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Morphological and physiological characteristics of two species of *Epiperipatus* from Costa Rica (Onychophora: Peripatidae)

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Abstract: *Epiperipatus biolleyi* and *Epiperipatus isthmicola* from Costa Rica were studied in the laboratory. Morphometric analyses of *E. biolleyi* show that: (1) larger animals have more legs and (2) females have 8 % more pairs of legs, and axe 24 % longer and 50 % heavier than males. An estimation of how alcohol preservation affects body length indicates less shrinkage in females. Physiological observations on *E. isthmicola* showed that (1) n a session these animals can lose a mean of 7.4 % of body weight (SW) by expelling shear adhesive secretion, (2) weight loss by water evaporation was in average 2 % of BW/min at 66 % relative humidity, and (3) larger animals lose water more slowly. A parturition of *E. isthmicola* was typical of the family.

Key words: Onychophora, *Epiperipatus*, weight, legs, body length, preservation, sexual dimorphism, water exchange, secretion, parturition.

The morphology and physiology of most onychophoran species are poorly known, probably in part because these animals are difficult to find *(e.g.* 0.016 to 0.58 specimens of the relatively abundant *Epiperipatus biolleyi* have been obtained per searching hour per person). *Epiperipatus biolleyi* (Bouvier, 1902) has been collected from altitudes of 250 to 1800 m (Bouvier 1905, Monge-Nájera *et al.* 1993) in the Central plateau and Pacific slope of Costa Rica. ft has been reported from eastern Panama and even Belice (Peck 1975), although these reports require confirmation. The species is characterized by a brilliant red coloration. Studies have been made on the genome of *E. biolleyi,* its secretion of adhesive and its behavior in the laboratory (Monge-Nájera *et al.* 1993, Mora and Leon 1994 in prep.).

Epiperipatus isthmicola (Bouvier, 1902) was originally described by Bouvier as *"Peripatus nicaraguensis* var. *isthmicola"* and has been recorded from altitudes of between 100 and 1200 m, mainly on the Caribbean side of southern Central America (Bouvier *1905,* Brues 1925, Peck 1975). Both sexes have brown bodies with yellow sensory papillae (Bouvier 1905), which are concentrated on the dorsal surface of the trunk and legs (pers. observ.).Very little is known of its biology (Bouvier 1905).

The specimens collected for this study in Coronado and Turrialba show that these animals can persist in cattle pasture and coffee plantations. Several onychophoran species are chiefly found in primary forest and do not survive deforestation, but there are exceptions (Endrödy-Younga and Peck 1983, Ruhberg 1985, Mesibov and Ruhberg 1991) which include these species.

This paper reports on the morphometry of *E. biolleyi,* and on the production of adhesive secretion, water loss and parturition in *E. isthmicola.*

MATERIAL AND METHODS

Between 1985 and 1992 more than 150 specimens of *E. biolleyi* were collected from under and inside rotten trunks, and from microcaverns in the soil, in the Las Nubes-Cascajal area, Coronado, San José, Costa Rica (83 57'37" W, 10 00' 18" N, 1750-1800 m elevation). The habitat is classified as Low Montane Very Moist Forest (Holdridge 1967) but is currently converted to cattle pasture with patches of secondary (basically riparian) forest (the onychophorans occur in both pasture and forest). The animals were transported to the laboratory in closed plastic containers (to avoid water loss), weighed shortly after arrival, and measured in length while walking. The sex was corroborated by dissection before use for other analyses. For comparison, length measurements were also obtained from alcohol preserved specimens, both from our own collection and from the literature (Bouvier 1905, Brues 1925, Clark 1937, Clark and Zetek 1946).

In the first week of April 1992 five individuals of *Epiperipatus isthmicola* were collected in Turrialba, Cartago, Costa Rica (9 54' 36" N, 83 41'12 W, Premontane Wet Forest, Holdridge 1967). The five were found in and under rotten logs: intensive subsequent searching in the same locality failed to reveal more individuals and for that reason we are publishing few observations. The specimens were kept in high humidity terraria according to methods outlined by Ruhberg and Nutting (1980). They were not fed in order to avoid interference with secretion production measurements. Eleven days after capture, two large females gave birth to two and one young respectively, which survived for a few days. Perhaps they were premature (onychophorans may give birth when stressed) or the laboratory conditions were unappropriate. The adults weighed 1.038 1, 0.8902, 0.7863, 0.2441 and 0.0678 g and newborns 0.0677, 0.0646 and 0.0592 g.

The animals were used for tests which included extraction of blood samples with a microsyringe (to be reported elsewhere) and anesthetized when necessary by placing them with a piece of paper moisted with a weighed amount of ethyl acetate (concentration 10.2g/mole) in a closed 60 cm^3 jar.

To extract the secretion the animals (which were not anaesthetized during extraction) were carefully pinched with the fingers. Read and Hughes (1987) forced their specimens to eject the secretion onto a pre-weighed piece of aluminum foil. We were unsuccesful with this technique (because some secretion fell outside the foil) and found it easier to weigh the animals before and after ejection of secretion. A correction was made for the weight loss caused by dehydration during the extraction time (using values presented here under "Water loss").

Water loss was also measured by weighing technique (Campiglia and Lavallard 1982): water loss values are the weight difference of animals after 1.0 mm of permanence at 66 % relative atmospheric humidity. The animals did not die inmediately after the dehydration tests and apparently recovered.

A sample of the liquid surrounding a newborn was stained with Giemsa for microscopic analysis.

All regressions are stepwise, which correct for strongly associated variables. Voucher specimens will be deposited in the Museum of Zoology, University of Costa Rica at San José, and in the American Museum of Natural History (New York).

RESULTS

E. biolleyi

Morphometry: No physiological observations were carried out on *E. biolleyi* because the specimens were required for immediate genetical analysis by other researchers. In comparison with males, the females have 8 % more leg pairs, and are 24 % longer and 50 % heavier (Table 1).

Length and weight can be related by the following empirical regression equations (all $p<0.05$)):

Females

Length = -3.23 Legs + 0.0063 Weight + 129.62

Weight = 441.93 Legs + 109.77 Length - 0.00016

Leg pair values were too variable to allow an equation.

Males

Leg pairs = 0.00025 Weight + 27.4

Length = 0.00789 Weight + 26.15

Weight = 280.63 Legs + 49.82 Length - 8130.4

TABLE 1
Morphomethc wihes for Iive Epiperipatus biolleyi*

Character	Mean	SD	Min	Max	N
Legs (pars)					
Females	30.33	0.66	28	32	95
Males	27.76	0.60	27	30	58
Length (mm)					
Females	52.27	13.25	18	75	84
Males	38.49	8.62.	18	55	53
Weight (mg)					
Females	2851	1905	100	8352	94
Males	1358	855	58	3369	57

Mean = arithmetic mean, SD = Standard deviation. Mm = minimum, Max = maximum, N = sample size

* All cases different between sexes (Mann-Whitney U test, p<0.001)

Effect of alcohol preservation: Alcohol preserved females (N=13) have a mean length of 38.50 mm, 26 % shorter than live females (I'able 1), while males in alcohol (mean 22.78 mm, N=9) are 41 % shorter than live specimens (see Table 1).

E. isthmicola

The small sample of *E. isthmicola* did not allow a detailed morphometric study, but physiological data were obtained for this poorly known species.

Anaesthesia: A dosage of *5* mg of ethyl acetate per 100 mg of animal body weight produced immovability in 80 s. The sequence of effects is the same for *E. isthmicola* and *Epiperipatus biolleyi:* (1) begining slightly behind the head and advancing towards the rear, the trunk twists turning upside down, (2) saliva is expelled in a bubble, mandibles emerge and move slowly, (3) adhesive secretion is slowly released, often predominantly on one side, (4) the body Is extended longitudinally and assumes an arc shape with legs outermost, while urine droplets appear at leg bases.

Overexposure to ethyl acetate causes death and has been recommended for relaxing specimens prior to fixation (Wagstaffe and Fidler 1955). In our experience, direct contact with ethyl acetate during anaesthesia should be avoided because it dissolves the onychophorans' pigment, whose solubility in this substance suggests that it is a non-polar chemical compound.

Adhesive secretion: *E. isthmicola* had to be pinched more times than *E. biolleyi* to squirt secretion (non-quantified personal observation). Animals with full reservoirs produced 0.017±-0.016 (0.003-0.047) g of secretion in a session (N=7, format for this and similar values: mean ± standard deviation, minimum-maximum, N number of cases), or a mean of 7.4 % (range: 1.3-13 %) of their body weight, and squirted 0-5 times in a session. When dissected after extraction, one individual had semi-filled reservoirs. The secretion was recognized during dissection because it solidified into a sticky ball upon exposure to air. It was only possible to estimate re-filling time in one female, which recovered 0.09 % of its original amount of secretion per day.

Water loss: Weight loss by water evaporation (66% relative humidity) was 0.403±-0.384 (0.059-0.924) g / mm (N=7) or a mean of 2.1 (mm. 0.3-max. 5.3)% of body weight in that time. Larger animals lose less water (Pearson Correlation = -0.41, p<0.05).

Parturition: Just before the onset of a birth observed in April 1992, a female *E. isthmicola* bent the body into an *U* with head and tail higher than the rest of body. The young began to emerge head *first,* advancing 1 mm per mm. It advanced with the help of maternal peristalsis and its own contractions, which the newborn supplemented 30 mm after the onset of parturition by twisting around its longitudinal body axis; 16 mm later it also began moving those legs closest to its parent. The female remained motionless most of the time; once she moved the head towards the young and after 83 mm of parturition briefly oscillated the rear part of her body laterally. She died (because of captivity stress?) after 103 mm. The newborn reduced its emergence rate to 0.07cm/mm, then it stopped and was extracted with forceps. A sample of the liquid covering the young showed no signs of the blood corpuscles which would have been expected if tissues were ruptured during the process, as occurs in many vertebrates.

In the young the yellow pigment is concentrated in the apical part of the papillae. Like adults, the young avoid air currents and can walk backwards.

DISCUSSION

E. biolleyi

Morphometry: In females, the number of legs is so variable that it can not be predicted by length or weight (both variables eliminated by the regression model). Similarly, Campiglia and Lavallard (1973) were unable to detect a clear correlation between number of legs and weight in *P. acacioi.*

In general, these results agree with the conclusion that longer animals require more legs for a constant distribution of weight per leg (Ghiselin 1974), a result of the lack of a rigid skeleton. The larger body size of female *E. biolleyi* is close to the 63 % weight advantage reported for females of *P. acacioi* (Campiglia and Lavallard 1973).

The theoretical basis for sex dimorphism in onychophorans is simple and applies to many other organisms (Ghiselin 1974). Natural selection appears to have favored larger females which are able to produce more offspring and evidence suggests that this helps them capture more profitable prey (see Ghiselin 1974, Read and Hughes 1987, Havel *et al. 1989).* Additionally, larger females may be more succesful colonizers of new habitats because they carry more offspring. Larger females may have larger individual offspring with more legs, but there are exceptions (Laval lard and Campiglia 1975, Read 1985).

In comparison with their male siblings, newborn females are often larger, have more legs and grow faster (Laval lard and Campiglia 1975, Read 1985, Havel *et al.* 1989). It is unclear why some larger females do not have larger individual offspring with more legs, and why newborn females sometimes are not larger and with more legs than their brothers.

In males the trend has been toward early reproduction, which is associated with small size, precocious mating and high motility (Ghiselin 1974).

The modal distribution of length, weight and number of legs according to sex *(e.g.* Campiglia and Lavallard 1973) suggests polygenic determination (or plastic expression) and sex linkage.

Effect of alcohol preservation: The problem of how to measure these contractile animals has been discussed in the literature, with the general result that data on the length of the resting and walking animal, length of exuvia and weight are considered of value (Manton 1938, Campiglia and Lavallard 1973, Ruhberg 1985). For many species of onychophorans the only available length measurements were performed on alcohol preserved specimens (see van der Lande 1993). For that reason we decided to examine the difference between body length measurements done in live animals and an independent sample of preserved specimens (surprisingly, there has been no previous attempt to statistically estimate the effect of preservation on this parameter). A previous observer had the impression that shrinkage in alcohol could reach 50 % in other species, but there were no statistical data (see Ruhberg 1985). The unexpected result that males suffer a greater contraction could mean that larger individuals *(i.e.* females) are less affected because of their lower surface/volume ratio, which possibly reduces the amount of alcohol which can penetrate their body wall. The amount of contraction also affects the appearance of some taxonomical characters (Read 1988). Although pre and post fixation measurements would optimally be done in the same individual, and not in independent samples as in our study, these data give a preliminary idea of the degree by which the taxonomic literature underestimates length.

If the percent reduction estimates obtained here are validated by future studies' with other species, they could be used to reconstruct values for those taxa which are only known as alcohol specimens. Unfortunately, not all collectors indicate the preservation techniques, and these vary greatly, from direct immersion in alcohol *(e.g.* our specimens unless labeled otherwise) to the previous use of relaxing chemicals (Wagstaffe and Fidler 1955, Ruhberg 1985), immersion in water slightly below boiling temperature (S.B. Peck, pers. com. 1994) or injection with preservative (van der Lande 1993). Nevertheless, this subject deserves more attention, because overall length can be a useful parameter in ecological studies and in comparisons with fossils, for which length at preservation is one of the few available measurements.

E. isthmicola

Anaesthesia: Ethyl ether, but not low temperatures or C02 produces similar effects in *P. acacioi* (Campiglia and Lavallard 1982). A newborn *E. isthmicola* expelled 4.6 % of its body weight in secretion when anesthetized, similar to the 5.7 % recorded for adult *P. acacioi* anaesthetized with CO2 (Campiglia and Lavallard 1982).

Adhesive secretion: The biochemistry of secretion in other onychophorans has been described by Manton and Heatley (1937) and Roper (1977). León *et at.* (1994 in prep.) showed that the secretions of *E. biolleyi* and *E. isthmicola* contain species-specific small peptides which may act as gelators and could be useful for taxonomic analysis. The evolutionary history of the secretion is discussed by Monge-Nájera (1994).

Manton and Heatley (1937) erroneously believed that the secretion was exclusively used for defense, but it is also used to capture prey as stated by early researchers (review in Read and Hughes 1987). The defensive secretions of several arthropods are often directed specifically at the attacker and released in larger amounts with stronger stimuli, because such secretions are physiologically expensive (Eisner and Meinwald 1966). The same applies to the few onychophoran species for which detailed observations are available (see Manton and Heatley 1937, Read and Hughes 1987, Monge-Nájera ci at. 1993, and this paper). Secretions with a similar drying mechanism are also known in Diplopoda and Isopoda, while a similar trapping function is also known in some Diplopoda and Isoptera (Eisner and Meinwald 1966). Nevertheless, a double function (defense and prey capture) is only known in the Onychophora and the reduviid hemipteran genus *Platymeris* (Eisner and Meinwald 1966).

In comparison with *E. biolleyi, E. isthmicola* appeared reluctant to squirt. The difference might be at the individual level (nutrition, health, etc.) or it may represent a differential species-level character, perhaps resulting from different levels of predator pressure. The few data available indicate a range of 1-31 discharges per individual in one session (Ruhberg 1985, Read and Hughes 1987), *E. Isthmicola* being in the lower part of the range. As a percentage of body weight, the secretion produced by *E. isthmicola* is half of that produced by *M. torquatus* (see Read and Hughes 1987), which could explain why the former species showed partly filled reservoirs upon dissection. For the single case of replenishment measured, it occurred slowly: our unfed *E. isthmicola* would have replenished its reservoirs in 60 days, while fed *M. torquatus* required 19 days. Nevertheless, feeding may be unrelated with secretion replenishment, according to Read and Hughes (1987), and onychophorans probably feed more frequently in nature (Ruhberg *1985,* Read and Hughes 1987), suggesting that they do not spend all their reserve in a single prey.

Water loss: In onychophorans, water loss is a function of air humidity *(e.g.* Manton and Heatley 1937, Manton and Ramsay 1937, Morrison 1946b) and occurs through tracheae. At least in one species the tracheae are concentrated in areas of higher metabolism and occupy more volume in larger animals (Bicudo and Campiglia 1985). The ratio of surface area to volume is lower in larger animals; this may explain why larger *E. isthmicola* lose and gain water more slowly. A similar suggestion was proposed by Newlands and Ruhberg (1978) for other species.

Water loss rates were 0.16 *(Peripatopsis),* 0.08-0.60 *(E. acacioi)* and 2.1 *(P. isthmicola;* all as *%* of body weight per mm) when tested at 27, 48 and 66 % relative humidity, respectively (recalculated from Manton and Heatley 1937, Campiglia and Lavallard 1982, this paper). *Peripatopsis moseleyi* can lose 34 % of its body weight by dehydrarion in 2 hr, any value above

33 % often being fatal (Doods and Ewer 1952). When returned to humidity-saturated terraria, recovery rates were 3.8, and 0.43%/mm in *Peripatopsis*, and *P. acacioi*, respectively (recalculated from Manton and Heatley 1937, Campiglia and Lavallard 1982). This fits the hypothesis that water loss is basically a function of air humidity (see Campiglia and Lavallard 1982).

No correlation was found between weight and rate of loss for *P. acacioi*, probably because there was little size variation in the sample (Campiglia and Lavallard 1982). This sample of *E. isthmicola* included a variety of sizes (see above), which can explain the correlation of weight with water loss.

Parturition: The parturition posture observed in this case appears to have no precedent in the literature. The female was in the moss of a terrarium (in nature its close relative *E. biolleyi* is sometimes found inside moss), not on a hard surface as might have been the case in other reports: is this a more natural posture or a result of captivity stress? On the other hand, females of other species elevate the rear end during parturition (Morera *et* at. 1988). There are no previous reports of parturition in this species, but births were also said to occur in September and November in one unidentified female which was probably *E. isthmicola* (see Calvert and Calvert 1917). That the species reproduces thoughout the year is also suggested by Bouvier's (1905) illustration of the female genital tract, in which he counted 20 embryos at various stages of development. However, unpublished observations indicate that some peripatids give birth over a period of several months, but that these are not Continuous throughout the year, despite having embryos at various stages of development (M. Walker, pers. corn. 1993).

Apparently females can mate shortly after birth (Bouvier 1905): therefore the species may be more precocious than *M. torquatus, P. acacioi* and *Peripatopsis moseleyi* which mate when aged 3, 5 and 9 months, respectively (Read 1985, Manton 1938, Lavallard and Campiglia 1975). The gestation time in *E. isthmicola* is unknown but gestation appears to be very constant within the phylum (10-14 months, Manton 1938, Lavallard and Campiglia 1975).

Maternal peristalsis, known in both onychophoran families (Manton 1938, Morrison 1946 a, Lavallard and Campiglia 1975, Morera *et* at. 1988), appears to be more important for a successful birth than the movements of the young (Campiglia and Lavallard 1989), an idea supported by this observation of *E. isthmicola*. The initial speed of embryo emergence is the same as that reported for *Epiperipatus brasiliensis* (recalculated from Morrison 1946 a).

The ability of the young to move their legs during birth is also known in both families and neotropical species are characteristically born head first (reference to films and literature in Morera *et* at. 1988). Parturition is often briefer in the peripatopsid *P. moseleyi* (15 mm reported by Manton 1938, but a 15-30 mm range has been observed: H. Ruhberg 1993 pers. comm.) than in the peripatids *E. brasiliensis* (30 mm, Morrison 1946 a) and *E. acacioi* (30-45 mm, Lavallard and Campiglia 1975). The death of the mother during parturition suggests that this longer case for *E. isthmicola* was not typical.

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RESUMEN

Se estudió en el laboratorio dos especies costarricenses de onicóforo, *Epiperipatus biolleyi* y *Epiperipatus isthmicola.* El análisis morfométrico de *E. biolleyi* muestra que (1) animales más grandes tienen más patas y (2) las hembras tienen 8% más pares de patas y son 24% más largas y 50% más pesadas que los machos. Una estimación de cuánto disminuye la longitud corporal por la preservación en alcohol indica que las hembras se encogen menos. Las conclusiones fisiológicas sobre *E. isthmicola* fueron que (1) en una sesión estos animales pueden perder una media del 7.4% de su peso corporal (PC) al lanzar la sustancia adhesiva típica del filo, (2) la disminución de peso por perdida de agua fue en promedio 2% del PC/mm a una humedad relativa del 66% y (3) los animales grandes pierden y ganan agua más lentamente (recuperación media 1.2% 1 mm en una atmósfera saturada). Un parto de *E. isthmicola* siguió el patrón típico de la familia.

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