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Amber from western Amazonia reveals Neotropical diversity during the middle Miocene

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Tertiary insects and arachnids have been virtually unknown from the vast western Amazonian basin. We report here the discovery of amber from this region containing a diverse fossil arthropod fauna (13 hexapod families and 3 arachnid species) and abundant microfossil inclusions (pollen, spores, algae, and cyanophyceae). This unique fossil assemblage, recovered from middle Miocene deposits of northeastern Peru, greatly increases the known diversity of Cenozoic tropical–equatorial arthropods and microorganisms and provides insights into the biogeography and evolutionary history of modern Neotropical biota. It also strengthens evidence for the presence of more modern, high-diversity tropical rainforest ecosystems during the middle Miocene in western Amazonia.

Pebas Formation | Peru | Hexapoda | Arachnida | microorganisms

Ambers and other fossilized natural tree resins are common, documented in hundreds of Upper Paleozoic to Recent localities from around the globe. In exceptional cases, they can entomb pollen (1) or delicate and soft-bodied organisms that are poorly sampled or absent in the fossil record (2–4). Most of these amber-bearing deposits are restricted to the Northern Hemisphere: Only three South American Cenozoic localities have been reported, from the Eocene of Patagonia, Miocene of eastern Brazil, and Pleistocene of French Guyana (4, 5). We report the previously undescribed occurrence of fossil-bearing amber from the vast western Amazonian basin, a region of extraordinary biological diversity today, but whose fossil record has been virtually unknown for most modern groups. Although the Miocene Pebas Formation of northeastern Peru had long been investigated in paleontological studies [mollusks, fishes, and pollen (6–10)], amber clasts with organic inclusions are known from only a single level that we discovered in 2004. This amber is especially noteworthy for containing a diverse fossil arthropod fauna [at least 13 different families of Hexapoda (in the Collembola, Coleoptera, Diptera, Hemiptera, Hymenoptera, Orthoptera, Psocoptera, and Trichoptera) and 3 arachnid species] and abundant microfossil inclusions [pollen, spores (30 morphotaxa, including >20 fungi), algae, and cyanophyceae].

Results and Discussion

Three large and 25 smaller clasts (≈150 g, in 50-g + 50-g + 30-g + smaller clasts) were recovered, two of which include trapped arthropods and pollen (see Figs. 2B, 3, and 4 and Tables 1 and 2). Others include spores or dispersed organs of cyanobacteria, fungi, and freshwater algae, as well as a few unicellular organisms (see Fig. 4 and Table 1). All of the amber clasts originate from a single level of the Pebas Formation [18–10 million years ago; “Solimões Fm” in Brazil (10, 11)] in the Tamshiyacu locality on the eastern bank of the Amazon River, ≈30 km upstream of Iquitos in northeastern Peru (Figs. 1 and 2). This outcrop has

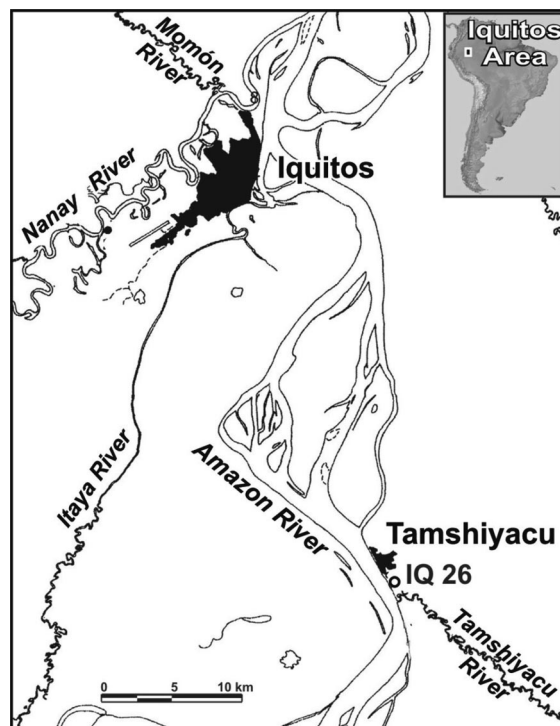


Fig. 1. Map of the Iquitos area (northeastern Peru) showing the geographic location of the middle Miocene amber-bearing locality of Tamshiyacu (IQ 26), denoted by an open circle. Map was redrawn from ref. 10.

been intensively studied for biostratigraphy and lithogenesis (7, 10, 11); it consists of two coarsening-upward parasequences, together referred to the middle Miocene *Crassoretitrites* Zone (≈15–12 Ma), based on the occurrence of *C. vanraadshoovenii* pollen (7, 10, 11). The amber-bearing level corresponds to a transgressive lag in the upper parasequence (TmB) (11), just above bottom lignites (Fig. 2A). “Rare detrital amber” was already mentioned within this parasequence (11), but it was not investigated further, and no fossil inclusions were reported. In fact, it appears to be relatively abundant and of large size within the locality. Even though the nature of the depositional environments of Pebas strata has been widely debated throughout the last decade (7, 10–14), with inferences ranging from fluvial,

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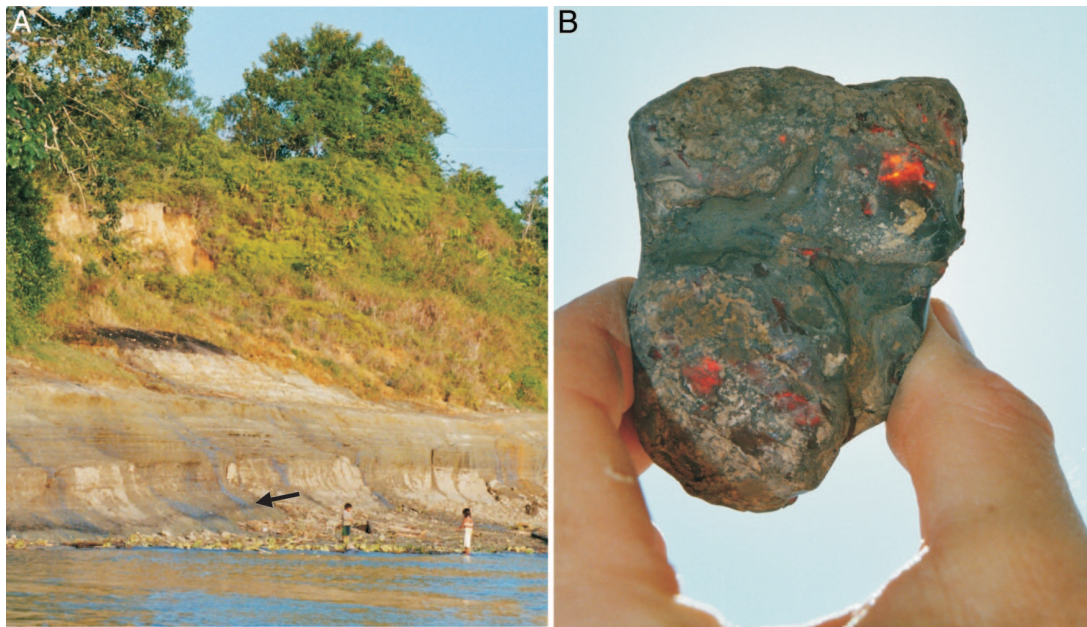


Fig. 2. Amber-bearing Tamshiyacu section (IQ 26, Iquitos area, northeastern Peru). (A) Middle Miocene amber-bearing level is indicated by black arrow. (B) Large amber clast from the level in A (length \approx 70 mm) at natural size.

lacustrine, and brackish to tidal environments, most authors acknowledge the occurrence of episodic marine incursions, most likely of Caribbean origin (9–16).

Amber allows the fossilized preservation of delicate plant structures [flowers or pollen (1, 17)], soft-bodied animals [e.g., nematodes, annelids, gastropods, arthropods, and small verte-

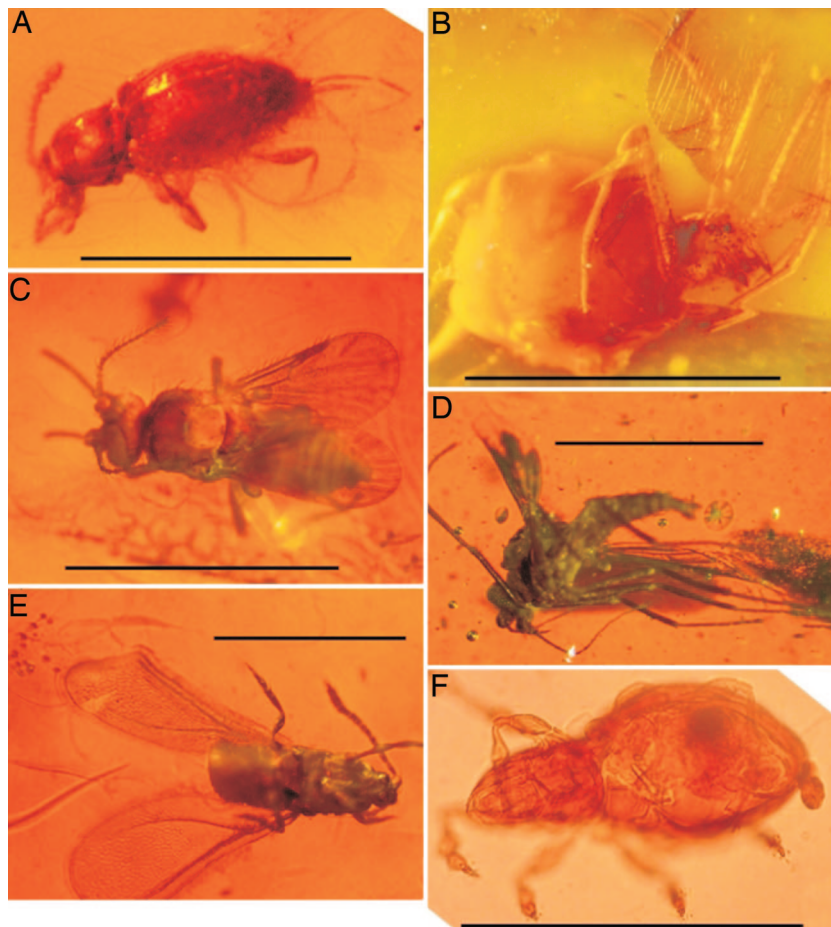


Fig. 3. Photographs of Euarthropoda in amber from the Miocene of Iquitos (northeastern Peru). (A) Coleoptera: Cucujoidea: Sphindidae. (Scale bar, 0.6 mm.) (B) Psocoptera, family undetermined. (Scale bar, 4 mm.) (C) Diptera: Ceratopogonidae (female). (Scale bar, 0.7 mm.) (D) Diptera: Chironomidae (male). (Scale bar, 1 mm.) (E) Hemiptera: Aleyrodidae (male). (Scale bar, 0.8 mm.) (F) Arachnida: Acarina (mite). (Scale bar, 0.2 mm.)

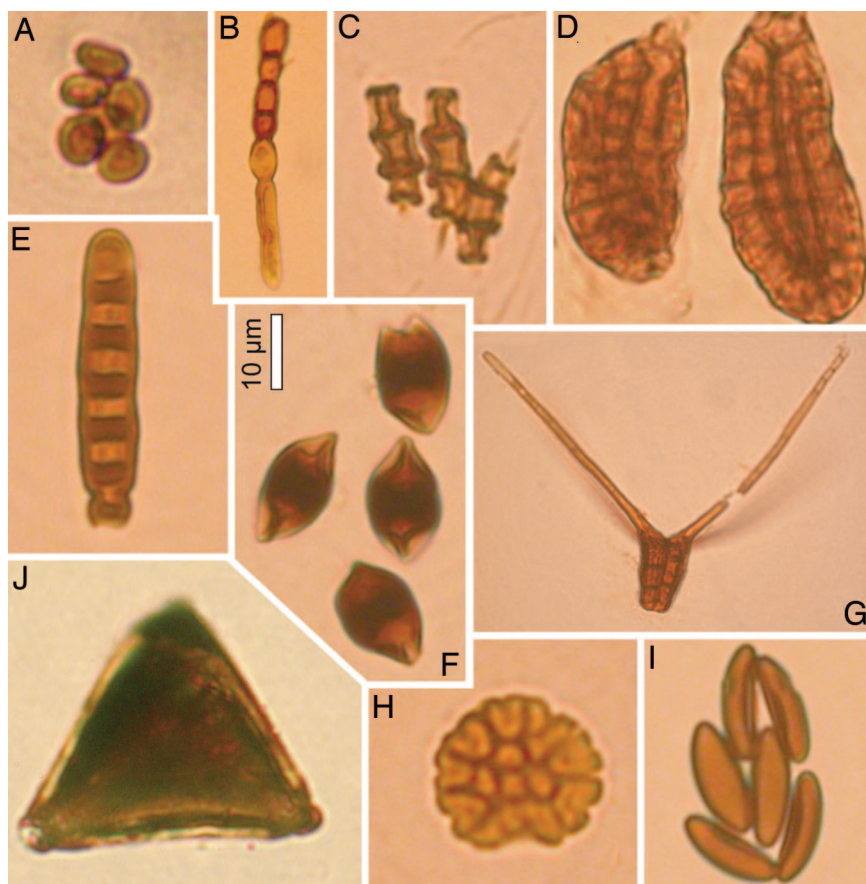


Fig. 4. Microfossils in Miocene amber from western Amazonia (Iquitos, northeastern Peru) in photographs taken under a light microscope. (A) Eubacteria. (B) Nostocaceae (Cyanobacteria). (C) *Quilonia* sp., pluricellate spores, specimens close to the modern *Alternaria*. (D) *Polycellulaesporonites* sp., also found in modern *Alternaria* species. (E) *Pluricellulaesporites* sp. (F) *Scenedesmus* sp. (G) *Frasnacritetrus* sp., four-branched spore (only two are visible here in the microscope focus). (H) *Phragmothyrites* sp., small subcircular ascostroma. (I) *Hypoxylonites* sp., fungal or algal spores. (J) *Triporopollenites* sp., pollen grain of a Proteaceae (Eudicotyledons: Magnoliophyta).

brates (4, 17–19)], and microorganisms (20), which allows their comparison with recent organisms. Contrary to what occurs in Dominican amber, which preserves membrane structures, musculature, and nerve tissue of arthropods (4), the amber clasts from Iquitos only preserved cuticles. However, these organisms are sufficiently well preserved to be identified precisely and used as paleoenvironmental markers. In addition, this fossilized resin from Iquitos preserves partial cell contents of some microorganisms and pollen grains, as also observed in Baltic and Paris basin ambers (21). Because it represents a previously undescribed Neogene insect assemblage from western Amazonia, the entomofauna is entirely unique and reflects only an initial sample of what is likely to be a much more diverse assemblage, necessitating broader taxonomic and phylogenetic analyses. Nevertheless, preliminary identifications already reveal significant taxonomic and ecological diversity, including two humid-environment, ground-living Hexapoda (Collembola) and a Trichoptera (Hexapoda with aquatic larvae). Among the Diptera, the families Mycetophilidae, Chironomidae (Fig. 3D), Ceratopogonidae (two specimens; Fig. 3C), Phlebotomidae, and Phoridae are represented. The first four of these dipteran families frequently live in humid environments. An adult Coleoptera (Cucujoidea: Sphindidae) is also present (Fig. 3A). These beetles are myxomycophagous specialists, living in forests on, or inside, mold sporocarps. There are also male and female specimens of Hemiptera: Aleyrodidae (Fig. 3E), and two parasitoid Hymenoptera, one Chalcidoidea: Aphelinidae (which live

in Hemiptera [Aleyrodoidea, Aphidoidea, Auchenorrhyncha, Psylloidea, and Coccoidea]), and one Scelionidae, plus four undetermined insects, including a Psocoptera (Fig. 3B). Representatives of the arachnids include at least three species of Acari (Fig. 3F). The numerous microorganisms found in the other amber clasts (Fig. 4) are fungi spores and conidia, cyanobacteria cells (Fig. 4B), eubacteria (Fig. 4A), and a few freshwater green algae. Among hundreds of individual spores and other microstructures, >30 different morphotaxa could be identified (Table 1). These include many previously undescribed species, which need to be studied comprehensively. The overall assemblage of known spore species documents an early and/or middle Miocene age (22), confirming contemporaneity for both this amber and the lithologic unit in which it is found (late early to early middle Miocene age Pebas Formation). A previously undescribed species of *Frasnacritetrus* (Staurosporea), a four-forked spore, is related to the modern genus *Tetraploa* [usually associated with Poaceae (grasses), Cyperaceae (sedges), or some tree species]. The rarity and fragility of these spores recovered from sediments suggest that they could represent contamination by recent *Tetraploa* (22). The presence of this specimen (Fig. 4G) within Miocene amber testifies to definitive occurrence of this genus in the early Neogene and could also indicate greater habitat complexity than might be expected in the dense rainforest-dominated environment suggested by the other amber organisms.

Arthropods and microorganisms play an exceptionally important role in modern terrestrial ecosystems (4), and amber-

Table 1. Microorganisms entrapped in amber from the middle Miocene of Tamshiyacu, nearby Iquitos (northeastern Peru)

Binomen	Higher-level taxon
Mycophyta	
<i>Psiamasporites fusiformis</i> (Salard-Cheboldaeff & Locquin, 1980)	Amerosporae ("Fungi imperfecti" fungal or algal spore)
<i>Inapertisporites clarkei</i> (Kalgutkar & Jansonius, 2000)	Amerosporae ("Fungi imperfecti" fungal or algal spore)
<i>Inapertisporites</i> spp.	Amerosporae ("Fungi imperfecti" fungal or algal spore)
<i>Monosporites</i> cf. <i>magnus</i> (Kalmghutkar, 1993)	Amerosporae ("Fungi imperfecti" fungal or algal spore)
<i>Monosporites</i> sp.	Amerosporae ("Fungi imperfecti" fungal or algal spore)
<i>Hypoxytonites</i> spp.	Amerosporae ("Fungi imperfecti" fungal or algal spore)
<i>Dicellaesporites</i> sp.	Amerosporae ("Fungi imperfecti" = Deuteromycetes)
<i>Dicellaesporites</i> cf. <i>obnixus</i> (Norris, 1986)	Didymosporae (Deuteromycetes)
<i>Dicellaesporites</i> cf. <i>perelongatus</i> (Kalgutkar & Jansonius, 2000)	Didymosporae (Deuteromycetes)
<i>Dicellaesporites africanus</i> (Salard-Cheboldaeff, 1980)	Didymosporae (Ascomycetes)
<i>Dicellaesporites inequabilis</i> (Martinez-Hernandez & Tomasini-Ortiz, 1989)	Didymosporae (Deuteromycetes)
<i>Dicellaesporites longus</i> (Trivedi & Verma ex Kalgutkar & Jansonius, 2000)	Didymosporae (Deuteromycetes)
<i>Dyadosporites</i> cf. <i>minor</i> (Salard-Cheboldaeff & Locquin, 1980)	Didymosporae (Ascomycetes)
<i>Kumarisporites</i> sp.	Phragmosporae (Deuteromycetes)
<i>Reduviasporonites</i> sp.	Phragmosporae (Deuteromycetes)
<i>Multicellites</i> sp.	Phragmosporae (Deuteromycetes)
<i>Pluricellulaesporites</i> sp.	Phragmosporae (Deuteromycetes)
<i>Quilonia</i> spp.	Phragmosporae (Deuteromycetes, 1 sp. cf. <i>Alternaria</i>)
<i>Multicellaesporites</i> sp.	Phragmosporae (Deuteromycetes)
<i>Diporicellaesporites fusoides</i> (Salard-Cheboldaeff & Locquin, 1980)	Dematiaceae (Phragmosporae)
<i>Diporicellaesporites</i> (Elsik, 1968) sp.	Dematiaceae (Phragmosporae)
<i>Dictyosporites</i> (Felix, 1894) sp.	Dictyoporeae (Deuteromycetes)
<i>Polycellulaesporonites</i> (Chandra, Saxena, & Setty, 1984) sp.	Dictyoporeae (Deuteromycetes)
<i>Frasnacritetrus</i> spp.	Staurosporae (Deuteromycetes)
<i>Trilobites</i> sp.	Staurosporae (Deuteromycetes)
<i>Phragmothyrites</i> sp.	Microthyriales (<i>Phragmothyrium</i> , Ascomycetes)
Lichen	
Gen. et sp. indet.	<i>Incertae sedis</i>
Chlorophyta	
<i>Scenedesmus</i> sp.	Scenedesmaceae
Magnoliophyta	
<i>Triporopollenites</i> sp.	Proteaceae

List is sorted by morphographic order for spores (22). Identification was by D.D.F.

preserved specimens provide key paleoenvironmental information for the middle Miocene ecosystems of the western Amazonian Basin. Resin entombment of an organism is a rapid preburial process (4). Further, amber is insoluble in water (3) but with a density close to it (1.04–1.10; Iquitos clast density = 1.06), which allows its long-distance transportation in running water and preservation in various proximal and downstream depositional environments (often associated with wood debris), including delta-plain and/or tidal environments (4). Occurrence of amber containing terrestrial organisms is consistent with previous reconstructions of the depositional environment of the Tamshiyacu sedimentary series (11, 14), accumulating near the shore of a tidally influenced “marine-like megalake” (10). Some amber deposits (notably Baltic amber) are known to be reworked, depending on both their density and the salinity of the transporting water. The Iquitos amber clasts are unlikely to be reworked from much earlier deposits because of the following: (i) the Iquitos resin flows have kept their original shape (Fig. 2B); (ii) several trapped spore taxa have an early to middle Miocene stratigraphical range, indicating contemporaneity with the surrounding sedimentary matrix (Pebas Fm.); and (iii) the composition and aspect of this Amazonian amber precludes the occurrence of any subsequent tectonic deformation and/or sediment burial effect, such as that often observed in reworked ambers (23, 24).

Many recent families of conifers and angiosperms generate resins (25), but only a few of them have been documented to be amber producers (4) through anatomical studies of associ-

ated amber and wood specimens [Pinaceae (17, 26); Caesalpinaceae (27)]. It is currently impossible to identify the specific amber-producing tree(s) for the Iquitos specimens, but the presence of fossil wood and excellent and laterally extensive outcrops suggest that intensive sampling should permit recovery of such connected specimens in the near future. In the interim, however, infrared spectrometry (26), solubility, and chemical properties indicate that the Iquitos amber originates from an angiosperm tree. Resin production is known to have both seasonal and diurnal fluctuations [resin exudations are more frequent during the warm season and in higher daily temperatures (4)]. The alternating bands observed in the Iquitos amber clasts can be inferred to represent successive resin flows, as proposed for similarly banded ambers (18). Periods of intensive amber production have been interpreted to be due to either frequent storm damage to source trees or intense forest fires [notably in relation to periods of drastic paleoenvironmental changes (28)] or to the abundance of mature trees in surrounding forests (23). The preliminary sample is too small to provide unequivocal conclusions regarding which of these causes might have been responsible for the resin exudation forming the Iquitos ambers.

The available insect sample (14 specimens) is sufficiently large to provide several additional paleoecological inferences. As in all other known amber insect associations, Hymenoptera and Diptera: “Nematocera” dominate. This dominance relates to a probable bias of attraction of these insect groups to the resin, particularly with respect to the position of the exudate in the tree or to the behavior

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