***Rariglanda jerseyensis* a new ericalean fossil flower from
the Late Cretaceous of New Jersey**

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Title

Rariglanda jerseyensis a new ericalean fossil flower from the Late Cretaceous of New Jersey

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Draft

Abstract

A new species, *Rariglanda jerseyensis*, is described from well-preserved fusainized fossil flowers collected from the Late Cretaceous of New Jersey. Phylogenetic analyses and comparisons with extant and extinct taxa place *R. jerseyensis* within the monophyletic Ericales, sister to Clethraceae. The most distinctive feature of *R. jerseyensis* is a dense covering of conspicuous multicellular trichomes on the abaxial surface of the calyx. These multicellular trichomes appear to be glandular, and similar trichomes are found in several other, unrelated, Late Cretaceous fossils. In particular, the ericalean fossil *Glandulocalyx upatoiensis* bears the most similarity to *R. jerseyensis*, although differences in androecium and trichome characters clearly separate the two taxa. In addition, phylogenetic analyses confirm the position of *G. upatoiensis* within the Ericales, but place it within the sarracenioid clade, in a polytomy with Actinidiaceae and Roridulaceae. Past ecological studies associating trichomes with defense against herbivores and pathogens, coupled with the prevalence of multicellular trichomes on flowers among different lineages of fossils in the Cretaceous, suggest that glandular trichomes could have been an important adaptation against herbivore feeding during the Cretaceous.

Key words

Clethraceae, Ericales, Late Cretaceous, New Jersey, glandular trichomes

Introduction

The Late Cretaceous was a remarkable time in the evolutionary history of the angiosperms. Most of the major angiosperm groups that today dominate the environment were already present during that time (Wing and Boucher 1998; Crepet et al. 2004; Doyle 2015). Important diversification processes occurred, together with numerous adaptations of angiosperms to occupy different ecosystems. The study of the fossil record from this time interval is therefore fundamental to improving our understanding of the ecological and evolutionary success of the angiosperms (Crepet 2000).

Flower fossils from the Old Crossman Clay Pit from New Jersey provide a significant opportunity to study the Late Cretaceous evolutionary history of the angiosperms, as the remarkable three-dimensional preservation of these fossils facilitates the identification process. Fossil plants from all major lineages of land plants have been documented from this locality, including mosses, ferns, gymnosperms (Gandolfo et al. 1997, 2000, 2001) and many angiosperms. Within the angiosperms, groups that have been described include both early-diverging lineages like Nymphaeaceae, Calycanthaceae, Lauraceae, Chloranthaceae and Magnoliaceae (Herendeen et al. 1993; Crepet and Nixon 1994; Herendeen et al. 1994; Crepet and Nixon 1998b; Gandolfo et al. 2004; Crepet et al. 2005), and more derived lineages such as monocotyledons, rosids and early ericalean asterids (Crepet et al. 1992; Nixon and Crepet 1993; Crepet and Nixon 1998a; Gandolfo et al. 1998a; Zhou et al. 2001; Gandolfo et al. 2002; Hermsen et al. 2003; Martínez-Millán et al. 2009; Crepet et al. 2013). Here, we describe a new fusainized (charcoalified) fossil flower morphotype, *Rariglanda jerseyensis* gen. et sp. nov., from the Old Crossman Clay Pit locality, using scanning electron microscopy (SEM) and CT-scans to

provide a detailed characterization of its morphological features. A comparison of *Rariglanda* with extant and other fossil angiosperms, as well as phylogenetic analysis, suggest a taxonomic affinity within the (traditional) Ericales sensu stricto. *Rariglanda jerseyensis* also bears a superficially close resemblance to another Cretaceous flower from Georgia, *Glandulocalyx upatoiensis* Schönenberger, von Balthazar, Takahashi, Xiao, Crane & Herendeen (Schönenberger et al. 2012).

Modern Ericales sensu lato (see APG III, 2009) contain approximately 6% of extant eudicot diversity (Magallón et al. 1999), with more than 11,500 species. Before the use of molecular phylogenetic analyses, the 22 families that are today within the expanded Ericales, were placed in 12 orders across three different classes (APG III, 2009), although all families originally placed in the traditional Ericales are still considered to form a monophyletic group. The deep incongruences in the classification of the groups external to the core Ericales, based on either morphological or molecular characters, are now understood as a consequence of the wide morphological diversity of this order. This situation brings with it the intrinsic challenge of finding synapomorphic characters to define the expanded order, given that these characters may have been obscured by divergent evolutionary trends that could have begun as early as the Cretaceous, when the Ericales originated (Schönenberger et al. 2005, Magallón et al. 2014). However, the traditional core Ericales retain several features which are either synapomorphies or occur in the vast majority of species. The ericalean fossil record is rich, with about 81 fossils described, and at least 49 of those based on whole or partial flowers and fruits (Martínez-Millán 2010). Some of the most important ericalean fossils include Cretaceous fusainized flowers from the United States, Sweden and Japan (Friis 1985; Nixon and Crepet 1993;

Crepet 1996; Keller et al. 1996; Takahashi et al. 1999; Martínez-Millán et al. 2009; Schönenberger and Friis, 2001; Schönenberger et al. 2012; Crepet et al. 2013). However, despite the exceptional preservation of these charcoalfied flowers, taxonomic placement can often be difficult as these fossils may have unique combinations of characters relative to those of taxa within existing families (Martínez-Millán 2010). Phylogenetic analyses are therefore essential for determining the fossils' affinities.

Materials and methods

Locality

The fossil bed is located in the Old Crossman Clay Pit, in Sayreville, Middlesex County, New Jersey, USA, south of the Raritan River, (40°28' N, 74°19' W; Fig. 1). The fossils were collected from the South Amboy Fire Clay Member. The member consists of massive unconsolidated to laminated, dark gray clay, and contains lignitized plant fragments, charcoalfied flowers, stems, wood fragments, fruits, and small pieces of amber that may have inclusions of plant or insect material (Sugarman et al. 2005). The unconsolidated clay-silt beds generally occur in channels, and are commonly adjacent to cross-bedded, fine to medium quartz sands with thin carbonaceous layers.

The *Complexiopollenites exigua*-*Santalacites minor* Zone has been consistently recognized in the South Amboy Fire Clay (Christopher 1979). The member is considered part of the upper member of the Raritan Formation (Christopher 1979), and the lowermost member of the Magothy Formation (Wolf and Pakiser 1971). The age of this zone has been mostly considered middle to late Turonian, possibly Coniacian

(Christopher 1977; Doyle and Robbins 1977; Christopher 1979; Sirkin 1991; Grimaldi et al. 2000) but also post-Coniacian (Christopher 1982).

The Raritan and Magothy formations probably represent fluvial/deltaic deposition environments (Christopher 1979). The South Amboy Clay Member may represent the filling of old meanders that would correspond with a phase of marine regression (Christopher 1979)

Fossil preparation

Bulk samples from the Old Crossman Clay Pit were prepared following the method proposed by Friis (eg. 1985; described in detail by Martínez-Millán et al. 2009), which includes several washing and sieving steps, and a treatment with hydrofluoric acid. The fossils were observed and sorted under a Zeiss SV-11 stereomicroscope. The specimens from the species described here were mounted on SEM stubs and sputter-coated with gold/palladium to observe them in a field-emission Hitachi (Tokyo, Japan) S-4500 and a Jeol NeoScope JCM-5000 scanning electron microscope. All specimens are deposited in the L. H. Bailey Hortorium Paleobotany Collection, Department of Plant Biology, Cornell University with numbers CUPC- 1508 and 1579–1585. Five specimens were dissected to study the internal structure of the flower: CUPC-1508, 1579–80, 1583 and 1585. The micro-CT scanning was in this instance conducted at Dartmouth College Electron Microscope Facility for the holotype specimen CUPC1579 on a GE eXplore Locus Specimen micro-CT Scanner.

Phylogenetic analysis

Preliminary exploratory analyses to identify families that included pentamerous and hypogynous flowers with free calices and corollas were undertaken by referring to literature and the herbarium collections of the L. H. Bailey Hortorium (BH). From these initial investigations we concluded that the fossil had a higher affinity with Ericales than with other orders of flowering plants.

Additionally, morphological similarities suggested that *Rariglanda* has a broad relationship to *Glandulocalyx upatoiensis* (Schönenberger et al. 2012), another Cretaceous fossilized flower from Georgia. *Glandulocalyx* was considered to be best placed within Ericales, and based on this as well as on our own preliminary study, we restricted our final phylogenetic analysis to Ericales sensu lato. Because of the shared characters, we also included *Glandulocalyx* in our final cladistic analyses. In their study of *Glandulocalyx*, Schönenberger et al. (2012) suggested a taxonomic affinity of the fossil with core Ericales, specifically Actinidiaceae or Clethraceae, but did not formally include it in a cladistics analysis. We conducted a morphologic phylogenetic analysis to estimate the phylogenetic position of the fossil, using as a scaffold a recent molecular phylogeny published by Löfstrand and Schönenberger (2015b). That topology included exemplar terminals for the major clades within core Ericales, while the outgroup comprised taxa from Ericales sensu lato, including Diapensiaceae, Styracaceae, Symplocaceae, Theaceae and Pentaphylacaceae. The terminals representing the fossil taxa were unconstrained in the analysis resulting in trees that were consistent with the molecular analysis proposed by Löfstrand and Schönenberger (2015b) for extant taxa, with placement of the two fossil taxa based solely on morphology. The matrix comprised

25 taxa (Appendix A1), representing exemplar genera from all families and major clades in the core Ericales, and 13 morphological characters (Appendix A2). The final morphological matrix included only characters that could be observed in the fossil taxa, and were scored based on published descriptions or matrices (e.g. Luteyn et al. 1995; Kron et al. 2002; Millán and Crepet 2014; Löfstrand and Schönenberger 2015a), and direct observations from herbarium specimens from BH. All molecular characters were coded as missing for both fossils. Parsimony analyses were performed using TNT (Goloboff et al. 1998) and the parsimony ratchet (Nixon 1999). In the TNT analyses, ten sets of 200 iterations using a 10% perturbation of characters were used for the ratchet analyses, and default values for drift, sectorial search and tree fusion were used. Visualization of character distributions was performed with Winclada ver. 1.99 (Nixon 2015).

Results

Systematics

Order — Ericales sensu APG (2003)

Family — Core Ericales, near Clethraceae

Genus — *Rariglanda* Martinez & Choo, gen. nov.

Type species — *Rariglanda jerseyensis* Martinez & Choo

Generic diagnosis — Flowers bisexual, actinomorphic, hypogynous, pentamerous. Calyx and corolla aestivation quincuncial. Sepals 5, free; adaxially glabrous, abaxial surface covered in shortly stalked multicellular capitate glandular trichomes, these mostly globose with an apical indentation. Petals alternate with sepals, free, and thin.

Androecium of ten stamens of uniform size; anthers with two sporangia and a hollow apical protrusion. Pollen small, spheroidal, tricolporate, striate/rugulate. Gynoecium syncarpous, tricarpellate, styles 3, basally fused; stigmas not observed. Ovary trilocular, placentation axile, ovules numerous.

Etymology — Named for the Raritan formation and the Raritan river of New Jersey and for the conspicuous glandular hairs on the calyx

Rariglanda jerseyensis Martinez & Choo, sp. nov. (Fig. 2–5)

Holotype — CUPC 1579. Deposited in the L. H. Bailey Hortorium

Paratypes — CUPC 1508, 1580–1585

Repository — Cornell University Paleobotany Collection, L. H. Bailey Hortorium, Department of Plant Biology, Cornell University, Ithaca, New York.

Type locality — Old Crossman Clay Pit, in Sayreville, Middlesex County, New Jersey, USA

Stratigraphic position — South Amboy Fire Clay Member, considered upper Raritan Formation

Age — Turonian–Coniacian, Late Cretaceous.

Etymology — Named after New Jersey, USA, where the fossil was collected.

Specific diagnosis — As for the genus.

Description — One charcoalfied flower, in unopened bud, was completely preserved (Holotype: CUPC 1579). Flowers bisexual, actinomorphic. Flower bud (late preanthesis) 1.2–1.4 mm in height by 0.9–2 mm in diameter. Sepals enclose remaining floral organs (Fig. 2a). The scan of the unopened bud showed a large preservational fracture through

the gynoecium, obscuring some of the gynoecium details (Fig. 4a: arrow pointing to the crack, supplementary video S1).

Calyx

The calyx is pentamerous and has quincuncial aestivation (Fig. 4f–g); all sepals are free and roughly triangular with an obtuse tip (Fig. 2a); sepals are approximately 0.9–1.3 mm in length and 0.6–0.9 mm in width, with a midvein; the outer sepals are slightly larger than the inner ones (e.g specimen 1579: outer sepal is 0.8 mm and inner sepal is 0.5 mm in width; Fig. 4); the adaxial surfaces of the sepals are glabrous (Fig. 2c), and the entire abaxial surface of each sepal is densely covered with large, multicellular, glandular trichomes (Fig. 2a,b) that are shortly stalked (Fig. 3a) and generally globose, but with a prominent central indentation (Fig. 3b). Glands average 241 μm in diameter, and with considerable variation in size (standard deviation: 59.3 μm). The smallest glands are located towards the margins and tips of the sepals; within the glands, the individual cells are smaller towards the differentiated center and appear to radiate spirally outwards from the central indentation (Fig. 3b); the cuticle layer of the glands is thick (Fig. 2b).

Corolla

The five petals are separated from each other and also show quincuncial aestivation (Fig. 4f–g); the bases of the petals are broad and alternately arranged with the sepals (Fig. 4a), and the apices of the petals are convolute in bud (Fig. 4e); the petals appear to be thin and obtusely shaped, comparable in size and shape to the sepals. The vascular trace of a mid-rib is visible in one specimen.

Androecium

Stamens are free and in a diplostemonous arrangement (Fig. 4); filaments are broad and short. Anthers are attached adaxially and composed of one longitudinally elongated pollen sac arranged on either side of the connective and have an apical protrusion or cavity (Fig. 2d–e). Pollen grains preserved on the outer surface of the gynoecium in two specimens are tricolporate and 12–14 μm in length; the pollen ornamentation is striate (Fig. 5).

Gynoecium

The gynoecium is superior and composed of three syncarpous carpels and is 2 mm in height and 1.1 mm in width; the ovary is ovoid and trilocular (Fig. 2f, g), with thick ovary walls and a prominent line dividing each carpel (Fig. 2g, h). Each locule bears numerous (>5) ovules on axile placentae (Fig. 2h). The styles are fused at the base, becoming separate presumably stigmas towards the apex. The cross section of the styles at the apex of the ovary shows three separate stylar canals that are surrounded by a ring of tissue (Fig. 2g).

Comparison with other similar fossils

We compared the floral characters of *Rariglanda jerseyensis* with eight similar fossil flowers from the Late Cretaceous that have previously been placed in Ericales (Table 1). The eight species included in the comparison all have a pentamerous calyx and corolla, and superior ovaries with numerous ovules in common with *R. jerseyensis*. Most of these species have calyces and corollas with quincuncial aestivation, multicellular trichomes on the abaxial surfaces of the sepals and three carpels. However, the number of stamens is very variable in these fossils, ranging from five to numerous (Table 1). Stamen number is extremely important in differentiating genera and families within Ericales.

Glandulocalyx upatoiensis is most similar to *Rariglanda jerseyensis* based on its overall morphology and presence of adaxial sepal glands but there are notable differences including stamen number, anther morphology, and the distribution and structure of the glandular trichomes. *Glandulocalyx upatoiensis* does not have glandular trichomes at the tips of the sepals and these glands lack the apical indentation characteristic of calyx glands of *R. jerseyensis*. The number of stamens in *G. upatoiensis* varies from 20–28, instead of ten as found in *Rariglanda*. Although the stamens observed in *R. jerseyensis* are in an earlier developmental stage than those observed in *G. upatoiensis*, they are clearly very different in morphology. *Glandulocalyx upatoiensis* has sagittate, dithecal, tetrasporangiate anthers, while *R. jerseyensis* has non-sagittate dithecal anthers with a hollow apical protrusion.

Parasaurauia allonensis, another Cretaceous ericalean fossil, also shares characters with *Rariglanda jerseyensis*, including the same floral formula (Keller et al. 1996, Fig. 31). However, the multicellular trichomes of *Parasaurauia* are completely different from those of *Rariglanda* being non-capitate and elongated. In addition, in *Parasaurauia* stamens are unequal, with 5 long and 5 shorter filaments; the anthers are deeply sagittate, and the styles are free.

Results of the phylogenetic analysis

Four most parsimonious trees of 3681 steps, 0.90 RI and 0.73 CI were found; the strict consensus tree is shown in Fig. 6. The analysis places *Rariglanda jerseyensis* within the monophyletic ericoid clade as the sister taxon to *Clethra alnifolia* (Clethraceae), while *Glandulocalyx upatoiensis* is nested within the monophyletic sarracenioid clade and is in an unresolved polytomy, alternatively as a sister to Actinidiaceae or to Roridulaceae in

the most parsimonious solutions. Characters such as presence of multicellular trichomes on the sepals, number of stamens and carpels, and style fusion were important characters determining the phylogenetic position of the fossils and are shown in Fig. 7.

Discussion

One of the most remarkable characteristics of *Rariglanda jerseyensis* is the presence of capitate multicellular trichomes on the calyx. Whether the multicellular trichomes are glands secreting enzymes, polysaccharides, sugar, oils or inorganic salts cannot be established based on the fossil material, however, their presence in both *Rariglanda* and *Glandulocalyx* suggests similar adaptations to some environmental factors. Ecological studies suggest that trichomes may serve as the first line of defense against herbivores and pathogens (Peiffer et al. 2009). High densities of trichomes like those observed in *Rariglanda jerseyensis* can directly impede herbivore feeding by serving as a physical and/or chemical barrier to their movement and feeding (Peiffer et al. 2009). The high number of flower fossils bearing multicellular and possibly glandular trichomes from the Cretaceous, such as *Glandulocalyx upatoiensis* (Schönenberger et al. 2012), *Parasaurauia allonensis* (Keller et al. 1996), *Paleoenkianthus sayrevillensis* (Nixon and Crepet 1993) and *Raritaniflora glandulosa* (Crepet et al. 2013), together with *Rariglanda jerseyensis* and other undescribed material from the Old Crossman Clay Pit, suggest that glandular trichomes may have been an important adaptation against herbivores during the Cretaceous. The Cretaceous is one of the most significant periods of insect evolution, since many modern families within phytophage lineages like Lepidoptera, Hemiptera and Orthoptera, appeared during this time (Grimaldi and Engel 2005). The high diversity of

phytophagous insects during the Cretaceous probably reflects the coevolutionary history of these with angiosperms, given that flowering plants are generally more digestible and have more nutritional value than other plant groups (Grimaldi and Engel 2005). The presence of these glands on flowers also may suggest that pollinators were less specialized, and their behavior included more generalized herbivory in addition to nectar and/or pollen collection.

The distribution of glandular hairs or multicellular trichomes on vegetative and reproductive organs tends to be variable within modern Ericales, sporadically distributed, and not strongly correlated with well-defined clades. Although in our analysis the absence of multicellular trichomes on the sepals appears as a synapomorphy for the ericoid clade (Fig.7b), there are various taxa within this clade, but not included in the analysis, that have multicellular trichomes on the sepals, such as *Rhododendron* and *Bejaria*. Remarkably, the evolution of related structures like the digestive glands of Sarraceniaceae containing proteolytic enzymes, and the prominent multicellular capitate glands of Roridulaceae shows the importance of these structures in certain groups within Ericales.

Within extant Ericales, Clethraceae was found to be most closely related to *Rariglanda jerseyensis*. Clethraceae includes two genera and 75 species and is today also distributed in temperate and montane tropical North and South America, where several species are present. The family is also distributed in tropical to subtropical regions of South East Asia, and most species occupy montane habitats, and are sometimes found growing in acidic soils (Gustafsson 2004). *Clethra* species typically have drooping or pendant flowers, with apical anther dehiscence, a syndrome commonly associated with buzz

pollination by bees. The pollination syndrome for *Clethra alnifolia* L. has been described as associated with bumblebees (Bhattacharya et al. 2003). The floral morphology of *Rariglanda jerseyensis*, with small flowers with free petals might also be associated with a bee-pollination syndrome, although the nature of anther dehiscence in the fossil is unknown.

Pollen in the ericalean clade is generally characterized by having small size, (2–) 3 (–5)-colporate apertures and variable surface ornamentation (Zhang and Anderberg 2002). Specifically, the pollen grains of *Clethra* are also small-sized and tricolporate, with surface ornamentation that varies by species, from psilate to rugulate (Zhang and Anderberg 2002). The pollen grains found associated with *Rariglanda jerseyensis* are spheroidal, small, tricolporate, and striate/rugulate (Fig. 5). Neither of the pollen grains from *R. jerseyensis* was found directly on the stamens, however, more than two of such pollen grains were found on more than one flower suggesting that the pollen was associated with *Rariglanda*. The shared characters between pollen from the core ericalean clade and the pollen found associated with *R. jerseyensis* are consistent with the phylogenetic placement proposed here.

Recent studies of the sarracenioid clade within Ericales that included morphological and molecular analyses also reviewed taxonomic affinities for the fossils *Glandulocalyx upatoiensis* and *Parasaurauia allonensis* and suggested likely affinities for both fossils with Actinidiaceae (Löfstrand and Schönenberger 2015a,b). Some of the floral characters supporting this suggested affinity are: late anther inversion; pendant placentae in *Glandulocalyx*; ovules arranged in longitudinal rows; pluriseriate trichomes present on sepals and capitate stigmas with ventral grooves (Löfstrand and Schönenberger 2015a,b).

Our phylogenetic analysis for *G. upatoiensis* is largely congruent with these studies, given that the fossil was found nested within the sarracenioid clade, although a sister relationship with either Roridulaceae or Actinidiaceae was equally parsimonious. In our analysis, other characters such as number of stamens and carpels and style fusion were informative for the phylogenetic placement (Fig. 7). Specifically, the difference in the number of carpels between *G. upatoiensis* and Actinidiaceae, was an important character placing *G. upatoiensis* outside Actinidiaceae (Fig. 7c). Other characters such as anther inversion, protruded placenta and a depression at the apex of the ovary were not included in the analysis because occurrence of these characters in *Rariglanda jerseyensis* was unknown, but should be considered for future analyses for *Glandulocalyx upatoiensis*. *Parasaurauia allonensis* shares its floral formula with that *R. jerseyensis*, but there are also numerous differences (see results). The great morphological variation within Ericales and the difficulties determining synapomorphic characters for the group might obscure the phylogenetic position of the fossil, however, given that the array of characters of *R. jerseyensis* is found in various ericalean lineages, it is safe to assume that *R. jerseyensis* is an early divergent lineage of the Ericales.

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Table 1. Comparative table of fossil flower species from the Late Cretaceous similar to *Rariglanda jerseyensis*

Species	Locality	Age	Reference	Calyx aestivation	Calyx	Calyx trichomes	Corolla	Anther attachment	Number of		
									Stamens	Carpels	Styles
<i>Rariglanda jerseyensis</i>	NJ, USA	Turonian	This study	Quincuncial	Free	Abaxial / capitate	Free	Basal	10	3	3
<i>Glandulocalyx upatoiensis</i>	GA, USA	Santonian	Schönenberger et al., 2012	Quincuncial	Free	Abaxial / capitate	Free	Ventral	20–28	3	3
<i>Parasaurauia allonensis</i>	GA, USA	Campanian	Keller et al., 1996	Quincuncial	Free	Abaxial / elongate	Free	Basal	10	3	3
<i>Pentapetalum trifasciculandricus</i>	NJ, USA	Turonian	Martínez-Millán et al., 2009	Quincuncial	Free	Absent	Free	Basal	∞	3	3
<i>Paleoenkianthus sayrevillensis</i>	NJ, USA	Turonian	Nixon and Crepet, 1993	Imbricate	Basally connate	Abaxial / multicellular?	Partially connate	Basal	8	4	4
<i>Paradinandra suecica</i>	Asen, Sweden	Campanian– Santonian	Schönenberger and Friis, 2001	Quincuncial	Free	Abaxial / unicellular	Partially connate	Basal	15	3	3
<i>Actinocalyx bohrii</i>	Asen, Sweden	Campanian– Santonian	Friis, 1985	Imbricate	Free	Absent	Connate	Basal	5	3	3
<i>Raritaniflora glandulosa</i>	NJ, USA	Turonian	Crepet et al., 2013	Valvate	Connate	Abaxial / capitate	Free	Dorsal	5	5	1

Figure captions

Figure 1. Location of the Old Crossman Clay Pit and surface geology of the area.

Modified from maps downloaded from

<http://www.state.nj.us/dep/njgs/pricelst/gmseries.htm>. The map on the left shows the surface geology of New Jersey, USA (New Jersey Geological Survey Map 1:1.000.000, 2005). In grey are Paleozoic rocks, Precambrian rocks and metamorphic and igneous rocks; in green are Mesozoic rocks; and in yellow are Cenozoic rocks. The map on the right shows the zoomed area of the grey square and the location of the Old Crossman Clay Pit (red arrow). Kms: South Amboy Fire Clay; Kmo: Old bridge sand; Krw: Woodbridge Clay (Sugarman et al. 2005).

Figure 2. SEM photographs from *Rariglanda jerseyensis*. (a) CUPC 1584: up-side view from the flower bud close to anthesis; (b) CUPC 1581: adaxial side of the sepal; (c) CUPC 1579: abaxial side of the sepal; (d) CUPC 1579: dissected flower bud showing the stamens; (e) CUPC 1579: close-up of the stamens in the early developmental stages; (f) CUPC 1508: gynoecium; (g) CUPC 1583: three free styles; (h) CUPC 1580: ovary with multiple ovules. Scales (a–c) 500µm; (d) 200µm; (e) 50µm; (f, g) 600µm; (h) 300µm.

Figure 3. SEM photographs of multicellular glands of *Rariglanda jerseyensis*. (a) CUPC 1504: side view of the sepal showing the short-stalked gland. (b) CUPC 1581: up-side view from the gland showing the central indentation and variation in cell size. (a and b) scales = 100µm

Figure 4. *Rariglanda jerseyensis* CUPC 1579 (a–e) Screenshots from the CT-scan movie (left; supplementary video S1) and drawings of the reconstruction of its floral characters (right). Calyx is in black with white border; corolla is in white; androecium is in gray; and gynoecium is in gray with white border. Scale = 0.5 mm. Screenshots are organized from base to apex of the flower bud. (a) basal section of the flower bud; (b–d) basal to middle sections; (e) apical section; (f) simplified floral diagram; and (g) simplified reconstruction.

Figure 5. SEM photograph of pollen of *Rariglanda jerseyensis* illustrating striate micromorphology and the endoapertural bulge in one of the apertures. Scale: 5µm.

Figure 6. Strict consensus tree of four equally most parsimonious trees of 3681 steps. CI 0.90, RI 0.73. *Rariglanda jerseyensis* (in bold font) is nested within the ericoid clade and is sister to the modern genus *Clethra*. *Glandulocalyx upatoiensis* (in bold font) is nested within the sarracenoid clade in a polytomy with Roridulaceae and Actinidiaceae.

Figure 7. Ancestral character-state reconstruction for: (a) number of stamens; (b) presence of multicellular trichomes on the sepals; (c) number of carpels; (d) style fusion. *Rariglanda jerseyensis* and *Glandulocalyx upatoiensis* are in bold font. See color code for character states.

Fig.1_Map fossil locality
86x42mm (300 x 300 DPI)

a

Botany

b

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Fig. 4_Ct scan B&W
154x130mm (300 x 300 DPI)

Pentaphylax euryoides] Pentaphylacaceae
Camellia japonica] Theaceae
Symplocos paniculata] Symplocaceae
Galax urceolata] Diapensiaceae
Styrax japonicus] Styracaceae
Clethra alnifolia] Clethraceae
Rariglanda jerseyensis
Cyrilla racemiflora] Cyrillaceae
Enkianthus campanulatus
Monotropa hypopitys
Arbutus unedo
Harrimanella stelleriana
Vaccinium vitis-idaea
Leucopogon amplexicaulis
Cassiope mertensiana
Erica carnea
Darlingtonia californica
Heliophora nutans
Sarracenia leucophylla
Sarracenia purpurea
Roridula gorgonias
Glandulocalyx upatoiensis
Clematoclethra scandens
Actinidia arguta
Actinidia chinensis
Saurauia pittieri
Saurauia subspinosa

Ericaceae

Sarraceniaceae

Roridulaceae

Actinidiaceae

Ingroup

Ericoid clade

Outgroup

Sarracenioid
clade

Appendix

Appendix A1

Appendix A1. Morphological matrix of extant Ericales and the fossils *Rariglanda jerseyensis* and *Glandulocalyx upatoiensis*

Species name	1	2	3	4	5	6	7	8	9	10	11	12	13
<i>Actinidia arguta</i> Miq.	1	1	1	1	1	0	1	2	0	1	2	1	1
<i>Actinidia chinensis</i> Planch.	1	1	1	1	1	0	1	2	0	1	2	1	1
<i>Clematoclethra scandens</i> Maxim.	1	1	1	1	1	0	1	1	0	1	0	1	2
<i>Saurauia pittieri</i> Donn.Sm.	1	1	1	1	1	0	1	2	0	1	0	1	1
<i>Saurauia subspinos</i> a J.Anthony	1	1	0	1	?	1	1	2	0	1	0	1	1
<i>Roridula gorgonias</i> Planch.	1	1	0&1	1	1	1	1	0	1	1	1	0	2
<i>Darlingtonia californica</i> Torr.	1	1	0	0	1	0	1	2	0	1	0	1	1
<i>Heliamphora nutans</i> Benth.	-	-	-	-	1	0	1	2	0	1	1	1	2
<i>Sarracenia leucophylla</i> Raf.	1	1	0	0	1	0	1	2	0	1	0	1	1
<i>Sarracenia purpurea</i> L.	1	1	0	0	1	0	1	2	0	1	0	1	1
<i>Clethra alnifolia</i> L.	1	1	0	1	1	0	1	1	0	1	1	1	1
<i>Cyrilla racemiflora</i> L.	-	1	0&1	0	1	0	1	0&1	0	1	3	0	1
<i>Enkianthus campanulatus</i> G. Nicholson	0	1	1	0	0	2	1	1	0	1	0	1	2
<i>Monotropa hypopitys</i> L.	?	1	0	0	?	2	1	1	0	1	0	1	2
<i>Arbutus unedo</i> L.	1	1	1	0	0	2	1	1	0	1	0	1	2
<i>Cassiope mertensiana</i> (Bong.) D.Don	?	1	1	0	0	2	1	1	0	1	0	1	2
<i>Erica carnea</i> L.	?	0	0	0	0	2	0	1	0	1	1	1	2
<i>Harrimanella stelleriana</i> Coville	?	1	1	0	0	2	1	1	0	1	0	1	2
<i>Vaccinium vitis-idaea</i> L.	0	1	1	0	0	2	?	1	0	0	0	1	2
<i>Leucopogon amplexicaulis</i> R.Br.	?	1	0	0	0	2	1	0	0	1	0	0	2
<i>Galax urceolata</i> (Poir) Brummit	1	1	0	0	1	0	1	0	0	1	1	1	2
<i>Styrax japonicus</i> Siebold & Zucc.	1	1	1	1	1	1	1	1	0	2	1	0	2
<i>Symplocos paniculata</i> Miq.	1	1	1	1	1	2	1	0	0	0	3	0	2
<i>Camellia japonica</i> L.	1	2	0	0	1	1	2	2	0	1	1	0	2
<i>Pentaphylax euryoides</i> Gardner & Champ	1	1	?	0	1	0	1	0	0	1	0	0	2
<i>Glandulocalyx upatoiensis</i>	1	1	0	1	1	0	1	2	1	1	1	1	1
<i>Rariglanda jerseyensis</i>	1	1	0	1	1	0	1	1	1	1	1	1	1

Appendix A2

List of characters included in the matrix

1. Calyx aestivation: valvate = 0; imbricate = 1
2. Number of sepals: <5 = 0; 5 = 1; >5 = 2
3. Calyx connation: free = 0; partially connate = 1; connate = 2
4. Multicellular trichomes on the sepals: absent = 0; present = 1
5. Corolla aestivation: valvate = 0; imbricate = 1
6. Corolla connation: free = 0; partially connate = 1; connate = 2
7. Petal number: <5 = 0; 5 = 1; >5 = 2
8. Number of stamens: <6 = 0; 6–10 = 1; >10 = 2
9. Anther apical protrusion: absent = 0; present = 1
10. Ovary position: inferior = 0; superior = 1; half-inferior = 2
11. Carpel number: 5 = 0; 3–4 = 1; >5 = 2; <2 = 3
12. Number of ovules: <6 = 0; numerous = 1
13. Style fusion: free = 0; partially fused = 1; fused = 2