NATURAL HISTORY

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

Daniel Rubinoff*, Michael San Jose, Camiel Doorenweerd

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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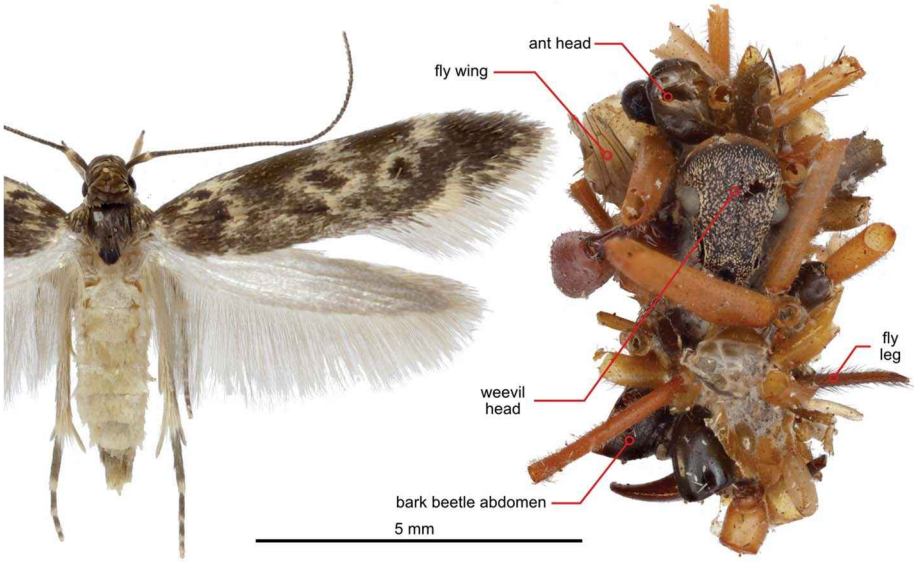

Fig. 1. Pinned adult female (left) of the bone collector caterpillar and portable case (right) in which the larva resides decorated with body parts from ants, bark beetles, weevils, and flies. Unlabeled parts are all host spider integument that has been shed.

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.

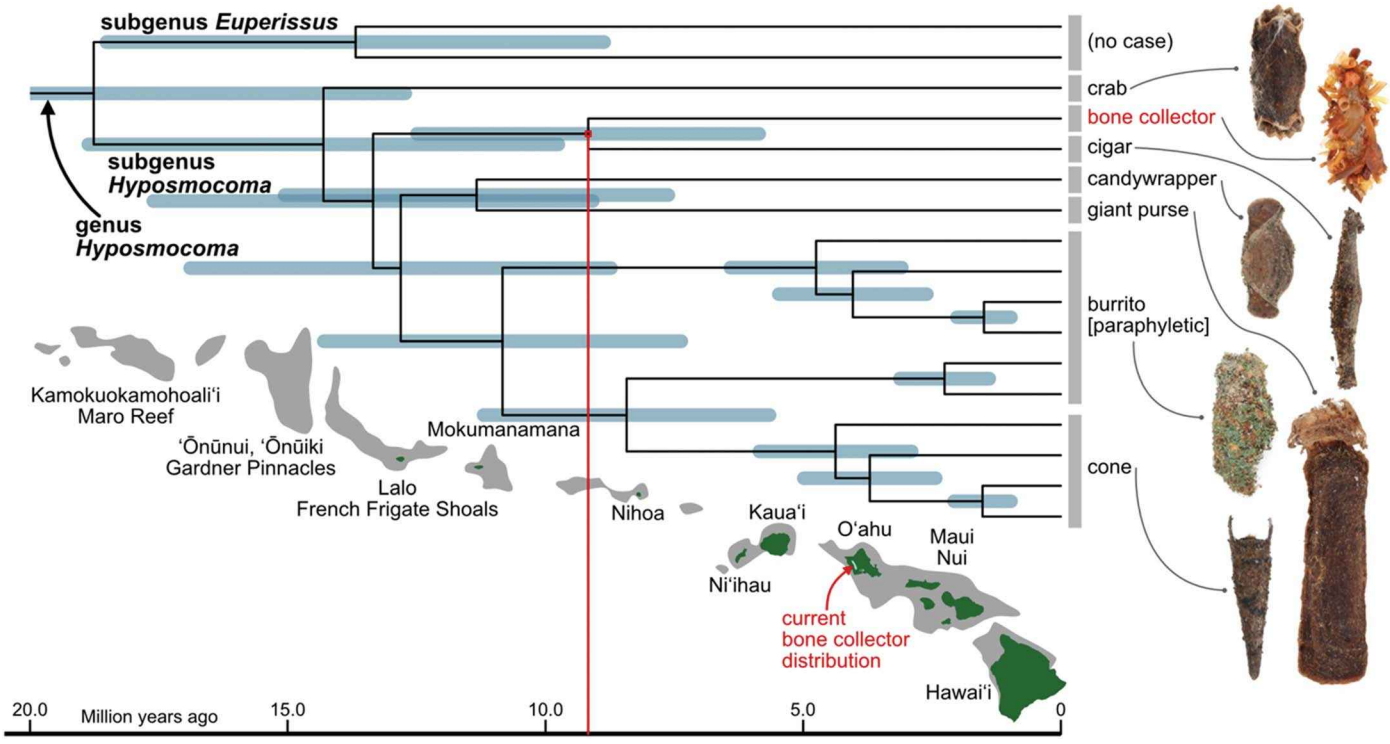

Fig. 3. Molecular phylogeny of *Hyposmocoma* lineages based on 38 genes and 82,875 aligned base pairs. The phylogeny was molecularly calibrated using age estimates from Kawahara *et al*. (*18*); 95% highest posterior density confidence intervals for the molecular dating estimates for nodes are indicated 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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19. Data for: A. Kawahara *et al*., Phylogenomics reveals the evolutionary timing and pattern of butterflies and moths. Dryad (2019); https://doi.org/10.5061/dryad.j477b40.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.ads4243
Materials and Methods
Fig. S1
Table S1
References (*20*–*30*)
MDAR Reproducibility Checklist
Movie S1

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10.1126/science.ads4243

Materials Design Analysis Reporting (MDAR)
Checklist for Authors

The MDAR framework establishes a minimum set of requirements in transparent reporting applicable to studies in the life sciences (see Statement of Task: doi:10.31222/osf.io/9sm4x.). The MDAR checklist is a tool for authors, editors, and others seeking to adopt the MDAR framework for transparent reporting in manuscripts and other outputs. Please refer to the MDAR Elaboration Document for additional context for the MDAR framework.

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Materials:

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The manuscript includes a dedicated "materials availability statement" providing transparent disclosure about availability of newly created materials including details on how materials can be accessed and describing any restrictions on access.	Data statement section	

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Cell lines: Provide species information, strain. Provide accession number in repository **OR** supplier name, catalog number, clone number, **OR** RRID.		x
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Animal observed in or captured from the field: Provide species, sex, and age where possible.	Supplementary material table S1	

Plants and microbes	indicate where provided: page no/section/legend)	n/a
Plants: provide species and strain, ecotype and cultivar where relevant, unique accession number if available, and source (including location for collected wild specimens).		x
Microbes: provide species and strain, unique accession number if available, and source.		x

Human research participants	indicate where provided: page no/section/legend) or state if these demographics were not collected	n/a
If collected and within the bounds of privacy constraints report on age, sex and gender or ethnicity for all study participants.		x

Design:

Study protocol	indicate where provided: page no/section/legend)	n/a
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Randomisation		x
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Studies involving human participants: State details of authority granting ethics approval (IRB or equivalent committee(s), provide reference number for approval.		x
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Attrition	indicate where provided: page no/section/legend	n/a
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Statistics	indicate where provided: page no/section/legend	n/a
Describe statistical tests used and justify choice of tests.	Material and Methods	

Data availability	indicate where provided: page no/section/legend	n/a
For newly created and reused datasets, the manuscript includes a data availability statement that provides details for access or notes restrictions on access.	Data statement	
If newly created datasets are publicly available, provide accession number in repository **OR** DOI **OR** URL and licensing details where available.	Data statement	
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Code availability	indicate where provided: page no/section/legend	n/a
For all newly generated custom computer code/software/mathematical algorithm or re-used code essential for replicating the main findings of the study, the manuscript includes a data availability statement that provides details for access or notes restrictions.		X
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MDAR framework recommends adoption of discipline-specific guidelines, established and endorsed through community initiatives. Journals have their own policy about requiring specific guidelines and recommendations to complement MDAR.

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Supplementary Materials for

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

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The PDF file includes:

Other Supplementary Material for this manuscript includes the following:

Materials and Methods

Taxon Sampling and DNA extractions

Genomic data from 16 species of *Hyposmocoma* were used for this study. *Hyposmocoma* were collected as larvae and reared following protocols from (*8*). Collecting permits were granted on a yearly basis from the Hawaii Department of Fish and Wildlife. Emerged adult moths were pinned, spread, and abdomens dissected and incubated in Macherey-Nagel T1 buffer and proteinase K for two hours up to overnight. Digested abdomens were then removed for morphological studies, and digested tissue was treated with RNAse. DNA purification was performed using the Macherey-Nagel NucleoMag kit on an OT-2 liquid handler (Opentrons Labworks, Brooklyn, NY). Extracted DNA was quantified using a Qubit fluorometer (Fisher Scientific, Waltham, MA).

DNA Sequencing

DNA extracts with > 5 ng/µl of double-stranded DNA were selected for whole genome resequencing. Illumina DNA libraries were prepared using NEBNext® Ultra™ II DNA Library Prep Kit using unique dual index primers from the NEBNext® Multiplex Oligos for Illumina® (New England Biolabs, Beverly, MA). Illumina sequencing was conducted at either the University of California Berkeley Genomics core facility using a HiSeq 2500 PE150 or at Novogene using an Illumina NovaSeq PE150. Raw reads are available on NCBI Genbank Bioproject PRJNA1143550.

Bioinformatics

In addition to our own data, we used sequence data from ten outgroup species from Gelechioidea, Pterophoroidea, and Alucitioidea from a previously published phylogeny (*18*) to establish an external calibration point for molecular dating. We cleaned and demultiplexed raw sequencing reads using the program BBduk from the package BBtools (*20*) prior to the alignment of our data to the published data. We used the program HybPiper v2.1.6 (*21*) to map and assemble reads corresponding to the loci used in (*18*). First, amino acid reference sequences from *Danaus plexippus* used in (*18*) were downloaded from the supplementary materials (doi:10.5061/dryad.j477b40). These sequences were then checked for low-complexity regions using the command "check_targetfile", any low-complexity loci were removed using the command "fix_targetfile". Loci that passed this filtering were then used as targets for extracting coding sequences from our clean reads. We assembled DNA sequences for each sample using the command "assemble" to map and assemble cleaned reads to the target *D. plexippus* loci in HybPiper. Sequences for each locus from each sample were extracted from assembled reads using the "retrieve_sequences" command in HybPiper.

Alignment, dataset generation, model selection, tree inference, and branch support

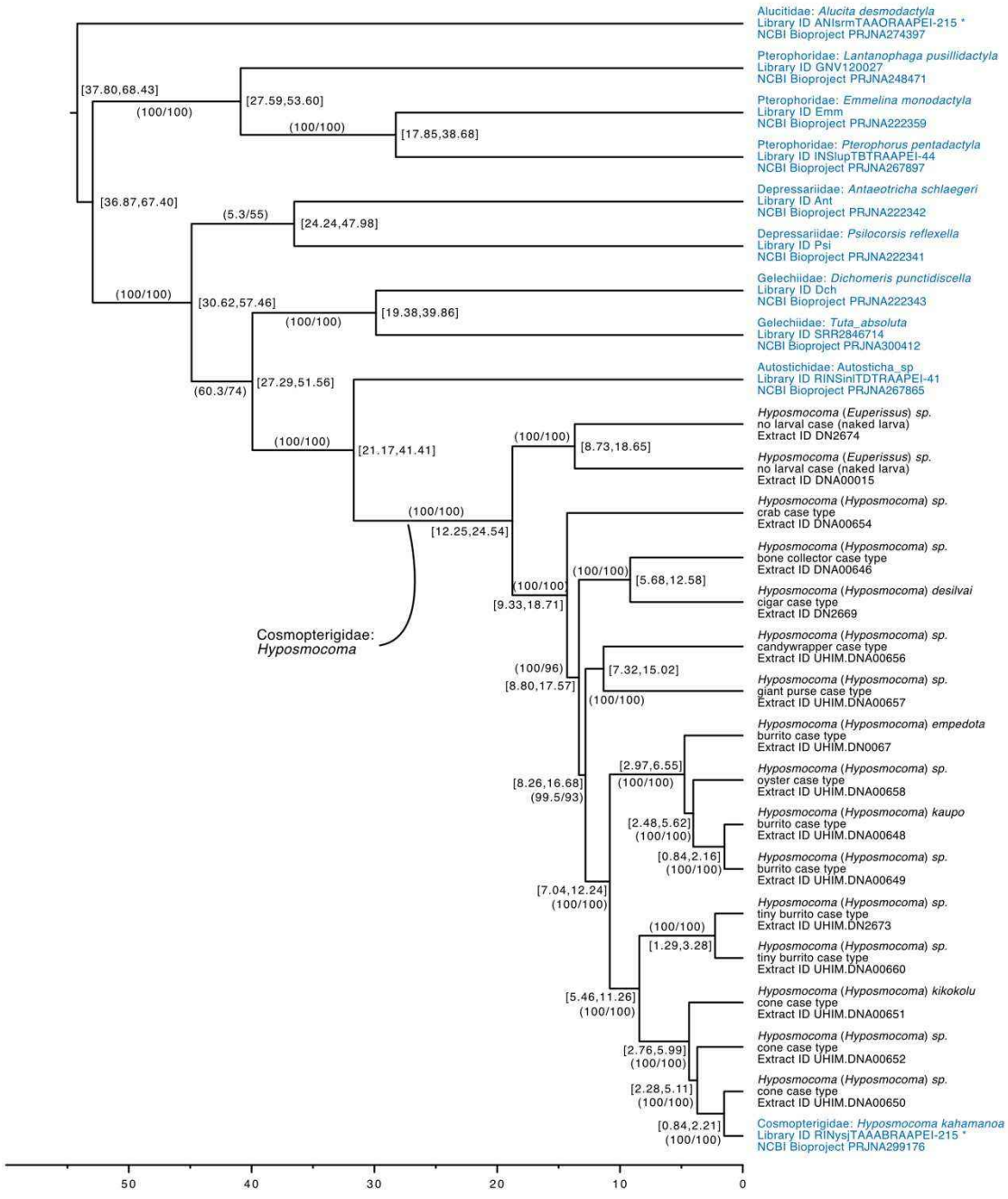
The HybPiper-assembled loci for *Hyposmocoma* and sequences from Gelechioidea, Pterophoroidea, and Alucitiodea from (*18*) were concatenated and aligned using MAFFT v7.520 (*22*) with the L-INS-I algorithm. To reduce the amount of missing data, we only used loci found in all *Hyposmocoma* samples. We used ModelFinder (*23*) implemented in IQ-TREE v2.2.3 (*24*) to infer the most likely model for the concatenated dataset using the Bayesian information criterion. We then used IQ-TREE to infer a maximum likelihood tree from the concatenated dataset. We conducted ten runs of IQ-TREE to find the most likely tree and assessed branch

support using two methods: the Shimodaira-Hasegawa-like approximate likelihood ratio test (*25*) and Ultrafast bootstrap support (*26*), with 1,000 replicates each.

Divergence time estimation

Because our dataset was too large to use in Bayesian divergence time estimation programs, we used the approximate likelihood method implemented in MCMCTree, part of the PAML software package, v4.9 (*27*), to estimate divergence dates in *Hyposmocoma*. We used the same DNA dataset used in the maximum likelihood analyses. We used the ModelFinder results on the concatenated dataset to select the most appropriate substitution model for dating analyses, which was the HKY model. The input tree topology from our partitioned ML analyses was time-calibrated using a single secondary root calibration with a lower bound of 37 Ma and an upper bound of 68 Ma, which is within the 95% confidence interval for the age of the Cosmopterigidae node in the dating analyses from (*18*). While the use of secondary calibrations is not ideal for divergence time dating (*28*), (*29*) found that the practice of increasing datasets to include primary calibrations produced divergence times with similar accuracy to secondary calibrations. We ran MCMCtree with a single chain for 20 million generations, sampling every 2,000 generations with a burn-in of two million generations and checked the posterior distribution for convergence using Tracer v1.4 (*30*).

Figure S1.



Un-cropped time calibrated molecular phylogeny. Scale bar indicates millions years ago. Bracketed numbers indicate the 95% highest posterior density of age estimates for the nearest node. Branch supports are given in parentheses along the respective branches; a-LRT values followed by Ultrafast bootstrap. Taxa indicated in blue indicate sequence data from (*18*) was used, for the remainder the sequence data was produced in this study.

Table S1.

Extract identifier	*Hyposmocoma* Species	Collecting locality	Date (yyyy-mm-dd)	Collector(s)
DNA00657	*H. sp.*	Lanaʻi, Puhielelu	2015-05-01	S. L. Montgomery
DNA00651	*H. kikokolu*	Nihoa, East Palm	2015-06-04	J. Sprague
DNA00015	*H. sp.*	Kauaʻi, Alakaʻi Swamp	2020-07-20	D. Rubinoff, R. Rubinoff, C. Doorenweerd
DNA00650	*H. sp.*	Kauaʻi, Hono o Nā Pali Natural Area Reserve	2018-03-20	W. Haines
DN0067	*H. empedota*	Oʻahu, Wiliwilinui Ridge Trail	2008-08-12	P. Schmitz, W. Haines, J. Kameoka, D. Nitta
DNA00649	*H. sp.*	Hawaiʻi, Pohakuloa	2016-04-27	W. Haines
DNA00658	*H. sp.*	Maui, Makawao Forest Reserve	2015-05-03	S. L. Montgomery, M. Bryce
DNA00660	*H. kukilakila*	Maui, Haleakalā National Park	2017-05-09	R. Kaholoaa
DN2669	*H. desilvai*	Maui	2010	
DN2674	*H. sp.*	Maui	2010	
DNA00652	*H. laysanensis*	Gardner Pinnacles	2016	C. Bird
DNA00648	*H. kaupo*	Maui, Kahikinui Forest Reserve	2018-03-26	F. Starr, K. Starr
DNA00646	"bone collector"	Oʻahu, Palikea	2016-04-16	D. Rubinoff
DNA00654	*H. sp.*	Kauaʻi, Kokeʻe	2015-09-01	S. L. Montgomery
DN2673	*H. sp.*	Maui	2010	

Collecting details on the specimens used for DNA sequencing.

Movie S1.

https://www.youtube.com/watch?v=J6JJSDQeKe8. Bone collector cases are cannibals. The video shows two bone collector caterpillars, with one attacking the other by biting a hole in the side of its silken cocoon, entering inside and killing and eating it.

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