

## Arecaceae Fossil Fruits from the Paleocene of Patagonia, Argentina

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**Abstract** We describe fossil fruits collected from outcrops of the Salamanca Fm. (Paleocene, Danian, 63.3–61.9 Ma) at the Estancia Las Violetas locality, Chubut, Argentina that show affinities with members of the Subtribe Attaleinae, Tribe Cocoseae, Subfamily Arecoideae within the Arecaceae. The fossils are preserved as permineralizations, and were examined by longitudinal, tangential and cross-sections, as well as by the application of Computed Tomography Scanning technology (CT Scan). The fruits are ovoid drupes with 3 longitudinal grooves delimiting three valves; displaying apical stigmatic remains and a single apical germination pore. The exocarp and mesocarp are fused and anatomically indistinguishable one from another; they contain longitudinal fibrous bands with brachysclereids. A centrally placed seed occupies the single locule entirely; the seeds are deltoid with a basal hilum and acuminate tip while the endosperm is ruminant. The taxonomic position of the fossils was explored using phylogenetic analyses of molecular sequences combined with morphological data. Along with the suite of morphological characters that points to an affinity with the Subtribe Attaleinae, Tribe Cocoseae, subfamily Arecoideae, the results of the combined phylogenetic analyses confirm the taxonomic placement. This report constitutes the first confirmed record for the Subtribe Attaleinae worldwide and the first record of fossil palm fruits from Argentina.

**Keywords** Arecaceae · Fossil fruits · Paleocene · Salamanca Formation · Patagonia · Argentina

### Introduction

Arecaceae is a large and economically important family of monocots with ca. 2300 species in 183 genera; with a worldwide distribution restricted to the sub-tropics to tropics (Dransfield et al., 2008). Of all monocots, Arecaceae has one of the richest fossil records both temporally and spatially (Daghlian, 1981); fossils assigned to it are found on every continent except Antarctica and interestingly often display a

previously higher level of diversity and distribution range than observed today (Pan et al., 2006). Harley (2006) provides a review of the fossil record of palms that includes several organs, although the most abundant are stems, fruits, seeds, leaves and pollen grains. Because of the distinctive diagnostic features of *Arecaceae*, taxonomic placement of fossils within the family is almost always guaranteed; nevertheless, due to character variability within the family the majority of the fossils assigned to *Arecaceae* cannot be placed with confidence within any modern taxa below familiar or subfamilial level (Harley, 2006; Dransfield et al., 2008). The earliest reliable macrofossils are stems placed within the morphogenus *Palmoxyton* Schenk dated to the Turonian of France (Crié, 1892) and Coniacian-Santonian of New Jersey (Berry, 1916) and palmate leaves appearing in the Coniacian-Santonian of South Carolina (Berry, 1914). Currently *Hyphaeneocarpum aegyptiacum* (Vaudois-Miéja & Lejal-Nicol, 1987) from the Aptian of Egypt is the oldest record of fossil palm fruits.

Although in South America modern genera of the family are highly represented, only 12 extant species within 8 genera are found naturally in Argentina (Zuloaga & Morrone, 1996) specifically in the north, northeast and in an area known as Mesopotamia (area that comprises the Misiones, Corrientes and Entre Ríos provinces; Fig. 1). Remarkably, the oldest fossil palm records from Argentina come from the Upper Cretaceous of Patagonia (Ancibor, 1995; Ottone, 2007) while the most recent ones are from the Pliocene of Mesopotamia (Lutz, 1980, 1984). Patagonian *Arecaceae* fossils are represented by stems, leaves and pollen grains. Based on the pollen record, the family is represented by several species of the genera *Arecipites*, *Confertisulcites*, *Liliacidites*, *Longapertites*, *Monosulcites*, *Psilamonocolpites*, *Sabalpollenites*, and *Spinozonocolpites* (Gandolfo et al., 2010). Argentinean fossil stems are referred to the morphogenus *Palmoxyton* Schenk 1882 and consist of 9 species that date from the Upper Cretaceous to the Pliocene (Ancibor, 1995; Argujio, 1979, 1981; Gandolfo et al., 2010; Lutz, 1980, 1984; Ottone, 2007; Petriella, 1972; Romero, 1968). The family is also represented by phytoliths (Zucol et al., 2007) and as of yet, undescribed pinnate and bifid palm leaves and fruits (pers. obs). Herein, we describe fossil fruits from Patagonia, Argentina with a clear affinity to the members of the subtribe *Attaleinae*, tribe *Cocoseae* within the subfamily *Arecoideae*.

## Material and Methods

### Geologic Background and Age

The fossil remains were collected from outcrops of the Salamanca Formation, which are exposed at the Estancia Las Violetas locality, Chubut province, Argentina (Fig. 1; Somoza et al., 1995). Here, a 10 m thick section composed of heterolithic facies (conglomerates and fine to medium grained sandstones) was deposited under littoral shallow marine conditions, including several tidal channel deposits represented by glauconitic bioturbated sandstones that bear the local fossil flora. The associated fossil logs have intense bioturbation of the *Terodolites* ichnofacies.

Based on paleomagnetic data, the section at Ea. Las Violetas has been assigned to Chron 27r of the Geomagnetic Polarity Time scale dated between 63.3 and 61.9 my (late Danian).

**Fig. 1** Map of Argentina showing the extant distribution of Arecaceae (*hash-mark*) and locality where fossils were collected (*circle*)



### Specimen Preparation and Examination

The examined specimens consist of 25 permineralized fossil fruits. Selected fossils were cleaned using traditional paleobotanical techniques, using a small pneumatic hammer, and degagement. Ultra thin and double polished longitudinal, tangential and transversal sections were performed on two selected specimens at Texas Petrographic Services, Inc. with the goal of observing anatomical and histological characters. Sections were examined using an Olympus BX60 microscope and photographed with a Nikon D70 a Sony DXC-9000. A section set is housed at the Paleobotanical Collection, Cornell University, USA (CUPC 1521 a–b) and the remainder set is housed at the Paleobotanical Collection of the Museo Paleontológico Egidio Feruglio, Trelew, Argentina under the numbers MPEF-Pb- 3767 a–c.

A fossil fruit and a fossil seed are housed at the Paleobotanical Collection, Cornell University, USA under the numbers CUPC 1522 and CUPC 1523 respectively; remainder fossils are housed at the Museo Paleontológico Egidio Feruglio under

the number MPEF-Pb-3766 (holotype) and numbers MPEF-Pb 3768, 3769, 3826–3830 (3829 and 3830 are two sets of several fossils each). Some of these fossils were subjected to X-ray tomography imaging that was conducted at the Cornell Imaging Center using a GE CT 120 eXplore, with 2 Gy to 8 Gy of radiation and 120,000 eV of voltage. This technique was used for observing rocks that contain fossils and isolated fossil fruits. They were placed within the CT Scan machine without any additional preparation. The images produced from the CT scan were viewed as series of still images or as movies. Within the rocks, the scan uncovered the presence of 2 fruits that could not be observed otherwise. Additionally, the scans revealed anatomical details such as the position of the germination pore, the thickness and relation to each other of the fruit layers and endosperm features that were not observed in the ultra thin sections. The use of CT scan technology was able to reveal and clarify several characters that were instrumental in describing and classifying these fossils while leaving the specimens fully intact.

Combined phylogenetic analyses were conducted using sequences downloaded from Genbank (Table 1) and morphological data that were compiled from literature and personal observation of herbarium material relevant to this study (Tables 2 & 3, Appendix 1). Nineteen taxa were selected from all five Arecaceae subfamilies with emphasis on New World species. Three members of Dasypogonaceae were selected as outgroups and coded from molecular data only. All taxa were scored at generic level, and some terminals are represented by more than a species, for example molecular data for the genus *Bactris* comes from a combination of the species *B. gasipaes* (*rbcL*) and *B. maraga* (PRK). The morphological matrix consisted of fourteen characters and was modified from Baker et al. (2009) with additional characters, of longitudinal grooves, mesocarp furrows, fibers in mesocarp, endocarp grooves, and number of seeds, coded by the examination of herbarium material and fossil specimens (Table 3). Two genes were selected to provide adequate resolution and taxa coverage: low-copy nuclear gene phosphoribulokinase (PRK) and chloroplast gene ribulose-bisphosphate carboxylase (*rbcL*). Both sequences were aligned using MUSCLE v.3.831 (Edgar, 2004). For the fossil taxon all molecular data was scored as absent. The combined matrix (Appendix 1) contained a total of 202 informative characters. Equal weighted parsimony analyses were conducted using NONA (Goloboff, 1998) as implemented in WinClada (Nixon, 1999). 300 heuristic search replicates (mult\*300) with random starting trees were conducted; a maximum of 10 trees were held in each replicate (hold/10) and TBR branch swapping (max\*) was conducted on all held trees. A strict consensus tree of the resulting most parsimonious trees was constructed using TNT (Goloboff et al., 2008), of 500 replicates with 10 replicates each and TBR branch swapping. The bootstrap values were placed on the strict consensus tree.

## Results

### Systematics

Family: Arecaceae Schultz 1832

Subfamily: Arecoideae

**Table 1** List of extant species used to compile the combined molecular and morphological data. All species used for coding morphological characters are housed at the L.H. Bailey Hortorium Herbarium, Cornell University (BH). Molecular sequences (rbcL and PRK) were downloaded from Genbank

Species	BH	Accession numbers Genbank rbcL	Genbank PRK
<b>Outgroup</b>			
<i>Calectasia intermedia</i>		AF206743	
<i>Dasypogon bromeliifolius</i>		AM110246	
<i>Kingia australis</i>		AM110245	
<b>Ingroup</b>			
<i>Acrocomia aculeata</i>	37261	AM110212	AY601224
<i>Attalea allenii</i>	37276	AJ404829	
<i>Attalea phalerata</i>			AY601240
<i>Bactris gasipaes</i>	37280	AM110214	
<i>Bactris maraga</i>			AY601214
<i>Barcella odora</i>	37275	AY044630	
<i>Butia yatay</i>	37262		
<i>Ceroxylon quindiuense</i>	37282	AJ404781	
<i>Ceroxylon amazonicum</i>			EF128386
<i>Chamaedorea microspadix</i>	37281	AJ404787	
<i>Chamaedorea metallica</i>			EF491095
<i>Cocos nucifera</i>	37283	AM110211	AY601232
<i>Copernicia macroglossa</i>	37278		
<i>Elaeis guineensis</i>	37263	AJ404830	AY601221
<i>Geonoma congesta</i>	37284	AM110219	
<i>Geonoma edulis</i>			HM140599
<i>Lytocaryum hoehnei</i>	37273; 37279		
<i>Lytocaryum insignis</i>	37264		
<i>Lytocaryum weddellianum</i>	37274; 37265	AY044633	AY601249
<i>Mauritia flexuosa</i>	37285	AJ404777	
<i>Nypa fructicans</i>	37286	AJ404778	AJ831357
<i>Pseudophoenix vinifera</i>	37277	AJ404780	
<i>Pseudophoenix sargentii</i>			EF128364
<i>Sabal bermudana</i>	37287	AJ404766	
<i>Sabal mexicana</i>			EF667947
<i>Socratea exorrhiza</i>	37288	AM110205	AF453378
<i>Syagrus flexulosa</i>	37266		
<i>Syagrus oleracea</i>	37269		
<i>Syagrus romanzoffiana</i>	37267; 37268		
<i>Syagrus smithii</i>	37270	AJ404827	AY601260
<i>Syagrus</i> sp.	37272		
<i>Synechanthus warscewiczianus</i>	37289	AJ404786	
<i>Synechanthus fibrosus</i>			EF491103
<i>Trithrinax campestris</i>	37271	AJ40474	

**Table 2** Morphological matrix compiled from herbarium observations. References to all previously published matrices serving as sources for the following defining and/or scoring the characters as well as primary literature consulted in scoring are listed following each character. All characters are nonadditive. Character numbering corresponds to WinClada numbering; numbering for NEXUS files will start with 1 rather than 0

	0	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Mauritia flexulosa</i>	0	1	0	0	0	0	0	0	–	0	0	1	0	0
<i>Trithrinax campestris</i>	0	0	0	0	0	0	0	0	–	0	0	1	0	0
<i>Sabal bermudana</i>	1	0	–	0	0	0	–	0	–	0	0	1	0	[01]
<i>Nypa fruticans</i>	1	0	–	0	0	1	–	0	–	0	0	1	0	1
<i>Ceroxylon quindiuense</i>	1	0	–	0	0	0	–	0	–	0	0	1	0	[01]
<i>Pseudophoenix vinifera</i>	1	0	–	0	0	0	–	0	–	0	0	1	0	1
<i>Geonoma congesta</i>	1	0	–	0	0	1	–	0	–	0	0	1	0	0
<i>Socratea exorrhiza</i>	0	0	–	0	0	1	–	0	–	0	0	1	0	0
<i>Chamaedorea microspadix</i>	1	0	–	0	0	0	–	0	–	0	0	1	?	0
<i>Synechanthus warszewiczianus</i>	1	0	–	0	0	1	–	0	–	0	0	1	[01]	0
<i>Barcella odora</i>	0	0	–	0	0	1	–	1	2	0	0	?	0	0
<i>Elaeis guineensis</i>	0	0	–	0	0	1	–	1	2	0	0	1	0	0
<i>Acrocomia aculeata</i>	0	0	–	0	0	1	–	1	1	0	0	0	0	0
<i>Bactris gasipaes</i>	0	0	–	0	0	1	–	1	1	0	0	1	0	0
<i>Cocos nucifera</i>	0	0	–	0	0	1	–	1	0	0	0	0	0	0
<i>Attalea allenii</i>	0	0	–	0	1	1	–	1	0	0	0	1	0	0
<i>Syagrus smithii</i>	0	0	–	0	1	1	–	1	0	1	0	0	[01]	0
<i>Lytocaryum weddellianum</i>	0	0	–	1	0	1	–	1	0	1	1	0	[01]	0
<i>Tripylocarpa aestuaria</i>	0	0	–	1	1	1	–	0	–	0	0	0	1	0

Tribe: Cocoseae Mart.

Genus: *Tripylocarpa* gen. nov. Gandolfo and Futey

Type species: *Tripylocarpa aestuaria* sp. nov. Gandolfo and Futey

**Generic Diagnosis.** One seeded ovoid drupe, exocarp and mesocarp fused and indistinguishable one from another; three external longitudinal grooves delimiting three valves, endocarp thin, not sculptured; apical stigmatic remains; one locule, seed deltoid; endosperm homogeneous and ruminant; apical germination pore and basal hilum.

**Specific Diagnosis.** As for the genus *Tripylocarpa*.

**Holotype:** MPEF-Pb-3766; Museo Paleontologico Egidio Feruglio, Trelew, Chubut Province, Argentina.

**Paratypes:** MPEF-Pb-3767 a–c; 3768, 3769, 3826–3830 and CUPC 1521 a–b and 1522–1523.

**Type locality:** Las Violetas, Salamanca Formation, Chubut Province, Patagonia, Argentina.

**Table 3** Morphological character list and characters coded

## Fruit surface, Exo-/mesocarp

0. Stigmatic remains: 0) apical to sub-apical; 1) lateral to basal [6, 15].
1. Pericarp scales: 0) absent; 1) present [6].
2. Pericarp warts: 0) absent; 1) present [6].
3. Longitudinal grooves: 0) absent; 1) present [6, 20, 32].
4. Mesocarp furrows: 0) absent; 1) present [6, 20].
5. Fibers in mesocarp: 0) absent; 1) present [6, 17].

## Endocarp

6. Endocarp sculpturing : 0) smooth; 1) sculptured [6, 20].
7. Endocarp pores: 0) absent; 1) present [6].
8. Endocarp pore position: 0) basal; 1) lateral; 2) apical [6, 15].
9. Endocarp grooves: 0) absent; 1) present [15].

## Seed

10. Hilum position: 0) basal; 1) lateral [6].
11. Raphe: 0) absent; 1) present [6, 15].
12. Endosperm: 0) homogenous; 1) ruminant [6, 20, 32].
13. Number of seeds: 0) one; 1) more than one [6].

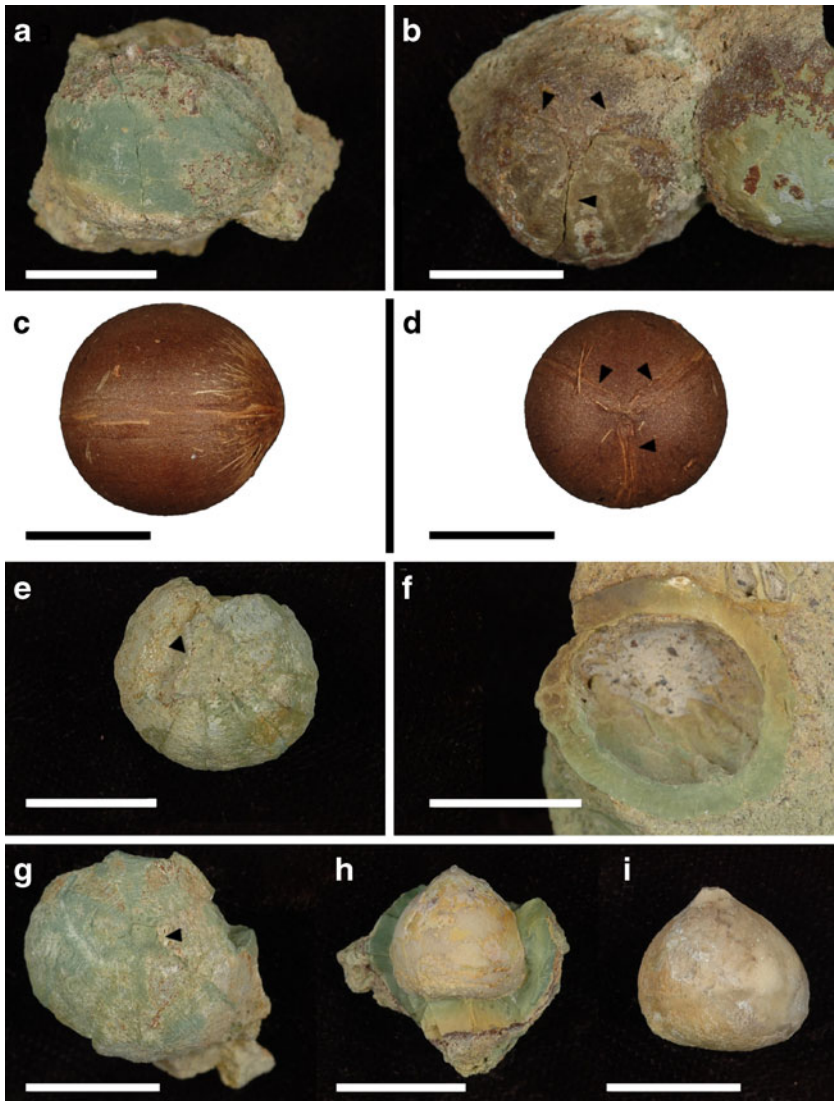
*Age and stratigraphy:* Danian, Early Paleocene, Salamanca Formation.

*Etymology:* *Tripylocarpa* refers to the three valves characteristic of the fruits (from the Greek *trion*+*pylo*+*karpus*); the specific epithet *aestuaria* refers to environment where the fossils were deposited.

*Description:* The fossils are petrified ovoid, drupaceous fruits, 17.1–23.2 mm long and 14.3–18.4 mm wide (Fig. 2a). The fruits have 3 main longitudinal grooves that delimit equal areas of exo/mesocarp, and extend from the apical pore to the most basal portion of the fruit (Fig. 2b). The three equal areas are interpreted as the fruit valves. A germination pore is clearly positioned on the apical area of the fruits and it is formed where the three valves reach each other (Fig. 3b & c). The fruits probably had a basal peduncle based on the presence of a constricted area opposite to the germinal pore that is interpreted here as part of the peduncle (Fig. 2e). The exocarp and mesocarp are fused and anatomically indistinguishable one from another (Fig. 3a). The exo/mesocarp is 1.5–3.0 mm wide with no distinct layers (Fig. 2f); while the endocarp is thin and unsculptured (Fig. 2h). Sclerenchyma bands with associated brachysclerids run longitudinally through the mesocarp and a layer of tanniferous cells internal to the endocarp (Fig. 3a). The stigmatic remains are apical (Fig. 2g). Each fruit carried a single seed; each seed is 10–16 mm long and 10–14 mm wide (Fig. 2h); they are deltoid in shape with an acute to acuminate apex, and basally truncate and they have a hilum that is basal (Fig. 2i). These correspond externally to the germination pore and basal peduncle respectively. The endosperm is ruminant (Fig. 3d).

*Comments:* Cocoseae fruits are more commonly preserved as endocarps and can often be easily identified due to the 3 pores and occasional ridges in the endocarp. While these fossils lack certain Cocoseae endocarp features, the exquisite preservation allows the observation of several key characters linking these fossils with

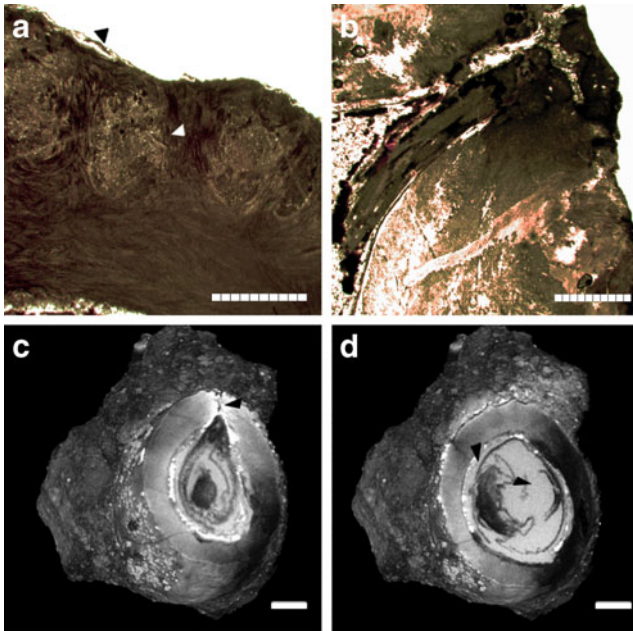




**Fig. 2** a–b, e–i: *Triplylocarpa aestuaria* Gandolfo and Futey. c–d. *Lytocaryum weddellianum* (H. Wendl.) Toledo. a–b. *Triplylocarpa aestuaria*. a. MPEF-Pb 3768- Side view of the fossil fruit showing a suture (arrow). b. MPEF- Pb- 3766- Top view of the holotype. Note the three longitudinal sutures (arrows) delimiting the three valves. The three sutures culminate at the germination pore. c–d. *Lytocaryum weddellianum*- BH #37247. Side view showing one suture (arrow). d. Top view showing 3 longitudinal sutures where the epicarp and mesocarp will split (arrows) and the germination pore. e–i. *Triplylocarpa aestuaria*. e. MPEF-Pb- 3769. Basal view showing peduncle remains (arrow). f. MPEF-Pb- 3826- Longitudinal section showing pericarp and seed cavity (locule). Note that there are no differentiation between the epicarp and mesocarp. g. MPEF-Pb- 3768- Top view showing the stigmatic remains (arrow) and germination pore. h. MPEF- Pb- 3827- Single seed surrounded by remains of pericarp, note the basal hillum. i. MPEF- Pb – 3828- Deltoid and basally truncate seed, note the acute apex. All scale bars=1 cm

Cocoseae. The fruits externally display several unique characters within Areceaceae, such as the furrowed surface and the three striations trisecting the fruit into equal





**Fig. 3** a–d: *Tripylocarpa aestuaria* Gandolfo and Futey. **a**- MPEF-Pb 3767a- Transversal section showing the fused exocarp and mesocarp layers and fibrous bundles (*arrows*). **b**. MPEF-Pb 3767b- Longitudinal section through the germination pore, note the channel left at the pericarp. **c–d**. MPEF-Pb- 3768- **c**. Still image from CT scan showing the germination pore (*arrow*), the pericarp, the single locule and remains of the seed. The white area is interpreted as the thin endocarp (*arrow*). **d**. Still image from CT scan showing endosperm ruminations (*arrows*). Scale bar figs. **a** and **b**=1 mm.; **c** and **d**=2.3 mm

areas. In longitudinal and transverse sections, it is possible to observe the central position of the unique seed and some anatomical characters of the exo, meso and endocarp. It is clear that there is no distinction between the exo and mesocarp, therefore we are interpreting them as fused (Fig. 3a). The sections also reveal the presence of parallel bands of longitudinal fibers in the mesocarp, along with the apical position of the germination pore (Fig. 3b & c)

Berry (1926) describes palm endocarps from the Middle Eocene of Peru that he compares with two modern genera of the tribe Cocoseae (*Astrocaryum* and *Attalea*) based on the size, the presence of longitudinal fibrous bands and overall appearance. Gómez-Navarro et al. (2009) and Tripathi et al. (1999) both describe *Cocos* fruits from the Paleocene of Colombia and Tertiary of Madhya Pradesh, India. While in both cases the endocarp pores are not preserved, the large size and longitudinal ridges on the fruit surface clearly indicate affinity with modern *Cocos*. The fruits described herein are clearly distinguishable from previous Cocoseae fossils based on the much smaller size and distinguishing characters found in these fossil fruits.

#### Phylogenetic Analysis

The heuristic search produced 21 most parsimonious trees with 689 steps with a consistency index (CI) of 76 and retention index (RI) of 64. The strict consensus resulted in the collapse of 11 nodes and 749 steps with a CI of 69 and a RI of 51. In all

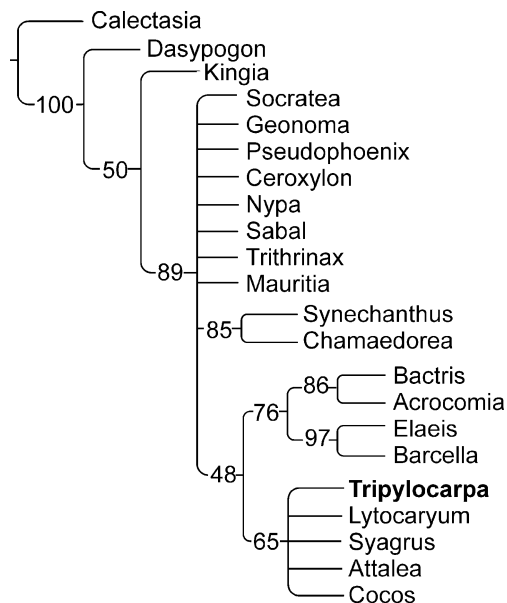
trees *Tripylocarpa aestuaria* is placed in the Attaleinae subtribe with 65 % support (Fig. 4)

## Discussion

The most recent taxonomic classification of palms based on molecular data, primarily from the chloroplast genome, resulted in the recognition of five subfamilies: Calamoideae, Coryphoideae, Nypoideae, Ceroxyloideae and Arecoideae, with the previously recognized subfamily Phytelephantoideae included in Ceroxyloideae (Asmussen et al., 2006). Inclusion of *Tripylocarpa* within Calamoideae and Nypoideae can easily be ruled out based on gross morphological characters; fruits of the Calamoideae have distinctive imbricate scales while the monotypic Nypoideae fruits are laterally compressed and irregularly angled (Dransfield et al., 2008), characters never observed in *Tripylocarpa*. Fruits of the remaining 3 subfamilies, Coryphoideae, Ceroxyloideae and Arecoideae, are typically one-seeded and not as strikingly distinct as those of the Calamoideae and Nypoideae. Longitudinal fibrous bands without bundle sheaths in the mesocarp are found throughout the Arecoideae and occasionally in Coryphoideae, but are lacking in fruits of the Ceroxyloideae (Essig, 1999). Additionally, all seeds of Ceroxyloideae have a homogenous endosperm (Dransfield et al., 2008). Fruits of Coryphoideae tend to be globose and often have a corky periderm, unlike the ovoid, smooth skinned *Tripylocarpa*.

The results of our phylogenetic analysis clearly place *Tripylocarpa* within the subfamily Arecoideae, tribe Cocoseae, subtribe Attaleinae. Although *Tripylocarpa* lacks the characteristic 3 or more well developed endocarp pores typical of tribe Cocoseae, the suite of anatomical and morphological characters point to an affinity with Cocoseae. The fossils are morphologically similar to fruits of Cocoseae, sharing

**Fig. 4** Strict consensus tree of 21 most parsimonious trees 689 steps long from combined morphological and molecular dataset as analyzed using NONA. CI=69, RI=51. Numbers on branches indicate bootstrap values



characters such as ovoid to obovoid shape, apical stigmatic remains and, excluding *Cocos*, a relatively small size. The fibrous bands running parallel and longitudinally through the mesocarp is also a typical character of Cocoseae fruits. While many arecoid fruits have a smooth epicarp surface, some members of the Cocoseae subtribe Attaleinae, such as *Attalea*, *Syagrus* and *Lytocaryum*, have furrows or striations in the epicarp similar to those found in *Tripylocarpa*.

Specimens of *Tripylocarpa* display a character found only in the genus *Lytocaryum*, a member of the subtribe Attalinae. *Lytocaryum* consists of 4 species (*L. itapebiensis*, *L. hohnei*, *L. insigne* and *L. weddellianum*) restricted to southeast Brazil (Noblick & Lorenzi, 2010) and has at times been placed in the larger, closely related genus *Syagrus* (Glassman, 1987). All 4 species have the 3 distinctive longitudinal markings running from apex to base on the epicarp which are strikingly similar to those found on these fossils (Fig. 2c & d). In *L. hohnei*, *L. insigne* and *L. weddellianum*, the exo/mesocarp dehisces at maturity along the grooves exposing the endocarp and releasing the seed. The shared presence of this unique character within Arecaceae is strong evidence for the affinity of these fruits to *Lytocaryum*. Additionally, *Tripylocarpa* has ruminant endosperm, which is also produced in *L. hohnei* (Noblick & Lorenzi, 2010).

While the Patagonian palm fossil record is extensive, the types of fossil remains found lack diagnostic characters that allow for precise taxonomic placement. In the case of both pollen and stems designation below the subfamily level is difficult. Seven species of *Palmoxylon* that have been described from Patagonia have been suggested to have an affinity to Sabaloid, Coryphoid, Phoenicoid, Bactroideae and Cocoseae palms based primarily on anatomical characters (Romero, 1968; Arguijo, 1979, 1981; Ancibor, 1995; Ottone, 2007), of those only three species come from Chubut (Gandolfo et al., 2010). Romero (1968) described fossil stem remains collected at the Cerro Abigarrado locality, also from the Salamanca Fm. (Chubut), and erected the species *Palmoxylon patagonicum*. This species shows intermediate characters with the tribes Sabaleae and Cocoseae, nevertheless the characters preserved do not allow a more precise taxonomical placement. Two other *Palmoxylon* species of Danian age are described for the Cerro Bororó Fm that outcrops in Chubut, *P. bororoense* and *P. vaterum* (Arguijo, 1979, 1981). Both species show affinities to the tribes Sabaleae and Cocoseae, but as with *P. patagonicum*, they cannot be placed with confidence in any one particular tribe. Although, at this time it is impossible to discuss potential relationships among the *Palmoxylon* species and *Tripylocarpa*, it is remarkable that the three Patagonian *Palmoxylon* species show potential affinities with Cocoseae as does *Tripylocarpa*. Therefore, the finding of *Tripylocarpa* provides unequivocal evidence of the presence of this tribe in Patagonia.

Although palm pollen is relatively variable when compared to other monocots, its taxonomic utility is limited when applied to the fossil record due to the tendency of morphologically distinct pollen types to be limited in phylogenetic range (Harley & Baker, 2001). While several species of palm pollen have been described from Patagonia, only in the case of *Spinozonocolpites* has any suggested affinities below the subfamily level affinities been ascribed, in this case to modern *Nypa* (Archangelsky, 1973).

Whether *Tripylocarpa* has any relationship with previously described palm macro- and microfossils cannot be made or ruled out due to the lack of taxonomic resolution.

Outside of Patagonia records of Cocoseae fruits, and more commonly endocarps, are reported from several localities. Coconut-like endocarps from both the North and South islands of New Zealand were found in deposits dated to mid-Eocene, Miocene and Pliocene (Ballance et al., 1981; Berry, 1926; Campbell et al., 2000). Fliche (1896) describes a coconut-like endocarp and fruit from the Cenomanian of northern France; which he compares to *Astrocaryum* and *Syagrus* based on size and shape of the fossil. Hollick (1928) and Maury (1930) described endocarps assigned to *Palmocarpon* from the Oligocene of Puerto Rico and the Maastrichtian of Brazil that they both compared with members of Cocoseae. However the poor preservation of all these fossils makes any assignment, even to Arecaceae, dubious. Comparisons among these species and *Tripylocarpa* are impossible to establish at this time due to the poor preservation of the previously described fossils and the lack of their reliable taxonomic placement; consequently, *Tripylocarpa* are the oldest and unequivocal record for fruits belonging to the subtribe Attaleinae and tribe Cocoseae.

In contrast to the current drier conditions found in Chubut today, several lines of evidence from the Salamanca Fm point to a moister, sub-tropical environment during the Paleocene. Many taxa found in the paleoflora, such as *Akania*, Malvaceae, and Lauraceae leaves and Araucariaceae cone scales (Berry, 1937; Iglesias, 2007) are associated with thermophilic families. Indeed the presence of palms alone is highly indicative of higher moisture and temperature levels as modern palm distribution is heavily influenced by water availability in addition to warm temperatures and therefore palms are rarely found outside of 34° latitude (Bjorholm et al., 2005). These suggested paleoclimatic conditions are also supported by leaf-margin and leaf-area analyses on the fossils from two localities in the Salamanca Fm, that predicted a mean annual temperature of 14.1 °C±2.6 °C and a mean annual precipitation of at least 115 cm (+50/−35 cm) (Iglesias et al., 2007).

## Conclusions

There is no doubt that the fossil fruits herein described belong to the Subtribe Attaleinae, Tribe Cocoseae, Subfamily Arecoideae. *Tripylocarpa aestuaria* taxonomic placement is based on the combination of morphological characters preserved as well as the results of the inclusion of the fossil within a phylogenetic context. Remarkably, to our knowledge, *Tripylocarpa aestuaria* is the first palm fossil taxon to be included in an analysis that includes molecular and morphological data. The detailed preservation of these fossils, which allows the observation of descriptive characters and its phylogenetic placement, makes it a prime candidate for use as a calibration point fossil in any future molecular clock analyses involving Arecaceae, the tribe Cocoseae or the subtribe Attaleinae.

This addition to the fossil record of Patagonia expands our knowledge of the Salamanca paleoflora and is further evidence of a previous subtropical environment in the Paleocene of Patagonia. Further work on any undescribed palm leaf, stem and endocarp fossils from Patagonia would only help to resolve the taxonomic affinities

of previously described fossil materials, especially stems, and will illuminate our understanding of the evolutionary history of the palms.

**Acknowledgments** The authors are grateful to Drs. S. Archanglesky and R. Somoza for making available the fossil remains studied herein. We thank Ing. M. Riccio for the CT Scan images, Dr. J. Reveal for helping with Greek for naming of the fossil, J. Svitko and P. Balcells for figure preparation. This research was supported by NSF grants DEB 0830020, DEB- 0918932 and DEB 0919071, and the Fulbright Foundation (MAG).

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**Appendix 1. Combined Molecular and Morphological Matrix**

*Calectasia* -----

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*Kingia* -----

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