NATURAL HISTORY

Hawaiian caterpillar patrols spiderwebs camouflaged in insect prey's body parts

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Lepidoptera is the most herbivorous of all the insect orders, with predatory caterpillars globally comprising less than 0.13% of the nearly 200,000 moth and butterfly species. Here, we report a species in which caterpillars are carnivorous inhabitants of spider's webs, feeding on the arthropods that they find there. This Hawaiian lineage also boasts an unprecedented and macabre practice of decorating its portable larval home with the body parts of the spider prey it harvests from the web where it resides. Phylogenomic data suggest that the origin of this unique spider cohabitant is at least six million years old, more than one million years older than Hawaii's current high islands. After decades of searching, only one species has been discovered, and it is restricted to 15 square kilometers of a single mountain range on the island of Oʻahu, meaning that other members of the lineage have disappeared from older islands. Conservation action to save this globally unique lineage is imperative and overdue.

Hawaii's geographic isolation has fostered the evolution of an array of unusual invertebrates, including spiders that spear prey from the air (*1*), terrestrial rather than aquatic damselfly nymphs (*2*), caterpillars that hunt snails (*3*), amphibious caterpillars (*4*), and caterpillars that ambush prey (*5*). Now, the "bone collector" caterpillar (Fig. 1) adds an additional dimension with a bizarre housekeeping regimen not reported for any other insect (*6*) and an ecology not recorded elsewhere in the order Lepidoptera. These newly discovered caterpillars are the first known to depend on spider webs, using only those located in tree hollows, logs, or rock cavities and never leaving their immediate vicinity. Carnivorous caterpillars are an extremely rare evolutionary phenomenon, and although caterpillars and spiders are common in the same environments all over the world, only this single caterpillar lineage in Hawaii is known to have made the leap to spider cohabitation.

Bone collector caterpillars crawl through the jumble of web and detritus (Fig. 2) and opportunistically eat any weakened or recently deceased insects they come across (e.g., cached spider prey), even chewing through silk to reach their meal if need be. Because they exclusively rely on cobwebs in enclosed spaces (not sheet webs), they can access the full three-dimensional space of the webs. We have identified body parts belonging to more than six different families of insect attached to the silk caterpillar cases, suggesting that they are adaptable scavengers and predators. In captivity, the caterpillars will attack and eat any live, slow moving, or immobilized insect prey, and they will even cannibalize each other (movie S1). This usually limits one caterpillar per web in the wild because a larger individual would make a quick meal of a smaller neighbor.

When decorating their silken portable cases, the caterpillars are particular. Body parts are carefully measured for size before the caterpillar weaves them into its collection. Each prospective new addition is rotated and probed with its mandibles several times, and parts that are too large are chewed down to a size that will fit its case. If denied access to arthropod body parts in captivity, the caterpillars do not accept other bits of detritus, suggesting that they recognize and exclusively use corpses in nature and that this decoration is important to their survival. Given the context, it is possible that the array of partially consumed body parts and shed spider skins covering the case forms effective camouflage from a spider landlord; the caterpillars have never been found predated by spiders or wrapped in spider silk. Bone collector caterpillars have been recorded from the webs of at least four different species of spider in three different families, none of which is native to Hawaii, so adaptability to non-native elements is likely crucial to their persistence. Many of Hawaii's ecosystems are now dominated by non-native species, and dependence on native spiders would have made the survival of the bone collector lineage even more tenuous. Still, these caterpillars are only rarely encountered; >22 years of fieldwork and >150 field surveys in the area where they occur have yielded only 62 individuals, and most apparently suitable spider webs do not host them.

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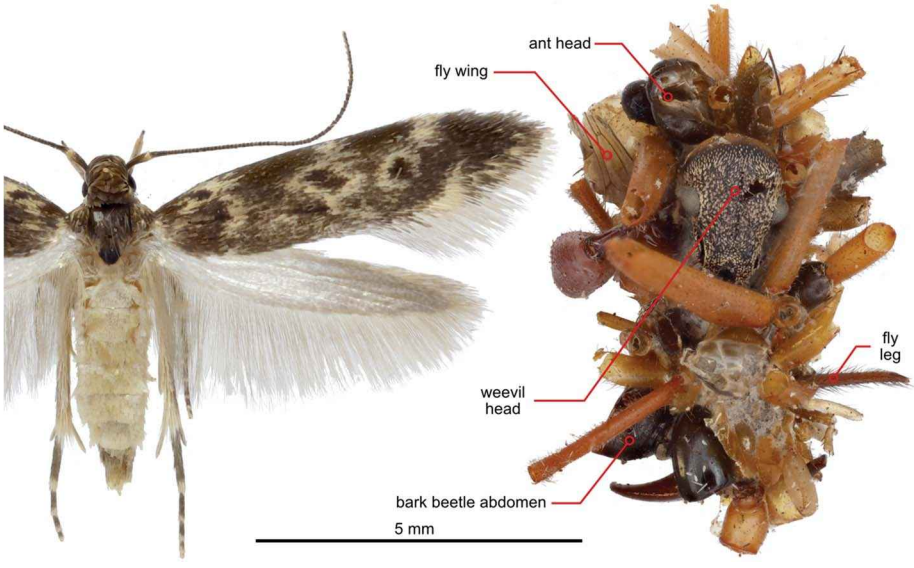

Fig. 1. Pinned adult female (left) of the bone collector caterpillar and portable case (right) in which the larva resides decorated with body parts from ants, bark beetles, weevils, and flies. Unlabeled parts are all host spider integument that has been shed.

Fig. 2. Rotting wood log broken open to expose a bone collector caterpillar resting on a clump of webbing next to a non-native spitting spider (*Scytodes* sp.) with its egg sac. The web is partially obscured by termite and other wood-boring insect frass.

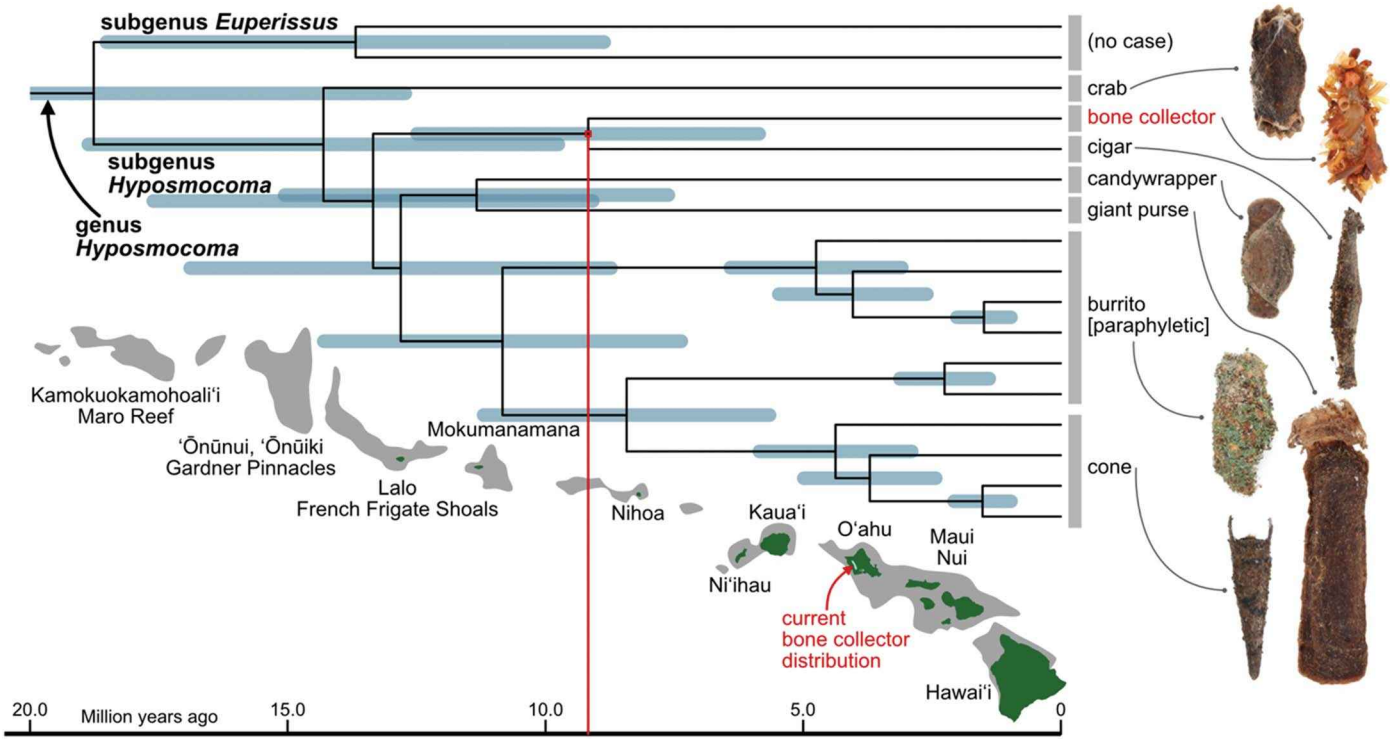

Fig. 3. Molecular phylogeny of *Hyposmocoma* lineages based on 38 genes and 82,875 aligned base pairs. The phylogeny was molecularly calibrated using age estimates from Kawahara *et al*. (*18*); 95% highest posterior density confidence intervals for the molecular dating estimates for nodes are indicated with blue bars. Outgroups are cropped, and the full tree is shown in the supplementary materials. Different lineages are indicated by their larval case type (*8*), and exemplar cases are shown on the right. Bone collector and cigar case species are the only ones that are carnivorous. Current terrestrial areas of the Hawaiian Island chain are shown in dark green; shallows that were once above sea level are shown in gray. The islands are placed along the timescale according to age and geographic position.

Ancient origins

The bone collector caterpillar belongs to *Hyposmocoma*, an endemic genus of small moths that is one of the most ecologically diverse adaptive radiations on the planet and, at 14 million years old, one of Hawaii's oldest (*7*). The genus contains >350 species occurring from the splash zones of the tropical shorelines to frigid alpine deserts on volcanic slopes >3200 m high, with each species typically restricted to a part of a single volcano on a single island (*8*, *9*). As shown by phylogenomic inference from 38 loci and subsequent molecular dating, there are nine major lineages of *Hyposmocoma*, most between 9 and 15 million years old, far older than the oldest current high island of Kaua'i (Fig. 3). The bone collector species is the only one known of its kind, representing a monotypic lineage without a sister species. Although it is related to the other carnivorous lineage of *Hyposmocoma*, their ancestors diverged more than 5 million years ago.

Uncertain future

Hawaii is an "extinction capital" of the world, with ongoing catastrophic losses of endemic flora and fauna [e.g., (*10*)]. This phenomenon extends to the archipelago's endemic invertebrate species, although their disappearances have gone largely undocumented. Despite >100 years of entomological surveys, the bone collector species has only been found in a 15-km^2 area of mesic forest in the Wai'anae mountain range on the island of O'ahu. Typically, an endemic Hawaiian lineage will contain multiple species with similar habits distributed across at least part of the archipelago [e.g., (*11*, *12*)], but no other member of the bone collector lineage has been found. Phylogenomic analysis shows that the bone collector lineage is at least 6 million years old, >3 million years older than the island of O'ahu (Fig. 3) (*13*). This suggests that the bone collector lineage once occurred on older islands such as Kaua'i or Nihoa, from which an ancestor dispersed to O'ahu. This ecology likely evolved on a now-subsided island in the Northwest Hawaiian Island chain, as did many lineages of *Hyposmocoma* (*8*) and other Hawaiian insects [e.g., *Drosophila* (*14*, *15*)]. The current range of the bone collector lineage is now limited to a single species holding on in a fragment of isolated forest that is increasingly beset with invasive species, exemplifying the vulnerability of many endemic Hawaiian insects and the ecosystems on which they depend. Although the bone collector species is able to use non-native spider hosts, it is still rarely found and its range is limited to a small area on one mountain on a single island. Population numbers may not be stable, and many factors leading to native insect decline in Hawaii (*10*) may also be affecting it, including introduced predators such as ants and parasitic wasps. It is unclear when bone collector caterpillars may have disappeared from Kaua'i, but it was before they could be discovered and may have been due to anthropogenic causes, as has been the case with most of Hawaii's historic extinctions [e.g., (*16*)]. Without conservation attention, it is likely that the last living representative of this lineage of carnivorous, body part–collecting caterpillars that has adapted to a precarious existence among spider webs will disappear.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
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MDAR Reproducibility Checklist
Movie S1

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