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CASUARINACEAE FROM THE EOCENE OF PATAGONIA, ARGENTINA

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Casuarinaceae, today restricted to the Australasian region, has an extensive fossil record. In this article, we evaluate previous records and recent findings from Patagonia, where Casuarinaceae are known from the Tufolitas Laguna del Hunco (early Eocene) in northwestern Chubut, Argentina. Based on characters found in numerous branchlets, infructescences, and male inflorescences with pollen of the *Haloragacidites harrisii* type, the presence of three fossil species within the genus *Gymnostoma* is confirmed: *G. patagonicum* comb. nov., *G. archangelskyi* sp. nov., and *G. argentinum* sp. nov. This is the oldest worldwide report of male inflorescences and the first record of vegetative branchlets and male inflorescences for South America. These fossils are of particular interest because Casuarinaceae is now extinct in South America, and they support the view that the family was diverse and had widespread distribution during the early Eocene climatic optimum. The diverse *Gymnostoma* described here further strengthens biogeographic links between Paleogene floras of Patagonia and Australasia.

Keywords: Casuarinaceae, *Gymnostoma*, megafossils, pollen, Eocene, Patagonia, Argentina.

Introduction

Casuarinaceae is a subtropical family of dioecious or, less commonly, monoecious trees and shrubs that includes four genera: *Casuarina* L., *Allocasuarina* L.A.S. Johnson, *Gymnostoma* L.A.S. Johnson, and *Ceuthostoma* L.A.S. Johnson. Originally, Casuarinaceae included only the genus *Casuarina* and was later split, based on numerous morphological studies. Recent molecular studies strongly support the distinctiveness of the four genera (Steane et al. 2003). Casuarinaceae members are easily distinguished from all other flowering plants because of their characteristic vegetative and reproductive morphology, including needlelike articulate branchlets with longitudinal ridges (phyllichnia) separated by furrows, teethlike reduced leaves arranged in whorls, highly reduced unisexual flowers grouped in male spikes, and female globular to ovoid "cones" that develop into woody infructescences at maturity (Wilson and Johnson 1989).

Although Casuarinaceae is today confined to the Malesian-Australian-Melanesian region, the fossil record indicates that the family had a widespread Gondwanic distribution earlier in the Cenozoic. Casuarinaceae megafossils have been found in Paleogene and Neogene deposits of Australia (Christophel 1980; Hill 1990; Christophel et al. 1992; Scriven and Hill 1995; Guerin and Hill 2003), the Miocene of New Zealand (Campbell and Holden 1984; Pole 1989, 1993), and the Eocene of South America (Frenguelli 1943; Zamaloa 1993; Wilf et al. 2003, 2005). Fossil pollen with casuarinacean affinity and dating from the Paleocene to the Miocene has also been reported in Australia, New Zealand, the Indian Ocean, South America, South Africa, the Antarctic Peninsula area, and the Ross Sea region (Johnson and Wilson 1989; Truswell 1990).

In South America, the palynological record is restricted to Patagonia (Argentina and Chile) and ranges from the early Paleocene to Eocene (fig. 1). Paleocene pollen grains assigned to the fossil species *Haloragacidites harrisii* (Couper) Harris have been reported from southeastern Chubut Province in Argentina (Archangelsky 1973; Zamaloa and Andreis 1995) and from central Chile (Doubinger 1972). This pollen type was also found in Eocene deposits from central and south-central Chile (Doubinger 1972; Doubinger and Chotin 1975; Palma Heldt 1980; Troncoso and Barrera 1980).

South American Casuarinaceae macrofossils were first recorded by Frenguelli (1943) and consisted of four articulated infructescences collected at the historic (Berry 1925) Laguna del Hunco locality in northwestern Patagonia, Argentina (fig. 1). Frenguelli assigned this material to *Casuarina patagonica*, and later, without detailed reinvestigation, several authors (e.g., Christophel 1980) considered these to belong to *Gymnostoma*. Likewise, Hill and Carpenter (1991) believe that *C. patagonica* has non-*Gymnostoma* affinities. Subsequently, two of us (E. J. Romero and M. C. Zamaloa) collected additional material from the same locality that represents a different species of Casuarinaceae (Zamaloa 1993; Hill 1994). Most recently, discoveries from several localities in a new measured section at Laguna del Hunco include abundant and diverse macrofossils referable to *Gymnostoma*. These were mentioned briefly in two reports (Wilf et al. 2003; Gandolfo et al. 2004).

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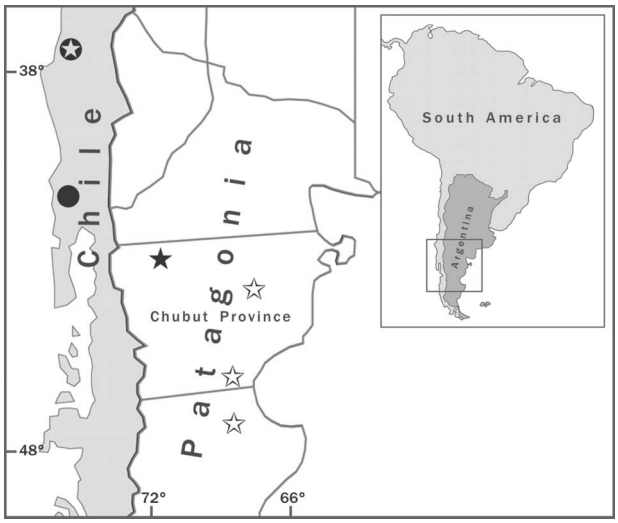


Fig. 1 Map of Patagonia showing the locations of Laguna del Hunco (solid star) and sites with *Haloragacidites harrisii* pollen records. Open stars indicate Paleocene pollen records. Solid circle indicates Eocene pollen records.

The past distribution of Casuarinaceae and the comparison of its fossil record to living representatives have been widely used as a basis for several phytogeographic and evolutionary scenarios in which the Patagonian record has an important role (e.g., Romero 1978, 1986, 1993; Christophel 1980; Campbell and Holden 1984; Coetzee and Muller 1984; Hill and Carpenter 1991; Hill 1994; Scriven and Hill 1995; Guerin and Hill 2003). Therefore, a detailed review of Frenguelli's material and descriptions of the new material are greatly needed to improve understanding of Casuarinaceae history. In this article, we restudy the type material of *Casuarina patagonica* Frenguelli and describe two new fossil species of *Gymnostoma* that were recently collected. Additionally, male inflorescences and vegetative branchlets also related to *Gymnostoma* are reported. The fossils are compared to the extant and fossil species within Casuarinaceae.

Material and Methods

Fossil Localities and Age

The studied material comes from nine different localities in the Tufolitas Laguna del Hunco, which previously were included in the Huitrera Formation, located in northwestern Chubut Province, Patagonia (fig. 1). These sediments derived from tuffaceous caldera lake deposits belonging to the volcanic-pyroclastic complex of the middle Chubut River (Aragón and Mazzoni 1997). The detailed stratigraphic position of the Laguna del Hunco sampling localities (LH 2, LH 6, LH 22, LH 25) was published by Wilf et al. (2005). Previously collected fossils came from the same stratigraphic horizon of the Tufolitas Laguna del Hunco but cannot be related to an exact source locality.

The age of these sediments has been the subject of several studies. Recently, based on $^{40}Ar/^{39}Ar$ analyses from tuffs located at three levels interbedded with the fossils, Wilf et al. (2003, 2005) determined that the Tufolitas Laguna del Hunco sediments are early Eocene. The most precise age, from sanidine, is 51.91 ± 0.22 Ma. This age places the flora in the sustained interval of global warmth known as the early Eocene climatic optimum (Zachos et al. 2001).

The Paleoflora and its Paleoclimate

Fossil plants from Laguna del Hunco show excellent preservation and high taxonomic diversity. When adjusted for sampling using rarefaction analysis (Wilf et al. 2003, 2005), the Laguna del Hunco flora has the highest known diversity of fossil leaf species for any Eocene site, and it ranks among the most diverse fossil macrofloras known from any time period. Dicots are the most diverse group, represented by Proteaceae, Myrtaceae, Cunoniaceae, Lauraceae, Akaniaceae, Sapindaceae, Sterculiaceae, and Fabaceae, among many other families. There are also monocots (i.e., palms), conifers (i.e., Podocarpaceae, Araucariaceae, Cupressaceae), *Ginkgo*, cycads, and ferns. Reproductive structures are abundant as well, including branches with flowers, fruits, and seeds. According to Wilf et al. (2005), the comparison of the fossil flora to the nearest living relatives, combined with the foliar physiognomy and the apparent absence of the austral beech *Nothofagus*, indicate a moist and equable climate with mean annual temperature of at least 16.6° ± 2.0°C, winter mean temperatures above 10°C, and abundant rainfall of more than 1.1 m/year.

Specimen Preparation and Examination

The studied fossils include 14 vegetative branchlets, 25 infructescences (of these, 14 are attached to branchlets as single cones or in clusters of two to four units), and three connected male inflorescences. Fossils are housed at the paleobotanical collections of the following Argentine institutions: Museo de la Plata, La Plata (LPPb), Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires (FCENCBPB), and Museo Paleontológico Egidio Feruglio, Trelew, Chubut (MPEF-Pb-Cz).

Although most specimens are preserved as impressions, several vegetative branchlets and cones and the male inflorescences are compressions from which superficial organic material was transferred to cellulose acetate (peel technique). Branchlets and cones contained amorphous organic material without any cellular detail, but the male inflorescences yielded abundant pollen masses. Because most infructescences and branchlets have pronounced surface relief, silicone rubber (RTV 3497; Dow Corning) casts were prepared for SEM observations. Observational and photographic equipment included a Wild Type 181300 Heerbrugg stereomicroscope at the Museo Paleontológico E. Feruglio, a Wild MPS 55 Heerbrugg stereomicroscope at the Universidad de Buenos Aires, a Canon PowerShot G2 digital camera, a Philips XL 30 scanning electron microscope at the Museo Argentino de Ciencias Naturales, and, for pollen study, a Dialux 20 microscope at the Universidad de Buenos Aires. Terminology used to describe macroscopic vegetative and reproductive structures follows Johnson and Wilson (1989), Dilcher et al. (1990), and Scriven and Hill (1995).

Systematics

Family—*Casuarinaceae R.Br.*

Genus—Gymnostoma *L.A.S. Johnson 1980*

Type Species—G. nodiflorum *L.A.S. Johnson 1980*

Species—Gymnostoma patagonicum *(Frenguelli) comb. nov. Zamaloa (Fig. 2)*

Synonymy. *Casuarina patagonica* (Frenguelli 1943, pl. I, figs. 1, 2; shown here in fig. 2*A*, 2*B*).

Holotype. LPPb-20415 (fig. 2*A*, 2*B*).

Paratype. MPEF-Pb-Cz-1461 (from LH 6; fig. 2*C*).

Type locality. Laguna del Hunco, NW Chubut Province, Argentina.

Age and stratigraphy. Early Eocene, Tufolitas Laguna del Hunco.

Emended diagnosis. Articles of branchlets with four prominent longitudinal phyllichnia and wide furrows, which alternate regularly in successive nodes. Articles 0.8–0.9 cm in length and 0.1–0.2 cm in width. Four leaves per whorl, leaves with acute apices. Infructescences spirally arranged and attached to the branchlets by stout axillary peduncles; peduncles up to 0.6 cm in length and 0.2 cm in width emerge from the axis at acute angles. Fruiting cones short cylindrical with slightly convex sides, 0.9–1 cm in length and 0.75–0.8 cm in width, length/width (l/w) ratio 1.2 : 1; six to seven whorls of fertile units per cone. Fruits with conspicuous bracts expanded laterally, broader than higher, longitudinally striate, and arranged in whorls of four. Bracteoles striate, subtriangular, with broad rounded apices, and slightly exserted from body of infructescences at 90° angles.

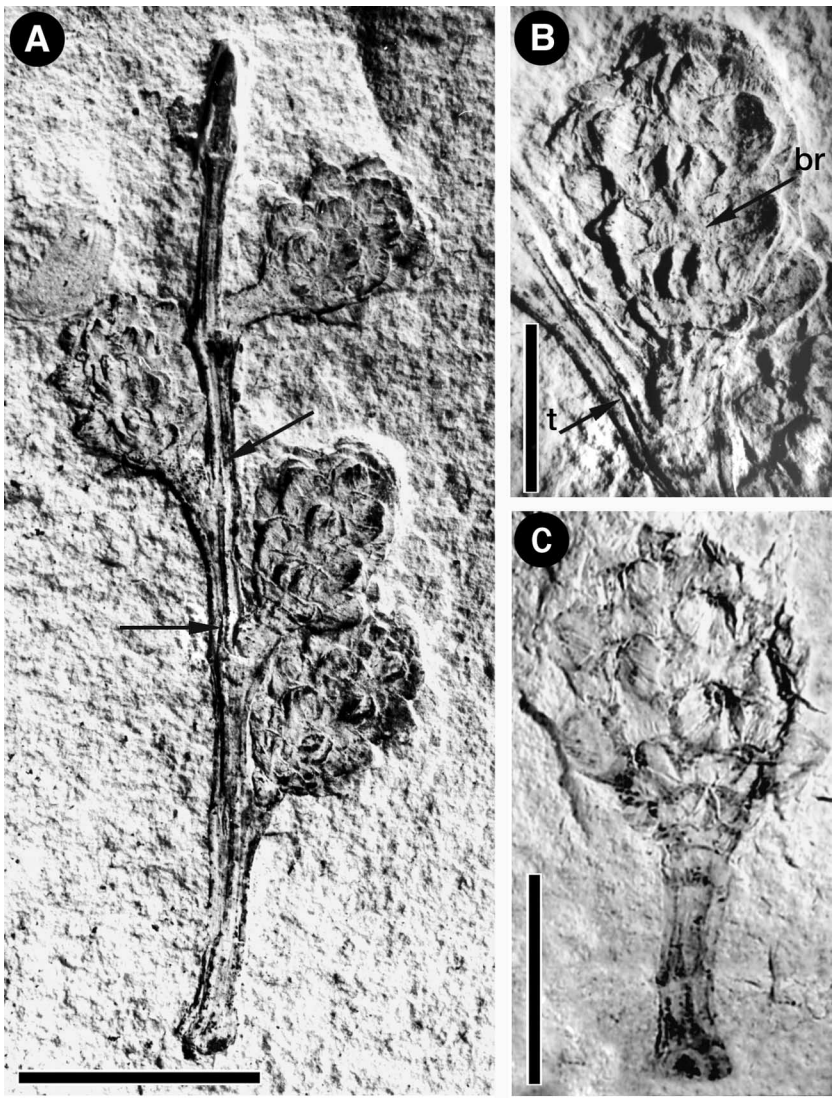
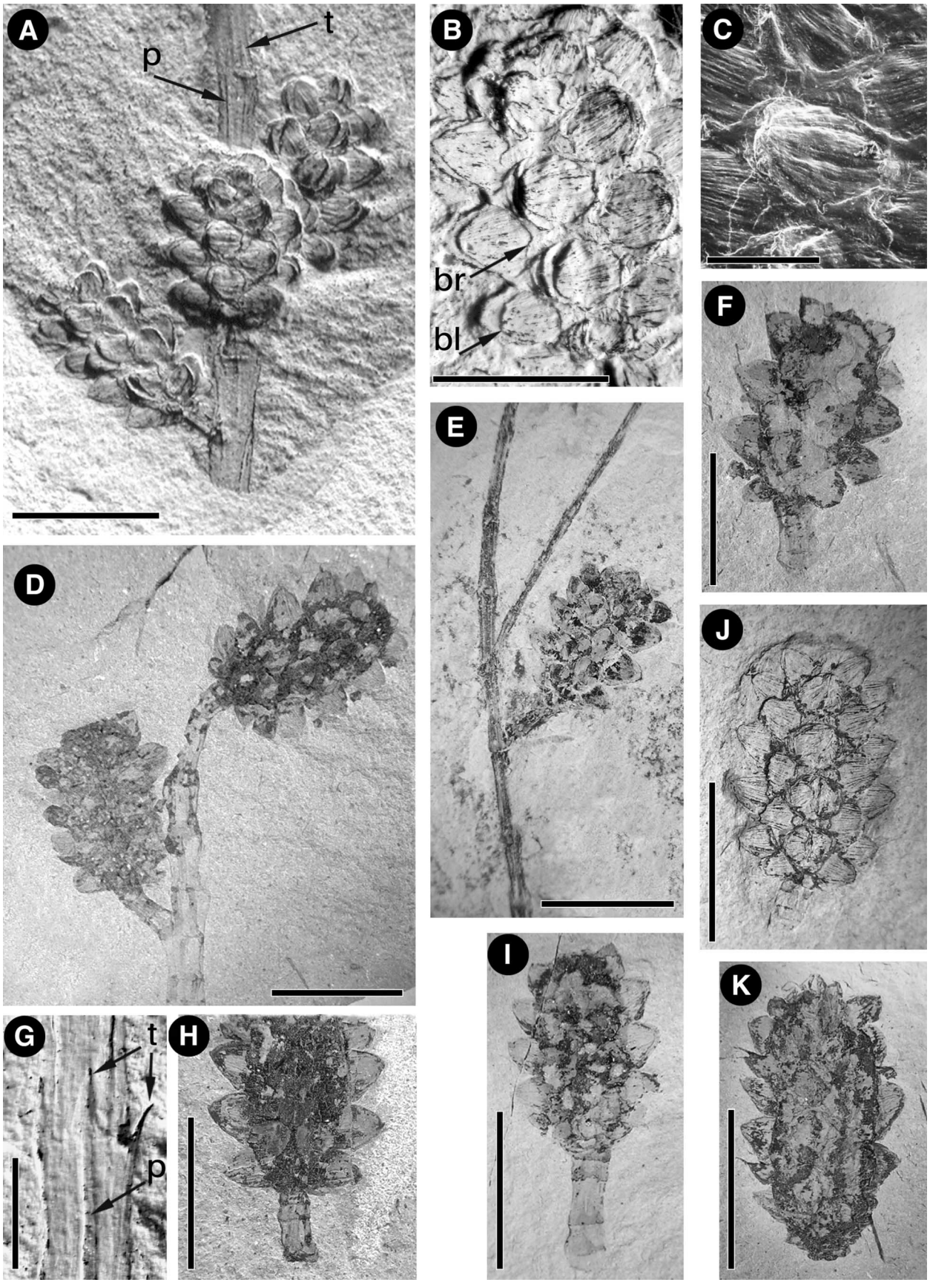


Fig. 2 Fossils of *Gymnostoma patagonicum* comb. nov. from Laguna del Hunco. *A*, Holotype consisting of a branchlet with acute teeth in whorls of four (arrows) and four articulated infructescences (specimen LPPb-20415). Bar = 1 cm. *B*, Close-up of the second basal infructescence in *A*, showing conspicuous broad bract (*br*), rounded and slightly exserted bracteoles and part of the subtending article with two prominent phyllicnia and teeth (*t*). Bar = 0.5 cm. *C*, Paratype in general view (specimen MPEF-Pb-Cz-1461). Bar = 0.5 cm.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Comments. The holotype (fig. 2*A*, 2*B*) is an impression of a reproductive branch. It consists of six articles and nodes, four of which bear infructescences (fig. 2*A*). The pronounced phyllichnia of the articles are separated by wide furrows, indicating that the articles were quadrangular in cross section (fig. 2*B*). The bracts of the infructescences are conspicuous (apparently woody) and wide, and each bract has two lateral expansions; each expansion bears two lobules, superior and inferior, that differ in size and morphology (fig. 2*B*). The superior lobule is larger, and the inferior is more rounded. The bases of the bracts are straight. The bracteoles are opened three-fourths of their length.

The original description provided by Frenguelli (1943) is detailed and coincided with our observations, except that the articles turned out to be slightly longer than measurements provided by Frenguelli (0.9–1.0 cm, in contrast to 0.7–0.8 cm of the original description). Nevertheless, since the infructescences slightly overlap the stem, these measurements depend on a subjective appreciation of the exact position of the nodes, especially those that carry the cones. Frenguelli interpreted the stem as a circular section crushed during the compression process; however, a quadrangular section seems to explain better the observed morphology, as was initially suggested by Christophel (1980). Additionally, Frenguelli described the infructescences as having the fruits arranged in whorls of probably seven elements, although after this revision, it is clear that the alternate position of the fruits indicates the presence of two successive whorls instead of the single whorl interpreted by Frenguelli. Among the recently collected materials, only one corresponds to *G. patagonicum*. This specimen (MPEF-Pb-Cz-1461) is probably an immature infructescence since it is rather small and the bracteoles are almost closed (fig. 2*C*). *Gymnostoma patagonicum* is characterized by the rounded and slightly exserted bracteoles (*sensu* Dilcher et al. 1990) and the large and conspicuous bracts.

Species—Gymnostoma archangelskyi *sp. nov. Zamaloa et Romero (Fig. 3)*

Holotype. FCENCBPB 168 (fig. 3*A*–3*C*, 3*G*).

Paratypes. MPEF-Pb-Cz-977 (from LH 22); MPEF-Pb-Cz-1457 (from LH 25); MPEF-Pb-Cz-1459, 1464, 1470 (from LH 6).

Type locality. Laguna del Hunco, NW Chubut Province, Argentina.

Age and stratigraphy. Early Eocene, Tufolitas Laguna del Hunco.

Etymology. Species epithet "archangelskyi" is erected in honor of Sergio Archangelsky, prestigious Argentinean paleobotanist, for his many contributions to the field of paleobotany.

Additional studied material. MPEF-Pb-Cz-1458, 1460, 1462, 1473, 1474 (from LH 6); MPEF-Pb-Cz-1468 (from unknown stratigraphic level).

Repository. The holotype is housed at the Departmento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Argentina.

Species diagnosis. Articles 0.5–0.65 cm in length and 0.12–0.25 cm in width. Leaves in whorls of four, with acute apices. Infructescences attached to the branchlets by axillary peduncles; peduncles of ca. 0.2–0.7 cm in length and 0.2 cm in width that emerge from the axis at acute angles. Fruiting cones cylindrical, 1.2–1.5 cm in length and 0.9–1.1 cm in width, l/w ratio 1.3 : 1–1.5 : 1, eight to nine whorls of fruit units per cone. Fruits with conspicuous bracts, bracts expanded laterally, broader than higher, longitudinally striate, apparently four bracts per whorl. Bracteoles longitudinally striate, subtriangular, with rounded apices, and moderately exserted from the body of the infructescences at 90° angles.

Comments. The holotype consists of a fertile branch bearing three cones arranged at different nodes (fig. 3*A*). The bracts are conspicuous, possibly indicating their woody nature, and they are wide and have two lateral expansions; each lateral expansion has two long and thin small lobes of similar size (fig. 3*B*). The base of the bract is concave and displays a central constriction, giving the bract the appearance of a butterfly (fig. 3*C*). The bracteoles are slightly opened. The cones show three to four lines of alternate valves; therefore, it is possible to interpret that each whorl was composed of four fertile units. The leaves are also arranged in whorls of four, although only one or two are visible in any given whorl (fig. 3*A*, 3*G*). In cross section, the branchlets are quadrangular, given that only two prominent phyllichnia are observed enclosing the wide furrows (fig. 3*A*, 3*D*, 3*E*, 3*G*).

During recent fieldwork (Wilf et al. 2005), ca. 15 specimens with similar morphology were collected. This type of cone is the most abundant in the Laguna del Hunco sediments. All are consistent in size, degree of exsertion and shape of the bracteoles, number of whorls per cone, and features of the branchlets in organic connection. The only observed variation is the length of the peduncle, which varies from 0.2 to 0.7 cm.

Two unattached cones (fig. 3*J*, 3*K*) display major differences in length (1.6–1.7 cm) and l/w ratio (1.6 : 1), and they are placed in *G.* cf. *archangelskyi*. They were not considered in the *G. archangelskyi* diagnosis. These specimens may represent larger cones of *G. archangelskyi* or may belong to a different species.

Fig. 3 Fossils of *Gymnostoma archangelskyi* sp. nov. and *G.* cf. *archangelskyi* from Laguna del Hunco. *A*, Holotype consisting of a branchlet with prominent phyllichnia (*p*), teeth in whorls of four (*t*) and three infructescences (specimen FCENCBPB 168). Bar = 1 cm. *B*, Close-up of the central "cone" in *A* showing broad lobulate bracts (*br*) and bracteoles protruding at 90° from the main axis (*bl*). Bar = 0.5 cm. *C*, Detail of a cast of the holotype showing bracts and bracteoles with SEM (10 kV). Bar = 0.2 cm. *D*, Paratype (specimen MPEF-Pb-Cz-1464). Bar = 1 cm. *E*, Paratype (specimen MPEF-Pb-Cz-977). Bar = 1 cm. *F*, Paratype (specimen MPEF-Pb-Cz-1457). Bar = 1 cm. *G*, Detail of the holotype showing an article with prominent phyllicnia (*p*) and teeth (*t*) in whorls of four. Bar = 0.2 cm. *H*, Paratype (specimen MPEF-Pb-Cz-1470). Bar = 1 cm. *I*, Paratype (specimen MPEF-Pb-Cz-1459). Bar = 1 cm. *J*, *Gymnostoma* cf. *archangelskyi* sp. nov. (specimen FCENCBPB 169). Bar = 1 cm. *K*, *Gymnostoma* cf. *archangelskyi* sp. nov (specimen MPEF-Pb-Cz-1463). Bar = 1 cm.

Species—Gymnostoma argentinum *sp. nov.*
Zamaloa et Gandolfo (Fig. 4)

Holotype. MPEF-Pb-Cz-1472 A and B (fig. 4*A*–4*F*).

Paratype. MPEF-Pb-Cz-1456 (from unknown stratigraphic level; fig. 4*G*, 4*H*).

Type locality. Laguna del Hunco (from LH 2), NW Chubut Province, Argentina.

Age and stratigraphy. Early Eocene, Tufolitas Laguna del Hunco.

Etymology. From the Latin, "from Argentina."

Repository. The holotype is stored in the MPEF, Chubut Province, Argentina.

Species description. Articles ca. 0.5 cm in length and 0.12 cm in width. Leaves in whorls of apparently four (one

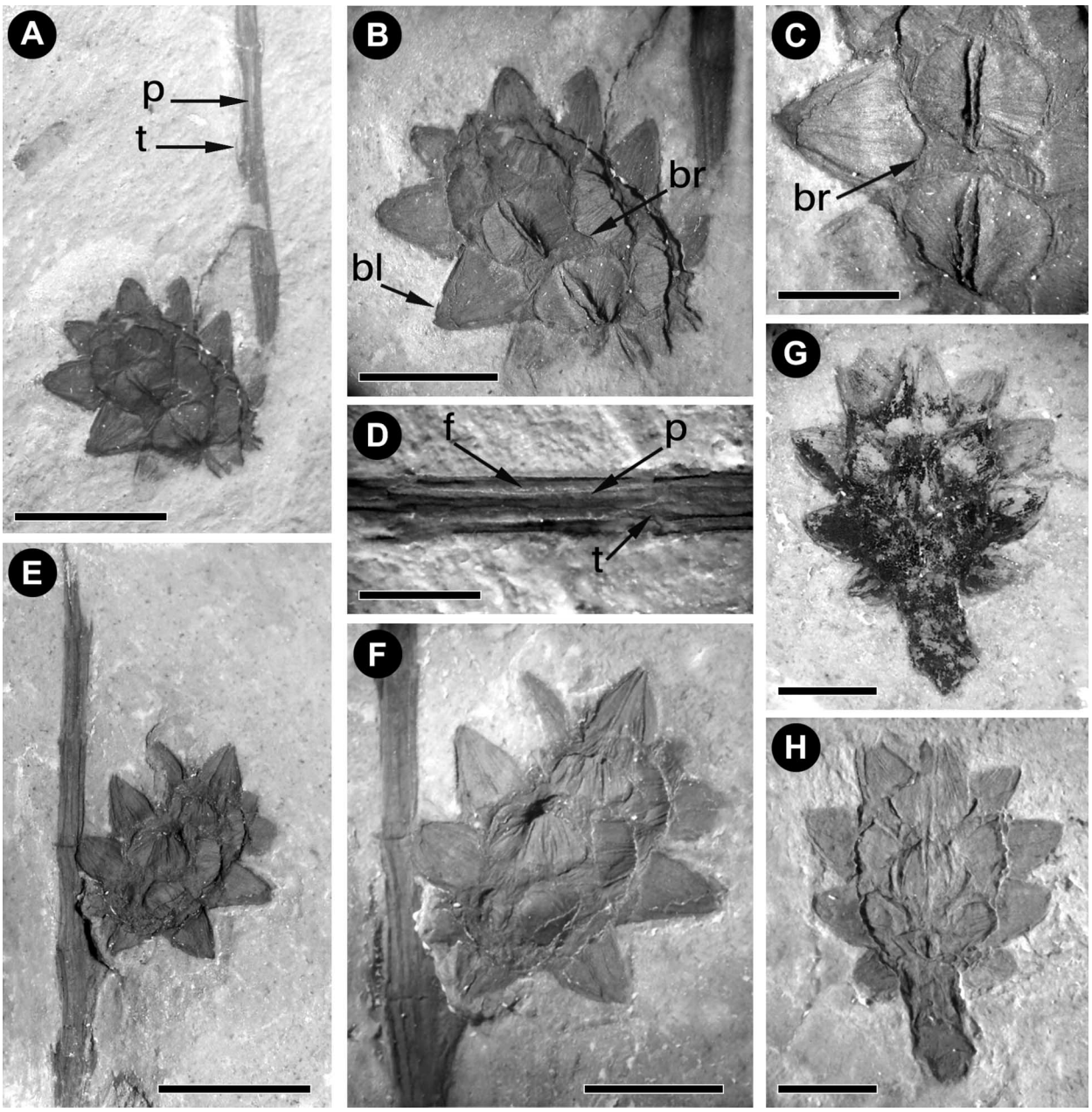

Fig. 4 Fossils of *Gymnostoma argentinum* sp. nov. from Laguna del Hunco. *A*, Holotype consisting of a slender branchlet with prominent phyllichnia (*p*) and teeth (*t*) and an attached infructescence (specimen MPEF-Pb-Cz-1472B). Bar = 1 cm. *B*, Close-up of the infructescence in *A* showing broad bracts (*br*) and highly exserted bracteoles (*bl*). Bar = 0.5 cm. *C*, Close-up of *B* showing striate bract (*br*) and acute triangular bracteoles. Bar = 0.3 cm. *D*, Detail of an article of the holotype showing prominent phyllichnia (*p*), wide furrows (*f*) and teeth (*t*). Bar = 0.2 cm. *E*, Holotype counterpart (specimen MPEF-Pb-Cz-1472A). Bar = 1 cm. *F*, Close-up of *E*. Bar = 0.5 cm. *G*, *H*, Paratype (specimen MPEF-Pb-Cz-1456); in *H*, surface carbonized material was removed. Bar = 1 cm.

or two visible) leaves with acute apices. Infructescences globose, 0.95–1.25 cm in length and 0.9–1.1 cm in width, l/w ratio 1.1 : 1; six to seven whorls of fertile units per cone and apparently four units per whorl. Fruit cone bracts longitudinally striate and broader than high. Bracteoles longitudinally striate, elongate triangular in outline, with acute apices, and highly exserted from the body of the infructescences.

Comments. The type material consists of an impression/compression and its counterpart with a shortly pedunculate infructescence in organic connection with a branchlet, which bears whorls of apparently four leaves. The articles have wide furrows and are probably quadrangular in cross section (fig. 4*D*). The bracteoles are relatively large compared with the other Patagonian species (fig. 4*B*, 4*C*). This species is the only Patagonian one with highly exserted bracteoles.

Gymnostoma *Male Inflorescences (Fig. 5*A–5D)

Studied material. MPEF-Pb-Cz-1467 (from LH 6).

Description. This specimen consists of a distinctive branchlet fragment of irregular shape, with abundant organic material on its surface. The branchlet is ramified and has three apices. At the lower portion of the branchlet, four teeth in every whorl are clearly noticeable. The article lengths diminish from the base (0.25 cm) toward the apex (0.15 cm) (fig. 5*A*). At the base of the distal articles, a small globose compression was found. Pollen masses were recovered from these structures (fig. 5*B*). The masses consist of immature pollen grains of the *Haloragacidites harrisii* type (fig. 5*C*, 5*D*). The pollen grains are oblate triangular, triporate, and irregularly scabrate. Therefore, this specimen is interpreted as a branchlet with three terminal male inflorescences composed of small unopened flowers, and the masses are interpreted as the contents of immature anthers.

Comments. Assignment of these male inflorescences to *Gymnostoma* is based on the organically attached occurrence of the inflorescences to branchlets of undoubted *Gymnostoma* affinity. Additionally, their intimate association with *Gymnostoma* female infructescences (*G. patagonicum* and *G. archangelskyi)* and abundant vegetative *Gymnostoma* sp. branchlets at the same locality (LH 6) reinforce their taxonomic placement within the genus.

Dispersed Vegetative Foliage Assignable to Gymnostoma *(Fig. 5*E–5I*)*

Studied material. MPEF-Pb-Cz-1465, 1466, 1475, 1476, 1477, 1478, 1479, 1480, 1481, 1482, 1483, 1485, and 1486 (from LH 6), MPEF-Pb-Cz-1484 (from LH 22).

Description. Branchlets with articles 0.15 (0.33) 0.8 cm in length and 0.04 (0.05) 0.07 cm in width; prominent phyllichnia separated by deep furrows, quadrangular in cross section. Teeth of about 0.4 (0.8) 1.2 mm in length and 0.2 (0.4) 0.6 mm in width, with acute apex and straight to slightly convex sides. Articles with leaves in whorls of four.

Observations. All studied branchlets are morphologically homogeneous; only one specimen (MPEF-Cz-1480) is slightly different from the others, as its articles are wider (up to 0.11 cm) and its teeth are longer (about 0.16 [0.18] 0.22 cm). The leaves arranged in whorls of four are evidenced when the articles are preserved disarticulated and teeth become free (fig. 5*H*).

Several branchlets have axillar or lateral ovoid-elongated buds (fig. 5*H*). These structures could represent young developing branchlets or immature female flowers such as those illustrated by Guerin and Hill (2003; fig. 2*A*).

Comments. All of these vegetative branchlets are isolated, although they were collected at the same localities and stratigraphic levels as the reproductive branchlets. They all share characters of *Gymnostoma*, but we cannot place any of them within any particular species of fertile branchlets described in this article. For now, we prefer to maintain them as *Gymnostoma* sp.

Discussion

The Patagonian Species

After the initial recognition that Casuarinaceae comprises four genera (*Casuarina*, *Allocasuarina*, *Gymnostoma*, and *Ceuthostoma*), a series of articles was published to establish differences among the genera and their species (e.g. Johnson 1980, 1982, 1988; Wilson and Johnson 1989; Dilcher et al. 1990; Scriven and Christophel 1990; Scriven and Hill 1995). Several of those articles had the major goal of providing information to interpret the fossil record of the family, and to accomplish this, the authors initially studied and systematized morphological vegetative and reproductive characters of the modern species. These articles emphasize the importance of cuticular features, especially those of the stomata, as the most reliable characters for distinguishing genera and species. Unfortunately, the Patagonian specimens lack cuticle. However, other relevant characters of definite systematic importance, such as those of the reproductive organs' morphology, are clearly observed. In particular, Dilcher et al. (1990) and Scriven and Hill (1995) provided lists of morphological characters that can be applied to fossils, allowing distinctions among the genera. These features include the number of teeth per whorl in the vegetative foliage, branchlet cross-section shape, position of the infructescences, nature and size of the bracts, and bracteole exsertion and angle of protrusion.

Gymnostoma L.A.S. Johnson 1980 is characterized by branchlets with square cross section and leaves in whorls of four, male inflorescences borne on branchlets similar to vegetative ones that can be simple or appear compound because of condensation of branching, female inflorescences on short or elongated branchlets that are similar to vegetative ones, infructescences with four bracts per whorl, conspicuous and laterally expanded bracts that are broader than high, and exserted bracteoles projecting at 90° from the vertical axis of the cone (Wilson and Johnson 1989; Dilcher et al. 1990; Scriven and Hill 1995). However, differentiation among species of *Gymnostoma* is more difficult because they differ in epidermal characters, l/w ratio of articles and infructescences, and anatomical and morphological features of the leaves (Scriven and Christophel 1990; Scriven and Hill 1995).

Gymnostoma is a tropical genus with 18 species recorded in Malesia, Fiji, New Caledonia, and northeastern Australia, with only one species endemic to Australia. Morphologically, *Gymnostoma* is considered to be the most primitive of the genera in the family and can be easily separated from the other three genera (Johnson and Wilson 1989), as indicated above. Molecular data also support *Gymnostoma* as the most

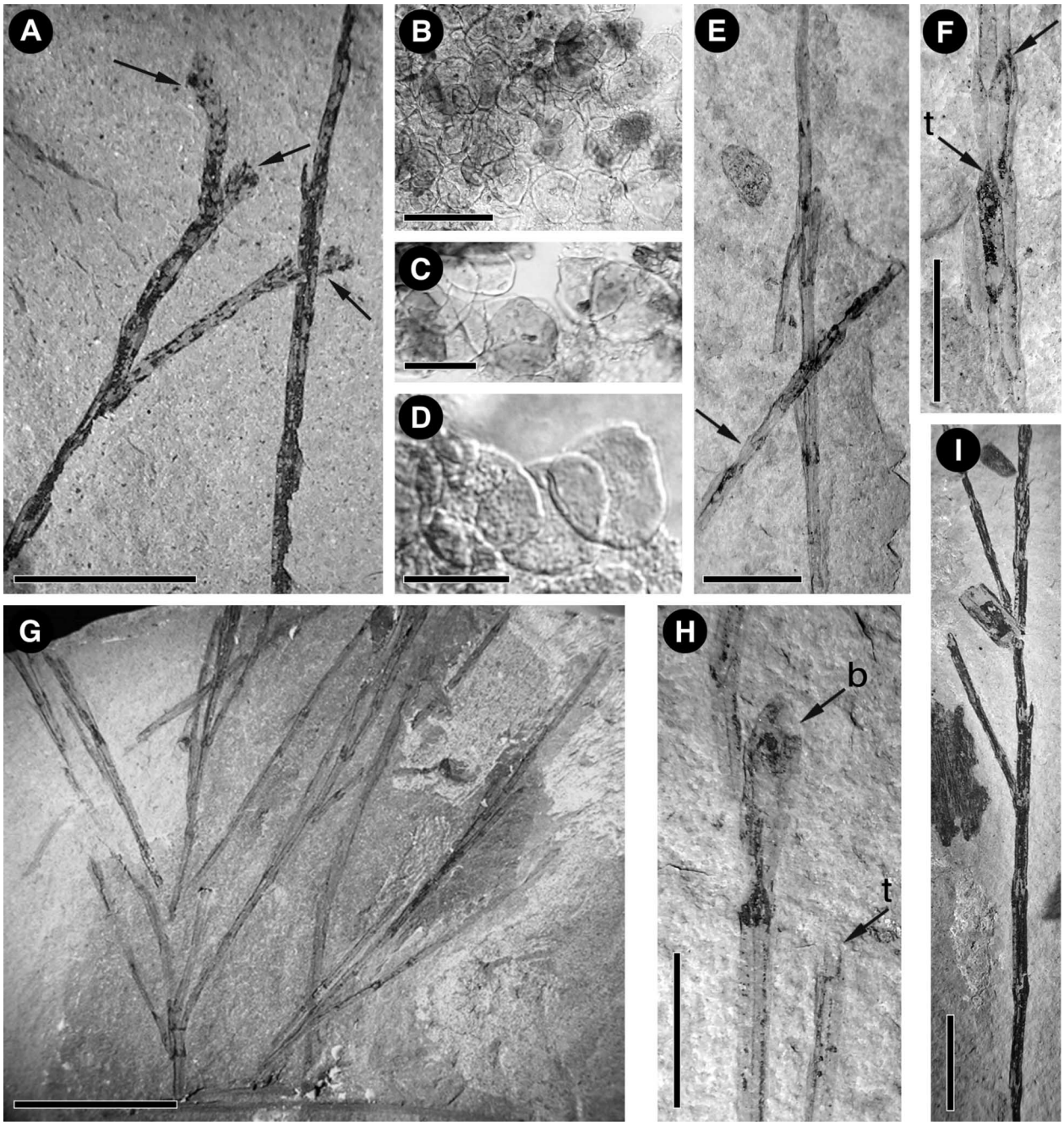

Fig. 5 *Gymnostoma* male inflorescences and dispersed branchlets from Laguna del Hunco. *A*, Branchlet with three terminal male inflorescences (arrows) (specimen MPEF-Pb-Cz-1467). Bar = 1 cm. *B*, Masses of pollen grains of *Haloragacidites harrisii* recovered from the apices in *A*. Bar = 20 μm. *C*, Close-up of the pollen grains. Bar = 20 μm. *D*, Pollen grains, triporate and with triangular outline, in interference contrast. Bar = 40 μm. *E*, Branchlets composed of articulated segments (specimen MPEF-Pb-Cz-1476). Bar = 1 cm. *F*, Close-up of articles noted with arrow in *E* showing teeth (*t*) in whorls of four. Bar = 0.5 cm. *G*, General view of vegetative branchlets (specimen MPEF-Pb-Cz-1479). Bar = 1 cm. *H*, Detail of a branchlet showing a bud (*b*) and four free teeth (*t*) at the top of an article (specimen MPEF-Pb-Cz-1477). Bar = 0.5. *I*, Vegetative branchlet with surface carbonized material (specimen MPEF-Pb-Cz-1481). Bar = 0.5 cm.

basal within the family because it is the sister group to the clade formed by Ceuthostoma + Casuarina + Allocasuarina (Steane et al. 2003).

Although fossil representatives of Casuarinaceae collected at Laguna del Hunco lack epidermal characters, they all have quadrangular articles and leaves in whorls of four, infructescences bearing four bracts per whorl, and bracts conspicuous and expanded laterally, and the bracteoles project at 90°. According to Johnson (1980) and Dilcher et al. (1990), these characters define *Gymnostoma* and can be considered synapomorphies for the genus; thus, all of the fossils can be placed confidently within it. The only difference is the position of the female

inflorescence, which is lateral in the Patagonian fossils and in one of the living species (*Gymnostoma* sp. A; Dilcher et al. 1990) but terminal in the remaining living species.

The infructescences found in Patagonia belong to different species. They differ in size, shape, and l/w ratio of the cones, bracteole shape and degree of exsertion, and length of the articles of the branchlets found in organic connection with the cones. These differences allow us to recognize three species (see "Key" [next]; table 1).

Key to the South American Fossil Casuarinaceae Infructescences

A. Infructescences (cones) with highly exserted bracteoles ..... *Gymnostoma argentinum*

A′. Infructescences (cones) with slightly to medium exserted bracteoles ..... B

B. Bracteoles slightly exserted, six to seven whorls of fertile units per cone ..... *Gymnostoma patagonicum*

B′. Bracteoles medium exserted, eight to nine whorls of fertile units per cone ..... *Gymnostoma archangelskyi*

Comparison to Fossil and Living Species

The most relevant casuarinacean fossils described so far, which were collected from the Australasian region, have been recognized as representatives of *Gymnostoma* (Scriven and Hill 1995). Nevertheless, only two species, *Gymnostoma antiquum* (Scriven and Hill 1995) and *Gymnostoma tasmanianum* (Guerin and Hill 2003), have proper diagnoses, which are mainly based on cuticular characters. Scriven and Hill (1995) discussed the fossil remains of Casuarinaceae mentioned in the literature and discounted several of them for lacking sufficient morphological data or being poorly preserved. Of the remaining taxa, we will consider *Casuarina stellata* (Campbell and Holden 1984) and *Casuarina avenaceae* (Campbell and Holden 1984) for comparisons.

Gymnostoma antiquum, from the Late Paleocene in New South Wales, are compressions in a clay matrix, often with cuticle remaining on the branchlets. Scriven and Hill (1995, p. 1047) did not find any organic connection: "Vegetative branchlet articles and one mature infructescence are confirmed as belonging to the same species by matching of cuticle features from unattached branchlets and the peduncle of the infructescence." Scriven and Hill (1995) compared *G. patagonicum* with *G. antiquum*. They found that the species differ in size and shape of the infructescences and therefore are not conspecific. Our personal examination of Frenguelli's samples and new samples of *G. patagonicum* supports Scriven and Hill's conclusion. *Gymnostoma antiquum* and *G. archangelskyi* cones are similar in gross morphology and size. *Gymnostoma argentinum* has more exserted bracteoles than *G. antiquum*.

Gymnostoma tasmanianum, from the Early Oligocene in Tasmania, is "organically preserved and three-dimensional material" (Guerin and Hill 2003, p. 630). The male inflorescences are attached to articles that are identical to the sterile ones; and although none of the few morphologically uniform infructescences are attached to articles, given that the articles occur in abundance in the deposit and are all of the same species, the authors considered that all these fossils probably belong to the same species. *Gymnostoma tasmanianum* has highly exserted bracteoles and hence is comparable only to *G. argentinum*, and *G. tasmanianum* has smaller cones and articles than *G. argentinum*.

Casuarina stellata, from the late Oligocene to early Miocene in New Zealand, are uncompressed molds of cones with highly exserted bracteoles. Campbell and Holden (1984) provided only generic-level characters for this species; however, in spite of their generic assignment, comparisons of these fossils were made with several extant species of *Gymnostoma*. In this regard, Scriven and Hill (1995) suggested that *C. stellata* could have closer affinities to *Gymnostoma* than to *Casuarina*. In our particular case, *C. stellata* is comparable only to *G. argentinum* in that both taxa show highly exserted bracteoles; however, *C. stellata* apparently has more rounded bracteoles and larger cones than this Patagonian species.

Casuarina avenaceae, from the Miocene in New Zealand, consists of compressed branchlets bearing laterally arranged cones with moderately exserted bracteoles. Its infructescences differ from those of *G. patagonicum* and *G. archangelskyi* in size, shape, and number of whorls per cone, and from *G. argentinum* in the degree of exsertion of the bracteoles. It is noteworthy that specimens of *C. avenaceae* were reidentified as *Allocasuarina* by Johnson and Wilson (1989) and Wilson and Johnson (1989).

The morphology of living species of *Gymnostoma* is fairly well known, but characters that are useful in comparisons to fossils preserved as compressions or impressions are little documented. Although the data given by Dilcher et al. (1990) and Scriven and Hill (1995) conflict with each other, they provide a good framework for establishing comparisons to the Patagonian fossils. We can compare the cone length/width ratio and the degree of exsertion of the bracteoles. Comparisons of living species to the Patagonian fossil species show similarities of *G. patagonicum* with *Gymnostoma intermedium*, of *G. archangelskyi* with *Gymnostoma leucodon* and *Gymnostoma*

Table 1

Distinctive Characters of the South American Fossil Species of *Gymnostoma*

	Infructescences							Attached articles		
Patagonian species	Position	Length (mm)	Width (mm)	Length/width	Bracteole exsertion	Bracteole shape	Whorls per cone	Length (mm)	Width (mm)	Length/width
G. patagonicum	Lateral	9–10	7.5–8	1.2 : 1	Slight	Rounded	6–7	8–9	1–2	5.7 : 1
G. archangelskyi	Lateral	12–15	9–11	1.3 : 1–1.5:1	Medium	Rounded triangular	8–9	5–6.5	1.2–2.5	3.1 : 1
G. argentinum	Lateral	9.5–12.5	9–11	1.1 : 1	High	Acute triangular	6–7	5	1.2	4.2 : 1

sumatrum, and of *G. argentinum* with *Gymnostoma poissonianum* and *Gymnostoma rumphianum*. Unfortunately, these similarities are based only on the two mentioned characters, and therefore, there is not sufficient evidence to reconstruct detailed phylogenetic or biogeographical relationships of the fossils.

Paleobiogeography

The presence of the family Casuarinaceae in South America during the Paleogene is confirmed by diverse fossil evidence: infructescences (or cones), staminate inflorescences, abundant vegetative material, and pollen grains. Most of these organs were found in organic connection (i.e., infructescences/branchlets, male inflorescences/pollen/branchlets) or as associated material in the same horizon and localities.

The megafossils described here are especially important in that they represent the only fossil Casuarinaceae reported from outside the Australasian region, and they are the first records of vegetative branchlets and male inflorescences with pollen from South America. Furthermore, this represents the second and the oldest known record for Casuarinaceae male inflorescences. While all the Patagonian megafossils come from the early Eocene Laguna del Hunco site, dispersed casuarinacean pollen grains have been found in at least five Patagonian localities (in latitudes from 37°S to 46°S), in sediments ranging in age from the early Paleocene to the Eocene.

The fossils described here show morphological traits sufficient to be included in the genus *Gymnostoma*; in addition, their wide morphological variability allows differentiation of three species. These species have a few similarities with four fossil species previously described from Australasia. It is noteworthy that in Patagonia, representatives of the three species were found at the same sites, and therefore, we interpret that the three species were living in the same time span. This diversity and abundance can be interpreted as evidence that *Gymnostoma* was an important and well-established component of the regional floras by at least the early Eocene in South America.

South American *Gymnostoma* were components of the so-called mixed floras, a term implemented by Romero (1978, 1993) to describe Patagonian Paleogene floras that combined the presence of taxa with tropical and Gondwanic affinities. According to Wilf et al. (2005), the nontropical but moist and equable climate at Laguna del Hunco may explain the presence of such a floristically distinct area in Patagonia. The absence of Casuarinaceae in the slightly younger (47.5 Ma) but equally diverse mixed flora of Río Pichileufú (Wilf et al. 2005), located 160 km northwest of Laguna del Hunco and at similar paleolatitude, indicates that the family became extinct in South America soon after the early Eocene climatic optimum. As indicated before in this article, the palynological evidence also supports this interpretation.

In summary, new South American Casuarinaceae fossils reinforce the previous hypothesis of a diverse and widespread occurrence for the family in middle Southern paleolatitudes during the Paleogene and provide valuable data for future reconstruction of the evolution of the family. Casuarinaceae extinction in South America could be related to paleoecological and paleoenviromental/paleoclimatic changes associated with cooling temperatures that followed the early Eocene climatic optimum.

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