SYSTEMATICS AND PHYLOGENY

Early evolution of Coriariaceae (Cucurbitales) in light of a new early Campanian (ca. 82 Mya) pollen record from Antarctica

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Abstract Coriariaceae comprise only *Coriaria*, a genus of shrubs with nine species in Australasia (but excluding Australia), five in the Himalayas, Taiwan, the Philippines, and Japan, one in the Mediterranean, and one ranging from Patagonia to Mexico. The sister family, Corynocarpaceae, comprises five species of evergreen trees from New Guinea to New Zealand and Australia. This distribution has long fascinated biogeographers as potential support for Wegener's theory of continental drift, with alternative scenarios invoking either Antarctic or Beringian range expansions. Here, we present the discovery of pollen grains from Early Campanian (ca. 82 Mya) deposits in Antarctica, which we describe as *Coriaripites goodii* sp. nov., and newly generated nuclear and plastid molecular data for most of the family's species and its outgroup. This greatly expands the family's fossil record and is the so far oldest fossil of the order Cucurbitales. We used the phylogeny, new fossil, and an Oligocene flowering branch assigned to a small subclade of *Coriaria* to generate a chronogram and to study changes in chromosome number, deciduousness, and andromonoecy. *Coriaria* comprises a Northern (NH) and a Southern Hemisphere (SH) clade that diverged from each other in the Paleocene (ca. 57 Mya), with the SH clade reaching the New World once, through Antarctica, as supported by the fossil pollen. While the SH clade retained perfect flowers and evergreen leaves, the NH clade evolved andromonoecy and deciduousness. Polyploidy occurs in both clades and points to hybridization, matching weak species boundaries throughout the genus.

Keywords Antarctica; biogeography; chromosome numbers; Cretaceous; deciduousness; Oligocene; pollen

■ INTRODUCTION

Coriariaceae have played an important role in biogeography, specifically in early discussions by botanists of Alfred Wegener's (1915) theory of continental drift and existence of the supercontinent Gondwana (Good, 1930). This was because of the unusually disjunct range of the family's sole genus, *Coriaria* (Fig. 1), which comprises 14–17 species (suppl. Table S1) that occur in the Western Mediterranean (one species in France, Spain, Morocco, Algeria); continental and insular Eastern Asia (five species in the Himalayas, Yunnan, Taiwan, the Philippines, and Japan); Australasia (nine species, mostly in New Zealand, the Chatham Islands, the Kermadecs, Fiji, the New Hebrides, Papua New Guinea, and also Samoa [fide Good, 1930]); and in South and Central America (one or two species) from lat. 45°S to lat. 23°N, with a gap of hundreds of kilometres between the northernmost Chilean and southernmost Peruvian populations. Despite these geographic disjunctions, the morphological similarity among populations is such that the most recent taxonomic revision (Skog, 1972) accepted only five species and considered the single New World species (*C. ruscifolia* L.) to have two subspecies, supposedly *both* extending to New Zealand. The type of *C. ruscifolia* was collected near Concepción (Chile) by Louis Feuillée in 1708.

As first suggested by Good (1930), a plausible explanation for the disjunct range of *Coriaria* is that it is the remnant of a former continuous range attained during the middle part of the Paleogene stretching from Eastern Asia to the Mediterranean and from Australasia to the New World via the Antarctic continent. "In *Coriaria* there seems little doubt that the present southern distribution is the result of the modification by climatic change of a more or less continuous distribution between New Zealand and South America in the early and middle parts of the Tertiary" (Good, 1930: 187). Good's inference of a Tertiary age was based on a remarkably

well-preserved fossil of a *Coriaria*-like flowering branch from the upper Oligocene Armissan beds (43°11′24″N; 03°05′24″E) in southern France (Saporta, 1866) (Fig. 2B). The Armissan fossil consists of a complete spray, about 41 cm long, with stems, leaves, and two long terminal racemes all organically attached. Such a terminal raceme is today only known from the Mediterranean *C. myrtifolia* L. and the Himalayan species *C. nepalensis* Wall., *C. terminalis* Hemsl., and *C. duthiei* D.K.Singh & Pusalkar (Singh & Pusalkar, 2009). Other fossils include late Miocene and Pliocene leaves from Japan that resemble *C. japonica* A.Gray (Ozaki, 1991), Miocene seeds from Germany that resemble *C. nepalensis* (Gregor, 1980), and *Corynocarpus*-like fruits from the Miocene of New Zealand (24 million years ago [Mya]; Campbell, 2002), *Corynocarpus* being the sister clade of *Coriaria* (below). Fossil pollen grains related to *Coriaria* have been reported from the late Miocene of Spain (Van Campo, 1976) and from the Quaternary of New Zealand (Zagwijn, 1963; Mildenhall, 1980). Other reports from the Maastrichtian of Canada (Srivastava, 1969; Jarzen & Norris, 1975) are doubtful (Muller, 1981).

Species of *Coriaria* (Fig. 2) are wind-pollinated shrubs with mostly bisexual (perfect) flowers (Thompson & Gornall, 1995), which is unusual in the order they belong to, the Cucurbitales, which mostly has animal-pollinated unisexual flowers (Zhang & al., 2006). Four species of *Coriaria*, however, are andromonoecious, having male and perfect flowers (Thompson & Gornall, 1995) (Table 1). As is typical of wind-pollinated plants, the flowers are strongly dichogamous, with the styles of each flower exposed long before the anthers. On any one plant, sequential flower maturation can lead to inter-floral protandry (Thompson & Gornall, 1995). Wood morphology and molecular data support a sister-group relationship with Corynocarpaceae, a family of five species of trees endemic to New Guinea, tropical Australia, New

Caledonia, New Zealand, and the Chatham Islands (Wagstaff & Dawson, 2000; Zhang & al., 2006; Schaefer & Renner, 2011), which have bisexual flowers that are visited, and probably pollinated, by birds (Matthews & Endress, 2004; Newstrom & Robertson, 2005). All but two species of *Coriaria* have had their chromosomes counted and so have most outgroup species (Table 1).

The first molecular-phylogenetic study of Coriariaceae, based on sequences of the plastid genes *rbcL* and *matK* with herbarium-vouchered material of 11 species, produced a well-supported phylogeny that showed Northern and Southern Hemisphere clades (Yokoyama & al., 2000). Unexpectedly, two accessions from the New World, one from Chile and one from Mexico, did not group together. When Yokoyama & al. excluded the outgroups they had used, *Begonia* and *Datisca*, and two *Coriaria* accessions (*C. terminalis* and an unnamed entity from Fiji), their DNA data did not reject the clock assumption of equal rates in sister taxa, and they then used Saporta's Armissan fossil to assign a minimal age of 30 million years (Myr) to the Himalayan *C. terminalis*. This calibration resulted in an age of at least 63 or 59 Myr for the genus, using either the *rbcL* or the *matK* alignment. Based on this inferred time frame and the tree topology, Yokoyama & al. proposed that *Coriaria* originated in either Eurasia or North America and that during the Paleogene, when the Arctic circumpolar region supported temperate plant species, it was continuously distributed between these northern continents. In North America, *Coriaria* gave rise to a species that then expanded south to South America across the Panamanian land bridge. Independently, *Coriaria* also reached Chile via transoceanic dispersal from one of the Pacific islands. This scenario disregards the Australasian distribution of the sister family Corynocarpaceae, which Yokoyama & al. briefly mentioned, but did not sample.
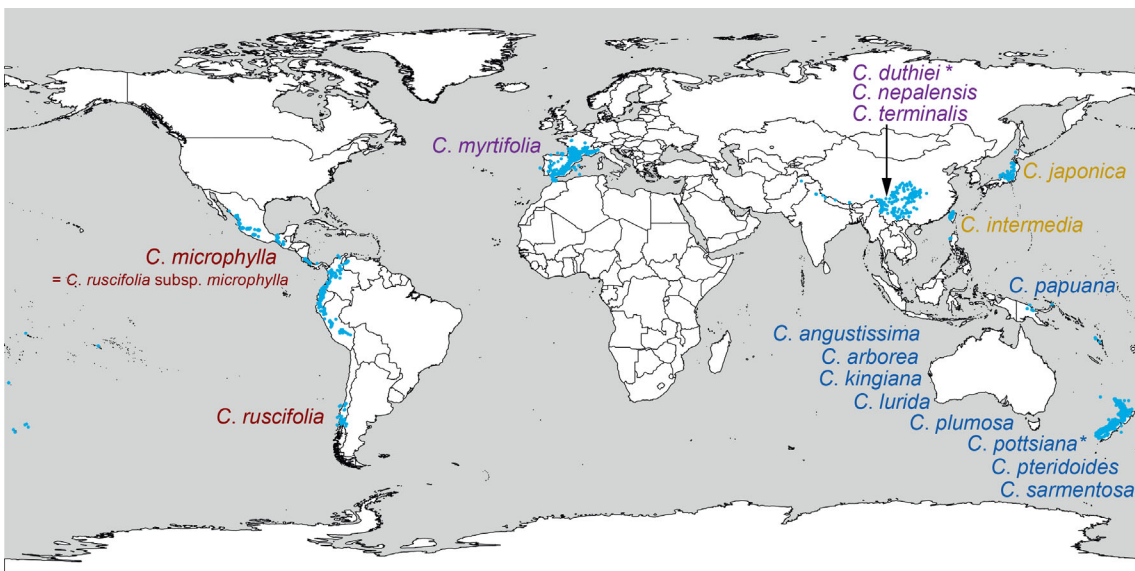

Fig. 1. Distribution map of *Coriaria* species generated from georeferenced data available in GBIF (accessed Jan 2019).

Fig. 2. Selected extant and fossil species of *Coriaria*. **A**, *C. myrtifolia* (photo by Tanja M. Schuster); **B**, Holotype of *C. longaeva* G. de Saporta, 1866, showing the characteristic venation pattern, leaf attachment, and terminal inflorescence; **C**, *C. sarmentosa* flowers showing protogyny (photo by Pieter Pelser, PhytoImages, Nickrent & al., 2006 –); **D**, Fruits of *C. sarmentosa* with accrescent corollas (photo by Tanja M. Schuster); **E**, The characteristically small leaves of *C. microphylla* or *C. ruscifolia* subsp. *microphylla* (photo by Axel Dalberg Poulsen); **F**, *C. ruscifolia* in Chile (photo by Mark Olson).

Table 1. Flower sexual system and chromosome numbers for the sister groups *Coriaria* (14–17 species) and *Corynocarpus* (5 species).

Species	Flower sexual system	Herbarium voucher (herbarium code)	Mitotic or meiotic counts	Reference
Coriaria				
C. angustissima Hook.f.	Perfect	no voucher	$2n = 40$	Oginuma (1993)
C. arborea Linds.	Perfect	*M. Suzuki & al. Co-1* (TI)	$2n = 40$	Oginuma & al. (1991)
C. arborea Linds.		no voucher	$2n = 40$	Oginuma (1993)
C. arborea Linds.		*L. Brunner & N. Westland 101502* (CHR)	$n = 20$	Beuzenberg & Hair (1983)
C. arborea Linds.		*J.A. Rattenbury s.n.* (AKU)	$n = $ ca. 22	Rattenbury (1957)
C. intermedia Matsum.	Andro-monoecious	*M. Suzuki & S. Suzuki s.n.*, 1989 (TI)	$2n = 40$	Oginuma & al. (1991), Oginuma (1993)
C. japonica A.Gray	Andro-monoecious	*M. Suzuki s.n.*, 1989 (TI)	$2n = 40$	Oginuma & al. (1991)
C. japonica A.Gray		*M. Nakata*, Japan, no voucher	$2n = 40$	Oginuma & al. (1991), Oginuma (1993)
C. kingiana Colenso	Perfect	(CHR: 527035)	$2n = 70$	De Lange & al. (2004)
C. lurida Kirk	Perfect	*M. Suzuki & al. Co-13* (TI)	$2n = 80$	Oginuma & al. (1991), Oginuma (1993 as $2n = 60$ but without a voucher specimen)
C. microphylla Poir. (*C. ruscifolia* subsp. *microphylla* of Skog, 1972)	Perfect	*M. Nakata 5201* (TNS)	$2n = 40$	Oginuma & al. (1991), Oginuma (1993)
C. myrtifolia L.	Andro-monoecious	*W.M. Bowden s.n.* (BH)	$2n = $ ca. 80	Bowden (1945)
C. myrtifolia L.		*Ron s.n.*, Morocco, no voucher	$2n = 80$	Oginuma & al. (1991)
C. myrtifolia L.		*Ron s.n.*, Spain, no voucher	$2n = 80$	Oginuma & al. (1991)
C. myrtifolia L.		Kew seed collection no. 36382, France	$2n = $ ca. 72	Hanson & al. (2001)
C. nepalensis Wall.	Andro-monoecious	*M. Suzuki & al. s.n.* (TI: 8840537)	$2n = 40$	Oginuma & al. (1991)
C. papuana Warb.	Perfect	*R. Watanabe s.n.*, 27 Nov 1989 (TI)	$2n = 40$	Oginuma & al. (1991), Oginuma (1993)
C. pottsiana W.R.B.Oliv.	Perfect	(AK: 256034)	$2n = 60$	De Lange & al. (2004)
C. pteridoides W.R.B.Oliv.	Perfect	*M. Suzuki & al. Co-5* (TI)	$2n = 80$	Oginuma & al. (1991), Oginuma (1993)
C. ruscifolia L.	Perfect	*K. Uemura s.n.*, Chile (TNS: 552756)	$2n = 40$	Oginuma & al. (1991), Oginuma (1993)
C. sarmentosa G.Forst.	Perfect	(AK: 250306)	$2n = 80$	De Lange & al. (2004)
C. terminalis Hemsl.	Perfect	no voucher	$2n = 40$	Oginuma (1993)
Corynocarpus				
C. cribbianus (F.M.Bailey) L.S.Sm.	Perfect	*Kimprani & al. 696J3* (LAE)	$2n = 44$	Oginuma & al. (1998)
C. dissimilis Hemsl.	Perfect	(CHR: 48109)	$2n = 46$	Dawson (1997)
C. lavigatus J.R.Forst. & G.Forst.	Perfect	(CHR: 200277)	$n = 22$ or 23	Hair & Beuzenberg (1960); Dawson (1997): recounted the original preparation as 23
C. lavigatus J.R.Forst. & G.Forst.		(CHR: 420516, 420517, 420518, 420527, 468722)	$2n = 44$ or 46	Dawson (1997)
C. rupestris Guymer	Perfect	Six vouchers from different locations (CHR)	$2n = 92$	Dawson (1997), a single hexaploid seedling ($2n = $ ca. 138)

The only species not counted are *C. duthiei* D.K.Singh & Pusalkar from the Western Himalayas, *C. plumosa* W.R.B.Oliv. from New Zealand, and *Corynocarpus similis* Hemsl. from Vanuatu.

Here we present a new fossil species described to accommodate pollen grains related to Coriariaceae from the Campanian/Maastrichtian sediments of Antarctica. In light of our fossil discovery, we test the contradictory biogeographic scenarios for *Coriaria* of Good (1930), who postulated a single arrival in the New World via Antarctica, and that of Yokoyama & al. (2000), who proposed two arrivals to the New World, one via Beringia and a second via transoceanic dispersal across the Pacific.

■ MATERIALS AND METHODS

Taxon sampling, DNA amplification, alignment, and phylogenetic analysis. — Appendix 1 shows the 25 samples of *Coriaria* (along with their herbarium vouchers), representing all but two species, that we used to sequence the plastid loci *trnL-trnF* and *matK* and the nuclear ITS locus coding for ribosomal RNA. We could not obtain material suitable for DNA extraction for *C. pottsiana* W.R.B.Oliv. from the North Island of New Zealand and *C. duthiei* (Singh & Pusalkar, 2009) from the Western Himalayas. Another entity not sampled, *C. kweichovensis* Hu, is based on a plant of *C. nepalensis* during its hermaphrodite phase (Thompson & Gornall, 1995). As outgroup, we used *Corynocarpus laevigatus* J.R.Forst. & G.Forst. to represent Corynocarpaceae, the sister clade of Coriariaceae, which consists of one genus with five species (Wagstaff & Dawson, 2000; Zhang & al., 2006; Schaefer & Renner, 2011). Coriariaceae and Corynocarpaceae in turn are sister clade to Begoniaceae, Datiscaceae, and Tetramelaceae (Schaefer & Renner, 2011). We also included one vouchered *matK* sequence of *C. arborea* Linds. from Yokoyama & al. (2000) downloaded from GenBank (AB016454; https://www.ncbi.nlm.nih.gov/genbank/).

Genomic DNA from leaf material was isolated using a NucleoSpin Plant II Kit (Macherey-Nagel, Düren, Germany), and sequences were generated using the primers in Table 2. Sequencing relied on Big Dye Terminator chemistry (ABI) and an ABI 3100 Avant capillary sequencer. Sequence assembly and editing were carried out in Geneious v.R11.1.5 (Kearse & al., 2012). The trace calls of the nuclear sequences were checked for ambiguous calls (which might suggest polyploidy), and all sequences were BLAST-searched in GenBank.

Sequence alignment was also performed in Geneious v.R11.1.5 using the E-INS-i alignment strategy with default settings in MAFFT v.7.388 (Katoh & al., 2002; Katoh & Standley, 2013). The two plastid regions were concatenated for a total aligned length of 1763 bp. The plastid and nuclear alignments were then analysed separately to check for topological contradictions. In the absence of statistically supported topological incongruence (i.e., maximum likelihood bootstrap support values >80%), we combined the plastid and nuclear data; the final concatenated matrix had 2483 aligned nucleotides; this alignment and resulting tree have been submitted to TreeBASE (https://www.treebase.org; accession number 25394. Phylogenetic analysis relied on RAxML v.8.2.11 (Stamatakis, 2014) to infer a best-scoring maximum likelihood (ML) tree and for nonparametric bootstrapping with 500 replicates, all under the general time-reversible model of substitution with unequal rates across sites (GTR + Γ).

Molecular dating. — Molecular-clock analyses relied on BEAST v.2.6.0 (Bouckaert & al., 2019), using the concatenated nuclear and plastid alignment but reducing *C. ruscifolia* from three accessions to one. Analyses used the relaxed clock lognormal model and were performed several times, with Markov chain lengths of 100 or 200 million generations, sampling every 1000th generation. Convergence was checked in Tracer v.1.7 by making sure that all effective sample sizes of the estimated parameters were higher than 200 (Rambaut & al., 2018). A burn-in fraction of 10% or more was removed before exporting the maximum clade credibility tree with mean heights using TreeAnnotator (both programs are part of the BEAST package). Trees were visualized with FigTree v.1.4.4 (Rambaut, 2019), and the priors were compared to the posteriors to confirm that the DNA data were informative as regards node age estimation.

Table 2. Primer sequences for the gene regions used in this study.

Primer name	Primer sequence	Primer source
matK (forward)	ACATTTAAATTATGTGTCAG	Nouioui & al. (2014)
matK (reverse)	TGCATATACGCACAAATC	Nouioui & al. (2014)
trnLc	CGAAATCGGTAGACGCTACG	Taberlet & al. (1991)
trnLd	GGGGATAGAGGGACTTGAAC	Taberlet & al. (1991)
trnLe	GGTTCAAGTCCCTCTATCCC	Taberlet & al. (1991)
trnLf	ATTTGAACTGGTGACACGAG	Taberlet & al. (1991)
ITS1	TCCGTAGGTGAACCTGCGG	White & al. (1990)
ITS2	GCTGCGTTCTTCATCGATGC	White & al. (1990)
ITS3	GCATCGATGAAGAACGCAGC	White & al. (1990)
ITS4	TCCTCCGCTTATTGATATGC	White & al. (1990)

To convert genetic distances into absolute time, we assigned an age of either 23 or 33 Myr to the stem of *C. myrtifolia*/*C. nepalensis*/*C. terminalis*, based on the rationale that the terminal inflorescence position uniquely shared by these species and the Armissan fossil (Saporta, 1866) must have evolved somewhere along the genetic branch subtending them. The Armissan beds, near Narbonne, have been dated to the late Oligocene, 23 to 33.9 Mya (Cohen & al., 2013), and we therefore used these ages as brackets, with a lognormal prior and either an offset of 23 Myr and a permitted range between 23.2 and 54.5 Myr or an offset at 33 Myr and a permitted range between 30.2. and 61.5 Myr. We also constrained the divergence of Corynocarpaceae/Coriariaceae (i.e., the root of our tree) to either 84 Mya based on the earliest fossils of Fagales, the sister group of Cucurbitales (Herendeen & al., 1995), with an offset of 84 Myr and a permitted range between 84.2 and 115 Myr, or to 82 Myr based on the newly discovered pollen record described in this study (Results), with an offset of 82 Myr and a permitted range between 82.2 and 113 Myr.

Distribution map for *Coriaria*. — To generate a distribution map, we downloaded georeferenced samples of *Coriaria* from the Global Biodiversity Information Facility (GBIF, 2019). The GBIF locations were restricted to collection material or living plants documented in their natural habitat, excluding specimens cultivated in botanical gardens or fossil records. GPS coordinates were excluded if they were clearly unreasonable, such as locations in the ocean. The map was generated with the online tool SimpleMappr (Shorthouse, 2010).

Inference of chromosome number change. — The chromosome numbers of most species of *Coriaria* have been counted (Table 1), and we used maximum likelihood and Bayesian phylogenetic approaches in ChromEvol v.2 (Glick & Mayrose, 2014) to infer changes in chromosome number in the genus, using the ML tree from the combined data. This software infers the expected number of polyploidy and dysploidy transitions along each branch of a given phylogeny and estimates ancestral chromosome numbers at internal nodes of the tree. The extended version 2 allows entering intraspecific variations in chromosome numbers within species. The chromosome numbers of the outgroup *Corynocarpus* vary between $2n = 44, 46$, and 92 in the four species that have been counted (Table 1), and to account for this variation, we generated pseudo-sequences for *C. cribbianus* (F.M.Bailey) L.S.Sm., *C. dissimilis* Hemsl., and *C. rupestris* Guymer by duplicating our sequences of *C. laevigatus*. These species' relationships are known from a phylogenetic study of *Corynocarpus* that included all five species (Wagstaff & Dawson, 2000).

ChromEvol implements eight models of chromosome number change that include the following six parameters: polyploidization (chromosome number duplication with rate ρ, "demi-duplication" or triploidization with rate μ) and dysploidization (ascending: chromosome gain rate λ; descending: chromosome loss rate δ) as well as two linear rate parameters, λ1 and δ1, for the dysploidization rates λ and δ, allowing them to depend on the current number of chromosomes. Four of the models have a constant rate, whereas the other four include the two linear rate parameters. Both model sets also have a null model that assumes no polyploidization events. We fitted all models to the data, each with 10,000 simulations to compute the expected number of changes of the four transition types along each branch. The maximum number of chromosomes was set to 10× higher than the highest number found in the empirical data, the minimum number to 1. The null hypothesis (no polyploidy) was tested with likelihood ratio tests using the Akaike information criterion (AIC).

Fossil and extant pollen samples. — Fossil pollen specimens were recovered from the Campanian/Maastrichtian Santa Marta, Snow Hill and López de Bertodano Formations on the James Ross and Vega islands, in Antarctica (Barreda & al., 2019). Slides containing the fossil specimens analysed and illustrated in this study are housed in the palynological collection of the Museo Argentino de Ciencias Naturales (BA; Buenos Aires, Argentina): BA-Pal, ex CIRGEO (Centro de Investigaciones en Recursos Geológicos), *Palin 611, 697* and *963*. Pollen grains were examined and photographed under a Leica light microscope, and photomicrographs were taken with a Leica DFC 290 camera. Coordinates of the illustrated pollen grains are from an England Finder slide, that is, a glass slide marked over the top surface in such a way that a reference position can be deducted by direct reading.

For comparison with extant material, we examined pollen from the following herbarium specimens: *Coriaria arborea*: *Suzuki & al. Co-14* (M); *C. intermedia* Matsum.: *A. Loher s.n.*, 1822 (M); *C. lurida* Kirk: *U. Schweinfurth 879* (M); *C. papuana* Warb.: *Watanabe s.n.*, 27 Nov 1989 (M); *C. plumosa* W.R.B.Oliv.: *R.M. Laing 9864* (M); *C. ruscifolia*: *P. Moreau s.n.*, Jan 1946 (BA); *C. sarmentosa* G.Forst.: *Suzuki & al. Co-13* (M), and *C. terminalis*: *Stainton & al. 980* (M). We also included pollen from a specimen of *C. myrtifolia* grown in the systematic section of the Botanic Garden of Munich (*S.S. Renner 2810* [M], no provenance data available). Pollen samples were acetolyzed following the technique outlined in Erdtman (1960) and mounted in glycerol jelly. Measurements of the polar axis (P) and equatorial diameter (E) were based on 20 grains, while measurements of exine thickness were based on 10 grains and made under a light microscope (LM). Sculpture details of fossil and living pollen were examined by scanning electron microscopy (SEM). For SEM examination, non-acetolyzed pollen was also included, air dried on the same stubs, because acetolysis causes pollen grains to shrink. Pollen grains were suspended in 90% ethanol, mounted on stubs, sputter-coated with gold palladium and examined with a Philips XL30 TMP SEM at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia".

■ RESULTS

Species relationships, key traits, and the biogeography of *Coriaria*. — The chronograms (Figs. 3, suppl. Figs. S1, S2) and phylogenies (suppl. Figs. S3–S5) include accessions of all

but two species (Materials and Methods) and show a Northern Hemisphere (NH) and a Southern Hemisphere (SH) clade that diverged from each other in the mid-Eocene to late Paleocene 46 to 57 Mya (Fig. 3, suppl. Fig. S2), depending on whether the Oligocene fossil (Fig. 2B) was set to 33 or 23 Mya (Materials and Methods). Using the oldest Fagales fossil (84 Mya) as a root constraint instead of the newly discovered pollen grains (82 Mya) made no difference to the inferred ages of nodes within the genus *Coriaria* (results not shown). Highest posterior density ranges (95%) around all node ages are shown in supplementary Fig. S1. Considering the inferred divergence times seen in the chronogram (Fig. 3), it appears that *Coriaria* entered the New World once, sometime before 36 Mya (late Eocene). While New Zealand harbours many young species, the divergence of a Papua New Guinean endemic, estimated as 8 to 9 Mya (late Miocene), is relatively

old (Fig. 3, suppl. Fig. S2). Deciduousness and andromonoecy each evolved once in the common ancestor of the Northern Hemisphere clade (Fig. 3).

Chromosome numbers and polyploidy. — Chromosome numbers of species of *Coriaria* and outgroup species are shown in Table 1 and in Fig. 4. We inferred at least three independent chromosome duplication events, one in the Western Mediterranean *C. myrtifolia*, and at least two in species occurring in New Zealand (Fig. 4).

Two accessions of *C. ruscifolia* from Argentina and Chile (with herbarium vouchers that we verified) place among accessions from New Zealand in the combined as well as the plastid and nuclear phylogenies (suppl. Figs. S3, S4, S5), apparently lacking synapomorphic substitutions that would place them with the two other American accessions (from Chile and Mexico).
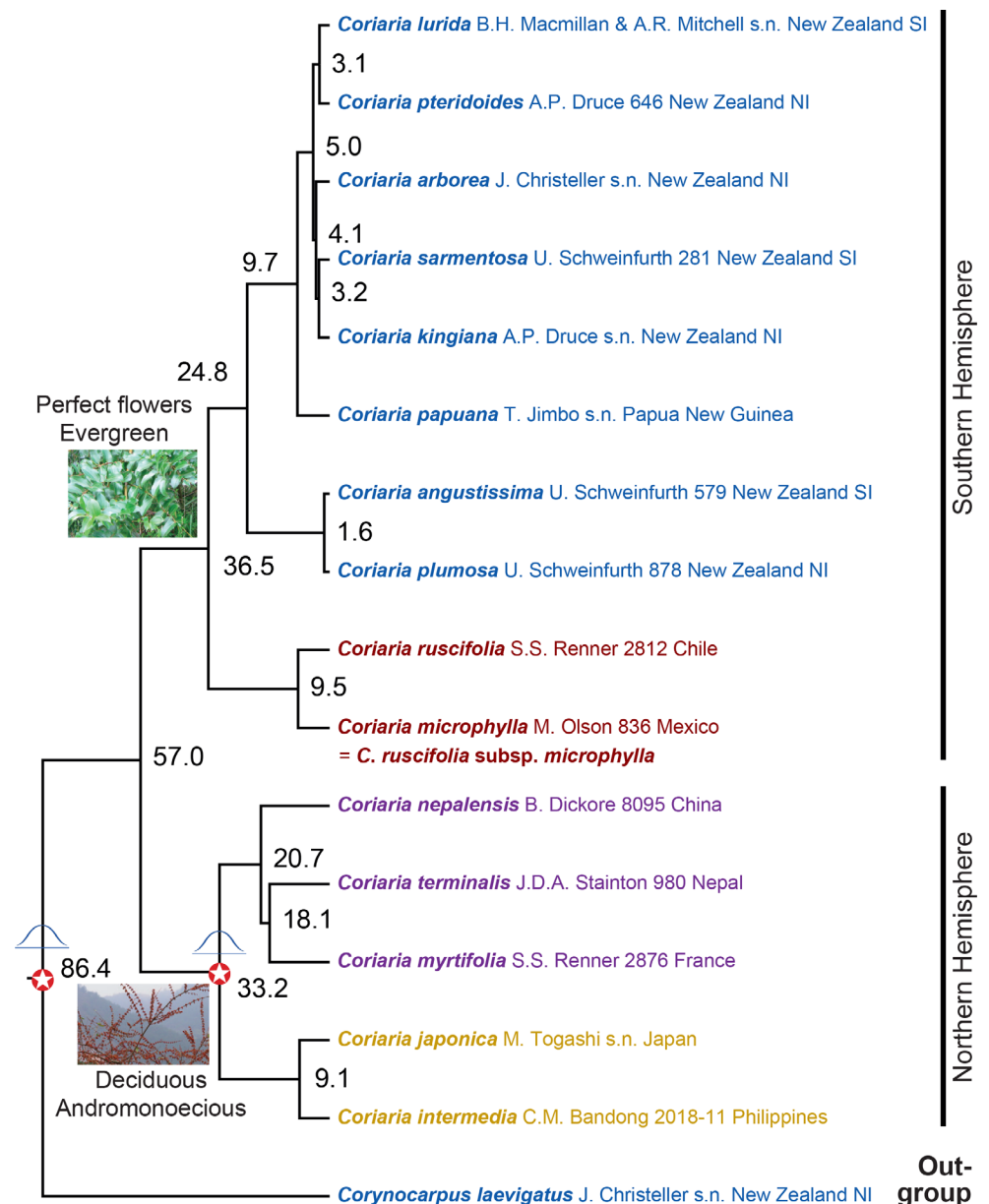

Fig. 3. Chronogram for Coriariaceae inferred from the concatenated ML alignment. The stars indicate a constraint based on the early Campanian (82 Mya) pollen described in this study and another based on the Oligocene flowering branch shown in Fig. 2B, which has been dated to 23 to 33.9 Mya. We here set this constraint to 33 Mya An alternative chronogram in which we set the same fossil to 23 Mya is shown in suppl. Fig. S2. We used a relaxed clock model; the permitted age ranges around the two fossil constraints are described in Materials and Methods and symbolized by the curves above the asterisks. Accessions in blue are from Australasia, in red from America, in purple from Eurasia, and in yellow from Eastern Asia. NI stands for North Island and SI for South Island. Error bars around age estimates are shown in suppl. Fig. S1.
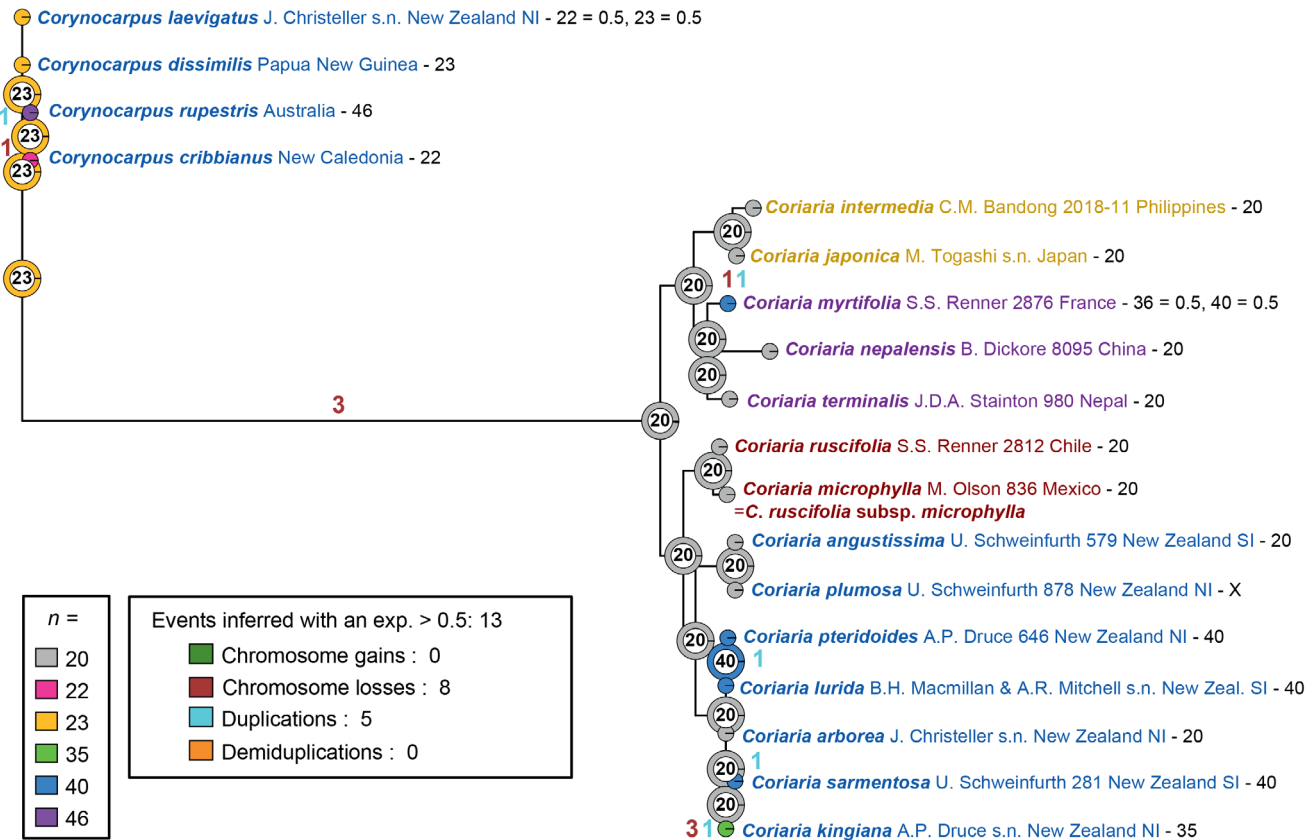
Fig. 4. The evolution of chromosome numbers in *Coriaria* inferred under a best-fitting maximum-likelihood model (Materials and Methods).

Pollen fossil. — The pollen grains we report here from the late Cretaceous of Antarctica are tri- or tetracolporate, fastigiate, scabrate-granulate, with very short colpi (Figs. 5, 6). The fastigium is a cavity in a colporate grain with a separation of the inner part of the exine from the domed sexine in the region of the endoaperture (Punt & al., 2007). We designate our specimens as a new species, *Coriaripites goodii*, which shows strong morphological similarities with pollen of extant *Coriaria* (see the Taxonomic Treatment for a full description and comments). These characteristic pollen grains first appear in the early Campanian (ca. 82 Mya), occurring in trace numbers.

■ DISCUSSION

Biogeography of Coriariaceae. — We set out to test the contradictory biogeographic scenarios of Good (1930), who postulated a single arrival of Coriariaceae in the New World via Antarctica, and of Yokoyama & al. (2000), who inferred one arrival to the New World via Beringia and a second via transoceanic dispersal across the Pacific. The discovery of 82-Myr-old Antarctic Coriariaceae pollen, together with the monophyly of our New World *Coriaria* accessions from Mexico and Chile and the restriction of the closest sister group, Corynocarpaceae, to New Guinea to New Zealand and Australia, supports a single entry into the New World

from Antarctica in line with Good's scenario. The hypothesis of Yokoyama and colleagues was based on a phylogeny in which their two New World accessions, one from Mexico and one from Chile (but not the same plants as sequenced here), did not form a clade. Their Chilean accession was instead nested among samples from New Zealand. Just like Yokoyama & al., we found that some of our New World plants yielded nuclear ITS and plastid sequences that failed to form a clade with our remaining American samples (suppl. Figs. S4, S5). Our sequences, like those of Yokoyama & al., come from verified herbarium collections and were generated at different times, reducing the chance of DNA contamination. As we argue below (Polyploidy and its possible effects on species boundaries), polyploidy and hybridization, which can lead to long persistence of ribosomal DNA (here ITS) polymorphisms through speciation events and/or the coexistence of different maternal plastid genomes in the same individual, probably explain the unexpected placement of some New World sequences in the phylogenies of both Yokoyama & al. and the present study.

The Cretaceous plant fossil record from Antarctica has received much attention (reviewed in Barreda & al., 2019). Palynological studies indicate that angiosperms there exceeded gymnosperms and seed-free plants in diversity for the first time by ca. 80 Mya (Barreda & al., 2019), with the persistence of warm-temperate conditions at least up to the early Eocene

(Pross & al., 2012). *Coriaria*-like specimens in Antarctica first appeared during the angiosperm diversity peak of the early Campanian (Barreda & al., 2019). Other East Gondwanan lineages, such as Nothofagaceae, Myrtaceae, and Proteaceae, underwent similar northward expansions from Antarctica to South America, and at least 28 angiosperm families are shared exclusively between South America, New Zealand and/or Australia (reviewed in Chacón & al., 2012). The gap in the range of Coriariaceae involving hundreds of kilometres between its northernmost Chilean and southernmost Peruvian populations (Fig. 1) may have been caused by the massive aridification of the late Neogene (Palazzesi & al., 2014).

Coriaria species typically occur in open woodland or coastal habitats on sandy soil, where their ability to fix nitrogen, with the help of their symbiotic *Frankia* bacteria that live in specialized root nodules, likely give them a competitive advantage. Experiments have shown that *Coriaria* shrubs can survive even in nitrogen-free pure quartz soils (Kataoka, 1930; Newcomb & Pankhurst, 1982; Mirza & al., 1994). The Oligocene plant preserved in the Armissan fresh-water limestone deposits from which Saporta (1866) (Fig. 2B) described *Coriaria longaeva* may have grown on sandy soils
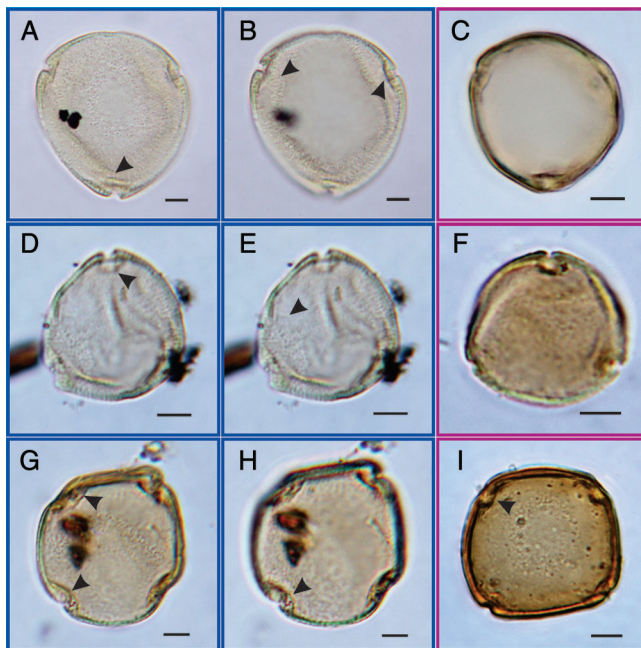
near a lake shore, and the expansion of the genus along the Northern Tethys margins may also have been facilitated by its symbiosis with *Frankia* bacteria.

Polyploidy and its possible effects on species boundaries. — Both Good (1930) and Yokoyama & al. (2000) invoked hybridization as a likely reason for weak species boundaries in *Coriaria*. Morphologically intermediate forms are known from New Zealand, for example, *C. sarmentosa × angustissima* (Allan, 1961: 305), and are also mentioned on herbarium labels (e.g., CHR 419709: *C.R. Mason s.n.*, 25 Mar 1985; Canterbury, Two Thumb Range, Firewood Stream). Hybridization is often associated with polyploidy, and indeed, several species of *Coriaria* from New Zealand have mitotic or meiotic counts suggesting polyploidy (*C. kingiana* $2n = 70$, *C. lurida* $2n = 80$, *C. pottsiana* $2n = 60$, *C. pteridoides* $2n = 80$, *C. sarmentosa* $2n = 80$; Table 1). Perhaps the *Coriaria* populations from Argentina, Chile, and Mexico (Appendix 1; suppl. Figs. S3–S5) have different ploidy levels, which might contribute to their placement among New Zealand species because of ancient polymorphisms persisting in duplicated genomes. In *Hordeum* from Patagonia, shared chloroplast types also occur between species, and persisting ancient polymorphisms have been proposed as the best explanation (Jakob & Blattner, 2006). Our attempts to obtain new chromosome counts from *C. ruscifolia* seeds obtained from Chile and Mexico and sown in Munich failed, because seeds either did not germinate or failed to reach a stage suitable for chromosome counts. Resolving these issues will require successful cultivation of relevant accessions and study of their chromosome numbers and genome sizes.

Andromonoecy and the deciduous habit parallel expansion into the temperate zone. — The evolution of a deciduous habit, which in *Coriaria* coincides with evolution of andromonoecy, has been interpreted as an adaptation to a seasonal climate (Thompson & Gornall, 1995), and our dated phylogeny fully supports this interpretation (Fig. 3). Both traits evolved at the same node and only in the Northern Hemisphere clade.
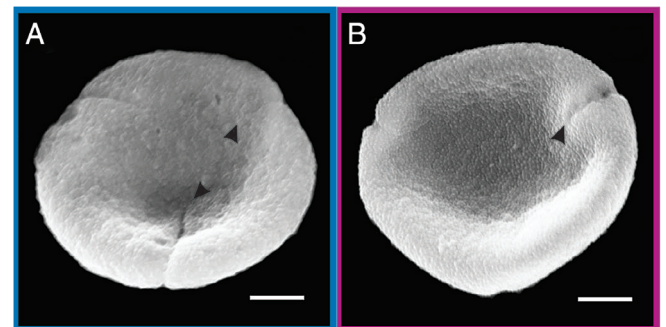

Fig. 5. Fossil and extant representatives of Coriariaceae observed with light microscopy. **A, B, D, E, G & H,** Pollen of *Coriaripites goodii* sp. nov. from the late Cretaceous of Antarctica (blue frames). **A & B,** Pollen on slide BA-Pal. ex CIRGEO *Palin 611b*: C54-1; **D & E,** Pollen on slide BA-Pal. ex CIRGEO *Palin 963b*: R31-1; **G & H,** Pollen on slide BA-Pal. ex CIRGEO *Palin 698b*: E30-2. All grains in polar view. **A & B,** Note the well-defined fastigium and short colpi with pointed ends (arrowheads); **D & E,** Note stratified thin exine and short colpi (arrowheads); **G & H,** Pollen with four apertures; note clearly defined fastigium and very short colpi (arrowheads). **C, F & I,** Pollen of extant species for comparison (magenta frames). **C,** Extant *Coriaria plumosa*; **F,** Extant *Coriaria ruscifolia*; **I,** Extant *Coriaria myrtifolia*, pollen with four apertures and clearly defined fastigium (arrowhead). — Scale bars = 5 µm.

Fig. 6. Fossil and extant representatives of Coriariaceae observed with scanning electron microscopy. **A,** Pollen of *Coriaripites goodii* sp. nov. from the late Cretaceous of Antarctica (blue frame); polar view showing details of sculpture, big apocolpium and short colpi (arrowheads); **B,** Extant pollen of *Coriaria arborea* (magenta frame); polar view showing details of sculpture and colpi length (arrowhead). — Scale bars = 5 µm.

■ TAXONOMIC TREATMENT

Coriaripites Sat.K.Srivast. in Santapau, J. Sen Memorial Volume: 49–50. 1969 – Type: *C. alienus* Sat.K.Srivast.

Comments on the genus. – Srivastava (1969) erected *Coriaripites* to include brevitricolporate pollen grains similar to those of extant *Coriaria*. Even though the presence of a fastigium and tetracolporate aperture type were not mentioned in the diagnosis of *Coriaripites*, we provisionally place our fossil pollen grains in this taxon because they exhibit most of its morphological features. The only genera similar to *Coriaripites* are *Sohlipollis*, defined by Christopher & al. (1999) to include brevicolporate, oblate pollen grains with well-defined colpi costae, and *Porocolpopollenites*, defined by Thomson & Pflug (1953) to accommodate tricolporate, vestibulate, and smooth pollen grains. According to Potonié, the latter is an earlier synonym of *Symplocoipollentites* Potonié (1951).

Coriaripites goodii Barreda, Palazzesi & M.C.Tellería, **sp. nov.** – Holotype: Specimen on slide 611b: C54-1 (sample 6 from Barreda & al., 2019) earliest Maastrichtian; occurs in trace numbers in early Campanian–early Maastrichtian sequences of the Santa Marta, Snow Hill Island and Lopez de Bertodano Formations, Snow Hill and Vega Islands, Antarctica. Paratype: Specimen on slide 698b: E30-2 (sample 23 from Barreda & al., 2019): early Campanian; same locality as the holotype.

For images of the holotype and paratype, see Fig. 5A,B and 5G,H, respectively.

Diagnosis. – Pollen grain free, isopolar, tricolporate, or tetracolporate, fastigiate, suboblate, amb circular to subcircular with convex sides. Colpi short and narrow (ca. 4–6 μm), slit-like, fastigium 4–8 μm wide, 2–3 μm deep in polar view, ora circular to subcircular, ca. 2–3 μm in diameter, with slightly thickened margins. Exine 1–1.5 μm thick, tectate, sexine as thick as nexine, sexine columellate, tectum scabrate, granulate (rugulate) (LM), bearing small spinules (SEM).

Dimensions. – Equatorial diameter: 21–34 μm (6 specimens observed).

Age. – Early Campanian–early Maastrichtian (ca. 82–70 Mya.; Barreda & al., 2019).

Etymology. – In recognition of R.D.O. Good, who first postulated a southern connection route for the Coriariaceae where these pollen grains come from.

Remarks and comparisons. — *Coriaripites alienus* Sat. K.Srivast. from the Maastrichtian of Canada (Srivastava, 1969) differs from the pollen grains described here in having aspidate instead of fastigiate apertures and obscure exine stratification. The illustration of pollen referred to as *Coriaripites* sp. cf. *C. alienus* (Jarzen & Norris, 1975: pl. 2, fig. 21), also from the Maastrichtian of Canada, shows broad similarities, but no description was provided. Muller (1981) considered these specimens to differ from modern *Coriaria* pollen by having a very thin exine wall and more pronounced colpi. Other brevitricolporate specimens with broad similarities to *Coriaripites goodii* were reported from the middle Turonian-Santonian of the Gulf and Atlantic Coastal Plain of North America, which are *Porocolpopollenites* (Leopold & Pakiser, 1964; Doyle, 1969), and aff. *Porocolpopollenites* (Doyle & Robbins, 1977), both later placed in *Sohlipollis* (Christopher & al., 1999). These fossils have similarities in pollen grain shape, size, and general sculpture, however they have subequatorial "nexinal costae" that border each colpus. More importantly, *Sohlipollis* lacks the fastigium typical of *Coraria*, because the nexine remains attached to the columellate layer at the apertural level (Christopher & al., 1999).

Botanical affinity. — *Coriaripites goodii* sp. nov. shows strong morphological similarities with pollen of extant *Coriaria*. They share similarities in shape, size, sculpture, exine thickness, and particularly in having tri- and/or tetracolporate fastigiate apertures, with very short colpi (Figs. 5, 6, suppl. Figs. S6, S7). Among Cucurbitales, the fastigium distinguishes *C. goodii* from most other members of the order (Schaefer & Renner, 2011), where only Begoniaceae also

Table 3. Morphological features of extant pollen of *Coriaria*.

Species	E: equatorial diameter (μm)	Mean	P: polar diameter (μm)	Mean	P/E	Exine thickness (μm)
C. arborea	19–28	24 ± 6	17–23	20 ± 2	Suboblate	ca.1–1.5
C. intermedia	22–34	33 ± 3	22–30	28 ± 6	Oblate-spheroidal	ca. 2
C. lurida	28–31	30 ± 4	23–27	24 ± 1	Oblate-spheroidal	ca. 1.5
C. myrtifolia	25–31	29 ± 4	21–26	23 ± 1	Suboblate	ca.1–1.5
C. papuana	22–27	25	19–23	22	Oblate-spheroidal	ca.1–1.5
C. plumosa	22–26	24	21–22	21	Suboblate	ca.1–1.5
C. sarmentosa	22–24	23	19		Suboblate	ca. 1.5
C. terminalis	20–25	23	19–20	19	Suboblate	ca. 1
C. ruscifolia	19–22	21	18–20	19	Suboblate	ca. 1

have a fastigium, but differ in pollen shape (prolate) and sculpture (striate) (Van den Berg, 1984, 1985). Pollen grains of Cucurbitaceae differ in size (ca. 50–200 μm) and sculpture (striate, reticulate, or echinate); Apodanthaceae in type of aperture (inaperturate, tricolpate) (Blarer & al., 2004), and Anisophyllaceae in size (ca. <20 μm), shape (subprolate), type of aperture (tricolporoidate, syncolpate), and sculpture (striate) (Vezey & al., 1988); Datiscaceae in the type of pollen dispersion (obligate tretrads) (Davidson, 1973); and Tetramelaceae in pollen grain size (ca. 10–12 μm) and shape (spheroidal) (Davidson, 1973). Furthermore, the sister family Corynocarpaceae differs in the number of apertures (dicolporate) (Nowicke & Skvarla, 1983). However, although *C. goodii* has all morphological features present in extant *Coriaria* pollen, we cannot exclude the possibility that the fossil pollen grains presented here represent a deeper diverging extinct lineage within Cucurbitales.

Pollen of extant *Coriaria*. — (Figs. 5C,F,I, 6B, suppl. Figs. S6, S7). Pollen grains are tricolporate, sometimes tetracolporate, suboblate to oblate-spheroidal, with a more or less elliptic or spheroidal outline in equatorial view and circular to semiangular outline in polar view. Polar axis ranges between 17 and 30 μm in length and equatorial axis between 19 and 34 μm in length (Table 3). The ectoaperture is always narrow with rounded ends and a scabrate membrane but it may be as long as the diameter of the pore (Fig. 6B, suppl. Fig. S7A,E,F). The endoaperture is circular to slightly lalongate, commonly forming a fastigium (Fig. 5). Exine is tectate, columellate, with the surface scabrate or rugulate-microgranulate. Ratio sexine/nexine: 1.

Conclusion. — Our Cretaceous record of Coriariaceae from Antarctica represents the oldest for the family and also the oldest record of Cucurbitales (Collinson & al., 1993). This fossil discovery reinforces the idea of Antarctica as a region of origin and/or dispersal during the Cretaceous of several lineages today occurring in the temperate regions of the Southern Hemisphere.

■ AUTHOR CONTRIBUTIONS

SSR conceived of the study, did the dating analyses, and wrote the first draft of the manuscript; VDB and LP analysed fossil pollen samples; MCT analysed extant pollen samples; VDB, MCT, and LP contributed to writing the manuscript; TMS contributed taxonomic knowledge, generated alignments, did the phylogenetic analyses, prepared all figures except those for pollen grains, and contributed to writing the manuscript. — SSR, https://orcid.org/0000-0003-3704-0703; VDB, https://orcid.org/0000-0002-1560-1277; MCT, https://orcid.org/0000-0003-3246-4144; LD, https://orcid.org/0000-0001-8026-4679; TMS, https://orcid.org/0000-0003-0851-3372

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Appendix 1. Sampling for this study with voucher information including *collector* and *collection number* (herbarium code) and GenBank accession numbers (nrITS, *trnL-trnF*, *matK*). *Coriaria* and *Corynocarpus* sequences beginning with MN were newly generated in this study; AB01645 and AY968448 were downloaded from GenBank. For *s.n.* collections, collection date is given. BG stands for botanic garden, NI for North Island, and SI for South Island. For a tabular version including species range, see suppl. Table S1.

Coriaria angustissima Hook.f., New Zealand: SI, Canterbury/Westland, Arthur's Pass, *U. Schweinfurth 579* (M): MN231906, MN231929, MN231886. *Coriaria arborea* Linds., New Zealand: NI, Palmerston North, Tennent Drive [S 40 26 47.29, E 175 37 18.81], cultivated at Massey University, Campus of Plants & Food Research, *J. Christeller s.n.*, 2004 (M): MN231907, MN231932, –; New Zealand: NI, Wakarewarea Forest Park, *M. Suzuki & al. Co-1* (TI): –, –, AB016454. *Coriaria intermedia* Matsum., Taiwan: Taiping Mountains [N 24 29 51.5, E 121 32 07.9], *H.-H. Lin & al. s.n.*, 08 Jul 2018 (S): MN231921, MN231947, MN231900; Philippines: Benguet - CAR, Poblacion, Atok, Benguet/Sto. Tomas, Tuba, *C.M. Bandong 2018-11* (S): MN231920, MN231946, MN231899. *Coriaria japonica* A.Gray, Japan: Honshu Island, Yamashi Prefecture, Yamabushi Pass, Yamanakako-mura, Mina-mitsuru-gun, *M. Togashi s.n.*, 13 Jun 1982 (M): MN231923, MN231948, MN231901; Japan, *K. Seto 36406* (M): MN231922, –, –. *Coriaria kingiana* Colenso, New Zealand: NI, Hawke's Bay Land District, The Lakes, Kaweka Range, *A.P. Druce s.n.*, Apr 1984 (CHR): MN231908, MN231933, –; New Zealand: NI, Eastern Volcanic Plateau Ecological Region, Whirinaki Ecological District, near Minginui, Whirinaki Forest, Waikaka Stream, *P.J. de Lange 7581* (CHR): –, MN231937, –. *Coriaria lurida* Kirk, New Zealand: NI, Taranaki, Mount Egmont, above Manganui Hut, *U. Schweinfurth 879* (M): MN231915, MN231934, MN231892; New Zealand: SI, Canterbury Land District, Lake Pukaki, Canterbury, Boundary Stream, *B.H. Macmillan & A.R. Mitchell s.n.*, 05 Nov 1969 (CHR): MN231909, MN231938, MN231888; New Zealand: SI, Canterbury Land District, Lake Pukaki, Canterbury, Tasman Downs, Boltons Gully, *B.H. Macmillan s.n.*, 06 Mar 1970 (CHR): MN231914, MN231939, MN231889. *Coriaria microphylla* Poir., Mexico: Jalisco, Talpa de Allende, *M. Olson 836* (MEXU): MN231918, MN231945, MN231898; Colombia: Cundinamarca, above Bogotá-Usaquen, *I.M. Idrobo & al. 83-100* (M): MN231917, MN231944, MN231896. *Coriaria myrtifolia* L., France: Lot et Garonne, Cancon; cultivated at Munich BG from wild-collected seed, *S.S. Renner 2876 & T.M. Schuster* (M): MN231924, MN231949, MN231902. *Coriaria nepalensis* Wall., Pakistan: Hazara, NW Himalaya, lower Kaghan Valley, N of Shogran [N 34 35, E 73 29], *B. Dickoré 13287* (M): MN231926, MN231951, MN231903; China: Sichuan, Lower Dadu He, Hanyuan (Fulin)-Kanding, Hanyan, Shimian [N 29 20, E 102 35], *B. Dickoré 8095* (M): MN231925, MN231950, MN231905. *Coriaria papuana* Warb., Papua New Guinea: Chimbu Province, Mount Wilhelm, Pengar River [S 05 48 52.6, E 145 04 53.1], *T. Jimbo s.n. & A.D. Poulsen*, 20 Apr 2016 (LAE): MN231916, MN231942, MN231894. *Coriaria plumosa* W.R.B.Oliv., New Zealand: NI, Taranaki, Mount Egmont, above Manganui Hut, *U. Schweinfurth 878* (M): MN231927, MN231931, MN231887; New Zealand: NI, Wellington, Tararua Range, Mount Holdsworth, *A.P. Druce 497* (CHR): –, MN231930, –. *Coriaria pteridoides* W.R.B.Oliv., New Zealand: NI, South Auckland, Hauhungaroa Range, Whenuakura (Whanganui Stream), *A.P. Druce 646* (CHR): MN231910, MN231941, MN231890. *Coriaria ruscifolia* L., Chile: Cultivated at Munich BG from wild-collected seed, *S.S. Renner 2812* (M): MN231919, MN231944, MN231897; Argentina: Province Chubut, Depart.Cushamen, P.N. Lago Puelo, Epuyén, Lago Puelo, NW shore and neighboring forests, between Hito Fronterizo (frontier with Chile) and Gendarmeria Nacional, *M. Weigend & al. 7035* (M): MN231912, MN231935, MN231893; Chile: Province Valdivia, Region de Los Lagos, Nilque [S 40 46, W 72 26], *K.H. & W. Rechinger s.n.*, 05 Dec 1987 (M): MN231911, MN231940, MN231891. *Coriaria sarmentosa* G.Forst., New Zealand: SI, Southland, coast S of Tokomairiro River mouth, *U. Schweinfurth 281* (M): MN231913, MN231936, MN231895. *Coriaria terminalis* Hemsl., Nepal: Lete, S of Tukucha, Kali Gandaki, *J.D.A. Stainton & al. 980* (M): –, MN231952, MN231904. *Corynocarpus laevigatus* J.R.Forst. & G.Forst., New Zealand: NI, Palmerston North, Tennent Drive [S 40 22 50.92, E 175 36 57.26], cultivated at Massey University, Campus of Plants & Food Research, *J. Christeller s.n.*, 2004 (M): MN231928, MN231953, AY968448.