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Damaeidae (Acari, Oribatida) from high mountains in Costa Rica and Panama – biogeographical considerations

Heinrich Schatz[1,*] and Jan Mourek[2]

[1] Institute of Zoology, Leopold-Franzens University of Innsbruck, Technikerstrasse 25, 6020 Innsbruck, Austria
[2] Department of Teaching and Didactics of Biology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44, Prague 2, Czech Republic
* Corresponding author, e-mail: heinrich.schatz@uibk.ac.at

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Abstract

More than 85% of all Damaeidae species are known from the Holarctic region, whereas in the tropics this family is poorly represented. Investigations on oribatid mites in Costa Rica and Panama revealed a surprisingly species rich material of Damaeidae. Altogether 78 specimens were found in 8 different mountain regions in Costa Rica and Panama. They belong to 11 species, which are presumably all new for science. The Damaeidae species occur almost exclusively in the upper vegetation belts of the Cordillera de Talamanca and nearby mountain ranges in tropical montane rain forest and subalpine paramo. It seems that the Central American high mountains offer refuges with insular effect which were possibly colonized during cooler climatic periods.

Keywords Central America | mountains | Cordillera de Talamanca | biogeography | insular effect

1. Introduction

The Central American landbridge is a transition zone and comprises elements of Nearctic and Neotropical origin. This exceptionally diverse composition is caused by the great variety of different habitats, but also by adequate dispersion routes for faunas of different provenance, ranging from cold-temperate mountains to humid tropical corridors (Halffter 1987). The shift of faunas and floras was facilitated during great climatic changes.

Different limits between the Nearctic and Neotropical regions are proposed for different taxa by various authors through different geographical barriers as the Isthmus of Tehuantepec (Halffter 1987: montane insects, Morrone & Marquez 2001: beetles) or the Balsas Depression (Marshall & Liebherr 2000: plants, insects, fishes, reptiles). The isthmus south of Lake Nicaragua which encompasses the Cordillera de Talamanca in Costa Rica and Panama is most isolated from other Central American regions and shows marked South American affinities. According to Halffter (1987) the insect fauna of the Cordillera de Talamanca was colonized in large part by taxa from the tropical lowlands which are frequently associated with the South American sphere of influence. The oribatid fauna of this mountain range is also broadly influenced by Neotropical elements, but this impact decreases at higher altitudes where the number of Nearctic taxa increases and some species even become abundant (Schatz 2007).

The oribatid mite family Damaeidae comprises more than 300 known species (and subspecies) (Subías 2015 updated, Schatz species database, unpubl.). The vast majority (264 spp., 85%) is known from the Holarctic region, among those 55 species are reported from the Nearctic region. The preponderance of the Damaeidae occurrence in the Northern hemisphere was already noted by some authors (e.g. Bulanova-Zachvatkina 1973, Norton 1979a). Only few species were recorded from tropical regions (Norton 1979a). Prior to this study three Damaeidae species were known from Mexico, and five

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species from South America, among some additional undescribed or doubtful records. From Central America the records of Damaeidae are known only at genus level (Tab. 1).

In the course of a large-scale study on oribatid mites in Central America (Schatz 1997, 2006, 2007) several specimens of the family Damaeidae were encountered. In this contribution biogeographical considerations on Damaeidae from the mountain regions of Costa Rica and Panama and their possible provenance are presented. Detailed species descriptions will be published successively.

Table 1. Damaeidae reported from the Neotropical region.

Mexico
Belba clavasensilla Norton & Palacios-Vargas, 1982: Volcán Popocatepetl, 3600 m a.s.l.
Epidamaeus mitlsensillus Palacios-Vargas, 1984: Volcán Popocatepetl, 3800 m a.s.l.
Epidamaeus palaciosi Iglesias & Guzman, 2012: in a cave near Taxco, ~1750 m a.s.l.
Vazquez (1999) reported *Damaeus* nr. *glycyphagoides* Bulanova-Zachvatkina, 1957 from the lowlands of the Yucatan Pensinsula in Sian Ka´an, Quintana Roo (originally described from the Caucasus). This record is doubtful and would have to be verified.
Central America
Belba (*Protobelba*) sp.: Pacific coastal forests from Central America and Mexico [Norton (1978, 1979a)]
Norton (1979a) mentions additional unpublished records of *Epidamaeus* sp. and other Damaeidae species from the neotropical region, especially from Central America.
Ecuador
Epidamaeus sp.: Reserva Biológica San Francisco, tropical montane rain forest, 2150 m a.s.l. (Illig et al. 2010)
Bolivia
Parabelballa flagellata (Balogh & Mahunka, 1969): near Puerto Linares, 600 m a.s.l., thick moss from roadside cliff in virgin forest (Balogh & Mahunka 1969)
Argentina
Trägårdh (1907) reported *Damaeus curtipes* Trägårdh, 1907 from Observatory Island, near Staten Island, Tierra del Fuego. The systematic position of this species is doubtful and would have to be verified.
Chile
Damaeus formica (Gervais, 1849): Prov. Santiago, in moss and under rocks (Gervais 1849)
Dyobelba armata Norton, 1979: Prov. Santiago, ~250–1900 m a.s.l. (Norton 1979b)
Epidamaeus flagelloides Norton, 1979: Prov. Santiago, ~250–600 m a.s.l., Prov. Tarapaca, 3000 m a.s.l. (Norton 1979b)
Epidamaeus meridianus Norton, 1979: Prov. Santiago, ~250–600 m a.s.l., Prov. Tarapaca, 3000 m a.s.l. (Norton 1979b)
Epidamaeus (*Akrodamaeus*) *flagellatus* (Balogh & Mahunka, 1969): Prov. Santiago, ~250–1900 m a.s.l. (Norton 1979b)

1.1. Environmental setting

The earliest stage of geological history in Central America is the Jurassic separation of North and South America. This was followed by a continuous movement and uplifting of plate fragments enlarging the puzzle-like land-bridge from North America towards south (Donnelly 1992). At present, the Central American land-bridge is a sequence of lowlands and mountain regions from Mexico to Panama: Sierra Transvolcanica – Balsas Basin – Sierra Madre del Sur – Isthmus of Tehuantepec – Chiapas-Guatemalan highland – Nicaraguan depression – Cordillera de Talamanca – Western Panamanian Isthmus. A chain of volcanic islands coalesced, probably as a result of tectonic uplifting, forming a land bridge between South and Central America (Coates & Obando 1996). Most estimates of the date of closure are at the Miocene-Pliocene boundary between 3 and 5 Ma. During the Pliocene the landform configuration was increased by the massive outpouring of igneous material. At present, a chain of explosive volcanoes stretches from the Mexican-Guatemalan border to Central Costa Rica. In Panama, the Volcán Barú is one of the centres of sub-recent activity. Once the land-bridge was formed, an interchange was possible by organisms that could traverse the narrow land-bridge (Kimsey 1992). The area investigated by one of us (H.S.) in Costa Rica and Panama is mainly situated in and around the volcanic mountain range of the Cordillera de Talamanca.

The Central American land-bridge is situated in the tropics, but geomorphology, oceanic currents, and wind systems form several zones of differing climate and vegetation (Lauer 1989, Khatun et al. 2013). Highland ridges are wet, especially the windward slopes in the northeast, while the leeward slopes in the southwest have an arid climate. Most regions have a rainy and a dry season. High mountain ranges reach into the orobiome of the 'cold tropics' with elevations of up to almost 4000 m a.s.l.

The highlands in the Cordillera de Talamanca belong to the life zones of tropical montane rain forest (in the high Talamancas, with small outliers round the summits of Turrialba, Irazú, Barva, and Poás) and tropical subalpine rain paramo. This life zone is the northernmost occurrence of the Andean paramo, originally restricted to the highest peaks (Chirripó) of the Talamancas, but extending downwards into the Cerro de la Muerte region owing to human disturbance. It is dominated by shrubs where drainage is adequate, but bogs occur where drainage is poor, e.g. on Cerro de la Muerte (life zones after Holdridge 1947, 1967 and Hartshorn 1983).

2. Material and methods

Several expeditions were carried out by H.S. in the main life zones of Costa Rica and Panama since 1986, collecting various soil and litter samples (Schatz 1997, 2007). The samples contained about one litre of organic material (mainly decaying leaf litter and wood, moss and samples of epiphytic growth). Altogether more than 500 samples were taken in different sites and vegetation zones, covering most life zones in different regions of the countries. The samples were extracted using modified Tullgren funnels.

Samples from lower elevations did not contain Damaeidae specimens and are not considered here. The collections in the Cordillera de Talamanca were mainly carried out along altitudinal transects on Volcán Chirripó, Costa Rica, and Volcán Barú, Panama. Additional samples were taken on other volcanoes and mountain regions in the Cordillera Centrál of Costa Rica and Panama (cf. Tab. 2).

Table 2. Sampled mountain regions of Costa Rica and Panama and occurrence of Damaeidae.

Mountain range	Country	Site	Samples total		Samples with Damaeidae	
			Samples total	elevation (m a.s.l.)	Samples	elevation (m a.s.l.)
Cordillera de Guanacaste	Costa Rica	Maritza	1	800	1	800
Cordillera de Tilarán	Costa Rica	Monteverde	6	1,550–1,700	3	1,550–1,700
Cordillera Centrál	Costa Rica	Volcán Poas	1	2,650	–	–
Cordillera Centrál	Costa Rica	Volcán Barva	2	2,720	1	2,720
Cordillera Centrál	Costa Rica	Volcán Irazú	2	3,400	1	3,400
Cordillera de Talamanca	Costa Rica	Tapantí	5	1,250–1,500	1	1,400
Cordillera de Talamanca	Costa Rica	Cerro de la Muerte	7	2,900–3,400	1	2,900
Cordillera de Talamanca	Costa Rica	Cerro Chirripó	13	2,500–3,800	3	2,510–3,000
Cordillera de Talamanca	Panama	Volcán Barú	22	1,750–3,475	8	2,200–3,475
Cordillera de Talamanca	Panama	La Fortuna	3	1,200–1,400	–	–

Table 3. Damaeidae species in mountain regions of Costa Rica and Panama. Species distribution in different mountain ranges and sites.

Mountain range	**Guanacaste**	**Tilarán**	**Centrál**	**Centrál**	**Talamanca**	**Talamanca**	**Talamanca**	**Talamanca**	**Total sites**	**Total Specimens**
Site	**Maritza**	**Monteverde**	**V. Barva**	**V. Irazú**	**Tapantí**	**C. Muerte**	**C. Chirripó**	**V. Barú**		
Altitude (m a.s.l.)	800	1,500–1,700	2,720	3,400	1,400	2,900	2,510–3,000	2,200–3,475		
Protobelba A						1	1	39	**3**	**41**
Epidamaeus B								5	**1**	**5**
Epidamaeus C							4	2	**2**	**6**
Epidamaeus D								1	**1**	**1**
Epidamaeus E								2	**1**	**2**
Epidamaeus F	10				1				**2**	**11**
Epidamaeus G				2					**1**	**2**
Epidamaeus J							2		**1**	**2**
Epidamaeus K		1							**1**	**1**
Belba H		2							**1**	**2**
Belba I			5						**1**	**5**
Species	**1**	**2**	**1**	**1**	**1**	**1**	**3**	**5**		**11**
specimens	**10**	**3**	**5**	**2**	**1**	**1**	**7**	**49**		**78**

3. Results

A total of 78 Damaeidae specimens (all adult) were found in 19 samples from 8 different mountain regions in the Cordillera de Talamanca and adjacent mountains in Costa Rica and Panama (Tab. 2). They belong to 11 species of the genera *Epidamaeus* (8 spp.), *Belba* (*Protobelba*) (1 sp.) and *Belba* sensu stricto (2 spp.). The inclusion of the two species to *Belba* sensu stricto is only tentative, because there are some differences from the current genus diagnosis. All these species are presumably new for science. Until the species are described properly they are named provisionally as morpho-species with letters (Tabs 3, 4).

Tab. 3 shows the species distribution in different mountain ranges and sites. Eight species were found in one site, two of those (*Epidamaeus* D and K) with one specimen only. The species *Protobelba* A and *Epidamaeus* C occur on both high volcanoes of the Cordillera de Talamanca (the mountain pass Cerro the la Muerte lies close to the Volcán Chirripó), and only the species *Epidamaeus* F was found in two sites far apart: Tapantí in the Cordillera Centrál and in the Cordillera de Guanacaste, the northernmost volcanic mountain range of Costa Rica. The vast majority of specimens belongs to *Protobelba* A (33 individuals in one sample of V. Barú), also *Epidamaeus* F was found in 10 individuals in one sample in Guanacaste, other species were represented by 1–6 individuals each.

The altitudinal distribution of the Damaeidae of Costa Rica and Panama (Tab. 4) shows an almost restricted occurrence at higher altitudes above 1550 m a.s.l., taking into account that most species occur above 2200 m a.s.l. The only exception is *Epidamaeus* F, which was found at 1400 m in Tapantí and at 800 m near Maritza (both in premontane rainforest, see discussion). *Belba* H occurs in Monteverde in the lower montane rainforest at 1600–1700 m, as well as *Epidamaeus* K (1550 m), the other 8 species were found at elevations above 2200 m a.s.l. in montane rain forest in different sites (*Epidamaeus* C, E, J, *Protobelba* A, *Belba* I) or in the subalpine rain paramo (*Epidamaeus* B, D on Volcán Barú, *Epidamaeus* G on Volcán Irazú).

4. Discussion

The results show clearly that the Damaeidae species in Central America occur almost exclusively at higher elevations. Although soil and litter samples were taken in large numbers in nearly all life zones of Costa Rica and Panama, no species of this family were found at lower elevations. This pattern corresponds with results of Schatz (2007) for several other taxa restricted to higher elevations above about 1900 m a.s.l., as observed for members of the families Achipteriidae, Camisiidae, Ceratozetidae, Liacaridae, Mycobatidae, Nodocepheidae, Phenopelopidae and some species of other families. The predominantly mountainous distribution of the Damaeidae was noted also by Miko et al. (2014) in the Ethiopian region of Africa.

The finding of *Epidamaeus* F at 800 m a.s.l. seems to be an exception. The sample with this species was

Table 4. Altitudinal distribution of the Damaeidae species in mountain regions of Costa Rica and Panama. Individual numbers are given for each species in different altitudinal belts. N: number of specimens in total.

Species	N	Altitude (m a.s.l.)																												
		800	900	1,000	1,100	1,200	1,300	1,400	1,500	1,600	1,700	1,800	1,900	2,000	2,100	2,200	2,300	2,400	2,500	2,600	2,700	2,800	2,900	3,000	3,100	3,200	3,300	3,400	3,500
Epidamaeus D	**1**																												1
Epidamaeus B	**5**																												5
Epidamaeus G	**2**																											2	
Epidamaeus C	**6**																		2		1	2		1					
Protobelba A	**41**															3	1			1		33	2	1					
Epidamaeus E	**2**																					2							
Belba I	**5**																				5								
Epidamaeus J	**2**																				2								
Belba H	**2**									1	1																		
Epidamaeus K	**1**									1																			
Epidamaeus F	**11**	10						1																					

taken in the Cordillera de Guanacaste. The presence of *Epidamaeus* F at a lower elevation might be explained by the generally lower altitude of the volcanoes of this mountain range – the highest peak, Volcán Miravalles, reaches an elevation of 2028 m. The place where *Epidamaeus* F was found is situated in the premontane rainforest on the slope of the Volcán Orosí (1659 m). But apart from this occurrence, nothing is known about the ecology of this species. Maybe it might be simply different than in other Damaeidae species.

The highlands of the Cordillera de Talamanca and nearby mountain ranges contain a distinct oribatid community from that of surrounding lowlands. A possible reason is the colder climate at higher altitudes. Temperate zones differ from cold tropical highlands in the duration and frequency of cold periods: the first have a seasonal climate, while the cold tropics exhibit a 'daytime climate' with strong daily temperature oscillations and can be classified as part of the 'cold highland tropics' where frosts occur (Lauer 1989). The fact that frosts occur - no matter if daily or seasonally - might limit the occurrence for many organisms.

The question arises how colder adapted taxa could disperse to the tropical highlands of the Cordillera de Talamanca and cross the tropical lowland barriers in Central America, particularly the Isthmus of Tehuantepec and the Nicaraguan depression. The vast majority of Damaeidae species occurs in the Northern hemisphere. It can be assumed that the ancestors of the present Damaeidae in the Central American highlands immigrated from the north. Except for single records in Bolivia and Ecuador, Damaeidae in South America are only known from Chile.

Colder climate periods probably provided more favourable conditions than present ones for crossing the lowland barriers. Cold-adapted taxa could immigrate from the north and survived until present in high mountain regions. We hypothezise that during dry interglacial and interpluvial periods the boreo-montane fauna was confined to the high, cold mountains. In these periods the barriers were extremely effective and the high mountain ranges offered refuges with insular effects for colder adapted taxa. Consequently, a potential speciation under isolated conditions can be assumed (Schatz 1998, 2007). This might be the case for the undescribed Damaeidae species recorded in the Cordillera de Talamanca and surroundings.

No Damaeidae species were recorded in the few studies carried out in the Chiapas-Guatemalan highland (compiled in Schatz 2006). The three Damaeidae species known from Central Mexico were described from the Mexican highland around the Volcán Popocatepetl (3600 – 3800 m a.s.l.) and in a cave near Taxco (~1750 m a.s.l.).

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