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the geothermal system is 41 kg s^{-1} (16). This implies a CO_2 flux of 1.1 kg s^{-1} or an annual flux of $3.5 \times 10^7 \text{ kg year}^{-1}$.

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Fossil Velvet Worms in Baltic and Dominican Amber: Onychophoran Evolution and Biogeography

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Velvet worms identified in Baltic and Dominican amber demonstrate that terrestrial onychophorans were present in the early Tertiary. Characters of the amber fossils are similar to those of the Cambrian *Aysheaia* and the Pennsylvanian *Helenodora*, which suggests that these Paleozoic lobopods are ancestral to extant velvet worms. The presence of slime secretions in the Dominican amber fossil shows that the slime gland-pore complex had developed by the mid-Tertiary and could have been an adaptation to terrestrial life. The Baltic amber fossil shows that the range for this now predominately gondwanan group was expanded in the Tertiary.

Members of the phylum Onychophora or velvet worms have incited debate for years regarding their position in the animal kingdom (1). Traditionally they have been regarded as a sister group to the monophyletic Arthropoda and a link between the Annelida and the Arthropoda, with the Cambrian *Aysheaia* possibly representing an ancient marine ancestor of today's velvet worms and of the entire Atelocerata (Myriapoda and Hexapoda) (2). However, there had not been any intermediate forms connecting the Cambrian *Aysheaia* and *Xenusion* (3–5), and Pennsylvanian *Helenodora* from (6), to present-day onychophorans.

Here, I describe terrestrial velvet worm fossils found in Dominican and Baltic amber and discuss their connection to Paleozoic forms (3, 7) and extant onychophorans. In addition, I will discuss the development of the elaborate slime gland-pore complex found in modern velvet worms, and the implications the Baltic amber fossil has regarding the distribution of onychophorans in the past.

The purple- to black-colored Baltic amber specimen (about 40 million years) (8) (Fig. 1) is represented by 8 mm of the anterior of the body. It contains a pair of antennae and nine pairs of legs. The brownish-tan-colored Dominican Republic amber specimen (20 to 40 million years) (8) (Fig. 2) is represented by 4.38 mm of the anterior of the body. The Dominican amber specimen bears a pair of antennae, oral papillae, and 19 pairs of legs.

One character that connects the two

amber fossils with the Paleozoic forms is the structure of the legs (sac-like, nonjointed extensions of the body). The leg of a typical present-day onychophoran consists of a proximal trunk portion and a dorsal foot portion bearing a terminal pair of claws and associated papillae. In the amber fossils, the foot is lacking and only the trunk is present (Figs. 1 to 3). The claws of the Dominican fossil are attached to the trunk, a condition similar to that reported in *Aysheaia pedunculata* (3) and *Helenodora* (6). This undifferentiated type of leg structure is also reminiscent of that found in some Tardigrada (*Haplomacrotus*) (9). A similarity be-

tween *Aysheaia* and tardigrades has already been proposed (10).

One of the unique characters (and certainly essential for survival) of extant onychophorans is the slime gland and pore complex (1). The slime glands are well developed in relation to the body size of velvet worms. These glands open to the exterior at the oral or slime papillae and produce a water-soluble sticky secretion that is used both to obtain food and for defense. There is no definite evidence of oral papillae in the two species of *Aysheaia* or in *Helenodora*. Slime would have been ineffective in an aquatic environment, and these organs evolved as the animal adapted to terrestrial life (11). The oral papillae are quite distinct in the Dominican amber specimen, and a thick, copious deposit extends from near the openings of each gland (Fig. 3). This deposit is interpreted as slime that had been emitted from the oral papillae as a triggered defense reaction at the time the animal fell into the sticky resin. This fossil establishes a minimum time for the evolution of this slime production system and connects the Dominican fossil to the modern velvet worms.

If the slime gland-pore complex did evolve as an adaptation to invasion of the land, then its primary function (aside from a possible use as a protective coating as the animal became terrestrial) was probably for

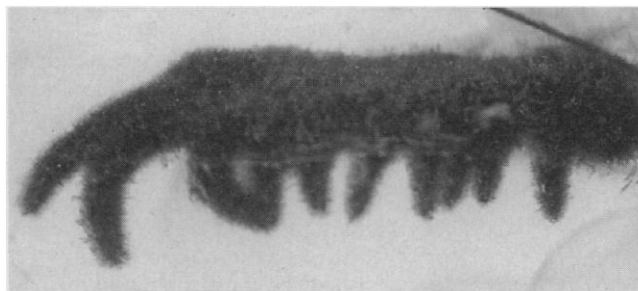


Fig. 1. Lateral view of a fossil onychophoran in Baltic amber (body = 8 mm).

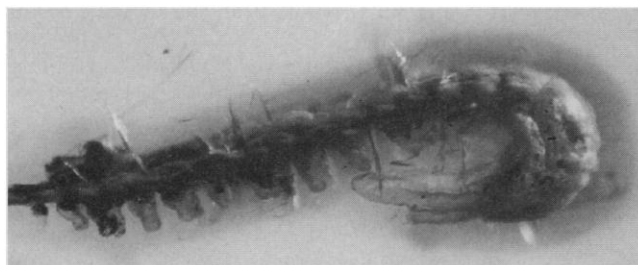


Fig. 2. Lateral view of the right side of a fossil onychophoran in amber from the Dominican Republic (body = 4.38 mm).

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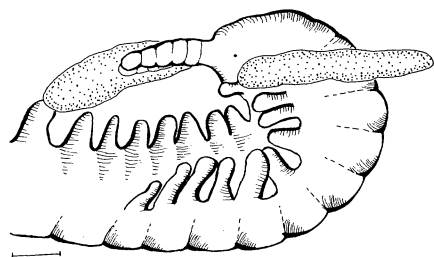


Fig. 3. Illustration of the lateral view of the left side of the fossil onychophoran shown in Fig. 2 (bar = 0.5 mm).

defense. An association of *A. pedunculata* with sponges has been suggested (3), but it is not clear whether *Aysheaia* actually fed on the sponges or scraped material such as algae deposits off the surface of sponges. Early terrestrial forms might have fed on decaying plant and animal matter. Plant remains do occur in the alimentary tract of extant velvet worms (11). At one point in their terrestrial evolution, onychophorans developed predatory habits, at which time the production of slime was used to capture prey.

Velvet worms have always presented an enigma because it was thought that they were not robust enough to survive rafting or transport (12, 13), and the eggs of oviparous forms are not durable (14). Yet, today velvet worms occur on several islands of the Greater Antilles, including Hispaniola (13). There are two basic schools of thought regarding the appearance of animals on the Greater Antilles: dispersion and vicariance. There is no plausible explanation of velvet worm distribution with the dispersal hypothesis, thus it appears that the present distribution supports the vicariance hypothesis: namely, that the velvet worms already formed a portion of the biota that occupied the ancient "proto-Antillean Archipelago" before it moved into its present position as the Greater Antilles (15, 16).

The present distribution of velvet worms is predominately gondwanan (13). Two hypotheses have been proposed to explain this phenomenon (17). The first is that the invasion of land by these creatures occurred in the Southern Hemisphere, whereas the alternative suggests that terrestrial invasion was universal but the environment of the Laurasian land masses somehow became unsuitable for the continued existence of velvet worms. The presence of a fossil velvet worm in Baltic amber provides evidence that these animals existed in northern Europe in the Eocene and indicates that their range was more extensive in the past, possibly even pantropical and pansubtropical.

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Threefold Electron Scattering on Graphite Observed with C₆₀-Adsorbed STM Tips

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The scanning tunneling microscope (STM) has been used to observe threefold symmetric electron scattering from point defects on a graphite surface. These theoretically predicted electronic perturbations could not be observed with a bare metal tip but could only be imaged when a fullerene (C₆₀) molecule was adsorbed onto the tunneling region (apex) of an STM tip. Functionalizing an STM tip with an appropriate molecular adsorbate alters the density of states near the Fermi level of the tip and changes its imaging characteristics.

The STM has recently enabled scientists to image local surface electronic phenomena on the nanometer scale. On metal surfaces, the STM has been used to image scattering of surface-state electrons around point defects and electron interference within and around "quantum corrals" (1). We report the observation of a threefold symmetric electron scattering process around point defects on graphite. These electron scattering patterns are in almost exact agreement with the theoretical predictions of this phenomenon by Mizes and Foster (2). The patterns were observable only when an STM tip had a C₆₀ molecule adsorbed onto its tunneling region. This result shows that molecular functionalization that controls the local density of states of an STM tip can permit the observation of an electronic effect not observable with a bare metal STM tip.

The functionalization of STM tips with C₆₀ to control the electronic interactions between the tip and surface is similar to the attachment of molecules to atomic force microscope tips to control the chemical

forces between the tip and surface (3). However, instead of exhibiting a sensitivity to chemical forces, the tunneling current of the STM is sensitive to the local density of states at the Fermi energy (E_F) of both the surface and the tip. The adsorption of a molecule such as C₆₀ onto an STM tip, which can act as a tunneling site, alters the local density of states of the tip in the vicinity of E_F , thereby modifying the tunneling current and changing the way the tip samples the electronic states of the surface it is imaging.

Resh *et al.* have reported improved atomic resolution on graphite when fullerenes were adsorbed onto STM tips (4). We have also reported the in situ characterization of C₆₀ adsorbed onto the active region of tunneling tips by "inverse imaging" (5). Inverse imaging of the C₆₀-adsorbed STM tips enables one to determine the number of fullerenes in the tunneling region and also shows that the adsorbed fullerene molecule or molecules can function as a tunneling site or sites. Inverse imaging is a robust and highly reproducible method for monitoring the structure of an STM tip at the tunneling junction (6).

To create the fullerene-adsorbed STM tips, we vacuum-deposited a thin fullerene film (100 to 500 Å) onto highly oriented

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