Like a glove: do the dimensions of male adanal suckers and tritonymphal female docking papillae correlate in the Proctophyllodidae (Astigmata: Analgoidea)?

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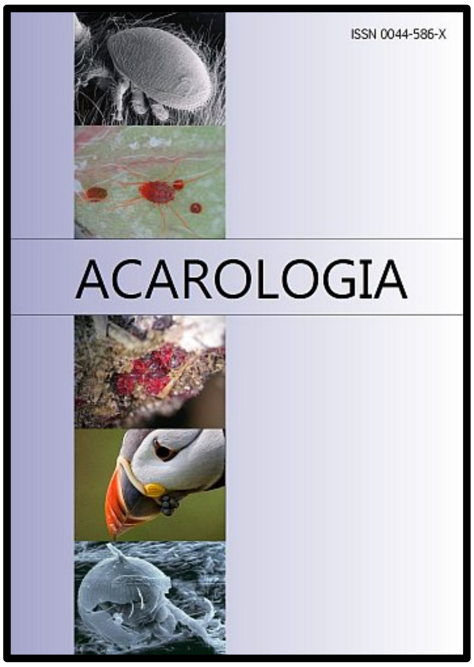

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LIKE A GLOVE: DO THE DIMENSIONS OF MALE ADANAL SUCKERS AND TRITONYMPHAL FEMALE DOCKING PAPILLAE CORRELATE IN THE PROCTOPHYLLODIDAE (ASTIGMATA: ANALGOIDEA)?

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ABSTRACT — Precopulatory guarding of tritonymphal females by adult males is common in feather mites (Acari: Astigmata). Within the Proctophyllodidae (Astigmata: Analgoidea), some genera possess morphological features in both sexes that have been suggested to enhance male attachment. One such structure in tritonymphal females is the development of a pair of fleshy lobe-like docking papillae, while males possess a pair of ventral adanal suckers that are proposed to fit over top of these projections. To determine whether these structures are strongly correlated in size, we measured the dimensions of the male adanal suckers and tritonymphal female docking papillae in three genera of mites: *Neodectes* spp. Park and Atyeo, 1971, *Proterothrix* spp. Gaud, 1968 (Proctophyllodidae: Pterodectinae), and *Proctophyllodes* spp. Robin, 1877 (Proctophyllodidae: Proctophyllodinae). We looked for correlations in these measurements as an indication of selective cooperation. Our results did not reveal strong positive correlations between the dimensions of these structures in tritonymphal females and adult males. We propose several reasons for why we may not have detected strong evidence of a good fit between anal suckers and tritonymphal papillae that are related to the biology of feather mites, and suggest steps to expand on this research in future.

KEYWORDS — Acari; cooperative; correlated morphology; feather mites; precopulatory guarding

INTRODUCTION

The mating strategies of precopulatory and postcopulatory mate guarding are common tactics employed by males to overcome sperm competition (Parker, 1970). Although both strategies aim to maximize male fertilization success, these behaviours are predicted under different reproductive conditions. Precopulatory mate guarding is expected when females mate only once, when females mate for a limited time (a brief fertilization window), or when there is little ability of the female to store sperm; these qualities encourage males to stake a claim to unreceptive females before they become receptive (Parker, 1974; Grafen and Ridley, 1983). In contrast, postcopulatory mate guarding is predicted when females mate repeatedly and are receptive to additional males following an initial copulation (Parker, 1974). In the case of precopulatory mate guarding, the fitness gained by guarding an unreceptive female exceeds that which is gained in a continued search for mates (Parker, 1974). This form of mate guarding is argued by Simmons (2001) to function more as a means of monopolizing females until they are receptive than as a tactic to avoid sperm-competition.

While mate guarding has been widely reported throughout the animal kingdom (beetles: Alcock, 1991; birds: Birkhead, 1979; Hammers *et al.*, 2009; cephalopods: Huffard *et al.*, 2008; lizards: Cuadrado, 1998; mammals: Schubert *et al.*, 2009), precopulatory guarding is especially common among invertebrates (Deinert *et al.*, 1994; Bel-Venner and Venner, 2006; Arnqvist *et al.*, 2007; Parker and Vahed, 2010; Takeshita and Henmi, 2010). Several studies in arthropods document that the onset of precopulatory mate guarding occurs when females are still juveniles (Evstigneeva, 1993; Fiers, 1998; Holdsworth and Morse, 2000; Zhu and Tanaka, 2002; Oku, 2009; Estrada *et al.*, 2010; Jones *et al.*, 2010). In some taxa this guarding is cued by the emission of pheromones by the immature female that announce her stage in the moult cycle to potential mates (Dunham, 1978; Thompson and Manning, 1981). Some immature female mites (Arachnida: Acari) also emit pheromones termed "arrestants" that stimulate guarding behaviour in conspecific adult males (Sonenshine, 1985).

In mites, precopulatory guarding has been found in many taxa where males guard the penultimate female stage, which depending on taxon can be the deutonymph (Helle, 1967; Potter *et al.*, 1976; Yasui, 1988; Oku, 2009) or the tritonymph (Witaliński *et al.*, 1992; Bochkov and OConnor, 2005). Some male spider mites (Tetranychidae: *Neonidulus* Beard and Walter, 2010) have enlarged legs I to guard nymphal females (D.E. Walter, Royal Alberta Museum, pers. obs.). Likewise, many male Astigmata possess enlarged legs III and/or legs IV to aid in guarding nymphal females (Krantz and Walter, 2009), while others use a pair of ventral adanal suckers to attach to immature and/or mature females (Witaliński *et al.*, 1992). In most male Astigmata, these suckers are composed of a thick exocuticle that forms slightly concave sucker plates that are covered by a flexible procuticle encompassing the sucker periphery, which facilitates attachment of the sexes through suction (Witaliński, 1990).

In the feather mite genus *Proctophyllodes* Robin, 1877 (Astigmata: Proctophyllodidae), the tritonymphal females possess a pair of dorsal, fleshy protuberances which are hypothesized to fit into the male adanal suckers (Atyeo and Braasch, 1966), which are particularly elongated in this genus. The protuberances of *Proctophyllodes* spp. and *Psoroptes* spp. Gervais, 1841 (Astigmata: Psoroptidae) have been described in detail by Witaliński *et al.* (1992) whose findings suggest that the dimensions of the docking papillae and the adanal suckers correspond in length, diameter and axis-to-axis distance. A comparable mechanism for attachment has been illustrated in the beaver fur-mite *Schizocarpus mingaudi* Trouessart, 1896 (Astimgata: Chirodiscidae) whereby the larval cuticle is drawn into a conical depression in the male's soft cuticle (Fain *et al.*, 1984). Some fur mites have an additional attachment site between the male's adanal suckers and discs on the immature female mite; in this instance, the discs are considerably larger than the adanal suckers, which makes their insertion into the suckers highly unlikely (Fain *et al.*, 1984).

Morphological traits associated with copulation and intromission are often correlated between the sexes (Eberhard, 2004). These correlated characters can arise through antagonistic coevolution wherein the sexes engage in an evolutionary arms race to gain control of reproduction (Rowe and Arnqvist, 2002; Bergsten and Miller, 2007; Tatarnic and Cassis, 2010); or these traits may be "selectively cooperative" arising through sexual selection by female choice (Eberhard, 1985). In this study, we measured the dimensions of the male adanal suckers and the tritonymphal female docking papillae in representatives of three genera of Proctophyllodidae (*Neodectes* spp. Park and Atyeo, 1971, *Proctophyllodes* spp., and *Proterothrix* spp. Gaud, 1968). These traits are supposedly beneficial to both sexes, as efficient coupling may increase the fertilization success of both sexes, and potentially reduce damage to the female's integument by localizing attachment to a particular area. As such, we hypothesized that these traits would be strongly correlated to improve attachment of the adult male to the tritonymphal female.

MATERIALS AND METHODS

Specimen collection

We collected three genera of mites in the family Proctophyllodidae, including *Neodectes* spp., *Proterothrix* spp. (Proctophyllodidae: Pterodectinae), and *Proctophyllodes* spp. (Proctophyllodidae: Proctophyllodinae). Mites were collected from 31 avian hosts captured in Australia, Canada, China, the Philippines, and Spain (Table 1). Mites were retrieved using a variety of methods depending on the host's place of capture. Birds collected in China and the Philippines were mist-netted and mites were removed by eye from the dead host. In Spain, feathers were plucked from live birds and soaked in 70 % ethanol to rehydrate specimens (see Galván *et al.*, 2008). In Australia, preserved bird specimens were sampled from either the Western Australian Museum or the Queensland Museum by one of the authors (HP). For these birds, mites were removed in two ways: if hosts were prepared as dry skins, the skins were ruffled over a sheet of white paper and the mites were picked out with fine forceps and placed into 80 % ethanol; if birds were preserved in ethanol, mites were sucked up from the bottom of the container using a syringe. Birds collected in Canada were stored individually after capture at -20 °C until processing by HP or KB. Frozen birds were thawed and then washed in a container with $\simeq$ 15 mL of 95 % ethanol, $\simeq$ 10 mL of Palmolive® dish detergent and sufficient water to submerge the bird. We massaged each bird thoroughly within solution to remove mites from the body, wing feathers, and retrices. We rinsed the bird body and poured the washing solution through a Fisher-Scientific 53-µm mesh filter. Mites were washed from the sieve with 80 % ethanol and stored in 75 mL screw-cap containers. For birds caught in Canada and Spain, the

TABLE 1: Taxonomic authorities and locality data for avian hosts of *Neodectes* spp., *Proctophyllodes* spp., and *Proterothrix* spp. (Analgoidea: Proctophyllodidae). The presence or absence of docking papillae in tritonymphs is indicated for each taxon.

Mite taxonomy and authority	Host genus	Host species	Authority	Locality	Docking papillae present
Neodectes spp. Park & Atyeo, 1971	*Acanthisitta*	*chloris*	(Sparman, 1787)	No data	Yes
	Pachycephala	*philippinensis*	(Walden, 1872)	Aurora Memorial Park, Philippines	Yes
	Sitta	*frontalis*	Swainson, 1820	Philippines	Yes
Proctophyllodes spp. Robin, 1877	*Acanthis*	*hornemanni*	(Hoiboil, 1843)	Smith, AB, Canada	No
	Bombycilla	*cedrorum*	Vieillot, 1808	Athabasca, AB, Canada	No
	Carpodacus	*purpureus*	(Gmelin, 1789)	Athabasca, AB, Canada	Yes
	Catharus	*ustulatus*	(Nuttall, 1840)	Edmonton, AB, Canada	Yes
	Certhia	*americana*	Bonaparte, 1838	Edmonton, AB, Canada	Yes
	Cincloramphus	*cruralis*	(Vigors and Horsfield, 1827)	Outcamp Creek, Australia	Yes
	Cyornis	*herioti*	Ramsay, 1886	Mt. Cagua, Philippines	Yes
	Melospiza	*melodia*	(A. Wilson, 1810)	AB, Canada	Yes
	Pica	*hudsonia*	(Sabine, 1823)	Edmonton, AB, Canada	Yes
	Sitta	*canadensis*	Linnaeus, 1766	Spruce Grove, AB, Canada	Yes
	Turdus	*migratorius*	Linnaeus, 1766	Edmonton, AB, Canada	Yes
P. glandarius (Koch, 1840)	*Bombycilla*	*garrulus*	(Linnaeus, 1758)	AB, Canada	No
P. megaphyllus Trouessart, 1885	*Plectrophenax*	*nivalis*	(Linnaeus, 1758)	Barrhead, AB, Canada	Yes
P. microcaulus Gaud, 1957	*Eremophila*	*alpestris*	(Linnaeus, 1758)	Manyberries, AB, Canada	Yes
P. musicus Vitzthum, 1922	*Turdus*	*migratorius*	Linnaeus, 1766	Edmonton, AB, Canada	Yes
P. pennifer (Trouessart and Neumann, 1888)	*Cinclidium*	*leucurum*	(Hodgson, 1845)	Jing Xin, China	No
P. schoenicli Atyeo and Braasch, 1966	*Emberiza*	*schoeniclus*	(Linnaeus, 1758)	Spain	Yes
P. sylviae Gaud, 1957	*Sylvia*	*atricapilla*	(Linnaeus, 1758)	Spain	Yes
P. vesca Atyeo and Braasch, 1966	*Myadestes*	*townsendi*	(Audubon, 1838)	Camp Creek, AB, Canada	No
Proterothrix spp. Gaud, 1968	*Rhipidura*	*cyaniceps*	(Cassin, 1855)	Aurora Memorial Park, Philippines	Yes
	Orthonyx	*temminckii*	Ranzani, 1822	Wilson's Peak, Killarney, Australia	Yes
	Cracticus	*quoyi*	(Lesson, 1827)	Gunn Point, Australia	No
Keys to *Proterothrix* spp. Gaud, 1968	*Conopophila*	*rufogularis*	(Gould, 1843)	Derby-West Kimberley, Australia	Yes
	Cyornis	*herioti*	Ramsay, 1886	Angat & Mt. Cagua, Philippines	Yes

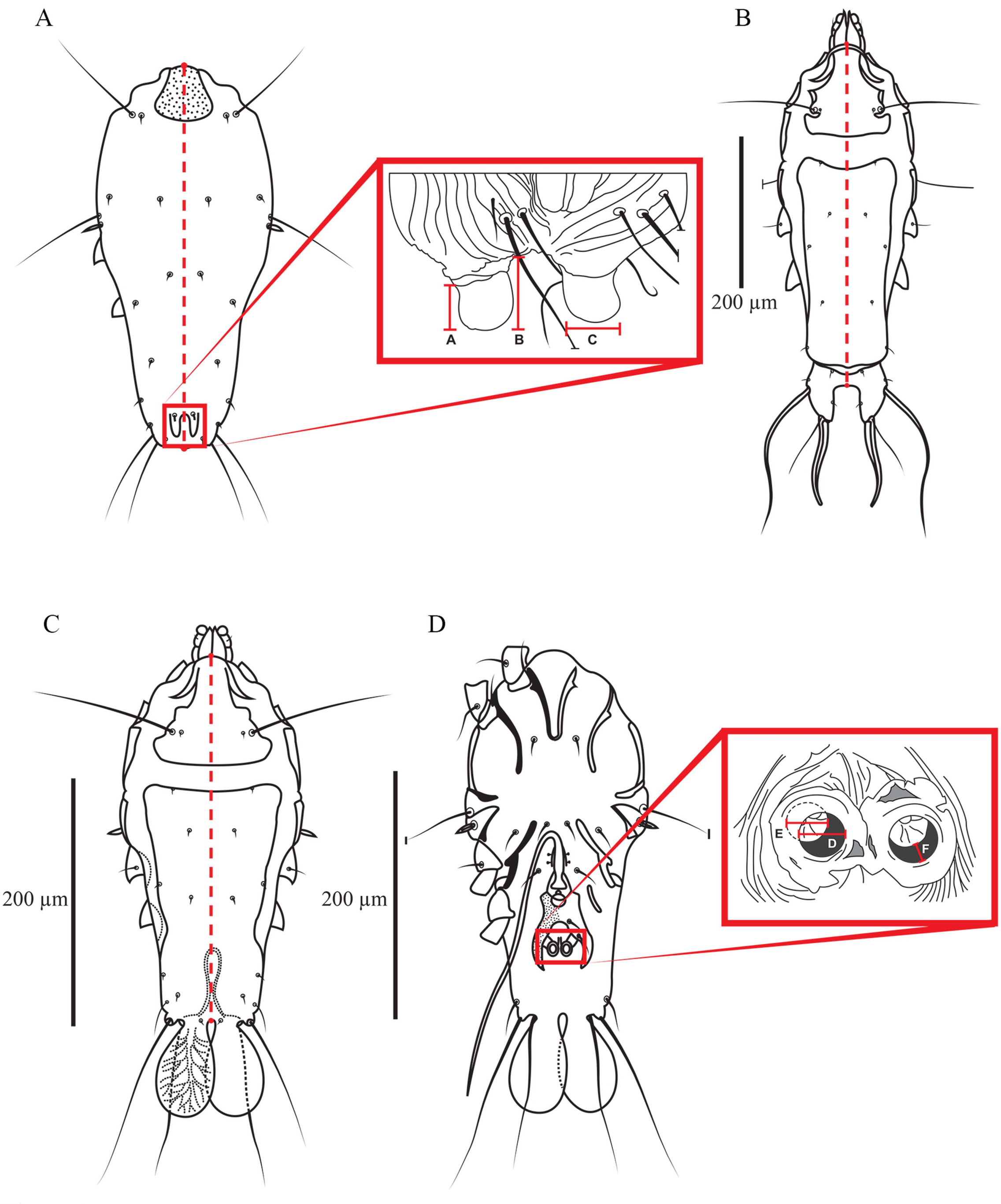

FIGURE 1: Length of the idiosoma in *Proctophyllodes* spp. in A. female tritonymphs, B. adult females and C. adult males. Measurements (dashed line) were taken from the margin of the prodorsum to the posterior margin of the body. In female tritonymphs we measured the lateral length (A), medial length (B), and width (C) of the docking papillae. In adult males (D; ventral), we measured the distal (D) and basal (E) widths of the adanal suckers as well as sucker depth (F). Line drawings are modeled after *Proctophyllodes glandarinus* for adults and from *Proctophyllodes pari* for tritonymphs (Atyeo and Braasch, 1996). Diagrams of the docking papillae and adanal suckers are drawn after scanning electron images published in Witaliński *et al.* (1992).

ethanol solution was examined at 20-40X magnification using a Leica MZ16 dissecting microscope.

We mostly selected pairs of mites that were in precopula (*i.e.*, male and tritonymphal female) for slide mounting. Mites were cleared in lactic acid overnight and mounted in PVA mounting medium (BioQuip Products; Rancho Dominguez, CA, USA) on glass slides. Slides were cured on a warming tray at 45 °C for a minimum of four days and were then examined at 400X on a Leica DMLB compound microscope (Leica Microsystems Inc., Richmond Hill, ON, Canada) using differential interference contrast (DIC). Mites were identified to genus in all cases and species when possible using relevant taxonomic literature (Atyeo and Braasch, 1966; Gaud and Atyeo, 1996). Most proctophyllodids from hosts outside of Europe and North America are undescribed, and are noted simply as 'sp.'. Exemplars of each taxon are deposited in the E.H. Strickland Entomological Museum at the University of Alberta.

Correlation measurements and analysis

To analyze whether the male adanal suckers and tritonymphal female docking papillae correlated morphologically, we took digital images at 200 and 400X of adult males and tritonymphal females from each bird using Image Capture (Apple Computer, Cupertino, CA, USA) and a Canon PowerShot S40. Images were uploaded to ImageJ (National Institutes of Health, Bethesda, Maryland) and measured for male and tritonymph body size as well as for dimensions of the male adanal suckers and tritonymphal docking papillae. For both sexes we measured the length of the idiosoma from the anterior margin of the prodorsum to the posterior of the body excluding the opisthosomal lamellae in males (see Figure 1a,b,c). For tritonymphs, we took three measurements of the docking papillae: the width, the longest (medial) length and the shortest (lateral) length (Figure 1a). For males, we measured the width at the adanal sucker tip and at the base as well as the depth of the sucker (Figure 1d). Spearman's correlation coefficient analyses were performed in SPSS version 20 (SPSS Inc., Chicago, IL, USA) to determine whether the dimensions of the male adanal suckers and female tritonymphal docking papillae were correlated.

Proctophyllodes troncatus measurements

In the literature, 'docking papillae' have been associated with the female tritonymph of *Proctophyllodes* spp. (Atyeo and Braasch, 1966); however, whether or not females are the only sex to possess these papillae has not been tested. To clarify whether docking papillae were restricted to female tritonymphs and not to any other nymphal stage or sex, we measured the length of the idiosoma in adult male, adult female and nymphal *Proctophyllodes troncatus* Robin, 1877 captured from house sparrows (*Passer domesticus* (Linnaeus)) in Romania (Figure 1). We measured a total of 20 adult male and female *P. troncatus*, as well as 196 nymphal *P. troncatus*. Ideally we would have been able to use the number of genital papillae to differentiate between protonymphs (which have one pair) and tritonymphs (which have two pairs), but the slightly degraded nature of the specimens rendered the nymphal genital papillae essentially invisible even under DIC lighting. The presence of two additional pair of ventral setae might also have been used for differentiating tritonymphs from protonymphs (Gaud and Atyeo, 1996); however, these setae were also difficult to observe, making their consistent use problematic. For all nymphs we determined whether docking papillae were present. We grouped mites into categories for adult males, adult females, nymphs with docking papillae, and nymphs without docking papillae and analyzed the distribution in a histogram produced in SPSS. We tested for differences in size between the adult sexes as well as between nymphs with and without docking papillae using unpaired t-tests. We hypothesized that adult females would be larger than adult males, that adult males would be larger than nymphs and that, if nymphs with docking papillae were tritonymphal females, that these nymphs should be on average larger than nymphs without docking papillae (predicted to be nymphal males or protonymphal females).

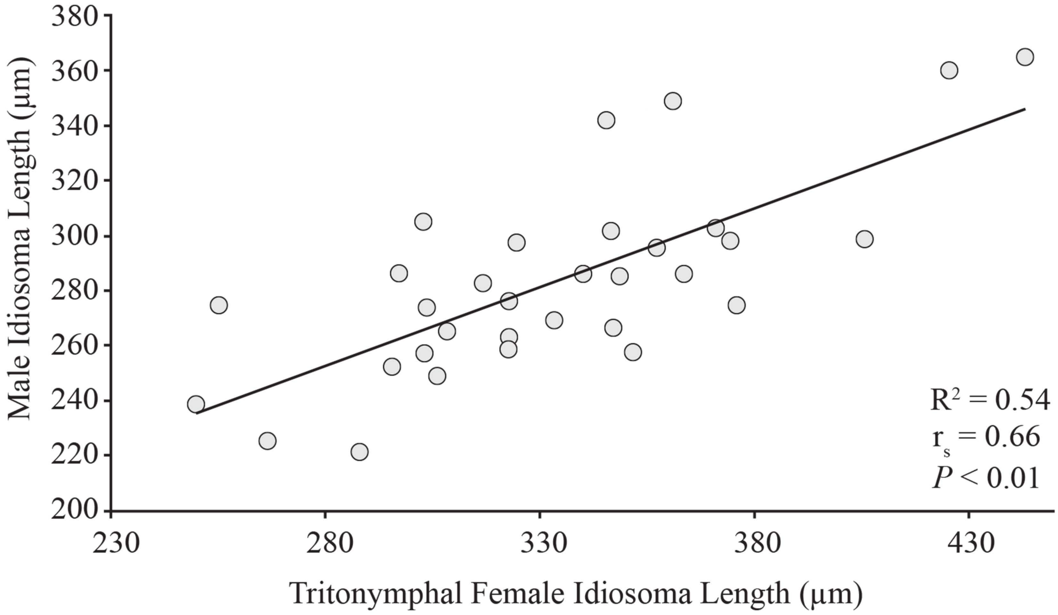

FIGURE 2: Correlation between adult male and tritonymphal female body length (µm) in *Neodectes* spp., *Proctophyllodes* spp., and *Proterothrix* spp. (Astigmata: Proctophyllodidae). Length of the idiosoma was measured from the anterior margin of the prodorsum to the posterior region of the body excluding the opisthosomal lamellae in males. Body size was positively correlated between the sexes (r_s = 0.66, n = 32, P < 0.01) whereby larger tritonymphal females were paired with larger conspecific males.

TABLE 2: Spearman's correlation coefficients (*rs*) and significance (*P*) of correlations between measurements of male adanal suckers and tritonymphal docking papillae in the genera *Neodectes* spp., *Proctophyllodes* spp., and *Proterothrix* spp. (Analgoidea: Proctophyllodidae).

Female tritonymph morphology	Male morphology	Adanal sucker distal width			Adanal sucker basal width			Adanal sucker length		
		n	r_s	P	n	r_s	P	n	r_s	P
Docking papillae width		19	0,47	0,85	18	0,43	0,07	17	-0,43	0,06
Docking papillae medial length		19	0,36	0,13	18	0,2	0,42	17	0,38	0,13
Docking papillae lateral length		19	0,06	0,81	18	-0,21	0,41	17	0,24	0,35

RESULTS

Correlation analysis

Of the 49 pairs of mites analyzed, 17 were omitted as the individuals were still firmly in precopula and the docking papillae were not observable. In the remaining pairs, body size was positively correlated between adult males and tritonymphal females (r_s = 0.66, n = 32, P < 0.01) (Figure 2). Among the tritonymphal females measured, four *Proterothrix* spp., one *Neodectes* spp. and eight *Proctophyllodes* spp. individuals did not have docking papillae. For correlation analyses we omitted specimens without docking papillae (n = 13) to remove the influence of zero counts. We also omitted males where we were unable to measure adanal sucker length (n = 2 of 19 pairs) or basal area of the sucker (n = 1 of 19 pairs). There were no correlations between the dimensions of tritonymphal docking papillae and male adanal suckers (Table 2). The medial and lateral lengths of the female docking papillae did not correlate with male adanal sucker length ($r_s > 0.24$, n = 17, $P > 0.13$; see Figure 3); nor was width of the docking papillae correlated with the distal ($r_s = 0.05$, n = 19, $P = 0.85$) or basal ($r_s = 0.43$, n = 18, $P = 0.07$) widths of the adanal suckers (Figure 3).

Proctophyllodes troncatus measurements

Distributions of body length for *P. troncatus* adult males, adult females, and nymphs are displayed in Figure 4. Adult males ranged in size from 250 – 285 μm in length and were significantly smaller than adult females in length which were 330 – 380 μm ($t_{38} = 22.6$, $P < 0.001$). For nymphs, there were two distinct size clusters; nymphs with docking papillae (n = 81) ranged in size from 240 – 375 μm in length and were significantly larger than nymphs without docking papillae (n = 115) which were 175 – 255 μm in length ($t_{194} = 20.6$, $P < 0.001$).

Discussion

Although copulation occurs between adult astigmatan feather mites, it is common for males to couple with tritonymphal females prior to mating (Atyeo and Braasch, 1966; Witaliński *et al.*, 1992). In our study of *Neodectes* spp. and *Proterothrix* spp. (Proctophyllodidae: Pterodectinae) and *Proctophyllodes* spp. (Proctophyllodidae: Proctophyllodinae) we observed dorsal docking papillae in tritonymphs of all genera similar to those described by Witaliński *et al.* (1992) in *Proctophyllodes stylifer* (Buchholz, 1869), *Proctophyllodes picae* (Koch, 1840), *Psoroptes cuniculi* (Delafond, 1859), and *Psoroptes natalensis* Hirst, 1919. Surprisingly, not all nymphs that we observed in precopula possessed docking papillae. This may be due to either intrageneric variability in the presence of docking papillae, or a result of males accidentally grabbing a nymph of the wrong sex or stage, a phenomenon which has been reported in male tarsonemids (Garga *et al.*, 1997).

It was surprising that we did not find a correlation between the dimensions of the female docking papillae and the male adanal suckers. In arthropods, several studies have documented correlations between the sexes in reproductive characters both internally (e.g. the genitalia of *Apamea* Ochsenheimer, 1816 moths (Mikkola, 1992)), and externally (e.g. the grooves and pits on female katydids which facilitate grasping by male clasping structures (Rentz, 1972)). In their study of *Proctophyllodes* and *Psoroptes* spp. mites, Witaliński *et al.* (1992) report size similarities between the docking papillae and male adanal suckers; however, these results were strongly categorical, whereby lengths and diameters of these structures were compared as ranges. We did not find any quantitative correlation between these structures in our study. Given that the mode of precopulatory attachment is likely the sucking force between the adanal suckers and the docking papillae (Witaliński *et al.*, 1992), one would expect that closely correlated dimensions would be integral to promoting a cohesive coupling. The absence of correlation between tritonymphs and adult males in dimensions of the docking papillae and adanal suckers may indicate that size is not the only characteristic that matters.

It is possible that we did not measure the size of the papillae as they would be when held within the adanal suckers. Witaliński *et al.* (1992) suggest that the docking papillae swell during attachment due to increased haemolymph pressure induced from suction of the male suckers. A similar suction-based mechanism of maintaining contact between adult males and immatures is hypothesized in *Schizocarpus* spp. Trouessart, 1896 fur mites (Fain *et al.*, 1984). If this is so, then it is possible that the papillae of independent tritonymphs are not representative of their size when swollen in copula. However, we would also expect that the width of the papillae would be consistently smaller than that of the adanal suckers, which we did not find. In some instances, the width of the tritonymphal docking papillae was greater than the width of the distal adanal sucker, a result which is in contradiction to our hypothesis. Another consideration is the role of glandular secretions in the attachment of males to females. In some uropodid mites, the phoretic deutonymph uses glandu-

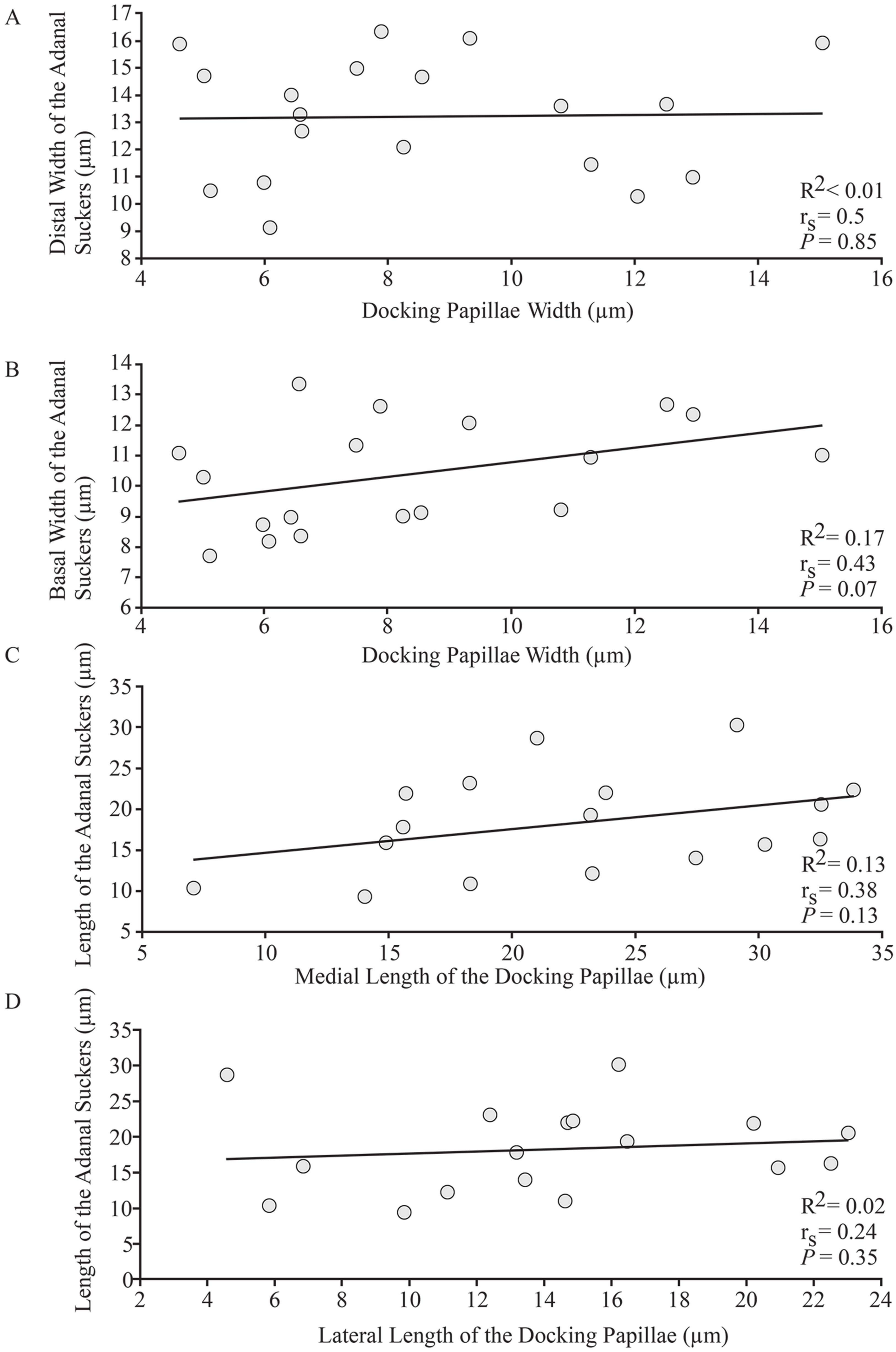

FIGURE 3: Correlations in morphology between adult male and tritonymphal female *Neodectes* spp., *Proctophyllodes* spp., and *Proterothrix* spp. feather mites (Astigmata: Proctophyllodidae). Correlations are illustrated between widths (A-B) and lengths (C-D) of the male adanal suckers and the female docking papillae. R^2 values indicate how well variation in one variable is predicted by that of the other variable.

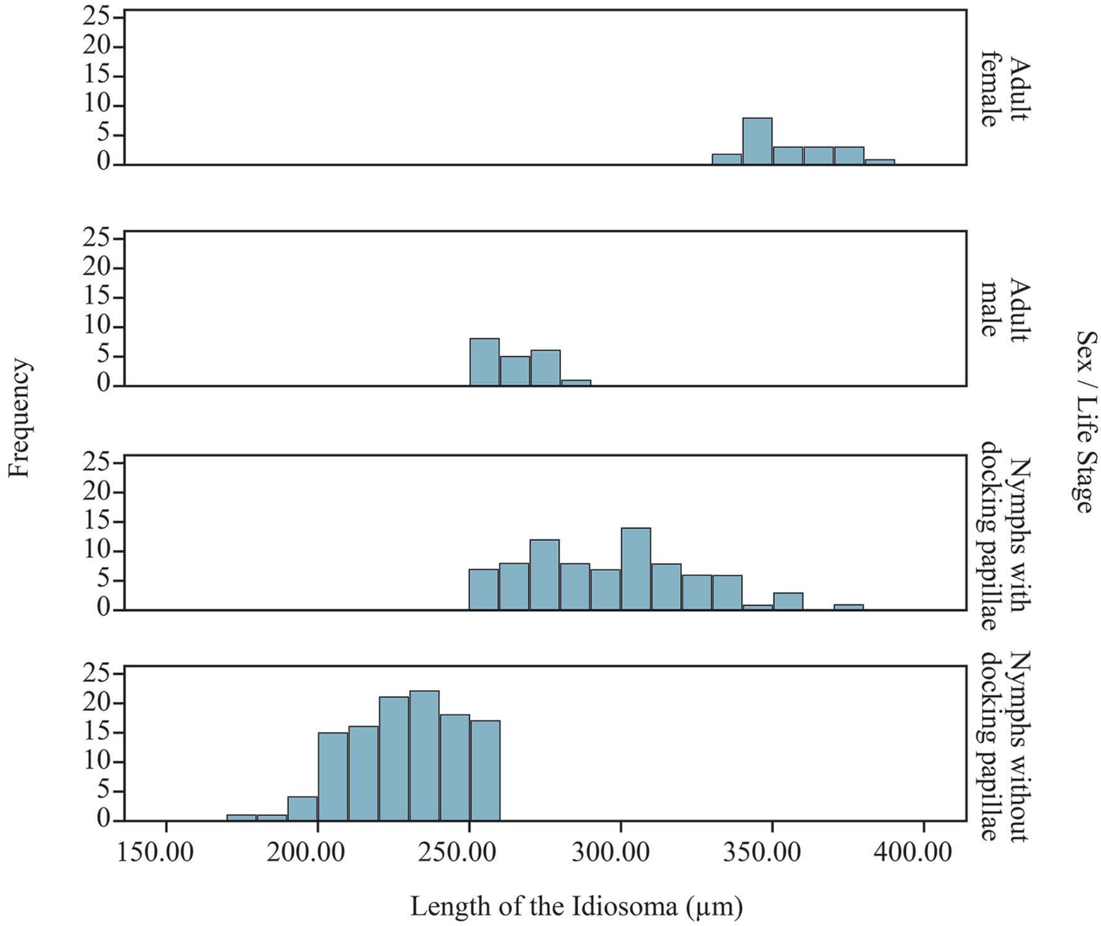

FIGURE 4: Size distributions of *Proctophyllodes troncatus* adult females, adult males and nymphs with and without docking papillae. Body size was measured as the length of the idiosoma (µm) from the anterior margin of the prodorsum to the posterior region of the body excluding the terminal hyaline appendages in adult females and the opisthosomal lamellae in males. Nymphs were categorized as having docking papillae or lacking docking papillae. Adult females were significantly larger than adult males as indicated by an unpaired t-test (t_{38} = 22.6, $P < 0.001$). Similarly, nymphs with docking papillae were larger on average than were those without docking papillae (t_{194} = 20.6, $P < 0.001$).

lar secretions from the pedicellar gland to attach to their carrier (Bajerlein and Witaliński, 2012). In *Pterodectes* spp. Robin, 1877 (Proctophyllodidae: Pterodectinae) glands associated with the adanal suckers are hypothesized to aid in male attachment (Popp, 1967), while sticky secretions exuded from the male suckers may also enhance fixation during coupling in fur mites (Fain *et al.*, 1984). If glandular secretions are used to improve adhesion between adult males and tritonymphal females in feather mites, then it is likely that the strict correlation between dimensions of the adanal suckers and docking papillae is unnecessary.

Another influence in why we did not detect a correlation between male and tritonymphal morphology may be that we assumed that all tritonymphs with docking papillae were female. Although both Atyeo and Braasch (1966) and Witaliński *et al.* (1992) refer to tritonymphs with dorsal papillae as female, they may not be exclusive to female tritonymphs. We tried to account for this by measuring body length of nymphal *P. troncatus* and grouping them by presence or absence of docking papillae. Our results show that docking papillae are present in larger nymphs and absent in smaller nymphs, suggesting that these larger nymphs with papillae are female (the larger adult sex) while the smaller nymphs without papillae are male (the smaller adult sex). It is also possible that when slide-mounting specimens, structures may have been distorted due to the orientation of the body and the flattening of the specimen on the slide, thus affecting our measurements. Moreover, the preservation of these mites prior to mounting may have influenced the dimensions of the docking papillae.

The results of this study are largely preliminary. It is likely that the tritonymphal docking papillae of females and the adanal suckers in males are indeed cooperative structures; however, if a close fit between the docking papillae and adanal suckers is evidence for cooperation, we are unable to provide any. To expand on this research, it will be beneficial to consider intraspecific as well as interspecific variations in traits to resolve the role of the docking papillae in precopulatory guarding and coupling in feather mites. Microscopic observation of the process of precopulatory coupling in live proctophyllodid mites may also provide clues about changes in dimensions of the docking papillae and/or adanal suckers before and after the male affixes to the tritonymph.

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