Recent findings of fossil angiosperms document a larger diversity than previously known from low latitude North America and support new hypotheses on the origin and diversification of ancient flowering plant lineages in the area (e.g., Magallón-Puebla and Cevallos-Ferriz, 1994a–c; Velasco-de León et al., 1998; Ramírez et al., 2000; Velasco-de León and Cevallos-Ferriz, 2000; Calvillo-Canadell, 2000; Calvillo-Canadell and Cevallos-Ferriz, 2002, 2005). This fossil record indicates the presence during Cretaceous and Paleogene of lineages otherwise thought to have arrived in low latitude North America during the Plio-Pleistocene (Cevallos-Ferriz and Ramírez, 1998; Ramírez and Cevallos-Ferriz, 2000). Furthermore, these discoveries aid in proposing new biogeographic routes and establishing the minimum time for the appearance of endemic and the so-called relict and refugee taxa in the area (e.g., Magallón-Puebla and Cevallos-Ferriz, 1994b; Martínez-Cabrera, 2001; Martínez-Millán, 2000, 2003; Ramírez and Cevallos-Ferriz, 2000; Ramírez et al., 2000; Calvillo-Canadell and Cevallos-Ferriz, 2005). They also offer evidence that links low latitude and high latitude paleofloras of North America, Asia, Europe, and South America (e.g., Magallón-Puebla and Cevallos-Ferriz, 1994a–c; Velasco-de León et al., 1998; Ramírez et al., 2000; Velasco-de León and Cevallos-Ferriz, 2000; Calvillo-Canadell, 2000).

Rhamnaceae is a family whose phylogenetic relationships have been difficult to establish. Recent molecular analyses confirm its monophyly, and infrafamiliar rearrangements have been proposed (Richardson et al., 2000a, b; Medan and Schirarend, 2004). In these studies, traditional classifications based on fruit types (Suessenguth, 1953) have also been questioned. Unfortunately, these analyses have used few morphological data, and more detailed studies based on larger sets of morphological characters with a more accurate coding may better reflect phylogeny (Richardson et al., 2000a, b). Because information from fossil plants (Table 1) was not used in these studies, and estimates of the time of origin and diversification of taxa within Rhamnaceae are based on few fossils not closely related to the family (e.g., Richardson et al., 2000a, b), the new records introduced here should aid our historical understanding of the group.

The study of new rhamnaceous fossils is important not only for reporting new taxa, but also for understanding character evolution within the family. However, analysis of character evolution requires a combination of both extant and fossil taxa so that ancestry–descendent relationships can be properly evaluated (e.g., Nixon, 1996; Manchester and Tiffney, 2001; Crepet et al., 2004; Graur and Martin, 2004). In the present study, we describe fossil flowers and fruits that are morphologically similar to those of extant Rhamnaceae. These findings expand our understanding of the combination of characters and taxa within this family, providing new information to refine future systematic and phylogenetic studies of the group.

**Key words:** Cretaceous; fossil flowers; Mexico; Oligocene; Rhamnaceae.
MATERIALS AND METHODS

The fossil material was collected at two different localities. The Late Cretaceous (late Campanian) El Alma´cigo locality (Cerro del Pueblo Formation) is located in General Cepeda County, Coahuila (25°8′31″N and 101°8′19″W, Fig. 1) (Boyd, 1959; Murray et al., 1962; McBride et al., 1974; Tidwell, 1984; Kirkland et al., 2000). The Oligocene Los Ahuehuetes locality (Coatzingo Formation) is located ca. 4.5 km NNE of Tepexi de Rodrı´guez, Puebla (18°8′35″00″N and 97°8′55″00″W, Fig. 2) (Calvillo-Canadell and Cevallos-Ferriz, 2005; Beraldi et al., 2006).

Table 1. Fossil record of some plant organs documenting history and variability of Rhamnaceae. Data followed by “?” are in need of review.

<table>
<thead>
<tr>
<th>Organ</th>
<th>Genus</th>
<th>Age</th>
<th>Location</th>
<th>Affinity</th>
<th>Author</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>Rhamnites</td>
<td>Cretaceous/Tertiary</td>
<td>North America</td>
<td>Rhamnaceae? vs. Annonaceae</td>
<td>Tidwell, 1984</td>
</tr>
<tr>
<td>Wood</td>
<td>?</td>
<td>Tertiary</td>
<td>North America</td>
<td>Rhamnaceae</td>
<td>Penhallow, 1903, 1907</td>
</tr>
<tr>
<td>Leaf</td>
<td>Ceanothus?</td>
<td>Oligocene/Miocene</td>
<td>SW North America</td>
<td>Rhamnaceae</td>
<td>Chaney, 1927; Nobs, 1963</td>
</tr>
<tr>
<td>Leaf</td>
<td>Paliurus</td>
<td>Oligocene/Miocene</td>
<td>SW North America</td>
<td>Rhamnaceae</td>
<td>Meyen and Manchester, 1997</td>
</tr>
<tr>
<td>Leaf</td>
<td>Hovenia</td>
<td>Oligocene/Miocene</td>
<td>SW North America</td>
<td>Rhamnaceae</td>
<td>Meyen and Manchester, 1997</td>
</tr>
<tr>
<td>Leaf</td>
<td>Berhanniphyllum</td>
<td>Eocene</td>
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<td>Rhamnaceae</td>
<td>Jones and Dilcher, 1980</td>
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<tr>
<td>Leaf</td>
<td>Karwinskia</td>
<td>Oligocene</td>
<td>Puebla, Mexico</td>
<td>Rhamnaceae</td>
<td>Velasco de León and Cevallos-Ferriz, 1998</td>
</tr>
<tr>
<td>Fruits</td>
<td>Paliurus</td>
<td>Eocene</td>
<td>Wyoming</td>
<td>Rhamnaceae</td>
<td>Manchester, 1990</td>
</tr>
<tr>
<td>Fruits</td>
<td>Paliurus</td>
<td>Eocene</td>
<td>Japan</td>
<td>Rhamnaceae</td>
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<tr>
<td>Fruits</td>
<td>Paliurus</td>
<td>Miocene</td>
<td>China</td>
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<td>Fruits</td>
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<td>Kazakhstan</td>
<td>Rhamnaceae</td>
<td>Zhilin, 1989</td>
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<tr>
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<td>Paliurus</td>
<td>Oligocene</td>
<td>Europe</td>
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<td>Kirchheimer, 1957; Bůžek, 1971; Mai, 1975, 1995</td>
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<tr>
<td>Fruits</td>
<td>Gouania</td>
<td>Eocene</td>
<td>North America</td>
<td>Rhamnaceae</td>
<td>O’Leary and Manchester, 2006</td>
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<tr>
<td>Flower</td>
<td>“Rose Creek Flower”</td>
<td>Cretaceous</td>
<td>North America</td>
<td>Rhamnaceae?</td>
<td>Basinger and Dilcher, 1984</td>
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<td>Flower</td>
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<td>Coahuila, Mexico</td>
<td>Rhamnaceae</td>
<td>This report</td>
</tr>
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<td>Flower</td>
<td>Nahinda</td>
<td>Oligocene</td>
<td>Puebla, Mexico</td>
<td>Rhamnaceae</td>
<td>This report</td>
</tr>
</tbody>
</table>

Fig. 1. Location of the El Almácigo locality, General Cepeda County, Coahuila, and section of the Cerro del Pueblo Formation in the Cerros de Los Dinosaurios locality (~500 m W of the El Almácigo locality; reproduced with authorization of Hernández Rivera [1977]) in Mexico.
The Cerro Huerta Formation has been dated as Maastrichtian based on the presence of a bivalve (*Exogyra costata* Say) and a cephalopod (*Sphenodiscus pleurisepta* Conrad), while a late Campanian age has been suggested for the Cerro del Pueblo Formation based on physical geology and the presence of *E. ponderosa* Römer (Boyd, 1959; Murray et al., 1962; McBride et al., 1974; Vega-Vera and Perrilliat, 1990; Kirkland et al., 2000).

The Los Ahuehuetes locality was formerly assigned to the Pie de Vaca Formation based on geological observations of Pantoja-Alor (1992); however, a review of the geology on a regional scale places Los Ahuehuetes as part of the Ahuehuetes Unit, Coatzingo Formation (Silva-Romo, 1998). Toward the base, this unit is composed of chert and limestone followed by fossiliferous volcanic ashes and sandstones. The sedimentary sequence has been interpreted as deposited in a low energy lacustrine basin (Beraldi et al., 2006). A minimum Oligocene age of these sediments has been suggested based on physical stratigraphic correlations, a preliminary palynological study, and plant macrofossil time ranges (Martínez-Hernández and Ramírez-Arriaga, 1996; Silva-Romo, 1998). However, this age still needs to be confirmed by radiometric dating.

Eighteen fossil flower impressions were collected from the Cerro del Pueblo Formation and 24 from the Coatzingo Formation. Additionally, from the latter, two different fruit types also related to Rhamnaceae have been distinguished, one represented by several drupes, while the second one is known from a single-winged fruit. The fossils were studied using an SHZ Olympus (Tokyo, Japan) stereoscopic microscope equipped with a camera lucida. Terminology follows Radford et al. (1974), Roth (1977), Moreno (1984), and Harris and Harris (2003). Comparisons with extant plants were based on material deposited in the National Herbarium of Mexico (MEXU) and data in the literature. When similarities between fossil and extant material were observed, all available extant flowers and fruits of these particular taxa were studied, as were those of closely related plants.
Figs. 3–17. Cretaceous flowers of *Coahuilanthus belindae* (light micrographs) from Coahuila, Mexico. Bar in all photographs = 1 mm. 3. Longitudinal section with floral cup and sepals. IGM-Pb 3456. 4. Longitudinal section with pedicel, spatulate clawed petals, and sepals. IGM-Pb 3456. 5. Flower in plane view with sepals having distinct thickened apex and nectariferous lobed ring. IGM-Pb 3456. 6. Longitudinal section with perigynous flower, sepals, and superior ovary. IGM-Pb 3456. 7. Longitudinal section of flower with deltoid to ovate sepals and ovary. IGM-Pb 3456. 8. Plane view of flower with keeled sepals. IGM-Pb 3456. 9. Flower with cupulate–campanulate floral cup and sepals in longitudinal section. IGM-Pb 3456. 10. Plane view of flower with nectariferous lobed ring. IGM-Pb 3456. 11. Central longitudinal section of flower with sepals and prominent lobed ring. IGM-Pb 3456. 12. Plane view of flower with keeled sepals and probable septa in ovary. IGM-Pb 3456. 13. Oblique section of flower with sepals and spatulated clawed petals. IGM-Pb 3456. 14. Longitudinal section of flower with long pedicel, sepals, and cupulate–campanulate floral cup. IGM-Pb 3456. 15. Oblique section with prominent sepals and floral cup. IGM-Pb 3456. 16. Longitudinal section of flower with anthers and style. IGM-Pb 3456. 17. Longitudinal section of immature flower with small floral cup and sepals. IGM-Pb 3456. a, anther; fc, floral cup; k, keel; o, ovary; p, pedicel; pt, petal; r, nectariferous ring; s, sepal; st, stigma; ta, thickened apex.
SYSTEMATIC DESCRIPTION

Family: Rhamnaceae
Tribe: Rhamninae/Zizipheae
Genus: Coahuilanthus gen. nov. Calvillo-Canadell and Cevallos-Ferriz

Species: Coahuilanthus belindae gen. et sp. nov. Calvillo-Canadell and Cevallos-Ferriz

Etymology: The generic name refers to the Mexican state of Coahuila where the fossils were collected; the specific epithet honors Belinda Martínez for her discovery of the El Almacligo locality and fossil conservation work in Coahuila.

Holotype: Paleontological Collection of the Instituto de Geología, UNAM, catalog no. IGM-PB 2573.

Other examined specimens: 17 (IGM-PB 2574–2590).

Locality: El Almacligo, Cerro del Pueblo Formation, General Cepeda County, Coahuila, Mexico, 25°31’ N, 101°19’ W.

Age: Late Cretaceous (late Campanian).

Number of examined specimens: 18

Diagnosis: Small actinomorphic, pedicelled, pentamerous, bisexual flowers; floral cup campanulate to cupulate; calyx lobes 5, lobes deltoid to ovate, slightly keeled, inserted in the margin of the floral cup; five spatulate, clawed petals, shorter than the calyx-lobes; epipetalous stamens with sub-basified anthers; nectariferous lobed ring.

Description: The fossil material consists of 18 specimens, some of them fragmented, some with possible negative or positive counterparts. These small, bisexual, and pentamorous flowers have actinomorphic symmetry, with fused perianth parts forming a slightly campanulate to cupulate floral cup, 2.5–3.5 mm long and 1.1–2.0 mm wide (Figs. 3, 6, 9, 14, 15, 17). The pedicel is 1.0–3.0 mm long (Figs. 3, 4, 6, 14). Five sepals are well preserved and fused in their lower part, forming part of the floral cup; their distal portion is free, and the lobes are deltoid to ovate with a slightly keeled surface (Figs. 3, 5, 7–9), reaching 0.8–1.2 mm wide and 1.2–1.8 mm long. The spatulate, clawed petals, when present, are very small, 0.3 mm wide and 0.7 mm long (Figs. 4, 13); frequently they are not well preserved, but some scars that alternate with the sepals strongly suggest their presence. Opposite and adnate to them are the stamens (obhaplostemonous) that are slightly shorter than the petals. They are composed of a subulate filament, 0.6 mm long, and sub-basifixed dicotal anthers, 0.08 mm in diameter (Fig. 16).

The insertion of perianth parts suggests a perigynous flower, with superior ovary; the presence of a flower cup could confirm this floral character even though it is difficult to corroborate based on the known fossil material. In some specimens, however, the attachment of floral parts can be observed in transverse section, where basal scars in the floral cup probably correspond with the ovary (Figs. 6, 7). These ovary scars are about 0.2 mm in diameter. The nectariferous ring is prominent (2.5–3.0 mm in diameter), lobed (approximately 10 lobules), and fills the floral tube cavity (Figs. 5, 10, 11). One almost mature specimen suggests, based on its rounded oval shape in lateral view, that the perianth parts are adpressed to the ovary and stamens occupy a distal position, as a consequence of which the flowers may ripen into a subglobose drupe, approximately 2.0 mm wide and 2.2 mm long (Fig. 16).

Comparative morphology: The floral morphology of Coahuilanthus belindae is consistent with Rhamnaceae (e.g., Rhamnus and Sageretia) (Figs. 40, 41) and Zizipheae (e.g., Berchemia) (Fig. 44). Floral cup structure and parts of the perianth are very much like those of Rhamnus and Berchemia. For example, they share five acute, triangular, slightly keeled sepals lacking a thickening on the adaxial surface, and an acute campanulate floral cup. Coahuilanthus belindae shares with Sageretia a nectariferous ring with an irregular crenate margin (Brizicky, 1964). Nevertheless, they differ in other floral characters like the conspicuously keeled petals in Zizypheae, obovate petals in Sageretia and Berchemia, or flat and bilobed petals in Rhamnus; these differences support the recognition of a new taxon.

Genus: Nahinda gen. nov. Calvillo-Canadell and Cevallos-Ferriz

Species: Nahinda axamilpensis gen. et sp. nov. Calvillo-Canadell and Cevallos-Ferriz

Etymology: The generic name derives from the word flower in the “mixteco” dialect; the specific epithet refers to the Axamilpa River along which the fossil flowers were collected.

Diagnosis: Small actinomorphic, pedicellate, pentamerous, bisexual flowers; campanulate floral cup, calyx lobes five, deltoid and clearly keeled with thickened apex, inserted in floral cup margin; five spatulate to cucullate, short-clawed petals with apical notch, generally shorter than calyx lobes; stamens opposite, adnate to and enfolded by petals, with subulate filament and sub-basifixed anthers; three-carpellate gynoeicum with a single style ending in three stigmatic lobes and three locules; pentagonal, lobed, nectariferous ring; pedunculate, cyma-like umbrella.

Description: The fossil material consists of 24 specimens with their counterparts, but some of them are fragmentary. Most flowers are at anthesis; a few represent fruits, and there is...
a single inflorescence. These small, bisexual, pentamous, and actinomorphic flowers are 2.0–6.8 mm long and have a campanulate floral cup 2.5–5.0 mm long by 1.5–3.5 mm wide (Figs. 22–24, 29, 34); some have a pedicel up to 6.0 mm long. The calyx consists of five triangular or deltoid sepalas up to 2.0 mm wide and 3.0 mm long (Figs. 18–26), with a conspicuous keel and notch near the sepal tip. The corolla generally consists of five petals; some petals did not persist in fossil material, but their attachment scars are evident. The petals are spatulate to cucullate, short, clawed, with an apical notch, 1.1 mm long and 0.9 mm wide (Figs. 21–24, 31, 34, 35). Adnate to and opposing them are the stamens; each one consists of a triangular or subulate filament, 2.0 mm long, and a bilocular ovary anther, 1.0 mm long and 0.5 mm wide, slightly longer than the petals (Figs. 19, 21, 26, 30, 31, 34).

The gynoecium has three carpels and a single style, which is longer than the rest of the flowers parts (1.0 mm long, Figs. 25, 27, 28) and ends in a three-lobed stigma. The ovary is 1.0 mm in diameter, tends to be spherical, and is composed of three locules, but five may be inferred from the flower symmetry (Figs. 20–24). It seems to be inserted in the deepest part of the floral cup, suggesting a probable perigynous flower, but to confirm this character we must clarify how the perianth and stamen parts, as well as their degree of the fusion, participate in the floral cup construction.

A nectary-bearing ring is prominent (4.5 mm in diameter) and highly lobed (Fig. 20).

One of the specimens is a well-preserved cyme or umbel-like inflorescence (Fig. 33), consisting of about four pedicelate flowers developing from the same point; two of them are missing, being represented by the persistent pedicel (4.0 mm long); the other two have flowers in different developmental stages. One is a mature flower with withered sepalas (4.0 mm in diameter), while juvenile flowers are still closed (2.0 mm in diameter). The largest flower is located in the middle of the inflorescence and could suggest the maturation sequence of the inflorescence (Fig. 33).

Comparative morphology: **Nahinda axamilpensis** fossils can be organized into an ontogenetic series to document how these reproductive organs grew and matured from a floral bud to mature perfect flowers in a small cyme-like inflorescence (Figs. 29, 33), and then how they ripened to an ovary drupe-like structure (Figs. 25, 27–28, 30, 32). However, their taxonomic affinities remain uncertain. The type of inflorescence (pedunculate “umbel-like cyme”) documented in the fossil plant is similar to that of *Adolphia*, which consists of very few small flowers. As the flower buds of *Adolphia* mature and reach anthesis, morphological similarities among the extant and fossil reproductive structures continue to be seen. At this stage, perhaps size is the most significant difference, but the fact that the fossil fruits seem to remain as a single unit, while in *Adolphia* they split into mericarps limits their similarity.

Morphological flower characteristics of *Nahinda axamilpensis* suggest further similarities to *Adolphia* (Colletiaea) and to some members of Zizyphaeae (Paliureae in Richardson et al., 2000a, b; Ziziphus, Berchemia, Karwinskia) (Figs. 36–39, 42–48), and Rhamnaceae (*Hovenia, Rhamnanus*) (Figs. 40–41). Though similarities of *Nahinda* to members of Zizyphaeae are important, no single extant taxon has all characters found in the fossil material. For example, in *Ziziphus amole* (Sesse & Mocíño) M. C. Johnston, *Z. obtusifolia* (Hook. ex. Torrey. & A. Gray) A. Gray, *Z. mexicana* Rose (Figs. 36–38, 43), *Berchemia racemosa* Sieb. et Zucc., and *B. scandens* (Hill) K. Koch (Fig. 44), the perianth structure, campanulate floral cup, and triangular-ovate sepalas with prominent keel and apical thickness are comparable morphologically to those of *Nahinda*, but otherwise the floral characters are different. Another morphological character found in the fossil material that can be compared with *Ziziphus amole* is the presence of a three-lobed stigma (Fig. 43). The flower of *Ziziphus mauritiana* Lam. is most similar to the fossil flowers in having subulate filaments with sub-basified anthers enfolded by petals, but further comparison limits their similarity. *Karwinskia* (Fig. 39) has petals comparable with those of the Oligocene material, but again, they are different otherwise. *Berchemia* reproductive organs (Fig. 44) are also similar to the fossils in having a drupeaceous elliptical fruit, but its flowers are unisexual by abortion and borne in a thyrs (Brizicky, 1964). These characters contrast with a cyme-like inflorescence bearing hermaphroditic flowers in the fossil material. The fossil drupe-like fruit can be compared with *Ziziphus mexicana*, *Z. amole* and *Condalia microphylla* Cav. (Figs. 45, 48, 49). The characters preserved in the fossil material and the inferred developmental sequence support affinities to Rhamnaceae, but the differences discussed justify the recognition of a new taxon within this family.

**Tribe:** Ventilagineae

**Genus:** Ventilago Bent.

**Species:** Ventilago engoto sp. nov. Calvillo-Canadell and Cevallos-Ferriz

**Etymology:** The specific epithet is in recognition of Enrique González Torres, for his interest in explaining Cenozoic geologic history of Mexico to biologists pursuing a more geologically grounded history of plant lineages growing at present in Mexico and introducing young paleontologists to geology.

**Holotype:** Paleontological Collection of the Instituto de Geología, UNAM, catalog no. IGM-PB 2875.

**Locality:** Los Ahuehuetes, Coatzingo Formation, in the southern part of the Axamilpa River, 4.5 km NNE of Tepexi de Rodríguez, Puebla, 18°35’15”N, 97°55’30”W.

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Morphological characters in both fossil flowers suggest affinities to Rhamnaceae; these characters include a very small, actinomorphic, perfect, and pentamerosous structure with a floral cup that ranges from cupulate to campanulate (Figs. 36–44, 46, 47). This taxonomic affinity is further supported by other characters, such as the deltoid to ovate, slightly to prominently keeled sepals, that have a pad of tissue covering the distal zones (especially in the Oligocene material; Cronquist, 1981), and the petals, that may be spatulate to cucullate, short clawed and with an apical notch. Of special interest are the adnate stamens opposite and always enfolded by petals; these features are a rare condition in angiosperms and are diagnostic of Rhamnaceae (Woodson et al., 1971; Richardson et al., 2000a, b).

Even with all of these characteristics, it is difficult to identify the fossil flowers to generic or specific levels within known taxa. However, it is clear that the known characters and their similarities to those of extant Rhamnaceae are sufficient arguments to accept the inclusion of the new fossil material within the family. Furthermore, it is possible to recognize morphological characters suggestive of a relationship with a few genera of some tribes within the family. As in the Suessenguth system (1953), our tribal divisions are based on fruit characters and consist of Maesopsideae, Ventilaginaceae, Zizyphoeae, Rhamnaceae, Colletieae, and Gouanieae. Some large tribes that are morphologically heterogeneous, like Zizyphoeae, exemplify the limitation of this classification. Richardson et al. (2000a, b) further documented this situation, recognizing only three groups within the family. Nevertheless, we follow Suessenguth’s classification while waiting for a complete review of this problem to avoid further taxonomic confusion.

It is important to note that a phylogenetic approach to resolve relationships within the family has been proposed based on rbcL and trnL-F sequences of the plastid genome but with reference to few morphological data (Richardson et al., 2000a, b). For this reason, it is difficult to integrate the morphology-based fossil material, and thus it would be premature to introduce the new plants using this phylogenetic scheme. All the new reports may represent plants with characters found in either the rhamnoid or ziziphoid groups of Richardson et al. (2000a, b).

The new taxa are referred here as morphotaxa with affinities to members of Rhamnaceae (McNeill et al., 2006). In doing this, we recognize flower variation between the fossil and extant plants, which is evident from comparison of their detailed descriptions to those of living taxa (e.g., Weberbauer, 1896; Brizicky, 1964; Woodson et al., 1971; Fernández-Nava, 1986; Medan and Hilger, 1992). Furthermore, this decision highlights variability through time in these reproductive structures. Further explanation of these differences needs a phylogenetic analysis that includes more morphological characters (e.g., Jeong et al., 1997; Richardson et al., 2000a, b; Richardson et al., 2004). These and other fossil materials will at this time be of great value in generating a hypothesis based on both extant and fossil evidence.

Flowers of these new fossil plants strongly suggest that the morphological pattern found in Zizyphoeae and Rhamnaceae was
underway during the Late Cretaceous and certainly was present during the Paleogene. The broad geographic distribution of Eocene fruits assigned to *Paliurus* (Manchester, 1999) supports an early differentiation of these tribes, especially of *Paliurea* (*Zyzypheae*). Among Rhamnaceae, the new winged fruit is characteristic of *Ventilago* (*Ventilagineae*) (Figs. 50–53), and its presence further documents the diversification that Rhamnaceae attained by the Oligocene. Furthermore, the reproductive structures of the new plants suggest varied strategies to interact with the biological and physical world. Most probably the drupe-like structure was dispersed by animals, while the winged fruit was carried by wind. The presence of a nectariferous disc in the flowers further suggests interaction with insect pollinators.

Unfortunately, *Nahinda axamilpensis* and *Ventilago engoto* have not been associated with leaves or other Rhamnaceae organs that would help us understand them as whole plants. Nevertheless, leaves from the same formation and assigned to *Karwinskia* are well known. Although the leaves have not been associated with leaves or other Rhamnaceae organs that would help us understand them as whole plants, their presence further documents the diversification that Rhamnaceae attained by the Oligocene. Furthermore, the reproductive structures of the new plants suggest varied strategies to interact with the biological and physical world. Most probably the drupe-like structure was dispersed by animals, while the winged fruit was carried by wind. The presence of a nectariferous disc in the flowers further suggests interaction with insect pollinators.

A great diversity of angiosperm flowers from the Cretaceous has been documented, adding new elements to understand angiosperm history (Friis et al., 2006). Flower structures of *C. belinda* and *N. axamilpense* can be compared with some Late Cretaceous mesofossils (Friis, 1990; Friis et al., 2006). Although Cretaceous mesofossils have not been discussed formally as members of Rhamnaceae, their common pentameric, actinomorphic, and bisexual condition with nectariferous rings suggests a probable common ancestor, reinforcing the identification of the new Cretaceous Rhamnaceae and supporting the idea that the family has a long geologic history. Furthermore, the Rose Creek flower (Basinger and Dilcher, 1984), which was originally compared to *Celastraceae*, has been reinterpreted as a bona fide member of Rhamnaceae, further supporting our determination of the fossils and our inference of a long evolutionary history of the family (Richardson et al., 2000a, b). Nevertheless, other authors do not agree that the Rose Creek flower is necessarily Rhamnaceae (Manchester, 2006; S. Manchester, Florida Museum of Natural History, University of Florida, personal communication).

Further work will certainly be needed to clarify the phylogenetic relationships of the Rhamnaceae, and the fossil record (Table 1) will provide important taxonomic information about reproductive and vegetative characters. For example, the phylogenetic work by Richardson et al. (2000a, b) can be reevaluated with our new data. Based on the data presented here, we can assume that the family originated at least 72 mya instead of 60–62 mya as suggested by these authors. Their analysis further suggests that some genera (e.g., *Gouania*, *Ziziphurus*, *Berchemia*, *Karwinskia*, *Paliurus*) originated about half way through this period of time, but our interpretation suggests an Eocene/Oligocene rather than a Miocene appearance for these taxa. Thus, the use of data from fossils and morphology can improve our understanding of phylogeny and biogeography.

**LITERATURE CITED**


