

The first fossil leaf insect: 47 million years of specialized cryptic morphology and behavior

Sonja Wedmann*[†], Sven Bradler[‡], and Jes Rust*

*Institut für Paläontologie, Rheinische Friedrich-Wilhelms-Universität, Nussallee 8, 53115 Bonn, Germany; and [†]Institut für Zoologie und Anthropologie, Georg-August-Universität, Berliner Strasse 28, 37073 Göttingen, Germany

Edited by May R. Berenbaum, University of Illinois at Urbana-Champaign, Urbana, IL, and approved November 15, 2006 (received for review August 11, 2006)

Stick and leaf insects (insect order Phasmatodea) are represented primarily by twig-imitating slender forms. Only a small percentage ($\approx 1\%$) of extant phasmids belong to the leaf insects (Phylliinae), which exhibit an extreme form of morphological and behavioral leaf mimicry. Fossils of phasmid insects are extremely rare worldwide. Here we report the first fossil leaf insect, *Eophyllium messelensis* gen. et sp. nov., from 47-million-year-old deposits at Messel in Germany. The new specimen, a male, is exquisitely preserved and displays the same foliaceous appearance as extant male leaf insects. Clearly, an advanced form of extant angiosperm leaf mimicry had already evolved early in the Eocene. We infer that this trait was combined with a special behavior, catalepsy or "adaptive stillness," enabling *Eophyllium* to deceive visually oriented predators. Potential predators reported from the Eocene are birds, early primates, and bats. The combination of primitive and derived characters revealed by *Eophyllium* allows the determination of its exact phylogenetic position and illuminates the evolution of leaf mimicry for this insect group. It provides direct evidence that Phylliinae originated at least 47 Mya. *Eophyllium* enlarges the known geographical range of Phylliinae, currently restricted to southeast Asia, which is apparently a relict distribution. This fossil leaf insect bears considerable resemblance to extant individuals in size and cryptic morphology, indicating minimal change in 47 million years. This absence of evolutionary change is an outstanding example of morphological and, probably, behavioral stasis.

crystallization | Eocene | Messel | Phasmatodea | stasis

Predator-prey interactions and the coevolution of insects and angiosperm plants are important driving forces in the evolution of insect diversity. Morphological, physiological, and behavioral adaptations are among the most striking examples of evolution (e.g., see ref. 1). One of the most elaborate methods of avoiding detection by visually hunting predators is seen in leaf mimics, which exhibit extreme modifications to mimic angiosperm leaves. The remarkable adaptations of leaf mimics not only concern morphological resemblance to leaves but also include a special behavior involving adaptive stillness at daylight or imitation of a leaf swaying in the wind (2).

Here we present the first fossil record of advanced angiosperm leaf mimicry in an insect. The fossil was collected in the lacustrine deposits at Messel in Germany, which are 47 million years old (3). The completeness and state of preservation of the fossil is exceptional (Fig. 1 *A* and *B*); the fossil shows almost exactly the same cryptic morphology as extant male leaf insects (Fig. 2*B*) of the order Phasmatodea. The huge majority ($>3,000$ extant species) of phasmids exhibits a stick-like habitus. Only 37 described species are assigned to the Phylliinae that engage in impressive leaf crypsis.

Possible stem-group representatives of phasmids have a geological record extending back to the Permian or Triassic (4, 5), but phasmid fossils that can be assigned to extant subgroups are extremely rare (6). Until now, only a few enigmatic members of the Euphasmatodea, a basal clade of the Phasmatodea (7), have been documented in the fossil record, mainly as nymphs from

Baltic and Dominican amber (8–10). The first fossil representative of Timematodea, the basal-most extant phasmid lineage, was recently described from Baltic amber (10).

Our specimen is the first fossil record of a phasmid pertaining to the euphasmatodean Phylliinae. Among the dicotyledonous angiosperm plants recorded from Messel (11), there are several families in which oblong leaves bear a resemblance to the fossil leaf insect. Its significant morphological similarity to these angiosperm leaves indicates a very strong selective pressure by visually hunting predators. The fossil illuminates the evolutionary progression of morphological characters within leaf insects (see Fig. 4*A*). Perhaps even modern sexual dimorphism in leaf insects (Fig. 2) was already present during the Eocene.

Systematic Paleontology

Insecta Linnaeus, 1758; Phasmatodea Jacobson & Bianchi, 1902; Phylliinae Kirby, 1904; *Eophyllium messelensis* gen. et sp. nov.

Holotype. Specimen MeI 12560 is curated in the Senckenberg Museum (Frankfurt-am-Main, Germany). This specimen is an almost complete adult male preserved in dorsal view, with many details of the head, antennae, thorax, wings, and legs intact, displaying a nearly unscathed abdomen and genital region (Fig. 1 *A* and *B*).

Ethymology. The generic name *Eophyllium* is derived partly from the Eocene, in reference of the age of the type specimen, and the phasmid genus *Phyllium*. The specific name *messelensis* is derived from Messel, the fossil site where the specimen was found.

Locality and Age. MeI 12560 was collected at Grube Messel near the town Darmstadt (Hesse, Germany). The fossil specimen was found in the Messel Formation (lower Middle Eocene, lowermost Geiseltalian, Mammal Paleogene level 11) in grid square E8/9, 1.5–2.5 m above local stratigraphic marker level Alpha. The sediments of the Messel Pit were deposited in a deep maar lake created by explosive volcanic activity (12, 13). Radiometric dating of a basalt fragment underlying the fossiliferous sediments from the Messel Pit indicates that the deposits are ≈ 47 million years old (3).

Diagnosis. *E. messelensis* gen. et sp. nov. is characterized by a leaf-shaped abdomen due to foliaceous expansions of the abdominal segments. Its fore femora are slender and covered sparsely with hairs but show no leaf-like dilations. The lateral margins of the mesothorax bear a row of compact spikes. The tegmina reach as far as abdominal segment 2. In the genital region, the vomer is basally rather broad with its apex ending in

Author contributions: S.W., S.B., and J.R. designed research; S.W. and S.B. performed research; S.W. and S.B. analyzed data; and S.W., S.B., and J.R. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS direct submission.

[†]To whom correspondence should be addressed. E-mail: sonja.wedmann@uni-bonn.de.

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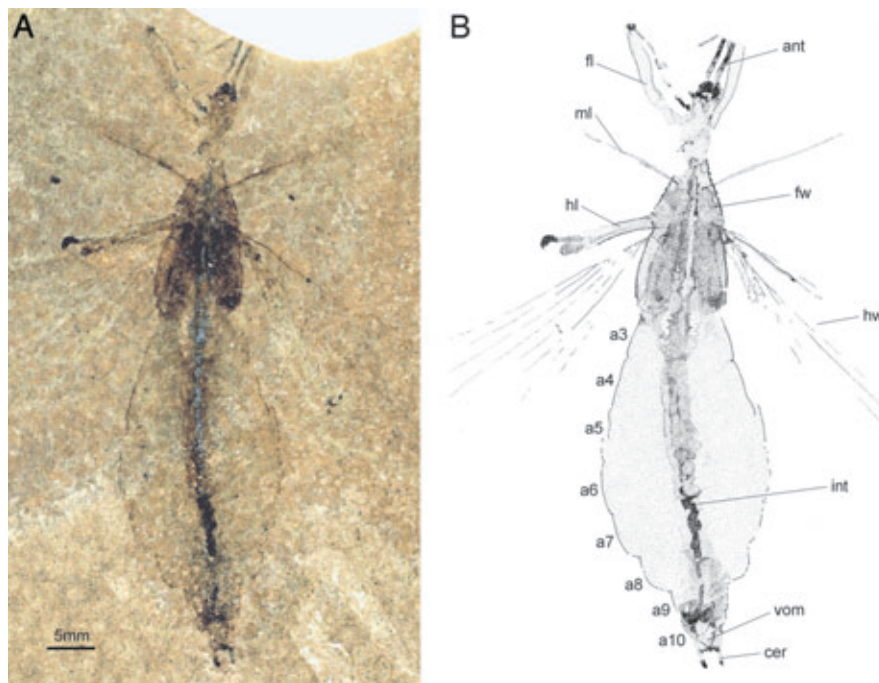


Fig. 1. Photo (A) and line drawing (B) of holotype of fossil leaf insect *E. meselensis* gen. et sp. nov. from the Eocene Messel Pit, Germany (Me1 12560). a3–a10, abdominal segments 3–10; ant, antennae; cer, cerci; fl, foreleg; fw, forewing; hl, hindleg; hw, hindwing; int, intestinal tract; ml, midleg; vom, vomer.

two sclerotized cusps. On both sides of the vomer, there is a thorn pad consisting of at least three rows of strongly sclerotized teeth. The unsegmented cerci probably were terete, and they are densely covered with robust setae.

Description and Comparisons. The fossil is an adult male with a body 63.1 mm in length (including cerci). It lies within the size range of extant *Phyllium* spp., e.g., *Phyllium celebicum* (Fig. 2).



Fig. 2. Extant female (A) and male (B) of *P. celebicum*. The fossil male leaf insect has the same size as extant male *P. celebicum*.

The body is essentially complete; only parts of the antennae and forelegs are missing. It is exposed from its dorsal side, but some ventral structures are visible as well.

The head and prothorax are incompletely preserved. Strongly sclerotized three-dimensional structures in the apical portion are probably parts of the mandibles. The eyes are not evident. The basal five segments of the antennae are preserved, densely covered with short, dark hairs. The outline of the prothorax is indistinct. The forelegs insert at the anterior part of the prothorax. In the right leg, the coxa, the trochanter, and the basal part of the femur are intact. In all euphasmatodean stick and leaf insects, the trochanter is small and fused with the femur (Fig. 3 B–E). The small size of the trochanter here indicates an equivalent condition for *Eophyllium* (Fig. 3A). A part of the tibia is preserved near the antennae. The left foreleg exhibits parts of the coxa and of the trochanter, the complete femur (showing the medial side), and the acute-angled remains of the hairy tibia and tarsus.

The fore femora show no leaf-like expansions; they are slender and covered sparsely with hairs. Some extant forms do not bear dilations on their legs either, or bear only slight expansions (e.g., Fig. 3C). The fore femora are slightly curved at their base (Fig. 3A), thus forming a notch for the head when the legs are longitudinally aligned during catalepsy. This notch is a common feature of stick insects, which is absent in extant Phylliinae for this specific construction. Besides being slightly twisted (Fig. 3 C and D), the fore femora are straight in extant Phylliinae (Fig. 3 B and E). Their fore femora usually bear lateral dilations (Fig. 3 B, D, and E), which also form a notch for the head and functionally allow the same cataleptic behavior.

The slightly incomplete mesothorax broadens posteriorly. Its margins (the mesepisternal sutures) bear a row of compact spikes, similar to extant males of *Phyllium* (Fig. 2) and *Chitoniscus*. The mid- and hindlegs are very fragmentary.

The tegmina (forewings) have a length of 13.5 mm, covering the metanotum and abdominal segments 1 and 2. This proportion corresponds to the condition found in males of *Chitoniscus*. The male tegmina of the examined *Phyllium* spp. are slightly

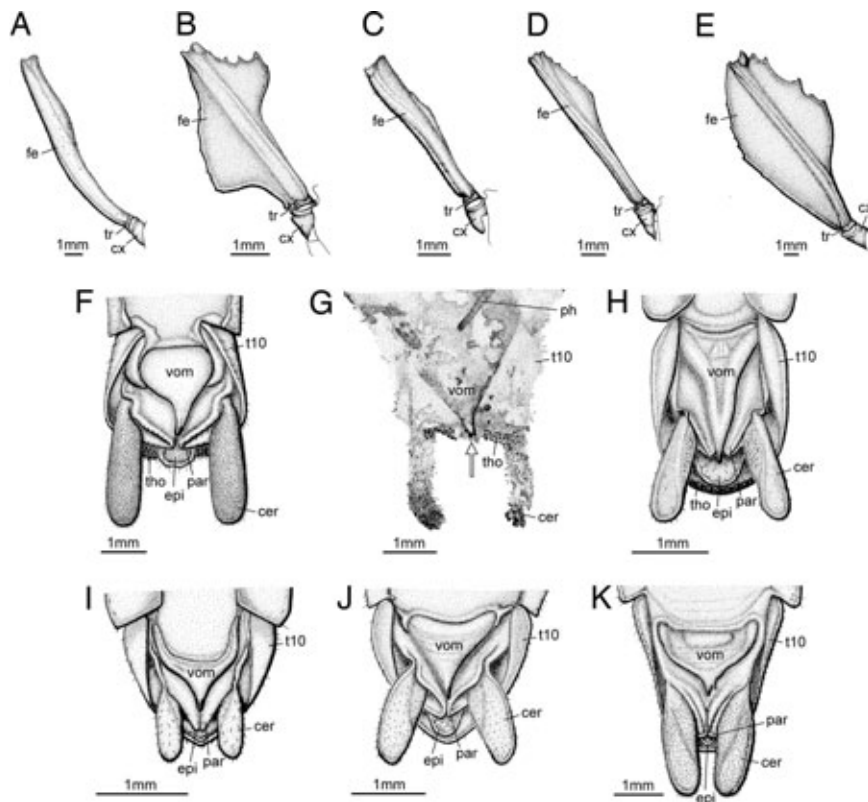


Fig. 3. Morphological details of *E. messelensis* gen. et sp. nov. compared with selected males of extant phasmid taxa, mainly members of Phylliinae. Basal portion of left foreleg of *E. messelensis*, reconstructed (A), *N. adisi* (B), *Microphyllium spinithorax* (C), *Chitoniscus feedjeanus* (D), and *P. celebicum* (E). Dorsal view of male terminal region of *E. messelensis* (G), ventral view of same region of *Aplopus* sp. (F), representing the euphasmatodean outgroup *N. adisi* (H), *M. spinithorax* (I), *C. feedjeanus* (J), and *P. celebicum* (K). cer, cercus; cx, coxa; epi, epiproct; fe, femur; par, paraproct; ph, phallic lobe; t10, abdominal tergum 10; tho, tergal thorn pad; tr, trochanter; vom, vomer.

longer, reaching the middle of abdominal segment 3 and ranging from 17 to 22 mm in length. The tegmina of *Nanophyllium* are considerably shorter, not reaching the abdomen. The hindwings of the fossil are both outspread, obviously showing the anal veins 2–7 that are basally merged, corresponding to the condition found in all extant phasmids with well developed wings (14). The remigium is not preserved.

The abdomen is leaf-shaped due to foliaceously lateral expansions of the corresponding terga and sterna. Abdominal segment 1, which is usually incorporated into the thorax, and segment 2 are not visible. The width of each segment increases consecutively until segment 6 and then subsequently decreases to the tip of the abdomen. This finding is consistent with the abdominal morphology of most living Phylliinae. Throughout the thorax and abdomen, the intestinal tract is visible, but no particulate contents are discernible.

The slightly asymmetric genital region is intact, showing details of the phallic organ as well as the accessory clasper composed of a triangular vomer on the venter of abdominal segment 10 and a pair of thorn pads at the hind margin of the corresponding tergum (Fig. 3G). A sclerotized oblong lobe of the phallus that is also present in living forms projects from right to left. The vomer of *Eophyllium* is similar in shape to that found in *Chitoniscus* (Fig. 3J). In addition, the vomer bears two cusps at its apex (arrow in Fig. 3G) as in *P. celebicum* (Fig. 3K). Each thorn pad consists of at least three rows of ventrally oriented, strongly sclerotized teeth (Fig. 3G). Tergal thorn pads are common in euphasmatodean taxa (e.g., *Aplopus* sp.; Fig. 3F); however, they are absent in most extant leaf insects (Fig. 3I–K). Only the male *Nanophyllium adisi* exhibits a single row of

sclerotized bumps on the slightly thickened hind margin of tergum 10 that can be interpreted as remnants of these thorn pads (Fig. 3H).

The unsegmented cerci appear to be terete, which is a common trait of stick insects (Euphasmatodea: *Aplopus* sp.; Fig. 3F), whereas living Phylliinae always possess dorsoventrally flattened cerci (Fig. 3H–K). Also, in contrast to living forms, the cerci of the fossil leaf insect are densely covered with rather robust setae.

Phylogenetic Relationships. *E. messelensis* gen. et sp. nov. shows convincing phasmatodean apomorphies, such as the vomer and one-segmented cerci (6, 7, 15–17). Furthermore, the fossil displays a combination of numerous synapomorphic characters of the Euphasmatodea: fusion of trochanter and femur, basally curved fore femora, merged anal veins 2–7 in the hindwing, and tergal thorn pads on abdominal segment 10 (7, 14, 18). The foliaceously dilated terga and sterna of the abdomen are an unambiguously apomorphic trait of Phylliinae. However, the fossil leaf insect lacks some synapomorphies shared by most extant Phylliinae, such as dorsoventrally flattened cerci and leaf-like dilations on fore femora. These characters collectively suggest a basal-most position for *E. messelensis* gen. et sp. nov. among the Phylliinae.

Discovery of *Eophyllium* provides insight into the poorly understood origin of leaf insects and allows an assessment of the temporal sequence of character transformations that led to the extant crown group (Fig. 4A). Although the exact phylogenetic position of the Phylliinae within the phasmid phylogeny is yet unknown, *Eophyllium* corroborates the hypothesis that leaf insects descend from stick insect-like ancestors and do not

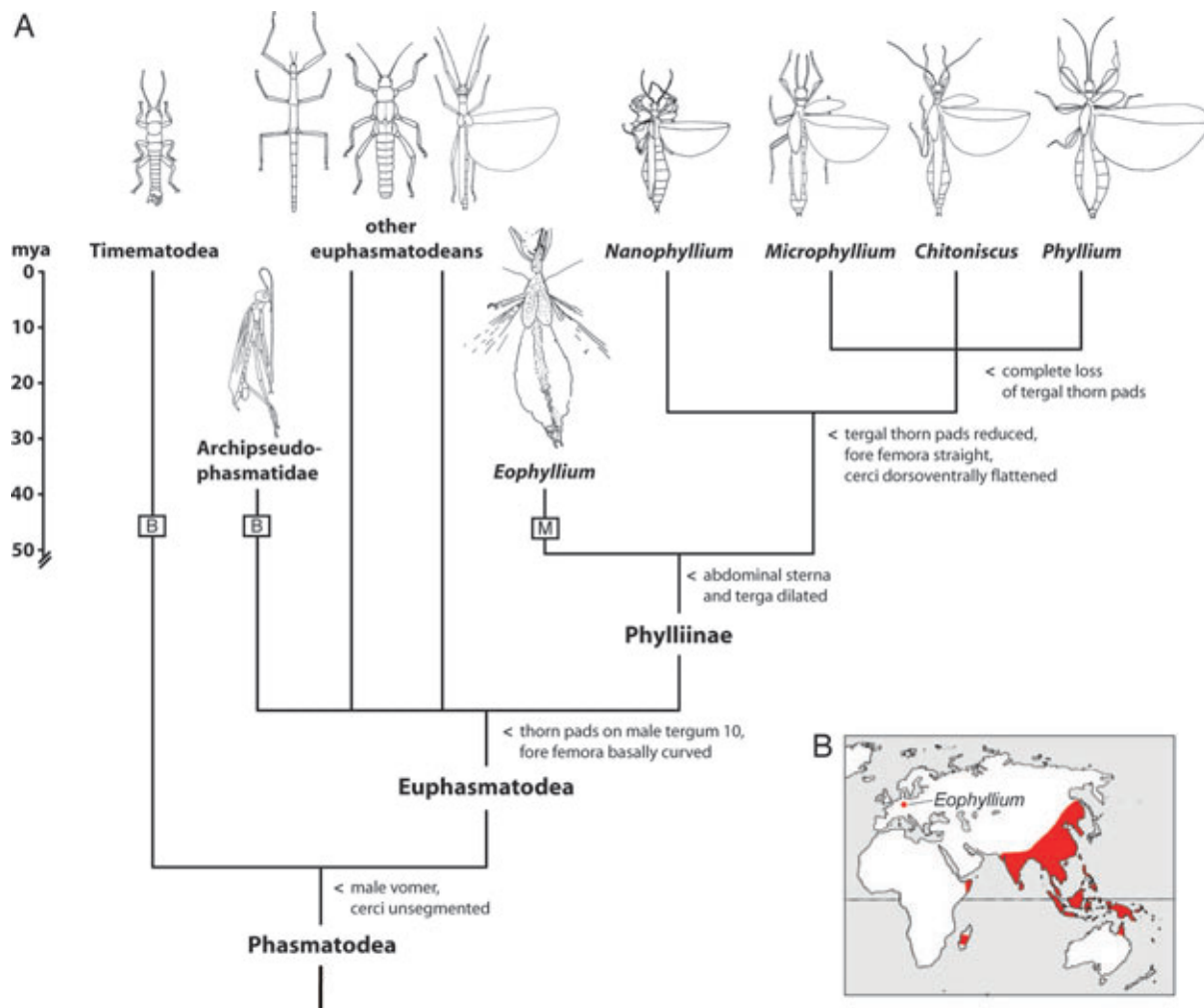


Fig. 4. *E. messelesensis* gen. et sp. nov. in evolutionary and biogeographical context. (A) Simplified cladogram with a partial geochronologic scale showing the phylogenetic position of *E. messelesensis* and the temporal sequence of character evolution. Oldest fossil records of determined adult representatives of Timematodea and Euphasmatodea are depicted (after refs. 8–10). M, Messel fossil site; B, Baltic Amber. Dating of splitting events of crown-group Phasmatodea is unknown. Euphasmatodea represent an unknown number of lineages. Figures are not to scale. (B) Distribution of extant and fossil leaf insects. Distribution of extant species mainly follow data from ref. 9, with amendments from ref. 41.

represent a basal lineage as has been proposed otherwise (9). The features of *Eophyllum* that are intermediate between typical stick insects and extant leaf insects indicate that presumably primitive characters of Phylliinae, such as straight fore femora and the absence of tergal thorn pads [remnants only present in *Nanophyllum*; Fig. 3H, see tergal thorn pad (tho)], are a secondary, derived condition. The assumed stick insect ancestry of leaf insects also has been supported by previous molecular and morphological studies (7, 17).

Discussion

The fossil leaf insect bears a physical resemblance to the oblong leaves of several angiosperm plants recorded from Messel, which are also potential food plants. These plant families include Lauraceae, Leguminosae, and Myrtaceae (11).

In all extant Phylliinae, the males look quite different and less like a leaf than in conspecific females, exhibiting a strong sexual dimorphism. Because of the substantial similarity of the fossil with extant Phylliinae males, we speculate that during the Eocene female leaf insects might have looked like extant females as well (Fig. 2A). It is possible that collectors have simply missed fossils of females because they were mistaken for angiosperm leaves.

It is rare that direct behavioral inferences can be made from fossils (e.g., ref. 19). The characteristically curved inner surfaces of the fore femora of this specimen form a notch where the head could be inserted. This finding indicates that, as in extant stick and leaf insects, a particular resting posture with a concealed head was adopted to strengthen its appearance as a leaf. Presumably the resemblance was perfected by catalepsy or “adaptive stillness” (2), i.e., their ability to remain motionless for prolonged periods of time, which is an essential part of their concealment during daylight. Occasionally a rocking motion is performed that probably enhances the resemblance to leaves swaying in the wind (2, 20). Extant leaf insects and the majority of stick insects are nocturnally active (e.g., 20).

In all probability, this advanced type of crypsis evolved in concert with angiosperm leaves on which the insects feed. It must have been caused by vigorous selection pressure by visually oriented predators. Common predators of adult phasmids are insectivorous birds (21), but also spiders, mantids, lizards, and bats (e.g., 20, 22–26) are documented. The defensive adaptations of phasmids are probably directed principally against predation by birds (21). The fossil bird fauna of Messel comprises potential predators like rollers (Coraciiformes) and related groups (see ref. 27; G. Mayr, personal communication), which may have

attacked large adult leaf insects. Leaf-mimicking orthopteroid insects like phaneropterines and pseudophyllinae (Orthoptera: Tettigoniidae) can constitute a large component of the diet of small neotropical monkeys (28). Thus, primates are among the potential predators of leaf insects, and early adapid primates (Prosimii: Notharctidae) are recorded by a few fossils from Messel (listed in ref. 29). Extant slow lorises (Prosimii: Lorisidae: *Nycticebus* sp.) have been observed to feed on leaf insects (F. Seow-Choen, personal communication).

Bats are another potential predator of large phasmids like leaf insects. Studies of the diet of extant insectivorous bats from the tropics have shown that gleanings can be important predators of herbivorous insects (26). Phasmids constituted only a small proportion of the diet of the observed bat species, but among the large prey stick insects were dominant. In Messel, bats are by far the most frequently found mammalian fossils, and eight species of bats are recorded from Messel (30). All species known from Messel used echolocation and were insectivorous (31, 32), but they certainly did not drive the visual mimicry of the leaf insects. Echolocating bats originated and diversified very rapidly during the Early Eocene (33, 34), and it has been suggested that the scope of this evolutionary diversification may have been caused by an increase in prey diversity (34). The Eocene insect fauna certainly was very diverse, and the record of a fossil leaf insect presented here is a further indication that much of the former biodiversity of Eocene insects is yet to be discovered.

Extant female leaf insects and nonadult males have short antennae with a stridulatory organ. In females, stridulation can be triggered by approaching males (35) or by disturbance (20). It is not known whether these sounds can be used by bats to locate leaf insects, but it is documented that gleanings use song to locate katydid orthopterans (36).

At present, all species of leaf insects are distributed primarily in southeast Asia and adjacent regions (9). The fossil record from the Eocene of Germany shows that their former geographical range was substantially more encompassing, most likely due to the significantly warmer climate at that time (37) and the more widespread distribution of their host plants. The fossil described here shows that today the leaf insects have a relict distribution (Fig. 4B).

Concerning the age of phasmatodean subgroups, indications from molecular dating are ambiguous. Molecular phylogenetics suggested that the basal genus *Timema* radiated only ≈ 20 Mya (38). Nevertheless, molecular datings of splitting events of

European species of more advanced *Bacillus* and *Leptynia* stick insects resulted in an age of ≈ 23 MyBP (39, 40). The present fossil record of a leaf insect sets a definite calibration point for this group. It indicates a minimum age of the origin of Phylliinae of 47 million years. The advanced systematic placement of Phylliinae among Euphasmatodea (7, 17) might contradict the assumption that pre-Cenozoic phasmids did not exist (8). This hypothesis may be supported by the record of a fossil member of the Timematodea from Baltic amber (10). However, very rapid evolution of Phylliinae at the beginning of the Cenozoic cannot be excluded.

The maximum age of Phylliinae dates back to the rise of angiosperm plants during the Lower Cretaceous (≈ 125 –90 Mya), with visually hunting predators being the main driving force for their evolution. Rapidly evolving groups like birds and mammals might have stimulated the evolution of leaf mimicry during the beginning of the Tertiary. In either case, the cryptic morphology of male leaf insects has scarcely changed since Eocene times. This phenomenon is an example of exceptional evolutionary stasis of a highly derived morphology, most likely coupled with very specialized cryptic behavior that lasted for ≥ 47 million years.

Materials and Methods

We have compared the fossil described here with all major Phylliinae taxa recognized at present. From the collection of the Museum für Tierkunde Dresden, we borrowed the extant male holotypes of *M. spinithorax* Zompro, 2001 and *N. adisi* Redtenbacher, 1906; also a male *C. feedjeanus* (Westwood, 1864) from the insect collection of the Museum für Naturkunde Stuttgart; and a male *Clarius brachysoma* (Sharp, 1898) from the collection of the Zoologisches Institut und Museum der Universität Hamburg. Additionally, several *Phyllium* species and other species of Euphasmatodea from the collection S.B. were examined.

The cladogram presented in Fig. 4A is based on mental analysis. Data exceeding this study are from refs. 6, 7, and 14–18.

We thank G. Oleschinski and C. Seiler for taking the photos, D. Kranz and B. Baumgart for help with the illustrations, R. Klug and F. Wieland for help with extant *Phyllium* species, and P. D. Gingerich and two anonymous reviewers for helpful comments on the manuscript. For the loan of the fossil and extant Phylliinae specimens, we thank S. Schaal, K. Klass, A. Staniczek, I. Rehmann, and H. Strümpel. This work was supported by a grant from the Deutsche Forschungsgemeinschaft (to S.W. and J.R.).

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