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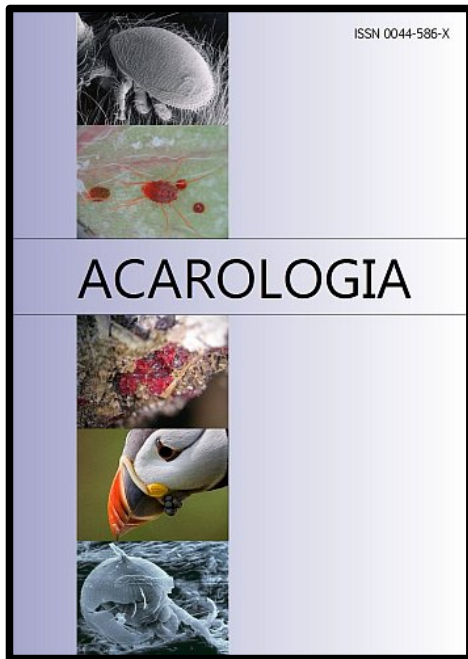
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Review of sexual dimorphism in brachypyline oribatid mites

Valerie M. BEHAN-PELLETIER

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*Invertebrate Biodiversity Program, Research Branch, Agriculture and Agri-Food Canada, K. W. Neatby Bldg., Ottawa, Ontario, Canada K1A 0C6.
Valerie.behan-pelletier@agr.gc.ca*

ABSTRACT — Expressions of strong sexual dimorphism have been found in 77 species of Brachypyliina, representing 36 genera, in the superfamilies Gustavoioidea, Ameroidea, Oppioidea, Limnozetoidea, Ameronothroidea, Licneremaeoidea, Oripodoidea, Oribatelloidea, Ceratozetoidea and Galumnoidea. There are many examples of convergences, e.g., modifications of tarsus I setae in *Cosmogmeta* (Autognetidae), *Hydrozetes* (Hydrozetidae) and *Erogalumna* (Galumnidae), and of possible behavioural constraints, e.g., the paraxial position of modified setae in sexually dimorphic species in these genera. Similarly, there is strong convergence in position and modification of presumed secretory porose organs in species of *Autogmeta* (Autognetidae), *Mochloribatula* (Mochlozetidae), *Symbioribates* (Symbioribatidae), *Oribatella* (Oribatellidae), *Zachvatkinibates*, *Nuhivabates* (Punctoribatidae), *Xiphobates* (Chamobatidae) and *Psammmogalumna* (Galumnidae).

The number of superfamilies with sexually dimorphic species and the range of expression of sexual dimorphism suggest multiple independent origins in Brachypyliina, as congeneric species in 20 of these 36 genera do not show such modifications. Despite 1% of brachypyline species being strongly sexually dimorphic, the evidence for courtship behaviour is limited to the Galumnidae and an undescribed species of *Mochloribatula* (Mochlozetidae). Evolution of strongly sexually dimorphic species in Oribatida seems to be in response to intermittent dryness, or aquatic habitats, or spatially discrete microhabitats. The littoral habitat is represented by 11 species showing strong sexual dimorphism, coastal vegetation by 6, the semiaquatic by 5, dry soil by 4 species and crustose lichens by 3 species. Arguably, these 29 species and some of the 19 species reported from arboreal habitats (including lichens and moss) live in microhabitats that can be intermittently dry, with wet-dry periods of varying lengths and intensity. Seven sexually dimorphic species of *Hydrozetes* are found in aquatic habitats; males of these all show modifications of one or more paraxial seta on tarsus I which may be used to orient the female. The 5 sexually dimorphic species of *Autogmeta*, and *Unguizetes mauritius* (Jacot) are associated with decaying wood, bark and fungal sporophores, suggesting evolution of sexual dimorphism in this spatially discrete habitat. Undoubtedly, there are many other undiscovered cases of sexual dimorphism in Brachypyliina, as microhabitats where they predominantly occur are rarely studied.

KEYWORDS — Gustavoioidea; Ameroidea; Oppioidea; Limnozetoidea; Ameronothroidea; Licneremaeoidea; Oripodoidea; Oribatelloidea; Ceratozetoidea; Galumnoidea; modified setae; secretory porose organs

INTRODUCTION

Oribatid mites are unusual among Acari in that the gender of adults is not readily determined in most species without examining genitalia, which are always hidden in the genital vestibule when

not in use. The majority of oribatid species are bisexual (Norton *et al.* 1993), about 10% reproduce parthenogenetically, and only 1% are distinctly sexually dimorphic. The rarity of distinct sexual dimorphism makes its nature and distribu-

tion interesting, as selective forces leading to appearance and convergence of traits may be more readily detected. The subject has been partially reviewed several times. Newell (1957) provided a brief first overview of sexual dimorphism in Oribatida in the introduction to his description of *Tuberemaus papillifer* (Newell, 1957). Travé (1959) provided the first summary of sexual dimorphism in Brachypylina in his study on *Pirnodus detectidens* Grandjean, 1956. Behan-Pelletier & Eamer (2010) described the first sexually dimorphic species of *Oribatella* and again reviewed sexual dimorphism in Brachypylina. Since 2010 a number of sexually dimorphic species have been described, and these highlight the diversity of expression even within a single genus. My goal in this paper is to review sexual dimorphism in Brachypylina and the little that is known of courtship behaviour in the sexually dimorphic species, highlight the ecological conditions where sexual dimorphism is most commonly expressed and discuss why sexually dimorphic species are apparently restricted to occasionally dry habitats, aquatic habitats and spatially discrete habitats.

Sexual dimorphism *per se* is evident in all bisexual Oribatida; the spermatopositor (male) and ovipositor (female) are morphologically and functionally different (Alberti & Coons 1999, Ermilov 2010, Norton & Behan-Pelletier 2009). In addition, females are usually larger on average and have relatively larger genital plates than conspecific males. In this review I focus on species showing additional morphologically distinct expressions of sexual dimorphism. A large number of the species showing distinct sexual dimorphism have the porose organs of the octotaxic system modified in the male, or have presumed porose organs on the ventral or anal plates. As Norton and Alberti (1997) outlined in detail, when these organs are modified it is always in the male and involves hypertrophied porose organs "or new organs may exist in males that have no known homologues either in females of the species or in males of related taxa". They suggested two

possible reasons for this sexual dimorphism, either a higher requirement for cuticular maintenance in males perhaps in response to more environmental exposure, or that the hypertrophied or novel porose organs of the males play a role in intraspecific communication producing "sex attractant or aggregation semiochemicals that are involved directly or indirectly in reproduction".

I focus on the Brachypylina as non-genitalic sexual dimorphism is most diverse and varied in this hyporder. It is also well recognized, though less common, in non-brachypylina taxa. For example, Grandjean (1954) noted that in the palaeacaroid *Aphelacarus acarinus* (Berlese, 1910a) the palptarsal eupathidium is forked in the female but not in the male. Wallwork (1962) studied three species of the epilohmanniid *Epilohmannia* in which the border of epimere IV is less strongly angled in the male than in the female. Schuster (1962) described the morphology and behaviour of *Collohmannia gigantea* Sellnick, 1922 which has a hypertrophied seta on genu IV of the male for holding nuptial fluid, as does the recently described *C. johnstoni* Norton & Sidorchuk, 2014.

MATERIALS AND METHODS

The data listed below are based on published literature on Oribatida. Undoubtedly sexual dimorphism is underrepresented in the literature as many species descriptions do not look for evidence of dimorphism. Brachypylina classification used below follows the broad outlines of Norton & Behan-Pelletier (2009), as updated in Schatz *et al.* (2011) and Norton & Ermilov (2014). Number of species in a genus is based on Subías (2014). Sexual dimorphism throughout the Results and Discussion below refers to morphological gender differences other than dissimilar genitalia, genital plates and overall size. A general overview of oribatid morphology is given in Norton & Behan-Pelletier (2009). Authorities for species given in Table 1 are not repeated throughout the text.

TABLE 1: Brachyhyaline species showing sexual dimorphism, and their habitats. (to be continued on the next two pages)

Superfamily	Family	Species	Habitat
Gustavioidea	Kodiakellidae	<i>Kodiakella dimorpha</i> Pérez-Iñigo & Subías, 1978	soil
Amerioidea	Amerobelbidae	<i>Hellenamerus ionicus</i> Mahunka, 1974	scrubland near seacoast
Amerioidea	Amerobelbidae	<i>Morgaillardia callitoca</i> Grandjean, 1961	clay, calcite soil at depth of 10–15cm
Amerioidea	Amerobelbidae	<i>Morgaillardia eveana</i> Grandjean, 1961	soil at depth of 10–15cm
OpPIOidea	Autognetidae	<i>Cosmogmeta impedita</i> Grandjean, 1960	litter under green oak
OpPIOidea	Autognetidae	<i>Cosmogmeta kargi</i> Grandjean, 1963	litter under oak
OpPIOidea	Autognetidae	<i>Autogneta schusteri</i> Behan-Pelletier, 2015	Decaying bark
OpPIOidea	Autognetidae	<i>Autogneta aokii</i> Behan-Pelletier, 2015	Forest litter, decaying bark
OpPIOidea	Autognetidae	<i>Autogneta flahertyi</i> Behan-Pelletier, 2015	Bracket fungi
OpPIOidea	Autognetidae	<i>Autogneta longilamellata</i> (Michael, 1885)	Decaying wood
OpPIOidea	Autognetidae	<i>Autogneta amnica</i> Jacot, 1928	Decaying bark
Hydrozetoidae	Hydrozetidae	<i>Hydrozetes confervae</i> Oudemans, 1896	aquatic
Hydrozetoidae	Hydrozetidae	<i>Hydrozetes dimorphus</i> Hammer, 1962	aquatic
Hydrozetoidae	Hydrozetidae	<i>Hydrozetes lacustris</i> Michael, 1882	aquatic
Hydrozetoidae	Hydrozetidae	<i>Hydrozetes lennae</i> (Coggi, 1898)	aquatic
Hydrozetoidae	Hydrozetidae	<i>Hydrozetes thienemanni</i> Strenzke, 1943	aquatic
Hydrozetoidae	Hydrozetidae	<i>Hydrozetes ringueleti</i> Fernandez, 1984	floating vegetation; aquatic
Hydrozetoidae	Hydrozetidae	<i>Hydrozetes (Heloribates) tamarae</i> Tolstikov, 1996	taiga sphagnum bog
Liceremaeoidea	?	<i>Glanderemaeus hammerae</i> Balogh & Csiszar, 1963	moss on bark and soil
Ameronothroidea	Fortuyniidae	<i>Fortuynia atlantica</i> Krisper & Schuster, 2008	intertidal zone
Ameronothroidea	Fortuyniidae	<i>Fortuynia yunkerii</i> Hammen, 1963	intertidal zone
Ameronothroidea	Ameronothridae	<i>Ameronothrus lineatus</i> (Thorell, 1871)	Intertidal zone
Ameronothroidea	Ameronothridae	<i>Ameronothrus nigrofenestratus</i> (L. Koch, 1879)	Intertidal zone
Ameronothroidea	Ameronothridae	<i>Podacarus auberti</i> Grandjean, 1955	Intertidal zone
Ameronothroidea	Ameronothridae	<i>Halozetes belgicae</i> (Michael, 1903)	intertidal zone
Ameronothroidea	Ameronothridae	<i>Alaskozetes antarcticus</i> (Michael, 1903)	intertidal zone
Oripodoidea	Mochlozetidae	<i>Mochloribatula bahamensis</i> Norton, 1983	ex. <i>Borrichia arborescens</i> , <i>Rachicallis americana</i> , <i>Tillandsia</i>
Oripodoidea	Mochlozetidae	<i>Mochloribatula metzi</i> Norton, 1983	ex. <i>Spartina</i> in salt marsh
Oripodoidea	Mochlozetidae	<i>Mochloribatula floridana</i> (Banks, 1904)	ex. <i>Typha</i> at edge of pond
Oripodoidea	Mochlozetidae	<i>Mochloribatula texana</i> (Ewing, 1909)	ex. coastal grass, mistletoe
Oripodoidea	Mochlozetidae	<i>Mochloribatula multiporosa</i> Mahunka, 1978	litter, soil

Superfamily	Family	Species	Habitat
Oripodoidea	Mochlozetidae	<i>Mochloribatula grandjeani</i> Mahunka, 1978	litter, soil
Oripodoidea	Mochlozetidae	<i>Mochloribatula</i> sp. (Oliviera et al. 2007)	ex. buildings
Oripodoidea	Mochlozetidae	<i>Unguizetes mauritius</i> (Jacot, 1936)	Under bark of <i>Eucalyptus</i>
Oripodoidea	Symbioribatidae	<i>Symbioribates aokii</i> Karasawa & Behan-Pelletier, 2007	Ex. branches of <i>Castanopsis sicboldii</i> , <i>Distylium racemosum</i>
Oripodoidea	Symbioribatidae	<i>Symbioribates papuensis</i> Aoki, 1966	Ex. fungi, algae on elytra of weevils in montane moss forest
Oripodoidea	Symbioribatidae	<i>Symbioribates yukiguni</i> Maruyama & Shimano, 2014	litter & soil
Oripodoidea	Scheloriibatidae	<i>Parpirnodus coniferinus</i> Behan-Pelletier, Clayton & Humble, 2002	twigs in conifer canopy
Oripodoidea	Scheloriibatidae	<i>Tuberemaus papillifer</i> (Newell, 1957)	Ex. bark and leaves of <i>Metrosideros collina</i> <i>polymorpha</i>
Oripodoidea	Scheloriibatidae	<i>Nasozetes sumatrensis</i> Sellnick, 1930	Ex. <i>Gardenia</i>
Oripodoidea	Scheloriibatidae	<i>Nasozetes lienhardi</i> Mahunka, 2006	Leaf litter in rainforest
Oripodoidea	Scheloriibatidae	<i>Nasozetes choerognathus</i> Willmann, 1932	Ex. sphagnum moss
Oripodoidea	Scheloriibatidae	<i>Nasozetes porcella</i> (Mahunka, 1966)	Under moss and lichens
Oripodoidea	Scheloriibatidae	<i>Nasozetes stunkardi</i> Sengbusch, 1957	Ex. <i>Artocarpus altitis</i>
Oripodoidea	Oripodidae	<i>Pirnodus detectidens</i> Grandjean, 1956	crustose lichens on rocks
Oripodoidea	Oripodidae	<i>Pirnodus soyeri</i> Travé, 1969	crustose lichens on rocks
Oripodoidea	Oripodidae	<i>Cryptoribatula euensis</i> (Hammer, 1973)	moss on bark of tree, 0.5m above soil on forested island
Oripodoidea	Oribatulidae	<i>Sellnickia caudata</i> (Michael, 1908)	arboreal
Oripodoidea	Parakalummidae	<i>Neoribates macrosacculatus</i> Aoki, 1966	Deciduous forest soil
Oribatelloidea	Oribatellidae	<i>Oribatella canadensis</i> Behan-Pelletier & Eamer, 2010	very dry soil
Oribatelloidea	Oribatellidae	<i>Oribatella oregonensis</i> Behan-Pelletier & Walter, 2012	?
Ceratozetoidea	Chamobatidae	<i>Xiphobates callipygis</i> Pavlichenko, 1991	?
Ceratozetoidea	Punctoriibatidae	<i>Nuhitabates hitaoa</i> Niemi & Behan-Pelletier, 2004	soil at base hanging ferns, ferns and moss of wet rock wall in cloud forest
Ceratozetoidea	Punctoriibatidae	<i>Nuhitabates nukuhiva</i> Niemi & Behan-Pelletier, 2004	moss and epiphytes in cloud forest, epiphytes on <i>Weinmannia parviflora</i> , epiphytic ferns
Ceratozetoidea	Punctoriibatidae	<i>Zachoaikinribates nortoni</i> Behan-Pelletier & Eamer, 2005	beach debris, littoral areas
Ceratozetoidea	Punctoriibatidae	<i>Zachoaikinribates maritimus</i> Shaldybina, 1973	beach debris, littoral areas

Superfamily	Family	Species	Habitat
Ceratozetoidea	Punctoribatidae	<i>Zachraatkribates quadrivertex</i> (Halbert, 1920)	marine salt marsh meadows
Ceratozetoidea	Punctoribatidae	<i>Zachraatkribates shalabyinae</i> Behan-Pelletier & Eamer, 2005	beach debris, littoral areas
Ceratozetoidea	Punctoribatidae	<i>Zachraatkribates schatzi</i> Behan-Pelletier & Eamer, 2005	beach debris, littoral areas
Ceratozetoidea	Zetomimidae	<i>Heterozetes aquaticus</i> (Banks, 1895)	subaquatic
Ceratozetoidea	Zetomimidae	<i>Heterozetes helios</i> Behan-Pelletier, 1998	Vegetation on surface of water in periodically dry swamp
Ceratozetoidea	Zetomimidae	<i>Heterozetes minnesotensis</i> (Ewing, 1913)	subaquatic
Ceratozetoidea	Zetomimidae	<i>Naiazetes reevesi</i> Behan-Pelletier, 1996	subaquatic
Galumnoidea	Galumnidae	<i>Centrorribates mucronatus</i> (G & R. Canestrini, 1882)	litter
Galumnoidea	Galumnidae	<i>Dicatozetes uropygium</i> (Grandjean, 1928)	moss
Galumnoidea	Galumnidae	<i>Dicatozetes numidicus</i> Bernini, 1984	moss
Galumnoidea	Galumnidae	<i>Erogalumna zeucta</i> Grandjean, 1964	Arboreal, ex. leaves in temporarily dry forest
Galumnoidea	Galumnidae	<i>Galumna tarsipennata gibbula</i> Grandjean, 1956	?
Galumnoidea	Galumnidae	<i>Galumna dimorpha</i> Krivolutskaya, 1952	Forest litter
Galumnoidea	Galumnidae	<i>Kabylogalumna rhinoceros</i> Bernini, 1984	moss
Galumnoidea	Galumnidae	<i>Psammogalumna hungarica</i> (Sellnick, 1925)	?
Galumnoidea	Galumnidae	<i>Psammogalumna iranica</i> (Akrami, Irani-Nejad & Mirzaie, 2011)	Litter, soil in orchard and cultivated field
Galumnoidea	Galumnidae	<i>Pergalumna rima</i> Fujikawa, 2007	Litter, humus, soil
Galumnoidea	Galumnidae	<i>Vaghia blascoi</i> Travé, 1981	litter beneath <i>Acacia mearnsii</i>
Galumnoidea	Galumnidae	<i>Vaghia simplex</i> Travé, 1957	moss in alpine
Galumnoidea	Galumnidae	<i>Vaghia carinata</i> Travé, 1955	rock, vertical face with moss, lichen
Galumnoidea	Galumnidae	<i>Vaghia stupendus</i> (Berlese, 1916)	under stones by stream

RESULTS

Strong sexual dimorphism is known in 77 species of Brachypylina, representing 16 families and 36 genera in the superfamilies Gustavoidea, Ameroidea, Oppioidea, Limnozetoidea, Ameronothroidea, Licnere-maeoidea, Oripodoidea, Oribatelloidea, Ceratozetoidea and Galumnoidea (Table 1). It is not yet reported for the other 15 brachypylina superfamilies (Schatz *et al.* 2011). In sexually dimorphic species modifications are often striking, are only found in the male, and encompass either modifications of the octotaxic system of dermal glands (Table 2) or leg, leg setal, prodorsal, hysterosomal or ventral modifications (Table 3). Usually a given species has only one type of modification; the combination of special male dermal glands with other modifications is known only in some sexually dimorphic species of *Autogneta*, *Symbioribates*, *Pergalumna*, *Fortuynia*, *Oribatella* and *Psammogalumna* (Akrami *et al.* 2011, Behan-Pelletier 2015, Behan-Pelletier & Walter 2012, Karasawa & Behan-Pelletier 2007, Krisper & Schuster 2008, Maryuma & Shimano 2014) (Tables 2, 3).

Taxonomic distribution of strongly sexually dimorphic species (Tables 1-3)

Gustavoidea: Kodiakellidae: Only one species in this large superfamily is sexually dimorphic, *Kodiakella dimorpha* Pérez-Iñigo & Subías, 1978 (1 of 2 described species), with the modification expressed as a broader bothridial seta in the male (based on 2 specimens) than the female (based on 2 specimens) (Pérez-Iñigo & Subías 1978).

Ameroidea: Amerobelbidae: Among this morphologically diverse superfamily sexually dimorphic species are known only in the amerobelbid genera *Hellenamerus* (monotypic) and *Mongaillardia*. Males of *H. ionicus* have a ventrolateral porose area on the ventral plate. In males of 2 (of 5 described) species of *Mongaillardia*, the lamellar seta is crochet shaped, with spines, and seta *pv'* of tarsus II is highly modified in shape. This is the only known modification of a seta on tarsus II; all other sexually dimorphic tarsal setae are on tarsus I (Table 3). Grandjean (1961) speculated that males of these species walked on the posterior 2 pairs of legs during courtship, in a "promenade à deux", and that the highly modified seta *pv'* could be used for positioning of spermatophores, but there were no observations of living mites.

Oppioidea: Autognetidae: In this large superfamily, strongly sexually dimorphic species are known only in the autognetid genera *Autogneta* (5 of 13 described species) and *Cosmogmeta* (2 of 4 described species). Travé (1959) made preliminary observations on an unidentified sexually dimorphic species of *Autogneta* from Madeira in which males have thickened integument in the humeral region, but the species was neither described nor illustrated. Male *Autogneta longilamellata* have a long, oval

porose area on the notogaster posteriorly. Four other *Autogneta* species show porose areas posteriorly, either flattened or in a concavity and associated with modified setae *h1* and *p1* (Behan-Pelletier 2015) (Fig. 1A, B). In contrast, males of the 2 strongly sexually dimorphic species of *Cosmogmeta* have a highly modified seta *a'* on tarsus I.

Limnozetoidea: Hydrozetidae: Seven of the 32 described species of *Hydrozetes* are sexually dimorphic, usually with one or more setae of tarsus I being modified in males (Table 3). The exception is *H. ringueleti* in which the male has a modified shape of femur II, modified claw with a large tooth on leg III, and a large ventral spine on femur IV (Fernandez 1984). Fernandez (1986) noted small variation in femur shape between male and female *Hydrozetes escobari* Fernandez, 1986, but found no consistent differences that would support the species being considered strongly sexually dimorphic. Surprisingly, different tarsal setae can be modified in males of dimorphic *Hydrozetes* species, with one or more of setae *it' pl' pv, v'* and *ft'* modified (Table 3). Males of two species of *Hydrozetes*, *H. dimorphus* and *H. ringueleti* are also larger than females (Fernandez 1984), which is the opposite of the usual pattern.

Hydrozetes also includes 5 species that are suspected parthenogens based on the absence or rarity of males in populations, including *H. lemnae* and *H. lacustris* (Norton *et al.* 1993). Whereas Fernandez (1984) noted an equal number of males and females in the population of *H. ringueleti* he studied, Grandjean (1941) reported 408 females to 3 males for *H. lemnae* (as *H. terrestris*) and 83 females to 1 male for *H. lacustris*, and considered males of these species non-functional and evolutionarily atavistic. He pointed out that rearing is essential to resolve whether a species of *Hydrozetes* could be both sexual and parthenogenetic. Fernandez & Athias-Binche (1986) considered *Hydrozetes lemnae* parthenogenetic in their detailed study of the demography of this species, and Ermilov (2006) confirmed parthenogenesis for the population of this species he reared. However, the juxtaposition of an atavistic male with evident dimorphism does raise the question of whether sexual reproduction occasionally occurs, or whether the modification of the tarsal seta in the male in this species is a genetic relic, and the closest relative of *H. lemnae* a sexual species. Based on adult and immature morphology, Seniczak & Seniczak (2009) and Seniczak *et al.* (2009) placed *Hydrozetes lemnae* in the "confervae" species group with *H. confervae* and *H. thienemanni*, whereas *H. lacustris* was placed in the "lacustris" group with other European species, *H. parisiensis* Grandjean, 1948, *H. octosetosus* Willmann, 1932, and *H. longisetosus* Seniczak and Seniczak, 2009. Clearly, sexually dimorphic species are found in both groups. The ecology of some of these species has been studied, e.g., in relation to water quality (Seniczak 2011), but there are no data on reproductive behaviour such as courtship.

TABLE 2: Brachypylinae species showing sexual dimorphism of the octotaxic system (A, porose area; S, saccule).

Superfamily	Family		Female	Male
Licneremaeoidea	?	<i>Glanderemaeus hammerae</i>	4 A	3 A, S3 large saccule
Ameronothroidea	Fortuyniidae	<i>Fortuynia atlantica</i>	absent	4 A, very large
Oripodoidea	Mochlozetidae	<i>Mochloribatula bahamensis</i>	5 or 6 small rounded A	4-6 A, variable shape; pair curving ventrad between setae <i>p1-p1</i>
Oripodoidea	Mochlozetidae	<i>Mochloribatula metzi</i>	6 small to elongate A	6 A, A2 + A3 long ribbon-like
Oripodoidea	Mochlozetidae	<i>Mochloribatula floridana</i>	6 A	6 A, A2 + A3 long ribbon-like; terminal pair vertically oriented
Oripodoidea	Mochlozetidae	<i>Mochloribatula texana</i>	4-6 A	4-6 A; pair curving ventrad between setae <i>p1-p1</i>
Oripodoidea	Mochlozetidae	<i>Mochloribatula multiporosa</i>	6 A	6 A, elongated, terminal pair in concavity
Oripodoidea	Mochlozetidae	<i>Mochloribatula grandjeani</i>	unknown	7 A, elongated, terminal pair vertically oriented, on tubercle
Oripodoidea	Mochlozetidae	<i>Mochloribatula</i> sp.	not described	terminal pair vertically oriented, on tubercle
Oripodoidea	Mochlozetidae	<i>Unguizetes mauritius</i>	4 A	A2 and A3 longer than in female
Oripodoidea	Symbioribatidae	<i>Symbioribates aokii</i>	4 A	4 A, A3 fused to single, concave, medial A
Oripodoidea	Symbioribatidae	<i>Symbioribates papuensis</i>	4 A small	4 A, large
Oripodoidea	Symbioribatidae	<i>Symbioribates yukiguni</i>	4 A	4 A, A3 closely adjacent A
Oripodoidea	Scheloribatidae	<i>Parapirnodus coniferinus</i>	2 A subequal	2 A, Aa longer than A2, Aa positioned medially seta c
Oripodoidea	Parakalummidae	<i>Neoribates macrosacculatus</i>	4 S small	4 S, very large, with large slit openings
Oribatelloidea	Oribatellidae	<i>Oribatella canadensis</i>	4 A	4 A, A3 fused to single, concave, medial A
Oribatelloidea	Oribatellidae	<i>Oribatella oregonensis</i>	4 A	2A, Aa and fused A1-A3
Ceratozetoidea	Chamobatidae	<i>Xiphobates callipygis</i>	unknown	4 A, A3 fused to single, concave, medial A
Ceratozetoidea	Punctoribatidae	<i>Nuhivabates hivaoa</i>	5-8 A	30 A, pair on large tubercles post.
Ceratozetoidea	Punctoribatidae	<i>Nuhivabates nukuhiva</i>	8 A	ca. 30 A, pair on large tubercles post.
Ceratozetoidea	Punctoribatidae	<i>Zachvatkinibates nortoni</i>	4 A	A2, A3 fused in band, covering posterior of notogaster
Ceratozetoidea	Punctoribatidae	<i>Zachvatkinibates maritimus</i>	4 A	Aa, A1 hypertrophied
Ceratozetoidea	Punctoribatidae	<i>Zachvatkinibates quadrivertex</i>	4 A, oval	Aa irregular long, A2 and A3 long oval
Ceratozetoidea	Punctoribatidae	<i>Zachvatkinibates shaldybiniae</i>	4 A	Aa, A1 hypertrophied
Ceratozetoidea	Punctoribatidae	<i>Zachvatkinibates schatzi</i>	4 A	4 A, A3 fused to single, medial A on tubercle
Galumnoidea	Galumnidae	<i>Centroribates mucronatus</i>	4 A	4 A larger; A3 long oval transverse in recumbant S
Galumnoidea	Galumnidae	<i>Dicatozetes uropygium</i>	4 A	> 4 A, porose areas medially Aa; A3 positioned anteriorly raised transverse arch
Galumnoidea	Galumnidae	<i>Dicatozetes numidicus</i>	4 A	> 4 A, porose areas medially Aa; A3 positioned anteriorly raised transverse arch
Galumnoidea	Galumnidae	<i>Vaghia blascoi</i>	unknown	A3 fused medially
Galumnoidea	Galumnidae	<i>Vaghia simplex</i>	4 A	>4 A, A1 and A2 maybe divided; 10-29 small A medially Aa
Galumnoidea	Galumnidae	<i>Vaghia carinata</i>	4 A	>4 A, A1 and A2 maybe divided; 10-29 small A medially Aa; A3 positioned medially
Galumnoidea	Galumnidae	<i>Vaghia stupendus</i>	4 A	> 4 A, 16-24 small A medially Aa; A3 close to posterior notogastral carinae
Galumnoidea	Galumnidae	<i>Galumna dimorpha</i>	4 A	3A, A2 and A3 fused and elongate
Galumnoidea	Galumnidae	<i>Galumna tarsipernata gibbula</i>	4 A	4 A, A3 positioned medially abutting transverse raised arch
Galumnoidea	Galumnidae	<i>Pergalumna rima</i>	2 A	4-5A, posteromedial A present or absent
Galumnoidea	Galumnidae	<i>Terrazetes mauritius</i>	4 A	A2 and A3 longer than in female
Galumnoidea	Galumnidae	<i>Psammogalumna iranica</i>	4 A	A2 and A3 longer than in female

TABLE 3: Brachypyline species showing sexual dimorphism, other than modifications of the octotaxic system (female state of character modified in male given in parenthesis; NG, notogaster).

Superfamily	Family		Male
Gustavioidea	Kodiakellidae	<i>Kodiakella dimorpha</i>	Head of bothridial seta wide (narrow)
Ameroidea	Amerobelbidae	<i>Hellenamerus ionicus</i>	ventrolateral porose areas (porose areas absent)
Ameroidea	Amerobelbidae	<i>Mongaillardia callitoca</i>	Seta <i>le</i> close to surface, crochet shape (seta unmodified); seta <i>pv'</i> of tarsus II spermadactyl shaped (seta <i>pv'</i> subequal to <i>pv''</i>)
Ameroidea	Amerobelbidae	<i>Mongaillardia eveana</i>	Seta <i>le</i> close to surface, crochet shape, with spines (seta unmodified); seta <i>pv'</i> of tarsus II spermadactyl shaped (seta <i>pv'</i> subequal to <i>pv''</i>)
Oppioidea	Autognetidae	<i>Autogmeta amnica</i>	Porose protuberance bearing setae <i>h</i> ₁ & <i>p</i> ₁ (no porose protuberance)
Oppioidea	Autognetidae	<i>Autogmeta aokii</i>	setae <i>h</i> ₁ modified, on porose plate (porose plate absent, setae <i>h</i> ₁ normal)
Oppioidea	Autognetidae	<i>Autogmeta flaheyi</i>	setae <i>h</i> ₁ & <i>p</i> ₁ modified, on porose plate (porose plate absent; setae <i>h</i> ₁ & <i>p</i> ₁ normal)
Oppioidea	Autognetidae	<i>Autogmeta longilamellata</i>	Long porose plate posteriorly (no porose plate)
Oppioidea	Autognetidae	<i>Autogmeta schusteri</i>	setae <i>h</i> ₁ & <i>p</i> ₁ modified, in porose cavity (porose cavity absent; setae <i>h</i> ₁ & <i>p</i> ₁ normal)
Oppioidea	Autognetidae	<i>Cosmogmeta impedita</i>	tarsus I modified seta <i>a'</i> (seta unmodified)
Oppioidea	Autognetidae	<i>Cosmogmeta kargi</i>	tarsus I modified seta <i>a'</i> (seta unmodified)
Limnozetoidea	Hydrozetidae	<i>Hydrozetes conferrae</i>	tarsus I modified seta <i>it'</i> (seta unmodified)
Limnozetoidea	Hydrozetidae	<i>Hydrozetes dimorphus</i>	tarsus I modified seta <i>pl'</i> (seta unmodified)
Limnozetoidea	Hydrozetidae	<i>Hydrozetes lacustris</i>	tarsus I modified seta <i>it'</i> (seta unmodified)
Limnozetoidea	Hydrozetidae	<i>Hydrozetes lemnae</i>	tarsus I modified seta <i>it'</i> (seta unmodified)
Limnozetoidea	Hydrozetidae	<i>Hydrozetes ringuleti</i>	femur II modified shape; leg III modified claw with large tooth; femur IV large ventral spine on femur IV (femora, claw unmodified)
Limnozetoidea	Hydrozetidae	<i>Hydrozetes thienemanni</i>	tarsus I modified setae <i>ft'</i> , <i>pl'</i> (setae unmodified)
Limnozetoidea	Hydrozetidae	<i>Hydrozetes (Heloribates) tamarae</i>	Tarsus I modified setae <i>pl'</i> , <i>ft' v'</i> and <i>pv'</i> (setae unmodified)
Ameronothroidea	Fortuyniidae	<i>Fortuynia atlantica</i>	pair lateral notogastral protuberances, distally lanceolate setae <i>la</i> , <i>lm</i> (notogaster normal)
Ameronothroidea	Fortuyniidae	<i>Fortuynia yunkerii</i>	Tibia IV shortened; tibia IV modified setae <i>l' (v)</i> (tibia IV normal; setae unmodified)
Ameronothroidea	Ameronothridae	<i>Ameronothrus lineatus</i>	Legs longer than body width (legs shorter than body width)
Ameronothroidea	Ameronothridae	<i>Ameronothrus nigrofemoratus</i>	Leg length equals body width (legs shorter than body width)
Ameronothroidea	Ameronothridae	<i>Podacarus auberti</i>	epimeral and aggenital neutrichy; male claw much larger than female (neutrichy absent)
Ameronothroidea	Ameronothridae	<i>Halozetes belgicae</i>	aggenital neutrichy (neutrichy absent)
Ameronothroidea	Ameronothridae	<i>Alaskozetes antarcticus</i>	aggenital neutrichy (neutrichy absent)
Oribatelloidea	Oribatellidae	<i>Oribatella oregonensis</i>	NG setae <i>lp</i> , <i>h</i> ₃ , <i>h</i> ₂ borne on fused A1-A3 (setae unmodified)
Oripodoidea	Oripodidae	<i>Pirnodus detectidens</i>	NG elongated; Sa anteromedial seta <i>c</i> (NG normal, Sa posteromedial <i>c</i>)
Oripodoidea	Oripodidae	<i>Pirnodus soyeri</i>	seta <i>h</i> ₁ scimitar-shape; seta <i>c</i> ₂ absent; genital & anal areas fused (seta <i>h</i> ₁ normal; seta <i>c</i> ₂ present; genital & anal plates separate)
Oripodoidea	Oripodidae	<i>Cryptoribatula euensis</i>	NG pear-shaped; genital plates abut anal plates (NG normal; genital & anal plates separate)
Oripodoidea	Oribatulidae	<i>Sellnickia caudata</i>	rostrum concave (flattened)
Oripodoidea	Symbioribatidae	<i>Symbioribates papuensis</i>	rostral setae modified (normal)
Oripodoidea	Symbioribatidae	<i>Symbioribates aokii</i>	rostral setae modified (normal)
Oripodoidea	Symbioribatidae	<i>Symbioribates yukiguni</i>	rostral setae modified (normal); setae <i>h</i> ₁ medially adjacent (normal)
Oripodoidea	Scheloribatidae	<i>Nasozetes sumatrensis</i>	rostral protuberance spatulate (not spatulate)
Oripodoidea	Scheloribatidae	<i>Nasozetes lienhardi</i>	rostral protuberance spatulate (not spatulate)
Oripodoidea	Scheloribatidae	<i>Nasozetes porcella</i>	rostral protuberance spatulate (not spatulate)
Oripodoidea	Scheloribatidae	<i>Nasozetes choerognathus</i>	rostral protuberance spatulate (not spatulate)
Oripodoidea	Scheloribatidae	<i>Nasozetes stunkardi</i>	rostral protuberance spatulate (not spatulate)
Oripodoidea	Scheloribatidae	<i>Tuberemaues papillifer</i>	pair posterior tubercles large (small)
Ceratozetoidea	Zetomimidae	<i>Heterozetes aquaticus</i>	anal plate porose (not porose)
Ceratozetoidea	Zetomimidae	<i>Heterozetes helios</i>	Ventral and anal plate porose (not porose)
Ceratozetoidea	Zetomimidae	<i>Heterozetes mimmesotensis</i>	ventral plate porose (not porose)
Ceratozetoidea	Zetomimidae	<i>Naiazetes reevesi</i>	rostrum modified; genital papilla Va modified (not modified)
Galumnoidea	Galumnidae	<i>Centroribates mucronatus</i>	posterior NG setae present (absent)
Galumnoidea	Galumnidae	<i>Psammogalumna hungarica</i>	shape <i>an</i> and <i>ad</i> different from female
Galumnoidea	Galumnidae	<i>Psammogalumna iranica</i>	shape <i>an</i> and <i>ad</i> different from female
Galumnoidea	Galumnidae	<i>Erogalumna zeucta</i>	tarsus I modified setae <i>ft'</i> , <i>pl'</i> , <i>v'</i> , <i>pv'</i> , <i>tc'</i> , <i>it'</i> , <i>a'</i> (setae unmodified)
Galumnoidea	Galumnidae	<i>Kabylogalumna rhinoceros</i>	Numerous macropores medially setae <i>la</i> ; rostrum with thickened crest (5-6 macropores; crest absent)
Galumnoidea	Galumnidae	<i>Pergalumna rima</i>	Rostrum medially rounded (rostrum medially concave)

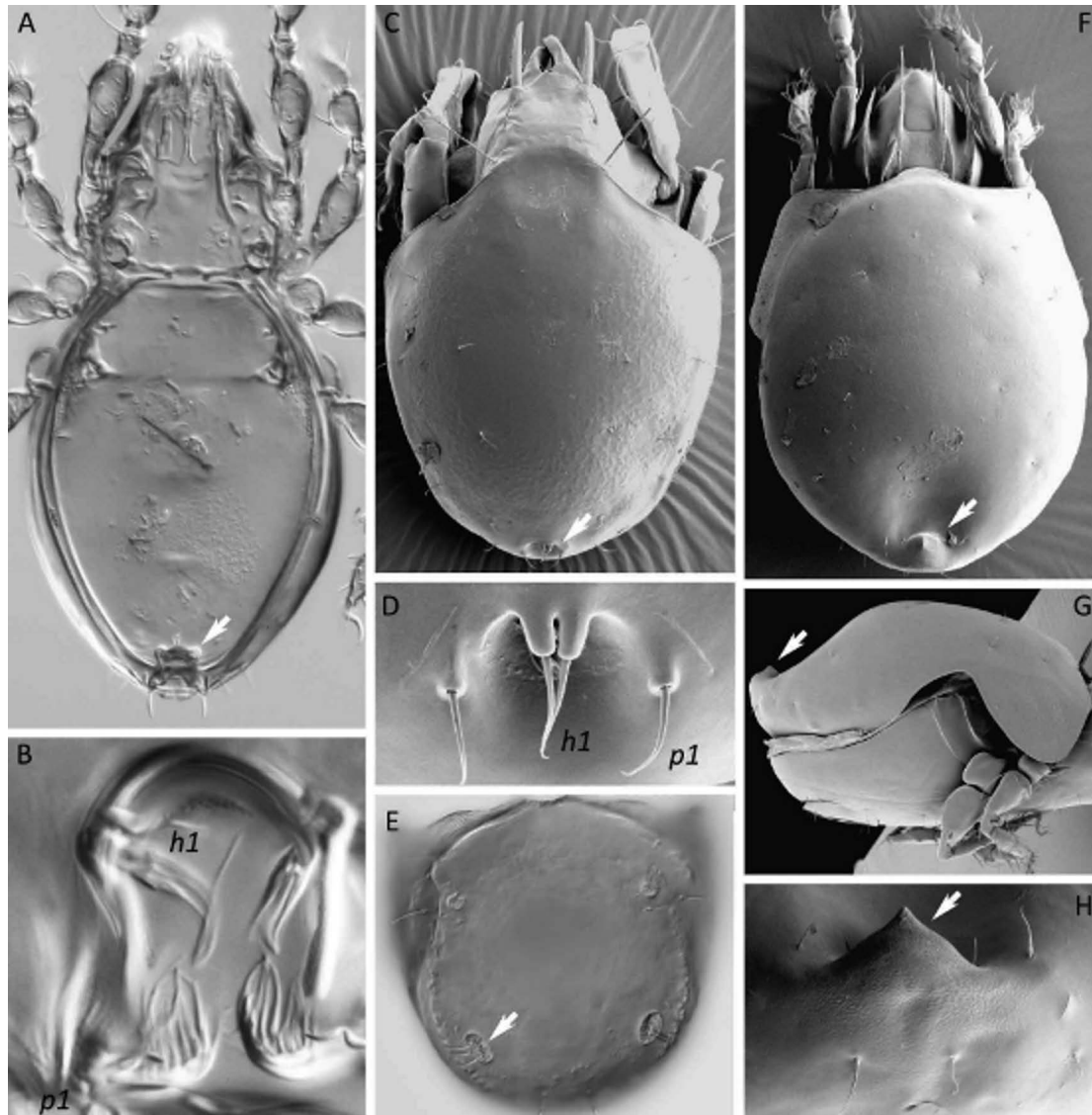


FIGURE 1: A, B, *Autogneta schusteri* Behan-Pelletier - adult male, differential interference contrast micrographs, A – habitus, B – detail of posterior of notogaster; C-H, Scanning electron micrographs, C, D, *Symbioribates aokii* Karasawa and Behan-Pelletier - adult male, C – habitus, D – detail of posterior of notogaster; E – *Oribatella oregonensis* Behan-Pelletier and Walter - adult male, notogaster; F-H, *Zachvatkinibates schatzi* Behan-Pelletier and Eamer - adult male, F – habitus, G – lateral of hysterosoma, H – detail of posterior of notogaster.

Hydrozetes is the only brachyppyline genus that includes sexual species, sexually dimorphic species and parthenogenetic species (Norton *et al.* 1993). Sexually dimorphic species are unknown in the sister family Limnozetestidae, where all species are suspected parthenogens based on absence of males in samples and collections (Norton *et al.* 1993).

Ameronothroidea: Distinct sexually dimorphic species are found in 2 of 4 ameronothroid families.

Fortuyniidae: Two species of *Fortuynia* (of 11 described) are strongly sexually dimorphic, but the expression differs significantly between species: males of *F. atlantica* have 4 pairs of porose areas on the notogaster, a pair of lateral notogastral protuberances, and lanceolate notogastral setae *la*, *lm*, whereas in males of *F. yunkeri* tibia IV is shortened and setae *l'* and (*v*) on this segment are modified (Hammen 1963, Krisper & Schuster 2008).

Ameronothroidea: Ameronothridae: One species in each of the genera *Halozetes* (of 16 described), *Podacarus* (monotypic) and *Alaskozetes* (of 3 described), and 2 (of 13 described) species of *Ameronothrus* are sexually dimorphic. Species in the former 3 genera show aggenital neutrichy in the male (*Podacarus* also with epimeral neutrichy); whereas in *Ameronothrus*, legs are longer than body width in the male of both *A. lineatus* and *A. nigrofemoratus* (Schubart 1975).

Licneremaeoidea: The octotaxic system is present to varying extent in most species of the 9 families comprising this superfamily, but only *Glanderemaeus hammerae* in the unplaced monotypic genus *Glanderemaeus*, is sexually dimorphic. The expression of dimorphism is unusual, with porose organ A3 being a sacculle in males but a porose area in females (Norton & Alberti 1997).

Oribatelloidea: Oribatellidae: Only 2 of 130 described species of *Oribatella* are strongly sexually dimorphic, *O. canadensis* and *O. oregonensis* (Fig. 1E). Both species show modification of the octotaxic system in the male, but in *O. oregonensis* there are additional modifications of notogastral setae *lp*, *h2* and *h3*, which are blade-like and borne on the fused porose areas A1-A3 (Behan-Pelletier & Walter 2012).

Oripodoidea: Of the 17 families comprising this superfamily, 6 include distinctly sexually dimorphic species with males having some modification of the octotaxic system (Table 2), combined or not with other modifications (Table 3).

Oripodoidea: Mochlozetidae: There are 10 genera in this family, yet strongly sexually dimorphic species are found only in *Mochloribatula* and *Unguizetes*. All described species of *Mochloribatula* are sexually dimorphic with modification of the octotaxic system in the male. In contrast, only 1 of 18 species of *Unguizetes*, *U. mauritius*, is sexually dimorphic, with A2 and A3 of the male longer than in the female (Table 2).

Oripodoidea: Sellnickiidae: *Sellnickia caudata* is strongly sexually dimorphic with a modified rostrum in the male (Grandjean 1958). It is possible that the second described species in this genus, *S. heveae* Oudemans, 1927 is also sexually dimorphic, but only the male was described (Oudemans 1927). This species was considered a junior synonym of *S. caudata* by Subías (2004) but Grandjean (1958) noted that Oudemans (1927) had described the shape of the palptibial seta to be thick, lanceolate and unilaterally ciliate unlike that of *S. caudata* which are setose, thus I reject this synonymy.

Oripodoidea: Oripodidae: Of the 27 oripodid genera, distinctly sexually dimorphic species are found in 3, *Cryptoribatula* (1 of 2 described species), *Oripoda* (2 of 37 described species), and *Pirnodus* (2 of 3 described species) (Table 1). The discovery of sexual dimorphism in *Pirnodus detectidens* by Travé (1959) and the subsequent description of *Pirnodus soyeri* by Travé (1969) highlighted the extent of morphological difference between the sexes in this family and in the expression of dimorphism between congeners, although this is evident in other congeners, e.g., sexually dimorphic species of *Oribatella* (Tables 2, 3). Both *Pirnodus* species show a modified hysterosomal shape in the male, as well as shifting of notogastral setae of *l* and *h* series, lyrifissures *im* and *ips*, notogastral sacculles and the opisthonotal gland opening medially, relative to the female. In addition, in male *Pirnodus soyeri* notogastral setae *c* and *h1* differ in shape from those of the female, and in contrast to the female the coxisternal region is elongated to the extent that the genital plates about the anal plates, the preanal plate is weakly sclerotized and thin and the genital and anal openings maybe separated only by a fine membrane (Travé 1969). It is possible that the third described species of *Pirnodus*, *P. andinus* Baranek, 1985 is also sexually dimorphic, but only females were collected and described.

Differences in body shape between sexes are possibly at their most extreme in *Cryptoribatula euaensis* which may be the senior synonym of *Euaella gitteae* Hammer, 1973 as suggested by Balogh and Balogh (1984) and accepted by Subías (2004). *Cryptoribatula euaensis* was described on the basis of a female specimen just prior to the description of *E. gitteae* in the same paper, based on a male specimen, both from the same habitat (Hammer 1973). Whereas the female has a typical oripodid habitus, the male has a pear-shaped body, different positions of notogastral setae, a coxisternum that is strongly directed posteriorly and genital plates that strongly about the anal plates.

Oripodoidea: Parakalummidae: Sexual dimorphism has been described for only one species in this family, *Neoribates macrosacculatus* (1 of 38 described), in which the notogastral sacculles of the male are much larger than those of the female (Aoki 1966a).

Oripodoidea: Schelorbitidae: This diverse family, with 49 genera, has 3 genera with sexually dimorphic

species, and the expression is different in each genus. One of 4 species of *Parapirmodus*, *P. coniferinus*, is sexually dimorphic with notogastral porose areas more elongated in the male and Aa positioned differently on the notogaster (Behan-Pelletier *et al.* 2002). In *Tuberemaeus papillifer* the posterior single pair of saccules are on well-developed tubercles in the male (1 of 30 described species) (Newell 1957). *Tuberemaeus* is considered a subgenus of *Hemileius* by Subías (2014), but is retained as a distinct genus by most authors, e.g., Ermilov and Anichkin (2013), and herein. The sexually dimorphic species of *Nasozetes* are particularly striking, with modification of the rostrum in the male forming a well-developed thumb-like projection (Table 3).

Oripodoidea: Symbioribatidae: The 3 described species of *Symbioribates* are sexually dimorphic. Their males have highly modified rostral setae, as well as modifications of the octotaxic system that are most striking in *S. aokii*, with A3 fused medially and in a concave depression (Aoki 1966b, Karasawa & Behan-Pelletier 2007, Maryuma & Shimano 2014)(Fig. 1C, D).

Ceratozetoidea: Chamobatidae: A single species in this family is sexually dimorphic, *Xiphobates callipygis* (1 of 8 described) Only the male of this species is known, but I infer sexual dimorphism because of the unusual, almost transverse position of notogastral porose areas A1 and A2 posteromedially on the notogaster and porose areas A3 being on a posterior protuberance (Pavlichenko (1991, his Fig. 4)), similar to what is known for males of some sexually dimorphic punctoribatid species, e.g., *Zachvatkinibates schatzi* and species of *Nuhivabates* (Behan-Pelletier & Eamer 2005, Niemi & Behan-Pelletier 2004).

Ceratozetoidea: Punctoribatidae: The 2 described species of *Nuhivabates* are sexually dimorphic with males differing in size, position and number of notogastral porose areas, and the presence of a pair of posterior tubercles (Niemi & Behan-Pelletier 2004). Similar modifications of the octotaxic system are found in the 5 (of 17 described) species of *Zachvatkinibates* that are sexually dimorphic (Behan-Pelletier & Eamer 2005, Weigmann 2009) (Table 2)(Fig. 1F-H).

Ceratozetoidea: Zetomimidae: The single species of *Naiazetes* and 3 of the 5 described species of *Heterozetes* are sexually dimorphic. In contrast with other ceratozetoids (the dimorphic Chamobatidae and Punctoribatidae), sexual dimorphism in Zetomimidae does not involve the octotaxic system, which is present in *Naiazetes* but lost in *Heterozetes*. *Naiazetes reevesi* shows modification of the rostrum, rostral setae and genital papillae *Va* in the male, whereas dimorphic *Heterozetes* species have either a porose anal plate or a porose ventral plate in the male, or a combination of both. These porose regions are presumed dermal glands, though there is no evidence supporting this as yet.

Galumnoidea: Galumnidae: Of the 50 galumnid genera, distinctly sexually dimorphic species are found in *Centrorribates* (monotypic), *Erogalumna* (monotypic), *Kabylogalumna* (monotypic), *Psammogalumna* (2 of 3 described species), *Pergalumna* (1 of 118 described species), *Dicatozetes* (2 of 2 described species), and *Vaghia* (4 of 5 described species). It seems likely that all *Vaghia* species are dimorphic, but *V. uniporosa* Arillo and Subías, 1993 is known only from a single female specimen. As in sexually dimorphic species of *Autogneta* and *Symbioribates*, some sexually dimorphic galumnid species combine modifications of the octotaxic system with modifications of the rostrum, setal modifications and differences in overall shape (Tables 2, 3).

General taxonomic patterns: Of the 1096 genera of Brachypylina, 36 include strongly sexually dimorphic species. Eight genera with strongly sexually dimorphic species are monotypic: *Hellenamerus*, *Glanderemaeus*, *Podacarus*, *Sellnickia*, *Naiazetes*, *Centrorribates*, *Kabylogalumna*, *Erogalumna*. In only 8 multispecies brachypylina genera are all species strongly sexually dimorphic: *Mochloribatula* (8 species), *Symbioribates* (3 species), *Pirnodus* (3 species, but males of only 2 species known), *Nasozetes* (5 species), *Nuhivabates* (2 species), *Dicatozetes* (2 species), *Psammogalumna* (3 species, but males of only 2 species known), and *Vaghia* (5 species, but males of only 4 species known). The remaining 20 genera include both mono- and dimorphic species. We have no evidence for close relationships between sexually dimorphic species or that they form distinct clades within genera as no relevant molecular studies and few phylogenetic analyses have been done.

Morphology of sexual dimorphism

A number of morphological characters are modified in males of sexually dimorphic species, and there is convergence and/or overlap in expression in taxa that do not seem to be closely related (Tables 2, 3). These morphological traits are reviewed below for the different body regions:

Prodorsum:

Modification of the rostrum: *Sellnickia caudata* (Oribatulidae), *Nasozetes sumatrensis*, *N. lienhardi*, *N. porcella*, *N. choerognathus*, *N. stunkardi* (Scheloribatidae), *Naiazetes reevesi* (Zetomimidae), *Kabylogalumna rhinoceros*, *Pergalumna rima* (Galumnidae).

Modification of prodorsal setae: Rostral setae: *Symbioribates aokii*, *S. papuensis*, *S. yukiguni* (Symbioribatidae); lamellar setae: *Mongaiillardia callitoca*, *M. eveana* (Amerobelbidae); bothridial setae: *Kodiakella dimorpha* (Kodiakellidae).

Notogaster:

Modifications of notogastral shape: *Fortuynia atlantica* (Fortuyniidae), *Cryptoribatula euaensis*, *Pirnodus detectidens* (Oripodidae).

Dermal glands absent in female; present in male: *Autogneta amnica* (1 porose area), *A. aokii* (1 porose area), *A. longilamellata* (1 porose area), *A. flaheyi* (1 porose area), *A. schusteri* (1 porose area) (Autognetidae), *Fortuynia atlantica* (4 porose areas) (Fortuyniidae).

Dermal gland porose in female; sacculae in male: Only known for octotaxic gland S3 of *Glanderemaeus hammerae* (Licneremaeoidea).

Number of dermal glands in male different from that in female: *Neoribates macrosacculatus* (Parakalummidae), *Oribatella oregonensis* (Oribatellidae), *Nuhivabates hivaoa*, *N. nukuhiva*, *Zachvatkinibates nortoni*, *Z. maritimus*, *Z. quadrivertex*, *Z. shaldybinae* (Punctoribatidae), *Dicatozetes uropygium*, *D. numidicus*, *Kabylogalumna rhinoceros*, *Vaghia simplex*, *V. carinata*, *V. stupendus*, *Galumna dimorpha*, *Pergalumna rima* (Galumnidae).

Difference in cuticular shape and/or position of porose areas in male vs. those in female: *Symbioribates aokii*, *S. papuensis*, *Parapirnodus coniferinus* (Schelorbatiidae), *Mochloribatula bahamensis*, *M. metzi*, *M. floridana*, *M. texana*, *M. multiporosa*, *M. grandjeani*, *M. calcyfera*, *Unguizetes mauritius* (Mochlozetidae), *Neoribates macrosacculatus* (Parakalummidae), *Oribatella oregonensis* (Oribatellidae), *Zachvatkinibates nortoni*, *Z. maritimus*, *Z. quadrivertex*, *Z. shaldybinae* (Punctoribatidae), *Centroribates mucronatus*, *Kabylogalumna rhinoceros*, *Galumna tarsipennata gibbula*, *Terrazetes mauritius*, *Psammogalumna iranica* (Galumnidae).

Posterior porose area of male in concavity: *Autogneta schusteri* (Autognetidae), *Mochloribatula floridana*, *M. multiporosa* (Mochlozetidae), *Symbioribates aokii* (Schelorbatiidae), *Oribatella canadensis* (Oribatellidae), *Xiphobates calipygis* (Chamobatidae), *Centroribates mucronatus* (Galumnidae).

Posterior porose area(s) of male on, or associated with, tubercle: *Autogneta aokii* (Autognetidae), *Mochloribatula grandjeani*, *Mochloribatula undesc. sp.* (Mochlozetidae), *Nuhivabates hivaoa*, *N. nukuhiva*, *Zachvatkinibates schatzi* (Punctoribatidae), *Dicatozetes uropygium*, *D. numidicus*, *Galumna tarsipennata gibbula* (Galumnidae).

Modifications of notogastral setae: Seta *c*: *Pirnodus soyeri* (Oripodidae); seta *la*, *lm*: *Fortuynia atlantica* (Fortuyniidae); seta *h1*: *Autogneta aokii*, *A. flaheyi*, *A. schusteri* (Autognetidae), *Pirnodus soyeri* (Oripodidae); seta *p1*: *Autogneta flaheyi*, *A. schusteri* (Autognetidae); setae *lp*, *h3*, *h2* *Oribatella oregonensis* (Oribatellidae).

Ventral Region:

Presence of porose areas: Ventrolateral: *Hellenacarus ionicus* (Amerobelbidae); anal plate: *Heterozetes aquaticus*,

H. helios (Zetomimidae); ventral plate: *Heterozetes minnesotensis*, *H. helios* (Zetomimidae).

Modifications in shape and/or position of anal and genital plates in male: *Pirnodus soyeri*, *Cryptoribatula euaensis* (Oripodidae).

Modifications of ventral setae in male: Shape anal seta: *Psammogalumna hungarica*; *P. iranica* (Galumnidae); shape adanal seta: *Psammogalumna hungarica*; *P. iranica* (Galumnidae); epimeral neotrichy: *Podacarus auberti* (Ameronothridae); aggenital neotrichy: *Podacarus auberti*, *Halozetes belgicae*, *Alaskozetes antarcticus* (Ameronothridae).

Genital papillae: Va modified: *Naiazetes reevesi* (Zetomimidae).

Legs:

Modifications of tarsus I setae in male:

Seta *a'*: *Cosmogmeta impedita*, *C. kargi* (Autognetidae), *Erogalumna zeucta* (Galumnidae); seta *it'*: *Hydrozetes conferoae*, *H. lacustris*, *H. lemnae* (Hydrozetidae), *Erogalumna zeucta* (Galumnidae); seta *pl'*: *Hydrozetes dimorphus*, *H. thienemanni*, *H. tamarae* (Hydrozetidae), *Erogalumna zeucta* (Galumnidae); seta *ft'*: *Hydrozetes thienemanni*, *H. tamarae* (Hydrozetidae), *Erogalumna zeucta* (Galumnidae); seta *pv'*: *Hydrozetes tamarae* (Hydrozetidae), *Erogalumna zeucta* (Galumnidae); seta *v'*: *Hydrozetes tamarae* (Hydrozetidae), *Erogalumna zeucta* (Galumnidae); seta *tc'*: *Erogalumna zeucta* (Galumnidae).

Modifications of tarsus II setae in male: Seta *pv'*: *Mongaillardia callitoca*, *M. eveana* (Amerobelbidae).

Modifications of tibia IV setae in male: Seta *l'*, *v'*, *v''*: *Fortuynia yunkerii* (Fortuyniidae).

Modifications in length and/or shape of leg segments: Leg length: *Ameronothrus lineatus*, *A. nigrofemoratus* (Ameronothridae); shape femur II, femur IV: *Hydrozetes ringueleti* (Hydrozetidae); shape tibia IV: *Fortuynia yunkerii* (Fortuyniidae).

Modifications in shape of claw: Leg III: *Hydrozetes ringueleti* (Hydrozetidae); all legs: *Podacarus auberti* (Ameronothridae).

Evidence for associative mating

Most oribatid mites have sperm transfer that is not only indirect, but usually done without male-female association, i.e., dissociative. Males produce stalked spermatophores (stalked sperm packages) deposited independently but without male-female association (also known as dissociative sperm transfer) on a substrate, which is usually humid (Alberti 1999, and included references). Despite this, oribatid spermatophores are morphologically complex structures, and often taxon specific (Alberti *et al.* 1991, Fernandez *et al.* 1991) and Alberti (1999) also referenced modifications to spermatophores

allowing their deposition in both aquatic and xeric habitats.

Although most evidence for spermatophore deposition appears to be dissociative (e.g., Pauly 1952, Woodring 1970), in some species deposition of spermatophores is proximal or associative, that is it is enhanced in the presence of females, for example in *Pelokylla malabarica* Adolph & Haq, 1982 (Haq & Adolph 1981), and *Pergalumna* sp. (Oppedisano *et al.* 1995) or not produced when females are absent, e.g., *Spatiodamaeus subverticillipes* Bulanova-Zachvatkina, 1957 (Shereef 1972). Furthermore, in an undescribed species of *Pergalumna*, Oppedisano *et al.* (1995), described a system of physical signals in the form of stalks deposited in a cross formation, guiding the female to the spermatophore in the centre of this formation. How this signal system precisely leads the female to the spermatophore is unclear, but the authors assumed that signaling chemicals are deposited on the signal stalks. However, none of these species is distinctly sexually dimorphic.

Proximal or associative sperm deposition and/or mating is assumed in the seventy-seven brachypylina species that are strongly sexually dimorphic but there is little evidence, although that available is tantalizing. Grandjean (1956, 1964, 1966b) observed a courtship dance in the sexually dimorphic *Erogalumna zeucta* and *Centroribatates mucronatus*, but there was no evidence of sperm deposition. Oliveira *et al.* 2007 described in detail the intricate courtship behaviour of an undescribed species of *Mochloribatula* from Brazil, with males having the modified terminal pair of porose areas raised medially. The female palpates the male's terminal porose areas with her palps, the stimulated male deposits a nuptial food on the substrate from his genital opening, walks forward a few body lengths, stands on his front two pair of legs, and the female eats the nuptial food. However, no spermatophores were deposited, and the authors speculated that sperm transfer may be direct. Extensive and prolonged courtship behaviour and deposition of nuptial food on modified seta of genu IV, but not associative mating, has been observed in the non-brachypylina *Collohmanna gigantea* and *C. johnstoni* (Collohmanniidae) (Schuster 1962, Alberti & Schuster 2005, Norton & Sidorchuk 2014). To date, associative mating has only been observed in a non-sexually dimorphic species of *Pilogalumna*, where the male forces a sperm package into the venter of the female, but does not precede this with courtship (Estrada-Venegas *et al.* 1996).

Habitat of sexually dimorphic species

Of the 77 strongly sexually dimorphic brachypylina species the microhabitat has been fairly well defined for 62, there is no habitat data for 4 species, and the remaining 12 species have been extracted from "litter and soil" without further specification (Table 1).

- The largest number of sexually dimorphic species (19) is found in a range of arboreal habitats including lichens, moss, bark, and leaves: *Glanderemaeus hammerae*, *Mochloribatula* sp., *Symbioribatates aokii*, *S. papuensis*, *Parapirnodus coniferinus*, *Tuberemaeus papillifer*, *Cryptoribatula euaensis*, *Sellnickia caudata*, *Nasozetes sumatrensis*, *N. choerognathus*, *N. porcella*, *N. stunkardi*, *Nuhivabates hivaoa*, *N. nukuhiva*, *Dicatzetes uropygium*, *Dicatzetes numidicus*, *Erogalumna zeucta*, *Kabylogalumna rhinoceros*, *Vaghia blascoi*, *Vaghia simplex*.
- Eleven species are associated with littoral habitats, either freshwater or marine, including: *Fortuynia atlantica*, *F. yunkeri*, *Ameronothrus lineatus*, *A. nigrofemoratus*, *Podacarus auberti*, *Halozetes belgicae*, *Alaskozetes antarcticus*, *Zachvatkinibates nortoni*, *Z. maritimus*, *Z. shaldybinae*, *Z. schatzi*.
- Six species are primarily associated with coastal vegetation, and were collected either from plants that are halophytic, or coastal shrubland or grasses: *Hellenamerus ionicus*, *Mochloribatula bahamensis*, *M. metzi*, *M. floridana*, *M. texana*, *Zachvatkinibates quadrivertex*.
- Five species live in semiaquatic habitats where water level varies on a seasonal basis, including: *Heterozetes aquaticus*, *H. helios*, *H. minnesotensis*, *Niazetes reevesi*, *Vaghia stupendus*.
- Four species are from dry soil, including: *Mongaiardia callitoca*, *M. eveana*, *Oribatella canadensis*, *Psammogalumna iranica*.
- Three species are from crustose lichens on rocks: *Pirnodus detectidens*, *P. soyeri*, *Vaghia carinata*.
- Seven species are found in continually aquatic habitats, these are the sexually dimorphic species of *Hydrozetes*, all of which show modifications of one or more paraxial seta on tarsus I.
- Seven species are from decaying wood, bark and fungus, including all 5 sexually dimorphic species of *Autogneta* and *Unguizetes mauritius*. *Symbioribatates papuensis* collected from cryptogamic plants growing on the elytra of the Papuan weevil *Gymnopholus* is included here.

DISCUSSION

Of the more than 8350 described species of Brachypylina (Subías 2014), only 77 are strongly sexually dimorphic, representing less than 1% of described species. They are found in 36 of 1096 brachypylina genera (i.e., ca. 3%), which represent 16 of 131 families (i.e., ca. 13% of families) found in 10 of 25 superfamilies (40%): Gustavioidea, Ameroidea, Oppioidea, Limnozetoidea, Ameronothroidea, Licneremaeoidea, Oripodoidea, Oribatelloidea, Ceratozetoidea, Galumnoidea (Table 1). We

can contrast this with the diversity of parthenogenetic species, about 10%, (Norton & Palmer 1991, Cianciolo & Norton 2006). In Brachypylina most parthenogens are isolated in otherwise sexual genera; there are few wholly parthenogenetic genera such as *Tectocephus* and *Limnozetes*, whereas there are 8 genera where all species are strongly sexually dimorphic. It is possible that parthenogenesis in Brachypylina is not as high as in Oribatida in general; but this has not been reviewed since Norton *et al.* (1993), though many subsequent studies have looked for males in populations of species, e.g., Cianciolo & Norton (2006), Maraun *et al.* (2013), Fischer *et al.* (2014).

In genera that also include monomorphic species, such as, *Autogneta*, *Hydrozetes*, *Ameronothrus*, *Parapirnodus*, *Zachvatkinibates*, do the dimorphic species form a clade? Analysis is hampered by the dearth of phylogenetic data. To date, there is no morphological or molecular analysis of phylogenetic relationships in Brachypylina *per se*, and other than Schäffer *et al.* (2010), who included 2 sexually dimorphic species of *Hydrozetes* in their morphological and molecular analysis, and Maraun *et al.* (2004) who included *Autogneta longilamellata* in their molecular analysis, no molecular studies include strongly sexually dimorphic species. Despite these caveats, the range of taxa showing strong sexual dimorphism and the fact that in many genera only some species are strongly sexually dimorphic indicates multiple origins of these traits. There is no evidence they are confined to any phylogenetic lineage in Brachypylina, other than that sexually dimorphic species are concentrated in the 3 closely related poronotic brachypylina superfamilies, Oripodoidea, Ceratozetoidea and Galumnoidea (Norton & Behan-Pelletier 2009), while being absent from the earlier-derivative poronotic taxa Achipteroidea and Phenopeloidea.

Expressions of strong sexual dimorphism are not random; as outlined in Results they are confined to modifications of dermal glands, setal modifications and the shape of legs and body. Furthermore, there is evidence of convergence; for example, tarsal setae are modified in Ameroidea (*Mongaiillardia*), Oppioidea (*Cosmogmeta*), Limnozetoidea (*Hydrozetes*), Galumnoidea (*Erogalumna*) and notogastral setae are modified in Oppioidea (*Autogneta*), Ameronothroidea (*Fortuynia*), Oripodoidea (*Pirnodus*). Grandjean (1960, 1963) noted that in all brachypylina species with tarsal setal modifications in the male, these setae are paraxial. He hypothesised (1963, 1964, 1966b) that during courtship behaviour males of these species walk behind the female on two or three pairs of legs with legs I or II on the flank of the female, and reported this behaviour for *Erogalumna zeucta* (1956, 1964). In contrast, females of a *Mochloribatula* sp. that touch the sides of the male during courtship do not show tarsal setal modifications (Oliviera *et al.* 2007).

Similarly, there is strong convergence in position and modification of secretory porose organs in sexually di-

morphic species of *Autogneta*, *Mochloribatula*, *Symbioribates*, *Zachvatkinibates*, *Nuhivabates*, *Xiphobates* and *Oribatella canadensis*, with a porose organ(s) on a posterior notogastral tubercle. In all cases of this type of sexual dimorphism, other than in *Glanderemaeus hammerae* and *Neoribates macrosacculatus* the dermal glands modified are surface porose areas, rather than invaginated sacculles (Norton *et al.* 1997, Norton & Alberti 1997) (Table 2).

Sexually dimorphic modifications of prodorsal structures are most developed in Oripodoidea and Galumnoidea, and again there is evidence of convergence. Adults of *Sellnickia caudata*, a species known from New Zealand and Australia, have a dimorphic rostral lobe with a porose leading edge (Grandjean 1958). The male lobe is strongly curved distally and has the appropriate size and shape to fit over the pygidial tubercle of the female (Norton and Alberti 1997). Males of *Nasozetes* (Schelorbitidae) have a distinct rostral protuberance (Grandjean 1970), which Bernini (1984) noted is similarly found in the galumnid *Kabylogalumna rhinoceros*. The dimorphism of rostral setae in species of *Symbioribates*, with those of the male enlarged and strongly birefringent throughout, is unique among known Oribatida; their morphology has not been examined in detail, but it is possible they function similarly to the modified tarsal setae in dimorphic species of *Hydrozetes*, steering females to, or in the direction of spermatophores.

Sexual dimorphism and habitat

Proctor (1998) captured the paradox of dissociative mating: "... the improbability that a small female arthropod will stumble across a much smaller droplet of sperm in a vast volume of soil or water". Dissociative sperm transfer and deposition of spermatophores is clearly evolutionarily viable in moist soil and litter habitats with high populations, habitats in which oribatid mites are particularly species rich. But some kind of association would seem to be advantageous in environments that can stress the sperm package with dryness or that are aquatic. In Proctor's (1998) terminology this "pairing with indirect transfer" occurs "when the male courts a particular female before, during, or after spermatophore deposition and often directs her towards his deposited spermatophore". Modifications shown by sexually dimorphic oribatid species would appear to have evolved for this type of association between males and females, and to be linked to particular non-soil microhabitats (Norton & Alberti 1997).

Arguably, species that are strongly sexually dimorphic and living in intermittently dry microhabitats, such as those associated with littoral habitats (11 species), coastal vegetation (6 species), semiaquatic habitats (5 species), dry soil (4 species) and crustose lichens (3) suggest that these are conditions where traits for associative mating are evolutionarily advantageous. To quote Norton and Alberti (1997) "sex pheromones and associa-

tive mating may be especially important in drier environments. The reason for this pattern is undetermined, but it may relate to instability of spermatophores or to the need for locating mates in low density populations." In species that live in semiaquatic habitats (*Heterozetes*, *Naiazetes*), or littoral habitats (e.g., *Fortuynia*, *Zachvatkinibates*), spermatophore deposition and reproduction may occur only at times when the habitat is drier, e.g., low tide, or when adults can aggregate in drier parts of the habitat, e.g., on surface vegetation. This has been postulated for *Fortuynia atlantica* by Pflingstl (2013) who observed adults and immatures of this species retreating into crevices to avoid submergence.

Whereas, some of the nineteen arboreal species listed in the Results are known from forests in the subtropics or tropics that may experience intermittent dryness, others are from rainforest or cloud forest. For example, *Parapirmodus coniferinus* is the only known sexually dimorphic arboreal species in temperate rainforests of western North America; a continually moist habitat. Similarly, *Nuhivabates hivaooa* and *N. nukuhiva* were collected from cloud forest, and *Nasozetes choerognathus* was collected from sphagnum moss in high altitude rainforest.

In discussing sexual dimorphism in species of *Hydrozetes*, Norton and Palmer (1991) suggested that oribatid spermatophores in hypotonic environments maybe osmotically stressed, but also noted that in freshwater Prostigmata dissociative sperm transfer is common, as are evolutionary trends towards more proximal sperm transfer. They suggested that the modified paraxial tarsal setae in *Hydrozetes* species may allow for direct sexual contact during mating. Or they may be used to guide the female to the spermatophore. It is possible that similar guiding (oribatid choreography) is accomplished by the modified seta on tarsal segments in species of *Mongaiillardia*, *Fortuynia yunkerii* and species of Galumnidae, and the modified rostral setae in *Symbioribates* (Table 3).

The five sexually dimorphic species of *Autogneta*, and *Unguizetes mauritius*, have similar modifications to those in intermittently dry habitats, i.e., modified dermal glands, with or without associated modified setae, and they possibly also encounter periods of dryness conducive to dissociative sperm transfer. However, decaying wood, bark and fungal sporophores can provide protected, food rich habitat patches for members of a population within a matrix of unsuitable space. These patches can be spatially discrete from similar microhabitats, populations can be isolated, and dispersal could be the life-history trait that is constrained (Holt 2003), thus limiting interaction between members of populations of a species and optimizing conditions for evolution of some kind of associative mating. Possibly the same applies to *Symbioribates papuensis* living on the fungi, algae and lichens growing on the pronotum and elytra of wingless *Gymnopholus* weevils in high altitude, moist, moss forests, where pop-

ulations of up to 60 mites can be found on a single weevil (Gressitt *et al.* 1965).

Many of the hypotheses on the habitat associations and distribution of sexual and parthenogenetic oribatid species proposed by Norton and Palmer (1991) have been tested in recent years e.g., Cianciolo and Norton (2006), Cianciolo (2009), Fischer *et al.* (2014), Maraun *et al.* (2013). Hopefully this review will stimulate ecological studies on sexually dimorphic species. For example, is it moisture *per se*, or longevity of spermatophores, or the chemistry of pheromones produced by either sex that is the constraining factor for sperm transfer in intermittently dry habitats? What are the differences in ecological conditions of microhabitats of sexual, sexually dimorphic, and parthenogenetic species of *Hydrozetes*? Is evolution of sexually dimorphic species of *Autogneta* and *Symbioribates* related to their spatially discrete microhabitats with dispersal constraints?

CONCLUSIONS

The range of expression of sexual dimorphism in oribatid mites suggests complex evolutionary histories and multiple independent origins in response to selective forces imposed by microhabitat. I suspect that the 1% strongly sexually dimorphic species known in Brachypyliina is an underestimation; many species descriptions do not indicate the sex being described, and/or both sexes are not examined for potential differences. Furthermore, microhabitats where sexually dimorphic species are most common (Table 1) are underrepresented in biodiversity studies. Brachypyliina families without known dimorphic species, yet present in non-soil habitats, e.g., Microzetidae, Licneremaidae, Tegoribatidae, warrant close attention, particularly when new species are described. Strong sexual dimorphism clearly has arisen many times in Brachypyliina; and the expression of this dimorphism does not appear restricted to any particular lineage, though this is hard to validate as phylogenetic data are generally lacking. Undoubtedly, there are many other undiscovered cases of sexual dimorphism in Brachypyliina and knowledge of their morphology is just a precursor to more interesting questions about their biology, evolution and ecology.

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