Paleocene *Ipomoea* (Convolvulaceae) from India with implications for an East Gondwana origin of Convolvulaceae

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The morning glory family, Convolvulaceae, is globally important in medicine and food crops. The family has worldwide distribution in a variety of habitats; however, its fossil record is very poorly documented. The current fossil record suggests an origin in North America, which is in contrast to molecular data that indicate an East Gondwana origin. We report *Ipomoea* leaves from the late Paleocene (Thanetian; 58.7–55.8 million years ago) of India, which was a part of East Gondwana during this time. This is the earliest fossil record for both the family Convolvulaceae and the order Solanales. This suggests that the sister families Convolvulaceae and Solanaceae diverged before the Eocene in Gondwana-derived continents. The evidence presented here supports the conclusion from molecular phylogenetic analysis of an East Gondwana origin of Convolvulaceae.

Convolvulaceae | sweet potato | *Ipomoea* | Paleocene | East Gondwana

Convolvulaceae, the morning glory family, consists of 57 genera and 1,880 species (1) with a worldwide distribution (*SI Appendix*, Fig. S1*A*) over a broad range of habitats. Most members of the family are perennial herbs, vines, or woody lianas, rarely annual herbs, shrubs, or trees that are endemic to the tropical regions (2), although weedy taxa from temperate regions are also known (e.g., *Calystegia* and *Convolvulus*). Traditionally, the family was placed in Solanales (3–5), but Takhtajan (6) created a new order, Convolvulales, for it. Recent molecular systematics places the family in the order Solanales (7). *Ipomoea batatas* (sweet potato) of the Convolvulaceae family is the world's second most important root crop (8). Despite a large number of species having worldwide distribution in varied environmental conditions, the fossil record of the family is very sporadic and is represented by a leaf from late Eocene sediments of the United States (9) and by pollen from Miocene sediment of Australia (10). Fossil records of its sister family Solanaceae are known from pollen and seeds from Eocene sediments of Colorado and of Lower Bagshot, United Kingdom (11). However, the recent discovery of *Physalis* fruit from the early Eocene (52.22 ± 0.22 Ma) sediments of Patagonia raises the possibility of a divergence in Gondwana (12).

Molecular phylogenetic studies suggest that the Convolvulaceae is monophyletic (13) and diverged from Solanaceae around 65 Ma (14), 85 Ma (15), 55.3 Ma (69.98–47.80 Ma) (16), or 66 Ma (17) in East Gondwana (18).

The Eocene fossil records of Convolvulaceae and Solanaceae from Laurasia, together with the Eocene *Physalis* fruit from Gondwana, raise an important question about the early divergence of both families and Solanales. Here we report fossil leaves of *Ipomoea* (Convolvulaceae) from the late Paleocene (Thanetian; ~58.7–55.8 Ma) of Meghalaya (25° 26′ 47.4″ N), India (Fig. 1 *A* and *B*), which was located ~7° S paleolatitude (19) (www.odsn.de) (*SI Appendix*, Fig. S1*D*). These fossil leaves represent the earliest record of Convolvulaceae and also Solanales, and they document the early divergence of Convolvulaceae and Solanaceae supporting the molecular inference of an East Gondwana origin of the Convolvulaceae (18).

Materials and Methods

A collection of 200 angiosperm leaves has been made from the Tura Formation exposed in Nangwalbibra (25° 26′ 47.4″ N; 90° 42′ 28.9″ E), East Garo Hills District, Meghalaya (Fig. 1 *A* and *B*). Here we describe a fossil leaf morphotype based upon 17 specimens, 2 of which have counterparts. The specimens are impressions/compressions. They were prepared with the help of a fine chisel and hammer and then photographed in natural low-angled light using a 10-megapixel digital camera (Canon SX110). An attempt was made to extract cuticle with no success. The terminology used in describing the fossil leaves is based on Dilcher (20) and Ellis et al. (21). The distance between adjacent secondary veins was measured, and a range (minimum–maximum) was taken while describing the fossil leaves. The fossils are housed in the museum of the Birbal Sahni Institute of Palaeosciences, Lucknow, India. Similar extant leaves were examined at the herbaria of the National Botanical Research Institute, Lucknow, India, and the Forest Research Institute (FRI), Dehradun, India. In addition, the website of the Royal Botanical Gardens, Kew (apps.kew.org/herbcat/navigator.do; accessed on August 18, 2014 and January 15, 2017) was also consulted.

Results and Discussion

Systematics.
Order. Solanales Juss. ex Bercht. et J. Presl.
Family. Convolvulaceae Juss.
Genus. *Ipomoea* L.
Species. *Ipomoea meghalayensis* sp. nov., Srivastava, Mehrotra, and Dilcher.
Holotype. Specimen no. Birbal Sahni Institute of Palaeosciences (BSIP) 40571 (Figs. 2*A* and 3*D*).
Paratypes. Specimen nos. BSIP 40572, 40573A, 40573B, 40574, and 40575–40586 (Figs. 2 *B–F*, 3 *A–C*, 4 *A–D*, and 5 *A–E*).
Repository. Birbal Sahni Institute of Palaeosciences, Lucknow.
Type locality. Nangwalbibra, Meghalaya, India (Fig. 1).
Horizon. Tura Formation.
Age. Late Paleocene (Thanetian; ~58.7–55.8 Ma).

Significance

The origin of the worldwide-distributed morning glory family (Convolvulaceae) has been a matter of debate. The fossil record from late Eocene sediments of North America argues for a Laurasian origin that is in contrast to a molecular phylogenetic study that favors an East Gondwana origin. This report of fossil *Ipomoea* from the late Paleocene of India supports the current molecular phylogenetic conclusions of an East Gondwana origin for Convolvulaceae.
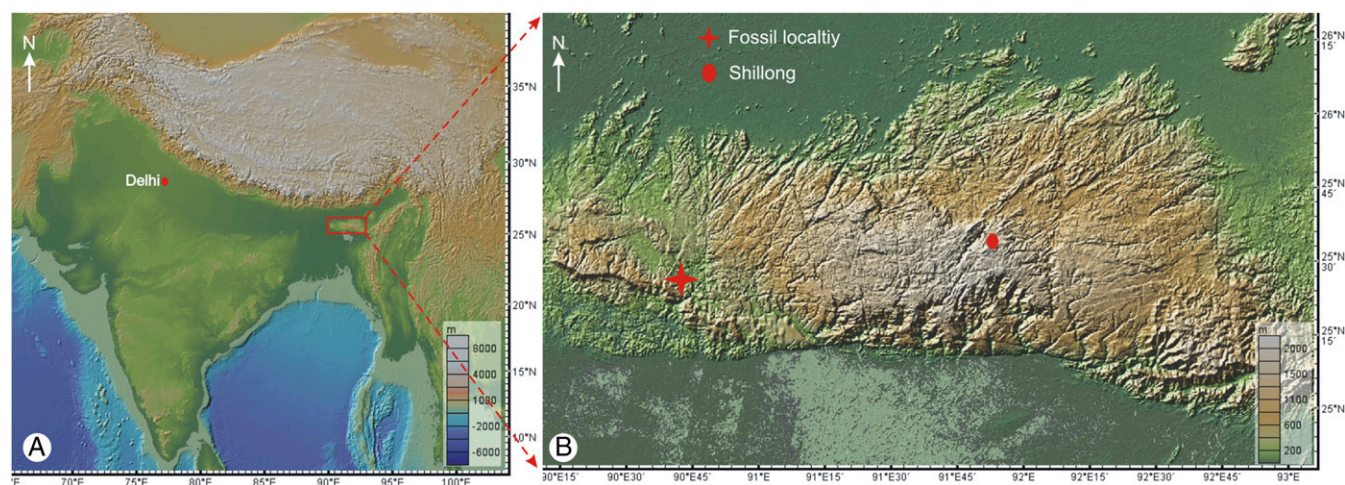
Fig. 1. Physiographic map showing the fossil locality. (*A*) Physiographic map of India and adjoining areas showing the fossil locality (red box). (*B*) High-resolution physiographic map showing the fossil locality (red asterisk) (map source: www.marine-geo.org/tools/maps_grids.php).

Etymology. The specific epithet is named for the locality.

Description. Lamina symmetrical, elliptic to ovate (widest at base or proximal 1/fourth); apex attenuate, arising somewhat abruptly from a broader leaf blade, rounded at the top (*SI Appendix,* Fig. S2*A*); base is deeply cordate, recurved leaf lamina joining the petiole (Figs. 2*D* and 5 *A* and *B* and *SI Appendix,* Fig. S2*D*). The basal lobes are rounded; margin entire, slightly wavy; midvein slightly curving, tapering, multistranded, and stout; leaf texture thin, appearing rough; petiole moderate to stout, short (0.03–1.78 mm); venation pinnate, eucamptodromous; secondary veins slightly more acute toward apex, angle of divergence often 57° to 67°, sometimes decurrent to midvein (Fig. 3*D*), course straight and arching upward at about two-thirds of the distance to the margin, forming loops close to the margin after joining with superadjacent secondary veins, two basal secondary veins at broad angles, each associated with a smaller more basal vein feeding the lobes (*SI Appendix,* Fig. S2*B*); tertiary veins percurrent (Fig. 3*D* and *SI Appendix,* Fig. S2*C*); one or two intersecondary veins may be present (Fig. 3*D*), sometimes joining the midvein with the secondary vein (Fig. 3*D*); glandular dots numerous (Fig. 2*C* and *SI Appendix,* Fig. S3 *A–C*).

Affinities. The characteristic features of the fossil leaves—such as their elliptic-to-ovate shape, attenuate apex, deeply cordate base with recurved leaf lamina joining the petiole, basal lobes, entire margin, pinnate, eucamptodromous venation, secondary veins slightly more acute toward apex, two basal secondary veins at broad angles feeding the lobes, percurrent tertiary veins, presence of intersecondary veins, and numerous glandular dots—exactly correlate with the same characters found in *Ipomoea*, therefore suggesting close affinity of the fossil with *Ipomoea* of the family Convolvulaceae. A large number of herbarium sheets of *Argyreia* Lour., *Calystegia* R. Br., *Convolvulus* L., *Ipomoea* L., *Merremia* Dennst. ex Endl., *Odonellia* Robertson, and *Operculina* Silva Manso of the Convolvulaceae were studied at the FRI and the National Botanical Research Institute, Lucknow, along with images of herbarium sheets from the website of the Royal Botanic Gardens, Kew.

The species of *Argyreia*, *Calystegia*, *Convolvulus*, *Odonellia*, and *Operculina* can be differentiated from the fossil on the basis of a combination of characters such as apex, length–width ratio, angle of divergence of secondary veins, distance between adjacent secondary veins, presence or absence of intersecondary veins, and reticulate tertiary veins (*SI Appendix,* Table S1). Modern species of *Merremia* such as *M. dissecta* Hallier f., *M. gemella* Hallier f., *M. hederacea* Hallier f., *M. peltata* Merr., and *M. tuberosa* Rendle

show superficial resemblance to our fossil, but the presence of an acute and rounded leaf base, moderately wide acute angle of divergence of secondary veins, and reticulate tertiary veins differentiate the modern species from the fossil (*SI Appendix,* Table S1).

A large number of modern species of *Ipomoea* were compared in detail with the fossil leaves, and a comparative chart of them is presented in *SI Appendix,* Table S1. Our fossil shows close resemblance with the modern leaves of *Ipomoea eriocarpa* R. Br. in the characters such as attenuate apex, deeply cordate base, pinnate eucamptodromous venation, narrow-to-moderate angle of divergence of secondary veins, distance between adjacent secondary veins, presence of intersecondary veins, and percurrent tertiary veins (Fig. 6 *A–D*). The petiole is short in the fossil, while in the modern leaf of *I. eriocarpa* the petiole length varies from short to long (0.6–6.5 cm) (*SI Appendix,* Fig. S4 *A* and *B*). There are also several other species of *Ipomoea* where length of the petiole varies from 2 mm to 14 cm (2). Secretory structures have been reported in *Ipomoea* species in the form of glandular trichomes (22–25), laticiferous canals and idioblasts (24, 26), floral nectaries on sepals (27), and extrafloral nectarines on petioles (24, 28–31). Glandular dots are present on the surface of *I. eriocarpa* leaves (*SI Appendix,* Fig. S5*B*). The glandular trichomes reported by Kuster et al. (25) in the *Ipomoea pes-caprae* and *Ipomoea imperati* are very similar to those of our fossil leaves (*SI Appendix,* Fig. S3 *A–C*).

In addition to Convolvulaceae, the fossil also shows some similarity with *Echinodorus grandiflorus* Micheli of the Alismataceae, *Centella asiatica* Urb. of the Apiaceae, *Arum dioscoroides* Sm. of the Araceae, *Dioscorea glandulosa* Ayala of the Dioscoreaceae, *Arcangelisia flava* (L.) Merr., *Cissampelos andromorpha* DC., *Cocculus carolinus* (L.) DC., *Odontocarya floribunda* Diels, *Odontocarya tamoides* (DC.) Miers, *Pericampylus glaucus* (Lam.) Merr., *Sarcopetalum harveyanum* F. Muell., *Tinospora dentata* Diels, *T. merrilliana* Diels of the family Menispermaceae, *Piper wichmannii* (C. DC.) Lebot of the Piperaceae, and *Smilax fluminensis* Steud. of the Smilacaceae.

The taxa from the families such as Alismataceae, Dioscoreaceae, Piperaceae, and Smilacaceae can be differentiated from the fossil in having campylodromous venation. *Centella asiatica* of the Apiaceae has festooned brochidodromous venation, which is in contrast to the fossil. In Araceae, the presence of a sagittate base and reticulate tertiary venation are major differences from our fossil. The genera from the family Menispermaceae have acrodromous to actinodromous venation in contrast to the fossil. However, *Tinospora dentata* shows superficial similarity, but the serrate margin clearly differentiates it from our fossil.
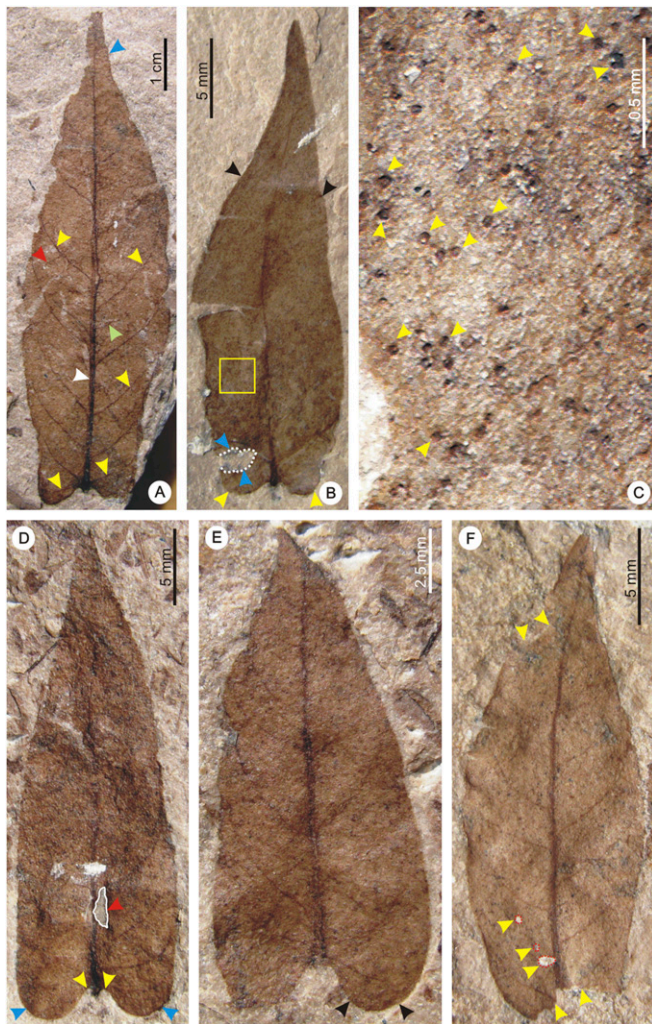
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Fig. 2. *I. meghalayensis* sp. nov. (*A*) Leaf showing elliptic shape, primary vein (white arrow), secondary veins (yellow arrows), percurrent tertiary vein (red arrow), intersecondary vein (green arrow), cordate base, and attenuate apex (blue arrow) (specimen no. BSIP 40571). (*B*) Fossil leaf showing shape, size, lobes of cordate base (yellow arrows), and insect damage (white dotted line with blue arrows); lamina showing shoulder portion (black arrows) (specimen no. BSIP 40572). (*C*) Enlarged portion (*B*, yellow box) of lamina showing glandular dots (yellow arrows). (*D*) Leaf showing elliptic shape, size, venation pattern, cordate base (blue arrows), recurved leaf lamina joining petiole (yellow arrows), and insect activity (red arrow) (specimen no. BSIP 40573A). (*E*) Leaf showing shape, venation pattern, and rounded basal lobe (black arrows) (specimen no. BSIP 40573B). (*F*) Leaf showing shape, size, venation pattern, and insect feeding (yellow arrows with red dotted line) (specimen no. BSIP 40574).

As far as the authors are aware, there is only one fossil (fruit) record of *Ipomoea* known from the Neogene sediments of India (32). Therefore, a new species—i.e., *I. meghalayensis* sp. nov., Gaurav Srivastava, R. C. Mehrotra, and D. L. Dilcher—is proposed for the fossil reported here.

Evolution and Dispersal of the Convolvulaceae and *Ipomoea*. According to Wikström et al. (14), the sister families Convolvulaceae and Solanaceae diverged during the Maastrichtian (~65.5 ± 0.5 Ma) while Bremer et al. (15) suggested their divergence during the Santonian (~85 Ma). This is also the time when social insects were first found and were important pollinators for these families (33). However, Eserman et al. (16) proposed a mean age of about 55.3 Ma (69.98–47.80 Ma) for

Convolvulaceae and Solanaceae and suggest a mean age for the divergence of the tribe Ipomoeeae is about 35 Ma (49.64–21 Ma), which is too young in comparison with the fossil record presented here. Moreover, the recent molecular data suggest that Convolvulaceae and Solanaceae diverged at ~66 Ma (17). Olmstead (18) has inferred that Solanales represents the best example of vicariance following the Gondwanan breakup, which resulted in emergence of Solanaceae in South America; Hydroliaceae, Sphenocleaceae, and Montiniaceae in Africa; and Convolvulaceae in East Gondwana.

In a comprehensive review of the fossil records of Asteridae, Martínez-Millán (11) has suggested that in Convolvulaceae only two fossils, namely *Convolvulites orichitus* (leaf) MacGinitie (9) from the late Eocene of Colorado and *Tricolpites trioblatus* (pollen) (10) from the Early–Middle Miocene of Lake Hydra, Australia, are reliable. However, in the sister family Solanaceae, Martínez-Millán accepted *Datura* cf. *D. discolor* (pollen) from the late Eocene of Colorado (34) and seeds of *Solanispermum reniforme* and *Solanum arnense* from the Eocene of Lower Bagshot, United Kingdom (35) as reliable fossil records (11). These fossil records suggest that both families were well established by the Eocene in Laurasia. However, the recent discovery of earliest fossil fruit of Solanaceae (*Physalis infinemundi*) from early Eocene
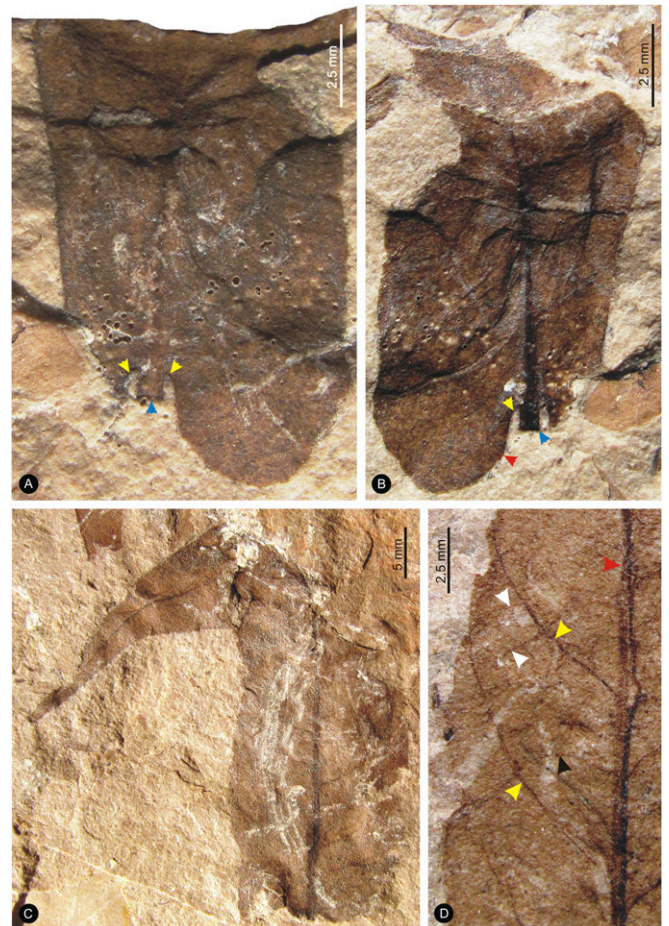

Fig. 3. *I. meghalayensis* sp. nov. (*A* and *B*) Part and counterpart of the fossil leaves showing shape, recurved lamina joining petiole (yellow arrow), lobed base (red arrow), and short petiole (blue arrows) (specimen nos. BSIP 40584 and 40585). (*C*) Fossil leaf in reflected natural light showing morphological details (specimen no. BSIP 40586). (*D*) Enlarged portion of the fossil leaf (Fig. 2*A*; specimen no. BSIP 40571) showing primary vein (red arrow), secondary veins (yellow arrows), percurrent tertiary veins (white arrows), and an intersecondary vein joining the midvein with the secondary vein (black arrows).
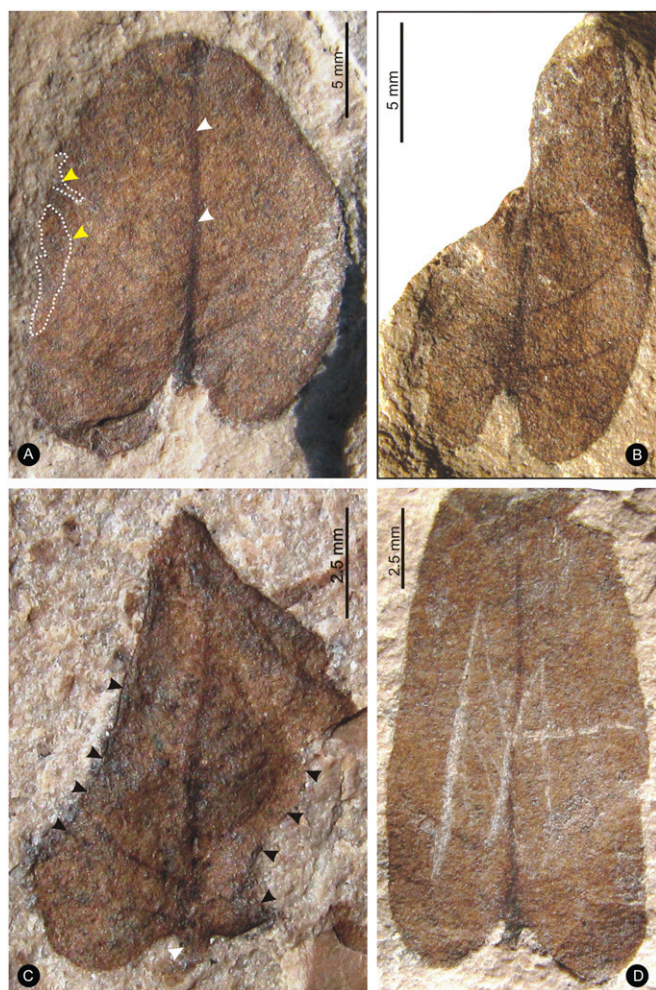
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Fig. 4. *I. meghalayensis* sp. nov. (*A*) Fossil leaf showing shape, size, thick midvein with insect mine (white arrows), and lots of insect damage (broken white line with yellow arrows) (specimen no. BSIP 40580). (*B*) Fossil leaf showing shape, size, and venation pattern (specimen no. BSIP 40581). (*C*) Fossil leaf showing shape, size, venation pattern, insect damage on the lamina (black arrows), and petiole bearing five ribs/veins (white arrow) (specimen no. BSIP 40582). (*D*) Fossil leaf in natural reflected light showing shape, size, and venation pattern (specimen no. BSIP 40583).

sediments of Patagonia suggests that the families Convolvulaceae and Solanaceae probably diverged before the Eocene in Gondwana-derived continents. The discovery of leaves similar to *Ipomoea* in the late Paleocene sediments (Thanetian; 58.7–55.8 Ma) of India represents the earliest record, not only of the family Convolvulaceae, but also of the order Solanales (11). It also suggests that Convolvulaceae and Solanaceae diverged before the Eocene in the Gondwana-derived continents, a theory already proposed from the molecular phylogenetic analysis (18). In light of the above facts, the fossil leaves reported here suggest an East Gondwana origin of the family Convolvulaceae.

The fossil records of Convolvulaceae from the Eocene of Colorado, the Miocene of Australia, and the Neogene of India (*SI Appendix*, Fig. S1 *A–D*), together with the Paleocene Indian fossil described above, suggest that the family had an early disjunct distribution during the Cenozoic. More fossil records are needed to hypothesize the dispersal pathway(s) of the family.

Ipomoea has a disjunct distribution today, and it is found in all tropical and subtropical areas of the world (*SI Appendix*, Fig. S1A). Phylogeographic analysis of Miryeganeh et al. (36, 37) based on molecular data for *I. pes-caprae* suggest that the species

has achieved long-distance dispersal, and they have also suggested an Old World origin for the species.

Geological Details. The Tura Formation overlies unconformably the Precambrian Gneiss complex at the junction of the Nangal stream and the Simsang River near Nangwalbibra where the plant-bearing beds are exposed. The formation is divided into lower, middle, and upper members (*SI Appendix*, Table S2). The lower member is about 16–20 m thick and consists of massive sandstones with pebbly interbeds, while the middle member is basically argillaceous and composed of lithomargic clays and argillaceous sandstones, along with coal seams. The upper member is again arenaceous with a few pebble-bearing layers. The Tura Formation is overlain by the Siju Limestone (early Eocene), which consists of intercalations of fossiliferous beds of marls, limestones, silts, and shales. The Siju Limestone is overlain by the Kopili Formation (late Eocene), which is composed of siltstones and shales (38–41). The generalized lithostratigraphic succession is given in *SI Appendix*, Table S2. In the Tura Formation, the plant megafossils are found in a grayish-white-to-buff claystone bed of the middle member, ranging from 3.0 to 3.66 m in thickness. It overlies a 1.83- to 2.13-m thick coal seam and underlies a 1.22- to 1.52-m thick white coarse-grained sandstone (42) (Fig. 7).
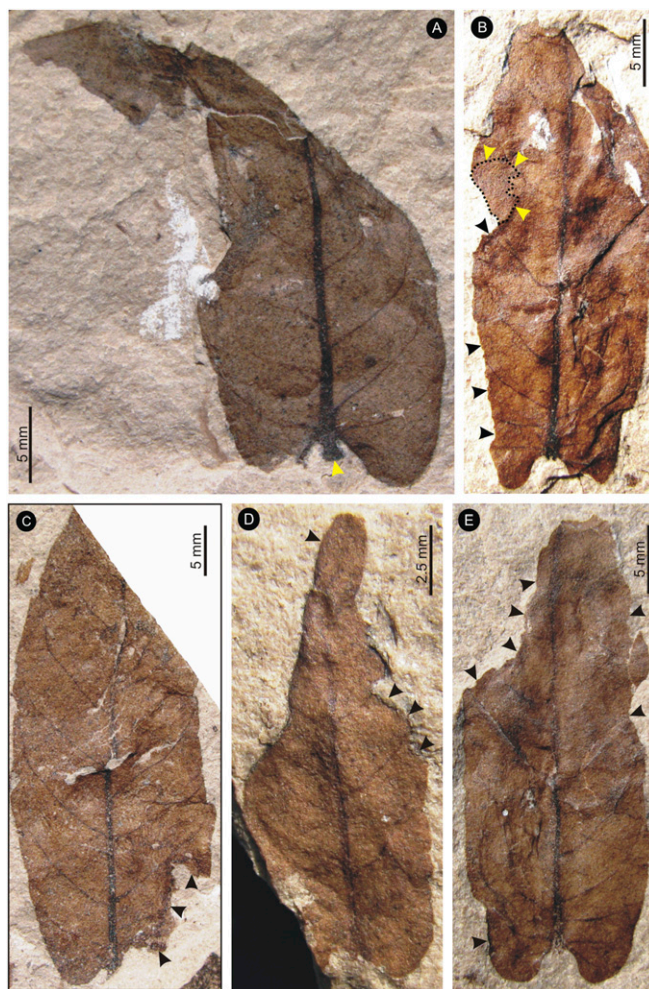

Fig. 5. *I. meghalayensis* sp. nov. (*A*) Fossil leaf showing characteristic shape, size, venation pattern, and displaced petiole bending down into the sediments (yellow arrows) (specimen no. BSIP 40575). (*B*) Fossil leaf showing shape, size, venation pattern, and insect feeding at margin of lamina (black arrows) (specimen no. BSIP 40576). (*C–E*) Fossil leaf showing shape, size, venation pattern and insect damage (black arrows) (specimen nos. BSIP 40577, 40578, and 40579).
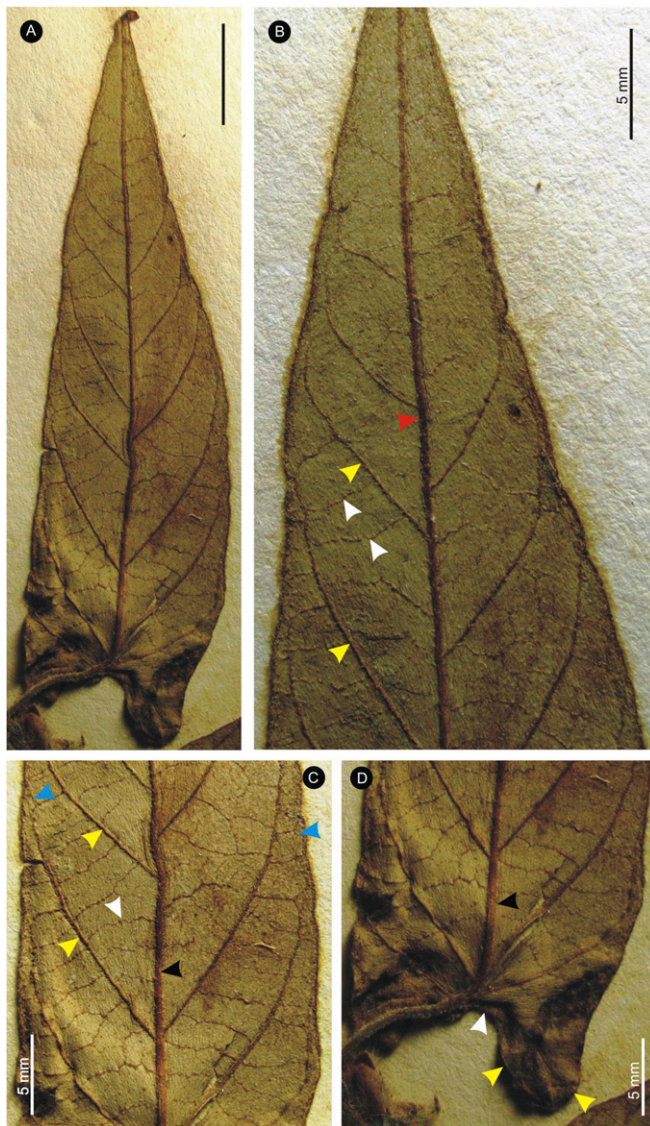
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Fig. 6. Modern leaves of *I. eriocarpa*. (*A*) *I. eriocarpa* showing shape, size, and venation pattern (Herbarium sheet no. FRI 24091). (Scale bar, 1 cm.) (*B*) Enlarged upper portion of the modern leaf showing primary vein (red arrow), secondary veins (yellow arrows), and tertiary veins (white arrows). (*C*) Enlarged middle portion of the leaf showing primary vein (black arrow), secondary veins (yellow arrows), recurved tertiary vein (white arrow), and eucamptodromous venation (blue arrows). (*D*) Enlarged basal portion of the leaf showing recurved lamina (white arrow) and basal lobe (yellow arrows).

Saxena et al. (43) conducted a detailed palynofloral work from the Tura Formation near Nangwalbibra and compared the assemblage with the already known palynofloral assemblages from the Cherra and Lakadong Sandstone Formations of the Khasi Hills (44–46), the Therria Formation of Jaintia Hills, Meghalaya
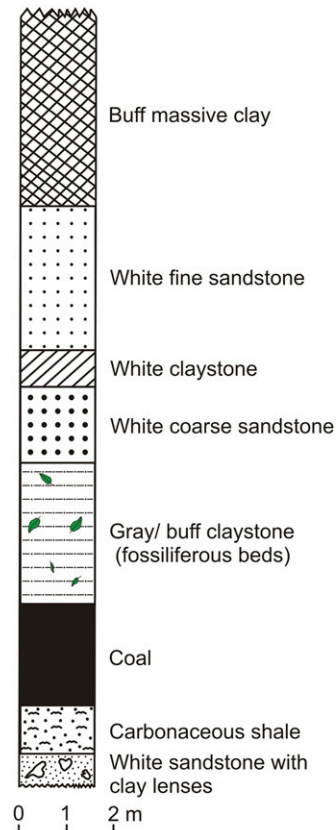

Fig. 7. Stratigraphy of the studied section at Nangwalbibra showing the strata from where the fossil leaves were collected (42).

(47), and the Mikir Formation of the North Cachar Hills, Assam (48) and suggested a taxonomic uniformity among them. Since all these formations are from the Paleocene age, Saxena et al. (43) suggested the same age for the Tura Formation of Garo Hills. Based on characteristic pollen taxa such as *Dandotiaspora telonata*, *Dandotiaspora pseudoreticulata*, *Dandotiaspora plicata*, *Polycolpites speciosus*, *Polycolpites cooksoniae*, *Lycopodiumsporites paleocenicus*, *Proxapertites microreticulatus*, *Matanomadhiasulcites maximus*, *Retitribrevicolporites matanomadhensis*, *Tricolpites levis*, *Neocouperipollis rarispinosus*, and *Neocouperipollis brevispinosus* described earlier by Sah and Singh (49) from Nangwalbibra, Ambwani and Kar (50) suggested a more specific age of the late Paleocene for the Tura Formation. Monga et al. (51) also suggested the same age on the basis of palynoassemblage recorded from the present fossil locality.

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