ABSTRACT: The terrestrial meiofauna of the Hawaiian islands is almost completely unknown to science. Water bears (Tardigrada) represent a phylum that seems preadapted for long distance dispersal to the Hawaiian islands, and here we present, for the first time, 31 species in 10 genera and four families. The diversity of species in an area smaller than 50 square miles means that the Haleakala site is the most tardigrade-rich location yet found on the planet. These species occupy a highly specialized niche in the Central Crater District of Haleakala National Park that involves alpine and subalpine cryptogams subject to extremes of temperature and desiccation. Several of the Hawaiian species are capable of anhydrobiosis, which is probably the mechanism that allows their occupation of alpine habitats. We present arguments that suggest that the richest habitats for Hawaiian water bears will be in subalpine and alpine settings of Maui and Hawai'i.
INTRODUCTION

The biota of the Hawaiian islands attracts biologists because of its diversity. We have all come to expect new and exciting things here; new species being among the more engaging discoveries. We report here a first glimpse of a fascinating phylum that has until now passed generally unnoticed in Hawaiian biology. The phylum is Tardigrada, comprised of small (50 to 1200 micron) creatures usually called water bears because of their appearance and deliberate "pawing" form of locomotion. They are part of the meiofauna (literally "small animals") loosely defined as any multicellular organism below about 2 mm in body length.

It is generally unknown among the scientific community in the Hawaiian islands, that tardigrade specialists have examined Hawaiian specimens and identified them. However, the most recent catalog of world tardigrades (Ramazzotti & Maucci, 1983) lists only five species from the Hawaiian archipelago: Bryocherus intermedius f. hawaiica (Thulin, 1929) from O'ahu, Echiniscus (?)perarmatus (Murray, 1907) from O'ahu, E. spinulosus (Doyere, 1840) from Hawai'i, E. viridus (Murray, 1910) from Hawai'i, and Macrobiotus crassidens (Murray, 1907) from O'ahu. All told, fewer than 500 species of tardigrades have been described in the world fauna.

The taxonomic position of water bears has long been argued (e.g., Morgan & King, 1976). They show some features of annelidan-arthropodan metamerism, but also show aspects of embryological development and final coelom structures more typical of nematodes or bryozoans. Tardigrades are free-living, and aquatic, but usually require only the thin film of water associated with mosses and other cryptogams, the habitat from which the majority of the world's species have been reported. Marine forms can also be found in capillary water between grains of sand. Water bears are generally plant feeders, piercing moss leaflet cells and sucking the contents by pharyngeal pumping. Some species prey on other small metazoans, likewise piercing and sucking the fluids of their victims.

MATERIALS AND METHODS

Tardigrades were collected in the course of a general survey of arachnids and associated arthropods of the Central Crater District of Haleakala National Park during July of 1985. Dry mosses and lichens were collected in plastic bags. Wet mosses were placed in
70% ethanol. Slurries of moss, detritus and soil from standing pools were filtered through a 44 micron screen, and the captured material was placed in 70% ethanol. All samples were sent to the Bohart Entomology Museum at the University of California at Davis, where the tardigrades were isolated and prepared using methods described in Horning, Schuster and Grigarick (1978). Representative specimens were slide mounted and photographed for this presentation. Detailed taxonomic work will entail preparing specimens for Scanning Electron Microscopy (SEM) at the University of California.

RESULTS

Thirty one species of Tardigrada in 10 genera and four families were identified to genus (Table 1). Among the specimens was a cosmopolitan species, Milnesium tardigradum Doyere, a predator. Because of a dearth of taxonomic specialists, and a poor understanding of the systematics and biogeography of Tardigrada, it is not yet possible to determine which of the Haleakala water bear species are new to science, and which are Hawaiian endemics. For example, some of the species collected resemble those known only from such localities as Finland, Tennessee, California and South America.

The four families of tardigrades encountered in the Maui sample are Echiniscidae, Milnesiidae, Macrobiotidae and Hipsibiidae. The Echiniscidae are easily recognized by the presence of dorsal plates, The Milnesiidae are best recognized by the presence of two cephalic cirri (whip-like sensory organs). Both the Macrobiotidae and Hipsibiidae lack cephalic cirri, and are distinguished by the patterns of their claws; Macrobiotidae with a 1-2-2-1 pattern, and Hipsibiidae showing a 2-1-2-1 pattern of claws per foot.

The number of species discovered by our brief survey is large when compared to the faunal diversity of other localities. For example, Puerto Rico has 8 species, the Galapagos islands show 15 species, the Dominican Republic shows 16 species, and New Zealand (including both North and South Island) shows 55 species. The state of California, which has received special attention from tardigrade specialists, shows more than 40 species. Pennack (1978) reported only 70 species from the United States as a whole.

Type specimens have been deposited at the Bohart Entomological Museum, Department of Entomology, University of California at Davis.
TABLE 1: Preliminary List of Tardigrada in the Central Crater District of Haleakala National Park, Maui, Hawaiian Islands.

<table>
<thead>
<tr>
<th>FAMILY</th>
<th>GENUS</th>
<th>NUMBER OF SPECIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milnesiidae</td>
<td>Milnesium</td>
<td>1</td>
</tr>
<tr>
<td>Macrobiotidae</td>
<td>Dactylobiotus</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Minibiotus</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Macrobioptus</td>
<td>5</td>
</tr>
<tr>
<td>Hypsibiidae</td>
<td>Doryphoribius</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Calohypsibius</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Diaphascon</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Hypsibius</td>
<td>1</td>
</tr>
<tr>
<td>Echiniscidae</td>
<td>Echiniscus</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>(arctomys group)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(other groups)</td>
<td>10</td>
</tr>
</tbody>
</table>
DISCUSSION

There are several reasons to believe that the Haleakala sample is not a complete representation of the Hawaiian tardigrade fauna. Only subalpine and alpine habitats were sampled, within an area of less than 50 square miles. No samples from wetter native ecosystems have been collected. For the taxonomic groups native to the Hawaiian islands, island endemism is the rule (Zimmerman 1948, Carlquist, 1972). Archipelago-wide distributions are the exception. If that pattern applies to tardigrades, then the number of water bears found in the Hawaiian islands may exceed 100 species. That would mean that Hawaiian species would represent more than 20% of the presently known world tardigrade fauna. Even if no further sampling were conducted, the Maui sample represents the highest known diversity of tardigrades per unit area on the planet. Why this should be the case is an open question.

It is not surprising that the Hawaiian water bears have escaped notice for so long. Being microscopic, they are not detected immediately in the field, but only after extraction and preparation in a laboratory setting. However, like other cryptic Hawaiian species, such as cave spiders, and flightless, nocturnal crickets of boulder beaches, the endemic Hawaiian water bears of Haleakala are the dominant species of their specialized habitat: periodically wet, subalpine cryptogams.

Anhydrobiosis:

When the moss habitats of water bears undergo drying, many species of tardigrades have the unusual ability to assume an inactive, resistant state called anhydrobiosis, literally "life without water". This reduced, nearly dehydrated state, may persist for months or years. In anhydrobiosis, water bears have resisted experimental conditions including strong brine solutions, and extremely low temperatures (190 degrees C below zero) (see review in Pennack, 1978). One can hardly think of a biological state more conducive to surviving a long voyage over the sea, for example, in the world's jet streams.

Vagility, Limiting Habitats and Endemism:

The great potential vagility of water bears is reflected in part by the cosmopolitan distribution of the "weedy" species, Milnesium tardigradum, and Macrobiotus hufelandii. However, it does not follow
that potential vagility is realized, and there are many species of tardigrades with limited geographical distributions. We know nearly nothing about the biology of Hawaiian water bears, especially with regard to their ability to compete with other organisms in their habitats. The preliminary data from Haleakala National Park shows that the greatest diversity of tardigrade species were from habitats that were dessicated much of the time: Rhacomitrium moss in unweathered 'a'a above 'Oili Pu'u. It is very interesting to add that in Britain, Rhacomitrium mosses are very poor tardigrade habitat (Morgan and King, 1976). This suggests that Hawaiian tardigrades may have been forced to shift adaptively to what was otherwise an inappropriate host.

Permanently wet habitats (as the spring behind Kapalaoa Cabin, or at Waikane Spring in Kaupo Gap) generally yielded a subset of the same species found in the dry habitats, and were never among the richest sites. Water was evidently not a limiting factor. Instead, the lack of water might limit those organisms incapable of anhydrobiosis, leaving the water bears with free reign as the dominant species, sharing the habitat with some very hardy nematodes, protists and bacteria (which also are capable of anhydrobiosis).

The implication is that wetter habitats may not prove to be the richest for Hawaiian tardigrades. Instead, habitats which are water-limiting to a majority of organisms, may be the best niches for Hawaiian species. In particular, we suspect that supra-alpine, alpine and sub-alpine habitats of Mauna Kea, Mauna Loa, Hualalai and Haleakala will each show their series of endemic species. Analogous systems at lower altitudes, for example, recent lava flows dominated by Stereocaulon vulcani, may prove to be rich water bear habitats. Thus, the sea-level to summit altitudinal coverage of both Haleakala and Hawai'i Volcanoes National Park provides an excellent setting for continued studies of tardigrades. In addition, we suggest that biologically water-limited habitats such as high-acid Rhacomitrium bogs might also yield a fascinating collection of water bears, probably with a unique assemblage of species not found in drier sites.

The significance of the new tardigrade fauna lies in what they can teach us about several aspects of evolution in the Hawaiian setting. They offer a study of habitat specialization, of diversification when released from competition or predation, and of the role of vagility in distribution between and within islands.
CONCLUSIONS

The finding of 31 species of Tardigrada in one short sojourn is a promising indication of the species remaining on other islands and other habitats. Bear in mind that the 31 species represent 6% of the known world fauna. The Central Crater District of Haleakala National Park already stands as the richest single locality for Tardigrada on the planet. Its unique status underscores the biological resource represented by the National Parks, and lends credence to the ecosystem approach for species management (for despite our ignorance of the species until this study, the National Parks have served to protect their habitats). The public appeal that water bears evoke may enhance education/interpretation efforts in the parks. To show the Mars-like environment of a lava field, coupled with the almost extra-terrestrial appearance of a water bear may be an effective introduction to a world unseen by the casual observer, but protected and preserved by the existence of a National Park.

ACKNOWLEDGEMENTS

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LITERATURE CITED


