SANTA MONICA MOUNTAINS NATIONAL RECREATION AREA INVERTEBRATE INVENTORY

TARDIGRADES SUBMITTED DEC. 1ST, 2009 BY FRESNO CITY COLLEGE

Carl Johansson

Introduction:

In response to a call for proposals for invertebrate studies of in the Santa Monica Mountains, issued jointly by the National Park Service, and the Santa Monica Mountains fund, Fresno City College was fortunate enough to be awarded a grant to inventory the Santa Monica Mountains National Recreation Area (SMMNRA) and surrounding areas for tardigrades.

Fresno City College (FCC) has been actively involved in sampling, collecting, cataloging and identifying tardigrades of North America since January of 2006. During that time FCC has built the largest known collection of tardigrades in North America, with over 12,000 specimens being collected identified, mounted onto slides or processed for DNA analysis. The SMMNRA specimens are entered into that database, with the slides, photographs and databases being deposited at the Philadelphia Academy of Natural Sciences (http://www.ansp.org/), which will house not only the physical slides and data, but will also host an on line accessible interactive tardigrade database, scheduled to become active in July of 2010.

Three surveys were conducted on different areas of SMMNRA and surrounding localities, between February 13th and June 29th 2009.

THE PHYLUM TARDIGRADA

The phylum Tardigrada is a little known, little studied group of microscopic metazoans that range from 150-1000 microns in length. Goeze, who first discovered them in 1773, referred to them as "kleiner wasser bär" or "little water bears" to describe their lumbering movement. Spallanzani (1776) named them "il Tardigrado" or "slow stepper".

The animals are generally ventrally flattened and dorsally convex (Dewel et al. 1993). The five segmented body is composed of a cephalic and four trunk segments. Each trunk segment supports a pair of legs, which are terminated in claws secreted by glands at its base. The taxonomy of tardigrades is based on morphology. The presence or absence of cephalic appendages and body armor separates the two major classes, the armored Heterotardigrada (Fig. 1.A.) and the unarmored Eutardigrada (Fig. 1.B) (Ramazzotti & Maucci 1983). The size, shape, and number of plates, appendages, claws, and mouthparts are used to distinguish levels of classification. Tardigrades lack a circulatory or respiratory system. They have a single (unpaired) gonad, are usually gonochoristic (rarely hermaphroditic) and in some cases parthenogenetic. Ornamented eggs (Figure 1.C.) are laid freely in the environment, whereas smooth eggs are deposited into the molted cuticle by some species (Kinchin 1994).



Figure 1. A. Heterotardigrade, B. Eutardigrade, C. tardigrade egg.

Limno-terrestrial tardigrades change stages of life in response to environmental stresses. In the active stage they move about, eat, grow, and reproduce. In times of excessive water (rain or flood) they swell into the asphyxia stage, become turgid, but survive until the water subsides. As their habitat desiccates they enter the cryptobiotic stage, shrivel to 1/3 original size, and have survived temperatures between –272C and +150C, 160,000 PSI of pressure, pure vacuum, high concentrations of gases and radiation (Crowe, 1975). The cryptobiotic stage has been recorded to last over 100 years and is described as the reversible suspension of metabolism (Kinchin, 1994). Cryptobiotic tardigrades are suspected of being distributed by wind (Miller, 1997).

Tardigrades are found on every continent, in marine, freshwater and terrestrial habitats such as sand, algae, aquatic vegetation, moss, lichen, soil, and leaf litter. They are known to occur from high altitude to abyssal depths. Tardigrades are herbivorous on bacteria, algae, mosses, and lichens or carnivorous on protozoans, rotifers, nematodes, mites, and other tardigrades.

Present status of tardigrade research: The literature comprises about 2500 published papers, most of which are in small, low volume, and difficult to locate journals. In about half of the papers, the tardigrade is but a note. Doyère wrote the first review in 1840, but it was Plate (1889) who classified them as primitive arthropods. Marcus (1929, 1936) identified 274 species and raised them to a class of arthropods. Ramazzotti (1962, 1972) elevated them to a phylum. In 1983, Ramazzotti and Maccui authored the most recent monograph, listed 514 species, and included the systematic ideas of Pilato (1969) and Schuster et al. (1980). Over a dozen new genera and 450+ new species have been described since Ramazzotti and Maccui (1983) (for example: Biserov, 1998; Claxton, 1998; Dastych, et al., 1998; Miller et al., 1995). The last and current monograph is a product of its time, it is text based on original descriptions and illustrations, and incorporates no data standardization beyond alphabetical order.

Present status of tardigrade research in North America: Compared to the 500+ species known from Europe (McInnes 1994), an area of much smaller size and diversity of habitat, it must be assumed there are many more species of tardigrades in North America than have been identified. It is highly likely that many of them are new to science. Such knowledge will add to our understanding of diversity, distribution and habitat requirements. As for the global data snapshot of the Phylum Tardigrada, the United States is still a black box.

Significance of Limno-Terrestrial Tardigrades: Tardigrades are lumped into the "Minor" phyla and treated as lacking economic or ecological importance (Madder, 1990; Hickman et al., 1998). Tardigrades are part of a large un-quantified path in the nutrient cycle of the planet. Tardigrades consume bacteria, algae, vascular plants, and microscopic animals. Mites, collembolans, insect larva, rotifers, nematodes, and other tardigrades in turn consume them. Krantz, Benoitt, & Beasley (1999) demonstrated that tardigrades carry plant pathogenic bacteria in their gut and suggested that in cryptobiotic distribution they may be an unrecognized vector. The physiological process of cryptobiosis, the reversible suspension of metabolism in response to environmental conditions such as: heat, cold, and humidity, is of interest for applications in medicine, aging, and space travel.

Preliminary studies in both temperate and tropical forests indicate that tardigrades are widely dispersed in the canopy (Miller, 2004). Steiner (1994a, b, c) and Hohl et al. (2001) demonstrated the value of tardigrades as environmental indicators, showing changes in tardigrade density and diversity relative to sources of pollution. Lichens and mosses are well known bioindicators of air quality; perhaps tardigrades, which live and feed on them, respond even quicker (Conti & Cecchetti, 2001; Onianwa 2001). In terms of phylogeny, biomass, economic contribution, vectors, trophic level energy transfer, food web relationships and role in ecosystem functioning our knowledge of tardigrades is inadequate. This dearth of information limits our understanding of the importance of these organisms and their contributions to global biodiversity and ecosystem stability.

The proposed project will systematically gather data on the distribution, diversity, and phylogeny of tardigrades in the United States and by inference North America and introduce many students to an animal for which novel observational discovery is still common.

SMMNRA Results:

Tardigrades were retrieved from ten of the eleven sites surveyed, yielding 1,180 specimens. Results for each genus are as follows: Genus Echiniscus is represented with two species E. arctomys grp. and E. postojnensis with seventy-six mounted, four exuvia mounted, thirty-one prepared for SEM photography and twenty-nine prepared for DNA analysis. Genus Isohypsibius is represented by five species I. bakonyiensis, I. deflexus, I. marcellinoi, I. solidus and an undetermined species with twenty-five, six prepared for SEM photography and eight prepared for DNA analysis. *Isohypsibius* is often undeterminable based on a lack of eggs, and presence of gibbosites which are used to identify species. Genus *Macrobiotus* is represented by eight species *M. harmsworthi grp*, M. coronatus, M. hufelandi grp., M. islandicus, M. mauccii, M. montanus, M. ovidii, M. richtersi and an undetermined species with 313 mounted, forty-nine eggs mounted, 108 prepared for SEM photography and 151 prepared for DNA analysis. Genus Macrobiotus is a very common, cosmopolitan genera, hence the large number collected. Eggs are required for some particular species, contributing to lack of identification. Genus *Milnesium* is represented by one undetermined species with ninety-five mounted, fourteen exuvia mounted, twenty-six prepared for SEM photography and thirty-seven prepared for DNA analysis. Identification of *Milnesium* is difficult to determine based on a lack of an updated key. Genus Minibiotus is represented by one species Mini. intermedius with two mounted and one egg mounted. Genus Ramazzottius is represented by two species R. oberhaeuseri and an undetermined species with ninety-seven mounted,

four eggs mounted, thirty-eight prepared for SEM photography and fourty-one prepared for DNA analysis. Order *Arthrotardigrada* is represented with one undetermined mounted species. At time of identification, laboratory lacked adequate technology to identify species. Specimen has been sent on to be properly identified. Genus *Hypsibius* is represented with one undetermined species with thirteen mounted, five eggs mounted, one prepared for SEM photography and six prepared for DNA analysis. Hypsibius is yet another tardigrade identified by presence of eggs, which were lacking in samples.

FAMILY, GENUS & SPECIES DESCRIPTIONS

Family *Hypsibidae*

Consists of six genera. Body types vary amongst genus and species. Double claws asymmetrically arranged to median plane of leg. Claw sequence follows 2121 arrangement, with primary claws elongated. Buccal tube rigid, sometimes with flexible pharyngeal tube. Various arrangements of placoids and pharynx. Eggs vary greatly between species. Genera include: *Hypsibius, Doryphoribius, Isohypsibius, Pseudobiotus, Itaquascon* and *Diphascon*. Only Exuvium found.



Genus *Hypsibius*

Hypsibius genus consists of twenty-eight species. Claws of each leg are more or less different form each other. Basal and primary branch of claws form a curve on which is inserted the secondary branch, with flexible junctions. Lunules always absent. Mouth without lamellae, buccal tube rigid, and reinforcement bar absent.



Genus Isohypsibius



Consists of eighty-five species. *Hypsibiidae* family member with rigid buccal tube, without reinforcement bar. Sequence of claws follows 2121. Some *Isohypsibius*' exhibit gibbosites with various arrangements, most notably either an even or odd distribution. Descriptions for *Isohypsibius* are often incomplete making identifying difficult at times. New to CA listing.

> Isohypsibius bakonyiensis



Length up to 250µ. Colorless, with eyes. Obvious reticulated sculpture, more dominant towards dorsal surface. Gibbosites occur in 9 rows as follows: 6, 6, 6, 4, 6, 2, 4, 4, 4. Middle gibbosites cone shape.

Two small conical gibbosites found on each side of head. Some gibbosities terminate with a group of short, slender spines. Buccal tube short and wide. Pharynx oval, apophyses present, 2 macroplacoids: 1st very constricted in center. No microplacoids. Small lunule at base of claws most obvious on 4th pair. Eggs smooth and laid in exuvium. New to CA listing.

Isohypsibius deflexus

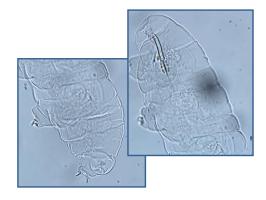


Length between 800-900µ. Colorless, eyes absent. Aquatic species. Steep "forehead" in profile. Buccal tube curved at entrance to pharynx. Pharynx oval with 2 macroplacoids, slender rod shaped. Variances in length of macroplacoids, sometimes equal, sometimes 1st longer than 2nd or they have 3 and the 3rd is longest. Microplacoids absent. Poorly developed apophyses. Claws principal branch is very long,

slender, slightly curved, no accessory points. Secondary branch much larger and curved. New to CA listing.

Isohypsibius marcellinoi

Max length 380µ. Colorless, eyes present with smooth cuticle. Lacks peribuccal lamellae. Pharynx short, oval with apophyses and 2 macroplacoids. Microplacoids absent. External claws larger than the internal. Smooth lunule at base of claws. Cuticular bar on first 3 legs, one smooth margin one notched. New to CA listing



> Isohypsibius solidus

Length between 220-300µ. Colorless, eyes absent, cuticle smooth. Short buccal tube, almost equal to pharynx which is elongated and oval shaped. Under developed apophyses, 2 angular macroplacoids, 1st nearly twice as long as 2nd, microplacoids absent. Legs short and stout. Double claws very small, equal shape and size on each leg. Basal part short principal branch slender. Lunules not described. Eggs not described. New to CA listing.



> Family *Macrobiotidae*

Consists of five genera. Lacking cephalic appendices not armored. Principal branch and secondary branch of claws united to form characteristic double claw. Each double claw is approximately equal in size and similar to the other, placed

symmetrically on median plate of leg. Variations are great amongst the different genera. Genera include: *Macrobiotus, Pseudodiphascon, Dactylobiotus, Adorybiotus* and *Haplomacrobiotus*



Genus *Macrobiotus*

Consists of ninety-two species. Buccal tube rigid for entire length. Reinforcement bar present. Double claws are deemed "*hufelandi* type". Lunules present on at least the fourth pair of legs.

Macrobiotus harmsworthi group

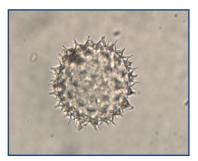


Length up to 650μ , with average being 400-500 μ . Eyes usually present. Colorless or white with smooth cuticle. Lamellae surrounding buccal aperture. Buccal tube wide. Pharynx oval. Apophyses present with 3 macroplacoids and one large microplacoid near 3rd macroplacoid. Claws in 2112 arrangement. Strong accessory points on principal branch. Medium lunule with fourth

legs crenate. Eggs with conical ornamentation, varying between subspecies.

> Macrobiotus coronatus

Animal belonging to *M. harmsworthi group*, with the same description. Eggs used as identifying quality within M. *harmsworthi group*. Eggs with conical ornamentations that are mammilliform.



Macrobiotus hufelandi group

Most common tardigrade species containing six subspecies. Cosmopolitan. Average size of 300-450µ. Colorless to white, sometimes with brown or gray pigmented rows. Eyes nearly always present. Smooth cuticle, with sparse "pearls"

(small raised bumps). Buccal aperture surrounded with lamellae. Buccal tube wide. 2 macroplacoids, 1 microplacoid. 1st macroplacoid longer than 2nd with 1st constricted in center, sometimes giving the appearance of 3 macroplacoids. Double claw with 2112 arrangement. Lunule medium sized. Eggs laid free,



sometimes in groups of up to 8. Ornamentation of eggs conical with "cups" on ends of projections. Egg base covered with pores, giving a mesh appearance. Many tardigrades are deemed a member of the "*hufelandi* group", being that many tardigrades are similar to *M. hufelandi*.

> Macrobiotus islandicus

Length of 500-560µ. Yellow, orange or yellowbrownish cavity spots. Cuticle smooth with miniscule "pearls" randomly placed across entire body. Peribuccal lamellae present. Buccal tube medium width. Oval pharynx with 2 macroplacoids, 1st longer than 2nd, sometimes with slight constriction. No microplacoids. Double claw of 2112 arrangement. Obvious accessory points. Large lunules with dentation. Egg projections thin cones narrow at base, spine like in appearance.



Macrobiotus mauccii

Animal belonging to *M. harmsworthi group*. Average length of 450µ. Colorless, eyes absent, smooth cuticle, no "pearls". Mouth with lamellae. Wide buccal tube. Oval pharynx and short with apophyses. 3 macroplacoids, rod shaped with microplacoids present. 1st macroplacoid longer than 2nd. Double claw with 2112 arrangement. Accessory points on



principle branch. Smooth lunules. Eggs projections cone shaped with narrow base. Mesh pattern of varying size directly on cones. Base with reticular sculpture. New to CA listing.

> Macrobiotus montanus

Average length of 300µ but up to 500µ. Juveniles colorless, but may acquire brown tint as maturity is reached. Eyes present. Buccal aperture with lamellae. Buccal tube very wide. Pharynx oval with a length to width ratio equaling 1.3:1. Apophyses and 3 ovals or short rod shaped macroplacoids all of similar length. May have small microplacoid. Double claws in the 2112 arrangement, large and robust. Principle branch displaying

prominent accessory points. Eggs projections are rounded mounds, with each separate projection nearly in contact with the next. Shell has pores with a reticular design. New to CA listing.



Macrobiotus ovidii

Length between 270-540µ. Juveniles without color, mature display brown pigmentation. Eye spots present with black coloring. Cuticle smooth. Buccal tube medium sized. Pharynx oval with ratio of 1.2-1.3:1. 3 rod shaped macroplacoids, 3rd the longest, 2nd the shortest. Very tiny microplacoid present. First macroplacoid may be constricted very deeply. Doubleclaws small on all legs, branches very curved. Lunules large and smooth. Principal branch with accessory points. Eggs large, yellowed. Projections slender, sharp cones with no bends and plenty of space between each projection. New to CA listing.



> Macrobiotus richtersi

Length varies between 750-1000µ. Colorless though mature specimens may exhibit brown pigment. Smooth cuticle with tiny "pearls", usually more dense towards caudal region. Eyes may be present. Mouth with

double ring of lamellae. Buccal tube very wide. Pharynx elongated oval with apophyses. 3 rod shaped macroplacoids and a microplacoid with the 3rd macroplacoid being the longest. Double claws robust, with obvious accessory points.



Lunules smooth though may be slightly crenate in large specimens. Eggs laid freely. Projections flattened mounds (truncated) sometimes with ring of papillae at base of cone. Reticular design on surface of egg.

Genus *Milnesium*

Cosmopolitan Tardigrade. Length usually between 500-600µ with some as large as 1000µ. Body elongated, tapering off at both ends. Cuticle smooth with the appearance of segments that are actually folds in the cuticle. Can be colorless but may range from tan to yellow coloring. Very wide, short, rigid buccal tube. Pharynx elongated, without placoids or apophyses. Branches of the claws separate, with primary very long with miniscule accessory points and secondary equipped with 2, 3, or 4 spurs. Eggs laid in exuvium, up to 18 at a time, spherical or oval, clear to white coloring. Exclusively carnivorous species, eating other microscopic animals, along with other tardigrades.



> Minibiotus intermedius

Extremely common. Length up to 350μ . White color, sometimes gray or brown pigment in transverse bands. Eyespots may be absent or almost unnoticeable.

Cuticle covered with small "pearls" dispersed regularly across body. In profile has a steep "forehead". Peribuccal lamellae present. Buccal armature absent. Buccal tube narrow and curved at entrance into the pharynx. Reinforcement bar short. Spherical pharynx with large apophyses. 3 round equal sized macroplacoids, with small microplacoid. Double claws small, hufelandi type with principal



branch displaying two large accessory points. Lunule smooth and incomplete. Eggs are deposited freely. Projections look like "screw with large head", often enclosed in transparent hyaline layer. New to CA listing.

➢ Genus Ramazzottius

Hypsibiidae family member. *Ramazzottius* genus is difficult to differentiate between without the presence of an egg. Species exhibit longitudinal and transverse, banding with granulation of varying degrees. Specimens are pigmented from red to reddish brown. Characteristic *Hypsibius* type claws, with primary branch elongated with

accessory points and secondary short with accessory points. Variation of buccal arrangement amongst species. Variation of ornamentation and depositing of eggs amongst species.

Ramazzottius oberhaeuseri

Maximum length 500µ but usually less. Cuticle often granulated either completely or caudally concentrated. Some have been found to be smooth. Mature specimens pigment varies between brown, reddish-brown or brownish-violet becoming more intense with age. Pigment is arranged in 5 longitudinal bands and 9 transverse. Eyes absent. Buccal tube narrow. Pharynx

short, oval contains apophyses and 2 granule macroplacoids usually of equal length. Double claws of each leg are very different,

length. Double claws of each leg are very different, long primary branch with two robust accessory points, short secondary branch with two accessory points, strongly curved. Eggs deposited freely, spherical exclusive of the projections which are numerous and diverse. Some cones transformed into short cones, truncated cones or hour glass shaped.

Order Arthrotardigrada

Order containing nine families and sixty species. Species unable to be determined based on lack of technology. Single mounted specimen. Aquatic species found amongst sand grains. Order is described as having median cirrus, internal and external medial cirri lateral cirrus A, cylindrical and long clava, lacking cephalic papilla. Legs on specimen are "flipper-like"

with each claw terminating in a spoon or disk shape and are connected directly on to legs without digits.









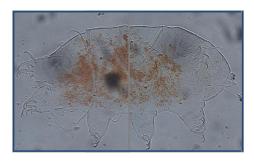
Echiniscus arctomys group

Difficult group to separate species. To date, we do not have a proper key for *Echiniscus arctomys group*, making it impossible for us to distinguish between species. Group placement distinguished by possessing cirri A, orange to red color, and granulation of various degrees. Same, "fork-like" placoids as all *Echiniscus* species. Listed in CA, seventy-two mounted specimens, twenty-four SEM prepared, twenty-eight molecular prepared, four mounted exuvia

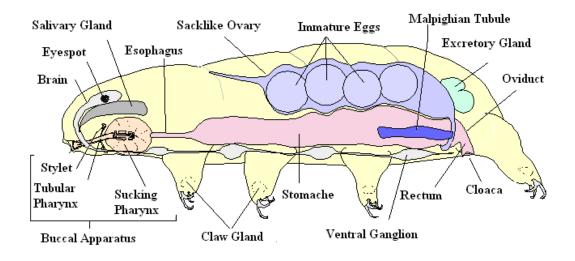


Echiniscus postojnensis

No length specified. Body armored. Facetted cephalic plate, median plate 1 triangular, robust. Median plate 2 subdivided by transverse band. Sculpture composed of various sized granules. Have a variety of cirri though not specified in which positions. New to CA listing.



Tardigrade Anatomy:



Claw Arrangement:

When referencing tardigrade "claw arrangement" followed by a series of 1's and 2's, we as identifiers are referring to the order of the tardigrades primary and secondary branches. Example, with *Macrobiotus*, their claw arrangement follows an order of 2121. This would be deciphered as secondary, primary, secondary, primary.

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