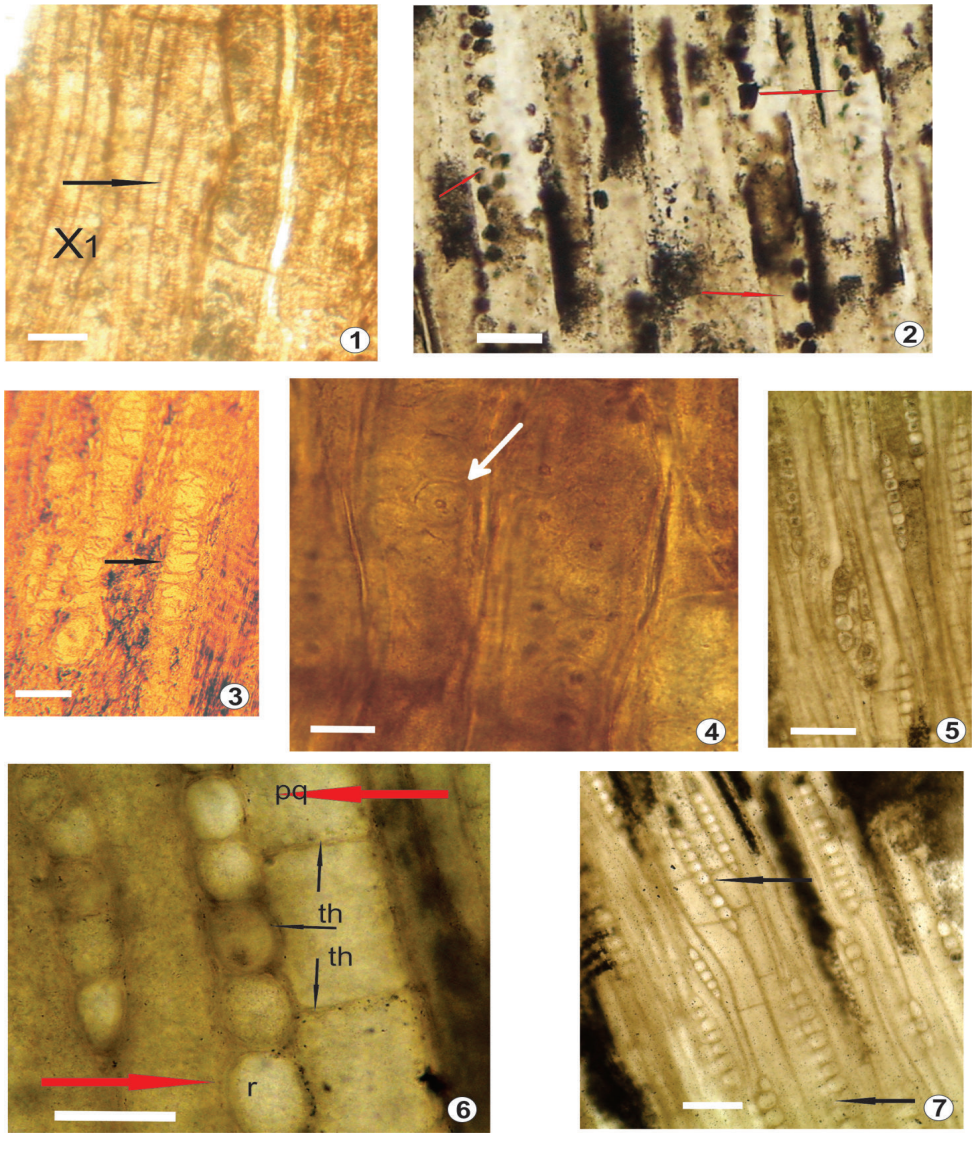

Figure 6. *Buckya austroamericana*, nov. gen et sp. (1, 2) CTES-PMP 3058. **1**. Longitudinal radial section of primary xylem showing scalariform thickenings on tracheid walls (arrows). **2**. Radial tracheid wall: uniseriate and opposite biseriate pits on tracheid walls (arrows). (3-4) CTES-PMP 3059: **3**. Longitudinal radial section showing mucilaginous cells (arrows). **4**. Radial section: biseriate and alternate pits on tracheidal walls (arrow). (5, 7) CTES-PMP 3060: **5**. Longitudinal tangential section showing ray cells with resin contents. **7**. Longitudinal tangential section showing height and frequency of rays (arrows indicate uni-and biseriate rays). 6. CTES-PMP 3061: **6**. Longitudinal tangential section: transverse end walls irregularly thickened (th) of axial parenchyma cells (pq) and low ray cells (r)./ **Figure 6.** Buckya austroamericana, *nov. gen et sp. (1, 2) CTES-PMP 3058*. **1**. *Sección longitudinal radial del xilema primario mostrando los engrosamientos escalariformes sobre las paredes traqueidales (flecha)*. **2**. *Pared radial: punteaduras uniseriadas y biseriadas opuestas sobre paredes traqueidales (flechas). (3-4) CTES-PMP 3059:* **3**. *Sección longitudinal radial mostrando células mucilaginosas (flechas)*. **4**. *Sección radial: punteaduras biseriadas y alternas sobre las paredes traqueidales (flechas). (5, 7) CTES-PMP 3060:* **5**. *Sección longitudinal tangencial mostrando las células de los radios con contenidos de resina*. **7**. *Sección longitudinal tangencial mostrando la altura y frecuencia de los radios (las flechas indican radios uni- y biseriados). (6) CTES-PMP 3061:* **6**. *Sección longitudinal tangencial: paredes terminales de las células del parénquima (pq) axial irregularmente engrosadas (th) y radios celulares bajos (r). Scale bars/ escalas: 1 = 70 μm; 2 = 30 μm; 3 = 60μm; 4 =15μm; 5, 7 = 120 μm; 6= 60 μm.*

Not with standing these differences, some characters are common to these three species: mucilaginous cells in the pith and cortex, absence of medullary bundles, endarch primary xylem and tracheids with scalariform pits in the primary xylem. Moreover traces are non-girdling, this being a character indicating that these species are not cycadean but bennettitalean as considered by Saiki and Yoshida (1999). A unique character of *B. austroamericana* is that the parenchymatic band surrounding the traces has sclerenchyma and crystals. It differs in several other aspects from all the other hitherto known species now included in *Buckya* (see Appendix below), with enough strong differences to separate them clearly from the Patagonian species.

Conclusions

A few general comments can be made regarding this new genus of the Order Cycadeoidales (=Bennettitales), Family Williamsoniaceae:

1) The taxonomical status of the Cycadeoidales (=Bennettitales) has long been a matter of debate, which at present is not solved. Several different classification schemes or higher systematic arrangements have been proposed, but most authors agree in accepting Cycadeoidales (=Bennettitales) as an independent Order, no matter where it may definitely be placed among the gymnosperms. Cycadeoidales (=Bennettitales) are informally associated with the Cycadales in the informal "Cycadophyta", but they generally constitute two independent classes.

2) According to the general anatomical characters that differentiate Bennettitales from Cycadales (Watson and Sincock, 1992; Watson and Lydon, 2004; Crisafulli *et al.*, 2008; Martínez *et al.*, 2012, among other authors), the genus *Buckya* with the herewith included species formerly known as *Bucklandia* (*pro parte*, Appendix 1) is a typical bennettitalean and different from the known extant and fossil true Cycadales.

3) The inclusion of *Buckya* (formerly *Bucklandia* pro parte) within the Williamsoniaceae is made following the criteria of Sharma (1991); Banerji (1992); Watson and Sincock (1992); Steward and Rothwell (1993) and Taylor *et al.* (2009) among others.

4) *Buckya austroamericana* is an interesting discovery as no other certain bennettitalean trunks of Upper Triassic age (or older) have been found before in southwestern Gondwana nor any other fossil which could represent an ancestral representative of the group. Potential exceptions are the many fossil fronds from the Gondwana Triassic ascribed to the group, but their position and relations to Bennettitales are still somewhat uncertain or debatable.

5) Anatomical characters such as mucilaginous cavities are considered primitive (Artabe *et al.*, 2004) as they disappear in time and are only relictual among extant Cycadophytes. These authors also consider the polyxylic condition to be derived from monoxyly, present in Triassic cycads (*viz.*, *Michelilloa*, *Antarcticycas*, *Vladiloxylon*, *Lissoxylon* and *Scalaroxylon*) and also in *Buckya*. Stems with more than one vascular cylinder are usually recorded in younger sediments (Crane, 1988; Stevenson, 1990). Thus, *Buckya* seems to share several primitive characters in accordance with its older age.

6) *Buckya austroamericana* is part of a lignoflora associated in a "fossil forest" composed of the osmundaceous fern *Millerocaulis herbstii* (Arch. and de la Sota) Tidwell, the pteridosperm *Tranquiloxylon petriellai* Herbst and Lutz, the araucarian conifers *Agathoxylon dallonii* (Boureau) Crisafulli and Herbst, *Agathoxylon lamainbandianus* Crisafulli and Herbst, *Agathoxylon amraparense* (Sah and Jain) Crisafulli and Herbst, the Podocarpaceae *Podocarpoxylon indicum* (Bardwaj) Bose and Maheshwari, *Podocarpoxylon paralatifolium* Vozenin-Serra and Grant-Mackie, *Protophyllocladoxylon* sp. and the ginkgoalean *Ginkgophytoxylon izychosianus* Crisafulli and Herbst (Crisafulli and Herbst, 2011) together with an impression flora with several species as *Neocalamites, Cladophlebis,*

Rochipteris, Dicroidium, Linguifolium, Yabeiella and *Heidiphyllum*. Jalfin and Herbst (1995) suggested that the tree flora (forests) grew on the levees and elevated sites whereas the rest of the flora developed on the flood plains and on hydromorphic soils close to open water bodies such as *Neocalamites* and some ferns.

7) Although many authors have proposed more or less dry temperate to warm climates for the Bennettitales in general, the sedimentological characters (Jalfin and Herbst, 1995) and the fossil flora of the Laguna Colorada Formation (leaf impressions and woods) indicate a somewhat temperate to warm climate. This is also in accordance with the location of this area during the Upper Triassic as proposed by Artabe *et al.* (2003) whereby the El Tranquilo area occurred in the "extratropical template to warm" belt at higher than 60º S latitude. Anderson and Anderson (1983) placed the area in their "temperate rain forest" between their 33º and 66º S latitude belt.

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Systematic Appendix

According to the above given diagnosis and arguments for the new genus *Buckya*, the following taxa have to be formally transferred. This list of changes is obviously not complete as some papers with reports of species included in *Bucklandia* (and eventually other generic names) may have escaped our attention.

ORDEN CYCADEOIDALES (=BENNETTITALES) Meyen, 1984
FAMILY WILLIAMSONIACEAE (Carruthers) Nathorst, 1913
GENUS *Buckya* Herbst and Crisafulli nov. gen. (this paper)

Type species: *Buckya austroamericana* Herbst and Crisafulli (this paper).

Buckya indica (Seward) Herbst and Crisafulli nov. comb.
1917. *Bucklandia indica* Seward
Basionym: Seward, 1917, *Fossil plants:* 488, fig. 579 A, B

Buckya sahnii (Bose) Herbst and Crisafulli nov. comb.
1953. *Bucklandia sahnii* Bose,
Basionym: Bose, 1953, *Paleobotanist* 2: 46, text-figs. 1-11, plates 1-7

Buckya guptai (Sharma) Herbst and Crisafulli nov. comb.
1967. *Bucklandia guptai* Sharma
Basionym: Sharma, 1967, Ameghiniana 4 (2): 36, text-figs. 1-12, plates I-III

Buckya dichotoma (Sharma) Herbst and Crisafulli nov. comb.
1969. *Bucklandia dichotoma* Sharma
Basionym: Sharma, 1969, Ameghiniana 6 (4): 303, fig. 1, plates I-II

Buckya choschiensis (Nishida) Herbst and Crisafulli nov. comb.
1969. *Bucklandia choschiensis* Nishida
Basionym: Nishida, 1969. Phytomorphology 19 (1): 29, figs. 1-5

Buckya kerae (Saiki and Yoshida) Herbst and Crisafulli nov. comb.
1999. *Bucklandia kerae* Saiki and Yoshida

Basionym: Saiki and Yoshida, 1999. American Journal Botany 86 (3): 326, figs. 2-21

Buckya tsuruokae (Nishida and Nishida) Herbst and Crisafulli nov. comb.
1983. *Bucklandia tsuruokae* Nishida and Nishida
Basionym. Nishida and Nishida, 1983. Botanical Magazine (Tokyo) 96: 94, figs. 1-4.

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