

# OBSERVATIONS ON GENITAL PAPILLAE OF PYCNONOTIC BRACHYPYLINA (ACARI : ORIBATIDA)

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EVOLUTION  
ORIBATIDA  
GENITAL  
PAPILLAE

**SUMMARY :** The morphology of genital papillae in adults of representatives of many pycnonotic brachypylina families and genera is analysed. The Oppioidea and Carabodoidea share the apomorphy of anterior genital papillae which are tapered and narrower than the medial and posterior papillae. Adults of Eremellidae and Caleremaeidae, presently included in the Oppioidea, have unmodified anterior genital papillae, indicating that their systematic position in the Brachypylina needs reevaluation. Within the Oppiidae genital papillae are reduced to two pairs, and the posterior genital papillae are very broad, in adults of *Aeroppia*, *Amerioppia*, *Oppia*, and *Ramusella*. Examination of genital papillae in immature instars of *Ramusella maculata* (Hammer) and *Oppia nitens* (C. L. Koch) indicates that reduction in number of genital papillae is first expressed in the adult, and that enlarged posterior genital papillae can be expressed in an earlier instar than the adult. The ontogenetic sequence of expression of genital papillae in *O. nitens* is hypothesized to be in a postero-anterior direction.

ÉVOLUTION  
ORIBATIDA  
PAPILLES  
GÉNITALES

**RÉSUMÉ :** L'auteur étudie la morphologie de papilles génitales chez les adultes de plusieurs familles et genres de brachypylines pycnonotiques. Les Oppioidea et les Carabodoidea possèdent une apomorphie commune, celle des papilles génitales antérieures qui sont effilées et plus étroites que les papilles médianes et postérieures. Les papilles génitales des adultes de deux familles d'Oppioidea, les Eremellidae et les Caleremaeidae, n'ont subi aucune modification d'où la nécessité de réévaluer leur position systématique dans les Brachypylina. Chez les Oppiidae, les papilles génitales sont réduites à deux paires, les postérieures étant très larges chez les adultes des genres *Aeroppia*, *Amerioppia*, *Oppia*, et *Ramusella*. L'examen des papilles génitales des stades juvéniles de *Ramusella maculata* (Hammer) et d'*Oppia nitens* (C. L. Koch) indique que la réduction du nombre de ces papilles n'apparaît que chez l'adulte, alors que les papilles génitales postérieures élargies peuvent s'observer chez des stades précédant l'adulte. On émet l'hypothèse que la séquence ontogénique de l'expression des papilles génitales chez *O. nitens* se produit dans une direction postéro-antérieure.

## INTRODUCTION

Genital papillae (also known as verrucae, aceta-bula, suckers, discs) appear to function for the uptake of water from the environment in terrestrial

acariform mites and may play a role in osmoregulation in fresh water acariform mites (ALBERTI, 1979 ; BARR, 1982). GRANDJEAN has written extensively on the origin, ontogenetic development, and influence of genital papillae on the morphology of the genital

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region of oribatid mites (for example, see GRANDJEAN, 1932 a, 1969). Although characters such as the shape and number of genital papillae have been used in studies on the systematics of early derivative oribatid mites (GRANDJEAN, 1932 a, b, 1954 a, b; O'CONNOR, 1981; NORTON *et al.*, 1983), their morphology has been overlooked in the taxonomy of Brachypyline, other than in certain works of GRANDJEAN (1960 a, b, 1963). It is recognized that generally adults have three pairs of papillae, and that the protonymph, deutonymph, and tritonymph have 1, 2, and 3 pairs respectively, but authors have rarely commented on structural differences among the pairs, or on changes in their form during ontogeny.

GRANDJEAN (1960 a) first recognized the unusual structure of genital papillae in adults of some brachypyline Oribatida. He noted that in *Autogneta penicillum* Grandjean the middle and posterior pairs, *Vm* and *Vp* respectively, have normal positions and dimensions, i.e., they are rounded and slightly expanded distally, and have a sclerotized band of integument along their length. In contrast, the anterior pair, *Va*, are different in size and taper distally. There is no sclerotized band, rather the tapered head is lightly sclerotized; the head is not the widest part of the papilla, rather the whole papilla gradually tapers distally. In addition, *Va* is positioned deeper in the body than *Vm* and *Vp*, at a different plane than the other papillae (GRANDJEAN, 1960 a), and as a result can often be overlooked. Subsequently GRANDJEAN (1960 b, 1963) observed similar development of *Va* in adults of *Rhaphigneta*, *Cosmogneta* and *Conchogneta*, (the former with *Va* having a sclerotized stylet apically), and considered the structure of *Va* to be one of the distinctive characters defining Autognetidae (GRANDJEAN, 1963).

I have surveyed adults of various brachypyline taxa for evidence of modified *Va* papillae and have found this character state to be much more widely distributed among pycnonotic Brachypyline than previously recognized. In contrast, all poronotic Brachypyline examined (representatives of the Oripodoidea, Ceratozetoidea, Galumnoidea, Oribatelloidea) have normal genital papillae, with *Va* subequal in size and shape to *Vm* and *Vp*. I have

also observed an additional character state, namely reduction in number of genital papillae to 2 pairs, in adults of certain genera of Oppiidae; this may prove useful to define genera or other lineages in this family. In this paper I will discuss the distribution of each of these character states in non-poronotic Brachypyline.

#### METHOD AND MATERIALS

Specimens were examined in two kinds of slide preparations. Specimens were examined in temporary mounts using cavity slides, but the shape of *Va* relative to *Vm*, *Vp* was more easily determined on permanently slide mounted, and slightly flattened, specimens. Unfortunately, in the latter preparations, the position of genital papillae may be shifted in respect to that of the genital plates. As GRANDJEAN (1960 b) indicated, the position of genital papillae can vary considerably among different preparations of the same species, depending on the position of the genital organs and whether or not the genital plates are in their normal retracted position. In all specimens examined for this study the genital plates were retracted.

This study includes only those brachypyline taxa available in the Canadian National Collection, Biosystematics Research Centre, Ottawa, and therefore, is not exhaustive. In the following results, genera examined are listed in parentheses after the appropriate family.

#### RESULTS

##### *Structure of anterior genital papillae.*

Genital papillae *Va* are unmodified, subequal in size to *Vm* and *Vp* and similarly rounded apically (though *Va* may be positioned slightly more dorsally than, and may be slightly tapered in comparison with *Vm* and *Vp*) in adults of: Hermanniellidae (*Hermanniella*, *Sacculobates*), Plasmobatidae (*Plasmobates*, *Solenozetes*), Liodidae (*Liodes*, *Platyliodes*, *Teleioliodes*), Gymnodamaeidae (*Gymnodamaeus*, *Joshuella*, *Nortonella*), Plateremaidae (*Pedrocortesella*, *Phereliodes*), Cepheidae (*Cepheus*, *Ommatoce-*

*pheus*, *Oribatodes*, *Sadocephus*, *Eupterotegaeus*), Polypterozetidae (*Polypterozetes*), Podopterotegaeidae (*Podopterotegaeus*), Ctenobelbidae (*Ctenobelba*), Liacaridae (*Adoristes*, *Liacarus*), Astegistidae (*Cultroribula*), Metrioppiidae (*Ceratoppia*, *Ceratorchestes*, *Metrioppia*), Gustaviidae (*Gustavia*), Kodiakellidae (*Kodiakella*), Tectocephidae (*Tectocephus*), Niphocephidae (*Niphocephus*), Oxyameridae (*Oxyamerus*), Eremellidae (*Eremella*) (Fig. 3), Caleremaeidae (*Caleremaeus*, *Veloppia*) (Fig. 4), Hydrozetidae (*Hydrozetes*), Limnozetididae (*Limnozetes*), Ameronothridae (*Ameronothrus*), Cymbaeremaeidae (*Ametroproctus*), Passalozetididae (*Passalozetes*).

Genital papillae *Va* are narrower than *Vm* and *Vp*, pointed and sclerotized distally, and positioned deeper than *Vm* and *Vp* in adults of Dampfiellidae (*Beckiella*) (pers. obs.), whereas *Va* are subequal to *Vm* and *Vp* in *Dampfiella* (GRANDJEAN, 1964). Papillae *Va* are shorter and wider than *Vm* and *Vp*, and sclerotized apically in adults of : Eremulidae (*Eremulus*), Eremobelbidae (*Eremobelba*), and Microzetidae (*Berlesezetes*). Papillae *Va* are subequal in size to *Vm* and *Vp*, but may be blunter and flatter apically in adults of Damaeidae (*Belba*, *Damaeus*, *Epidamaeus*, *Hungarobelba*, *Porobelba*). In adults of Amerobelbidae (*Grypoceramerus*, *Gymnodampia*) *Va* are shorter and the same width, or wider than *Vm* and *Vp*, but have a sclerotized band in the former genus, whereas in the latter they are sclerotized apically.

Genital papillae *Va* are narrower than *Vm* and *Vp*, strongly tapered rather than rounded apically, and displaced dorsad of *Vm* and *Vp* in adults of : all genera in the Autognetidae (GRANDJEAN, 1960 a fig. 1A, 1960 b figs. 2B, C, D, 1963 fig. 1B), Suctobelbidae (*Allosuctobelba*, *Rhinosuctobelba*, *Suctobelba*, *Suctobelbella*, *Suctobelbilla*), Oppiidae (*Arcoppia*, *Cosmoppia*, *Machuella*, *Micropoppia*, *Multioppia*, *Oppiella*) (Fig. 1), *Pulchropoppia*, *Quadropoppia*, *Striatoppia*, *Subiasella*), Anderemaeidae (*Carabodoides*), Spinozetidae (*Spinozetes*), Aceremaeidae (*Tecteremaeus*), Thyrisomidae (*Oribella*, *Banksinoma*) (Fig. 2), *Gemmazetes*, *Pantelozetes*, and Carabodidae (*Carabodes*, *Odontocephus*, *Pseudotocephus*, *Phyllocarabodes*).

#### Number of genital papillae and structure of posterior genital papillae.

Among the Oppiidae four genera (*Aeroppia*, *Amerioppia*, *Oppia*, *Ramusella*) are unusual in having only 2 pairs of genital papillae in the adult. The anterior of these two pairs is strongly tapered distally. The posterior pair is very broad, with a skull-cap shape (Figs. 5, 6). A cross-sectional view indicates that the shape of the latter is a long oval. This number and shape of genital papillae is independent of the sex of the mite, papillae being similar in males and females of the same species.

WOODRING and COOK (1962) reported two pairs of genital papillae in adults of *Oppiella nova* (Oudemans) (= *Oppia neerlandica* Oudemans). Their illustration (plate 5) of the adult shows two pairs of genital papillae of equal size, clearly indicating that they overlooked the tapered, more dorsally positioned papillae *Va* in their study. Unfortunately, this oversight has been perpetuated in acarological literature (WOOLLEY, 1988, p. 313).

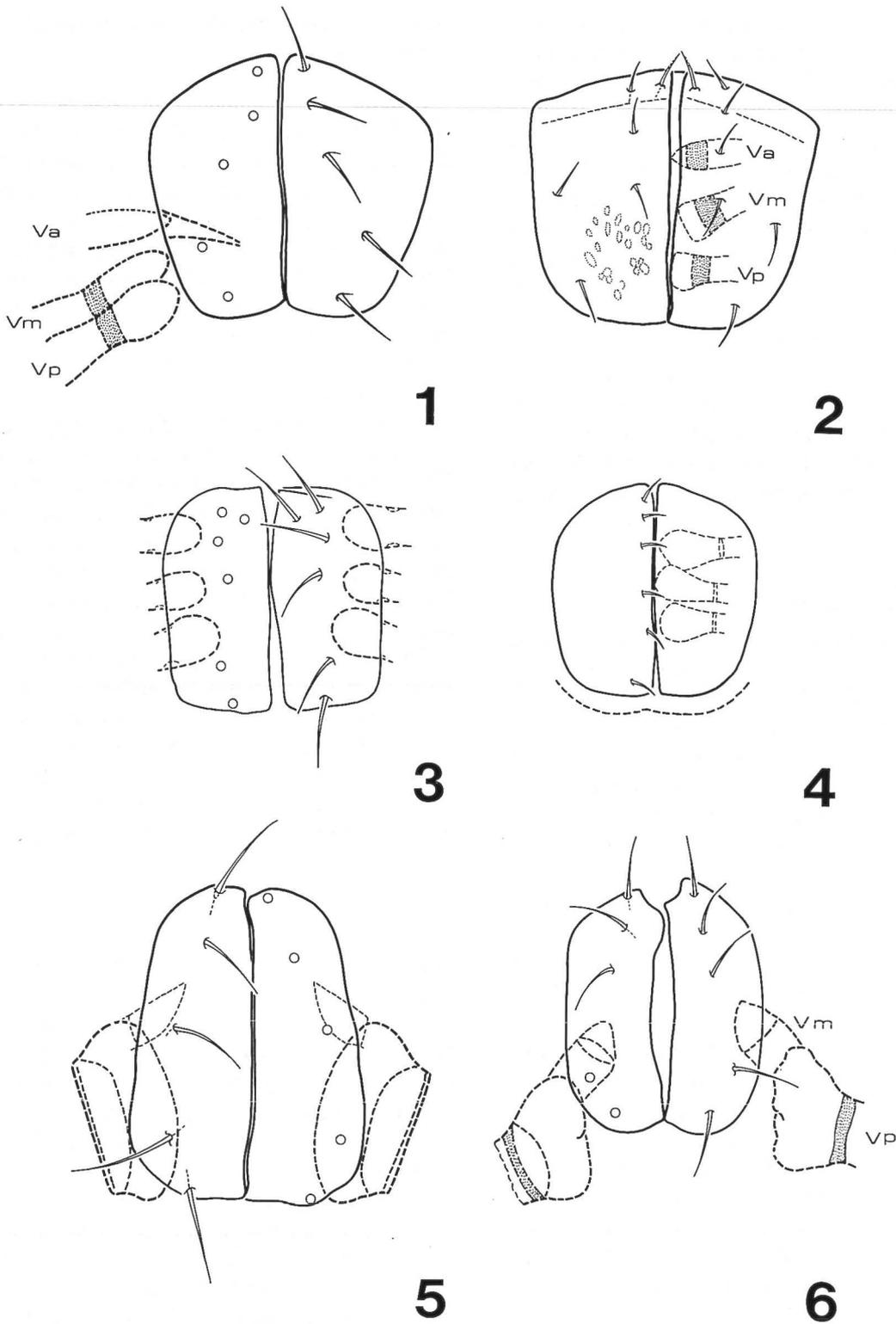
The presence of two pairs of modified genital papillae in adults raises the following questions : which pair of genital papillae is lost or consolidated in the adult, and in which instar is this loss or consolidation first expressed? To address these questions, I have examined laboratory reared populations of representatives of *Oppia* and *Ramusella*.

#### *Oppia nitens* (C. L. Koch)

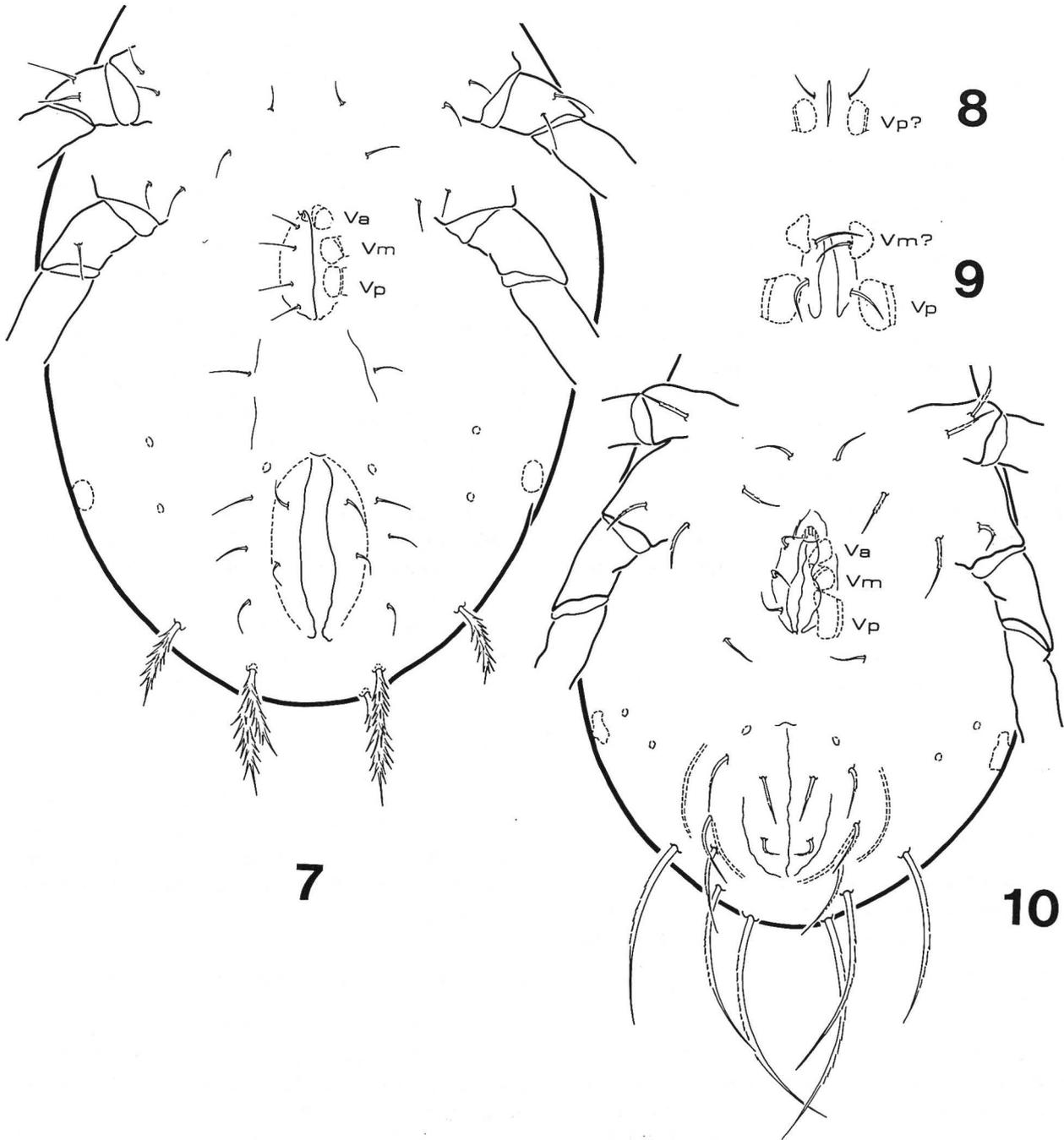
In the protonymph papillae are rounded apically, and 10-14  $\mu\text{m}$  wide at the sclerotized band ( $n = 3$ ) (Fig. 8).

In the deutonymph the posterior papillae are broad, 13-15  $\mu\text{m}$  wide at the sclerotized band ( $n = 6$ ). The anterior papillae are weakly sclerotized, positioned very slightly deeper than the posterior pair, and are 8-10  $\mu\text{m}$  wide at the sclerotized band ( $n = 6$ ) (Fig. 9).

In the tritonymph the posterior papillae are very broad, 15-19  $\mu\text{m}$  wide at the sclerotized band ( $n = 6$ ) (Fig. 10). The medial papillae are 9-10  $\mu\text{m}$  wide at the sclerotized band, and positioned very slightly deeper than the posterior pair. The anterior papillae are 8-12  $\mu\text{m}$  wide basally ( $n = 5$ ), positioned deeper than either the medial or posterior pair, and weakly



FIGS. 1-6 : Genital papillae of some genera of pycnonotic Brachypylina, ventral aspect ; 1. — *Oppiella* ; 2. — *Banksinoma* ; 3. — *Eremella* ; 4. — *Caleremaesus* ; 5. — *Aeropfia* ; 6. — *Oppia*.



FIGS. 7, 10 : Venter of opisthosoma of tritonymph; 7. — *Ramusella maculata* (Hammer); 10. — *Oppia nitens* (C. L. Koch).  
FIGS. 8, 9 : Genital papillae of *Oppia nitens* (C. L. Koch); 8. — Protonymph; 9. — Deutonymph.

defined and poorly sclerotized (in one tritonymph the anterior pair were not visible).

In the adult the posterior papillae are 20-24  $\mu\text{m}$  wide at the sclerotized band ( $n = 5$ ). The anterior papillae, 7-9  $\mu\text{m}$  wide at the sclerotized band, are positioned directly anterior of, and slightly deeper than, the posterior pair. The two pairs are positioned posteriad of the anterior two pairs of genital setae (Fig. 6).

The size progression observed in the posterior pair indicates that the papillae present in the protonymph are homologous with the posterior pair of the deutonymph, tritonymph and adult. Similarly the shape and development of the anterior pair in the deutonymph suggest that these papillae are homologous with the medial pair in the tritonymph, and the anterior pair of the adult. The position of the papillae in the adult indicates that they represent pairs *Vm* and *Vp*.

The gradual size progression observed in the posterior pair from protonymph to adult, and the presence of two and three pairs of papillae in the deutonymph and tritonymph, respectively, also indicate that the enlargement of genital papillae is independent of reduction in number of papillae, at least in this species. These observations also suggest that the reduction in number of genital papillae in the adult is the result of a loss, rather than the consolidation of two pairs of papillae. Thus it appears that papillae *Va* are lost in adult *Oppia nitens*.

#### *Ramusella maculata* (Hammer)

Only tritonymphs and adults are available for this species. There are three pairs of subequal genital papillae in the tritonymph, each about 10  $\mu\text{m}$  wide at the sclerotized band ( $n = 3$ ) (Fig. 7). There is no indication which pair of genital papillae is lost or consolidated in the adult, other than that the two pairs present are positioned posteriad of the anterior two pairs of genital setae. However, by comparison with *Oppia nitens*, it is probable that the papillae in adult *R. maculata* represent *Vm* and *Vp*, with loss of *Va*, rather than retention of *Va* and consolidation of the medial and posterior pairs.

#### *Modified anterior genital papillae :*

The above review of the morphology of genital papillae in the pycnonotic Brachypylina indicates that shape and size of papillae *Va*, relative to *Vm* and *Vp*, can be useful characters to define taxa at the genus level or higher.

The smaller size and tapered shape of papillae *Va* relative to *Vm* and *Vp* are particularly useful apomorphies to define the Oppioidea, sensu BALOGH 1972 (with the exclusion of at least the Eremellidae and Caleremaeidae) and the Carabodoidea, sensu MARSHALL *et al.*, 1987 (i.e., exclusive of the Tectocephidae and Niphocephidae). The unmodified papillae *Va* in adults of Eremellidae (Fig. 3) and Caleremaeidae (Fig. 4) indicate that these taxa should not be included in the Oppioidea and that their systematic position in the Brachypylina needs reevaluation.

A close relationship between the Oppioidea and Carabodoidea is suggested by this shared apomorphy. Other similarities include nymphs of both groups being unidifferent, smooth, and without sclerites (Group VIII of WALLWORK, 1969). However, the former and latter character states are plesiomorphic in the Brachypylina, and the polarity of a smooth versus plicate integument in the immatures of pycnonotic Brachypylina requires further study. Unfortunately, in his detailed analysis of characters in the Oppioidea and other Brachypylina, WOAS (1986) did not consider members of the Carabodidae, and, as with other systematists studying Oppiidae, did not examine genital papillae.

#### *Development of enlarged posterior papillae :*

Initial results on the ontogeny of genital papillae given above, indicate that there may be specific or generic differences in the stage of expression of the enlarged posterior papillae. Enlargement does not occur until the adult in *Ramusella maculata*, but may appear as early as the deutonymph, as in *Oppia nitens*. Although SENICZAK (1975 a, b), in his excellent studies on the morphology of juvenile

stages of species of *Oppia*, did not discuss the morphology of genital papillae, his illustration of the tritonymph of *O. nitens* shows enlarged posterior papillae. Those of the tritonymphs of *O. subpectinata* (Oudemans), *O. bicarinata* (Paoli), *O. glabra* (Mihelcic) and *O. fasciata* (Paoli) show the posterior papillae similar to the medial pair. These last four species are now considered as members of *Oppiella*, *Berniniella*, *Multioppia* and *Rectoppia*, respectively (BALOGH, 1983).

*Reduction in number of genital papillae :*

The synapomorphic loss of *Va* and enlargement of posterior papillae in adults possibly define a monophyletic lineage in the Oppiidae, including at least *Aeroppia*, *Amerioppia*, *Oppia* and *Ramusella*. At the minimum they are useful character states in generic classification. As yet, only genera of Oppiidae known from North America, and a few others, have been surveyed for these character states, representing only a fraction of the approximately 120 genera in this family. Reduction in number of genital papillae appears to be independent of the size of the posterior papillae. There may also prove to be specific or generic differences in the instar when reduction in number of papillae is first expressed.

*Development of genital papillae :*

In the analysis of the development of genital papillae in *Oppia nitens* in this paper, I hypothesise that pair *Va* are lost in the adult. It appears that papillae *Vp* are expressed in the protonymph, followed by *Vm* in the deutonymph and *Va* in the tritonymph, that is in a postero-anterior manner.

GRANDJEAN did extensive research on the ontogeny of genital papillae in the Palaeosomata and Enarthronota. In his study on *Ctenacarus araneola* (Grandjean), he hypothesized that the papillae appear in an antero-posterior manner, i.e., pair *Va* are formed in the protonymph, then pair *Vm* in the deutonymph, and lastly, pair *Vp* in the tritonymph (GRANDJEAN, 1932 b). He based this hypothesis of development on his observation that in adult and tritonymphal *C. araneola* *Va* are smaller than *Vm*

or *Vp*. Likewise, in the deutonymph, the anterior papillae are smaller than the posterior papillae. His study on *Aphelacarus acarinus* (Berlese) in the same paper, shows the presence of one pair of papillae in the protonymph and deutonymph, and two pairs of papillae in the tritonymph and adult of this species. GRANDJEAN (1932 b) indicates clearly that the *Va* papillae are not developed in the tritonymph and adult of this species, as supported by a comparison of the position of the papillae in *A. acarinus* with that in *C. araneola* (Fig. 4, p. 416 and Fig. 7, p. 420). In a later work (GRANDJEAN, 1954), he elaborated on the morphological variation in papillae and reduction in their number in the Palaeosomata. He also justified his hypothesis on antero-posterior appearance of the papillae in *A. acarinus* by considering that pair *Va* is formed in the protonymph, lost in the deutonymph, and the papillae appearing in the deutonymph are pair *Vm*, with *Vp* formed in the tritonymph.

Following GRANDJEAN it has been generally assumed that the ontogenetic sequence of expression of genital papillae is antero-posteriorly. In this paper a postero-anterior ontogenetic sequence is proposed for *Oppia nitens*. It is evident therefore, that further research on the ontogeny of papillae in other species of Oppiidae is necessary before conclusions can be drawn as to whether the ontogenetic sequence in *O. nitens* is autapomorphic, or a possible synapomorphy defining a broader taxonomic grouping.

ACKNOWLEDGEMENTS

My thanks to Dr. Roy A. NORTON, College of Environmental Science and Forestry, State University of New York, Syracuse, New York, and my colleagues Drs. Evert E. LINDQUIST and Ian M. SMITH for reviewing this manuscript; and to Mr. J. VANDERMEER for rearing material used in this study, and Mr. C. PAQUETTE for inking all illustrations.

REFERENCES

- ALBERTI (G.), 1979. — Fine structure and probable function of genital papillae and clapede organs of Actinotrichida. — Pp. 501-508 in *Recent Advances in*

- Acarology Vol. II, RODRIGUEZ (J. D.) (Ed.) Academic Press, New York, 569 pp.
- BALOGH (J.), 1983. — A partial revision of the Oppiidae Grandjean, 1954 (Acari : Oribatei). — Acta Zool. Acad. Scient. Hung., **29** : 1-79.
- BARR (D.), 1982. — Comparative morphology of the genital acetabula of aquatic mites (Acari, Prostigmata) : Hydrachnoidea, Eylaeoidea, Hydryphantoidea and Lebertioidea. — J. Nat. Hist., **16** : 147-160.
- GRANDJEAN (F.), 1932a. — Observations sur les Oribates (3<sup>e</sup> série). — Bull. Mus. nat. Hist. natur., (2), **4** : 292-306.
- GRANDJEAN (F.), 1932b. — Au sujet des Palaecariformes Trägårdh. — Bull. Mus. nat. Hist. natur., (2), **41** : 411-426.
- GRANDJEAN (F.), 1939. — Quelques genres d'Acariens appartenant au groupe des Endeostigmata. — Ann. des Sc. Nat., Zool., 11<sup>e</sup> série : 1-122.
- GRANDJEAN (F.), 1960a. — *Autogneta penicillum* n. sp. (Oribate). — Acarologia, **2** : 345-367.
- GRANDJEAN (F.), 1960b. — Les Autognetidae n. fam. (Oribates). — Acarologia, **2** : 575-609.
- GRANDJEAN (F.), 1963. — Les Autognetidae (Oribates). Deuxième partie. — Acarologia, **5** : 653-689.
- GRANDJEAN (F.), 1964. — Oribates mexicains (1<sup>ère</sup> série). *Dampfiella* Selln. et *Beckiella* n. g. — Acarologia, **6** : 694-711.
- GRANDJEAN (F.), 1969. — Observations sur les muscles de fermeture des volets anaux et génitaux et sur la structure progénitale chez les Oribates supérieurs adultes. — Acarologia, **11** : 317-349.
- MARSHALL (V. G.), REEVES (R. M.) and NORTON (R. A.), 1987. — Catalogue of the Oribatida (Acari) of continental United States and Canada. — Mem. Ent. Soc. Canada No. **139** : 418 pp.
- NORTON (R. A.), O'CONNOR (B. M.) and JOHNSTON (D. E.), 1983. — Systematic relationships of the Pediculochelidae (Acari : Acariformes). — Proc. Entomol. Soc. Wash., **85** (3) : 493-512.
- O'CONNOR (B. M.), 1981. — A systematic revision of the family-group taxa in the non-psoroptidid Astigmata (Acari : Acariformes). PhD Thesis, Cornell University, Ithaca, New York, 594 pp.
- WALLWORK (J. A.), 1969. — Some basic principles underlying the classification and identification of cryptostigmatid mites. — Pp. 155-168 in SHEALS (J. G.), (Ed.) Systematic Association Publication Publication No. 8, *The Soil Ecosystem*.
- WOODRING (J. P.) and COOK (E. F.), 1962. — The biology of *Ceratozetes cisalpinus* Berlese, *Schelorbitates laevigatus* Koch, and *Oppia neerlandica* Oudemans (Oribatei), with a description of all stages. — Acarologia, **4** : 101-137.
- WOOLLEY (T. A.), 1988. — Acarology. Mites and Human Welfare. — Wiley-Interscience (John Wiley & Sons), New York. 484 pp.

Paru en Avril 1991.