

SPERMATOPHORES AND SPERMATOZOA OF ORIBATID MITES (ACARI : ORIBATIDA). PART II : FUNCTIONAL AND SYSTEMATICAL CONSIDERATIONS *.

BY G. ALBERTI **, N. A. FERNANDEZ *** and G. KÜMMEL ****

FEINSTRUKTUR
FUNKTION
ORIBATIDA
SPERMATOPHOREN
SPERMATOZOEN
SYSTEM

ZUSAMMENFASSUNG : In dem vorliegenden zweiten Teil unserer Arbeit werden die Ergebnisse der feinstrukturellen Untersuchung der Spermatophoren bzw. Spermatozoen von 10 Arten, die im 1. Teil dargelegt wurden, unter funktionellen und systematischen Gesichtspunkten diskutiert. Bezugnehmend auf frühere Arbeiten können bisher 5 Spermatophoren-Typen unterschieden werden : *Phthiracarus*-Typ, *Hermannia*-Typ, *Damaeus*-Typ, *Achipteria*-Typ und *Punctoribates/Eupelops*-Typ. In dem *Achipteria*-Typ lassen sich verschiedene Subtypen unterscheiden. Die Spermatophore von *Scutovertex sculptus* wird vorläufig in den *Achipteria*-Typ mit eingereiht, obwohl sie von denen der anderen in diesem Typ geführten Arten etwas abweicht. Bemerkenswert ist die Übereinstimmung zwischen den *Hermannia*-, *Damaeus*- und *Achipteria*-Typen, während die *Phthiracarus*- und *Punctoribates/Eupelops*-Typen jeweils eigene Entwicklungen repräsentieren.

Es ist wahrscheinlich daß die verschiedenen Spermatophorenstrukturen wichtige Voraussetzungen für die erfolgreiche Übertragung der Spermien darstellen.

Die Spermatozoen besitzen meist eine discoidale, kugelförmige oder elliptische Gestalt. Innerhalb der Liacaroidea gib es jedoch längliche Formen. *Liacarus subterraneus* hat bandförmige Spermien, die in Gruppen angeordnet sind. Alle Oribatidenspermien sind von einer Sekrethülle umgeben, die bei *Adoristes ovatus* besonders kompliziert ist.

STRUCTURE FINE
FONCTION
ORIBATIDA
SPERMATOPHORES
SPERMATOZOÏDES
SYSTÉMATIQUE

RÉSUMÉ : Dans cette deuxième partie de notre travail seront discutés, en tenant compte des aspects fonctionnels et systématiques, les résultats des observations faites sur la structure fine des spermatophores et/ou des spermatozoïdes chez dix espèces présentées dans la première partie. Comme il découle d'autres travaux réalisés dans le passé, cinq types de spermatophores peuvent être retenus jusqu'alors : le type de *Phthiracarus*, le type de *Hermannia*, le type de *Damaeus*, le type d'*Achipteria*, et le type de *Punctoribates/Eupelops*. Pour le type d'*Achipteria* différents sous-types peuvent être décelés. Dans un premier temps, nous allons considérer le spermatophore de *Scutovertex sculptus* comme appartenant au type d'*Achipteria*, malgré le fait qu'il présente une légère différence par rapport aux autres types présents dans cette espèce.

* Part I of this paper has been published in *Acarologia*, vol. XXXII, 1991, fasc. 3, pages 261-286.

** Zoologisches Institut (Morphologie/Ökologie) der Universität Heidelberg, Im Neuenheimer Feld 230, D-6900 Heidelberg, Federal Republic of Germany.

*** Universidad Nacional de Mar del Plata, Facultad de Ciencias Exactas y Naturales, Laboratorio de Artropodos, Funes 3350 (7600) Mar del Plata, Argentina.

**** Zoologisches Institut der Universität Karlsruhe, Postfach 6380, D-7500 Karlsruhe, Federal Republic of Germany.

Une concordance remarquable existe entre les types de *Hermannia*, *Damaeus* et *Achipteria*, les types de *Phthiracarus* et de *Punctoribates/Eupelops* par contre se caractérisent chacun par un développement spécifique.

Sans doute les différentes structures des spermatophores constituent des préalables importants en vue du bon transfert des spermatozoïdes. En règle générale, les spermatozoïdes sont discoidaux, sphéroïdaux ou elliptiques. Chez les Liacaroidea existent également des formations allongées. Chez les *Liacarus subterraneus*, le contenu spermique est disposé en groupes et présente une structure filamenteuse. Chez les Oribates, tous les spermatozoïdes sont entourés d'une gaine secrétée, particulièrement complexe chez *Adoristes ovatus*.

INTRODUCTION

In the foregoing part of our study we described the fine structure of spermatophores and spermatozoa respectively of 10 species from Phthiracaridae, Hermannidae, Liacaridae, Hermannellidae, Scutoverticidae, Achipteriidae, Euzetidae, Chamobatidae, and Pelopidae. We were able to present distinctly differing types. In the following an attempt is made to sum up the available data on spermatophore structure in oribatids which were obtained by light and electron microscopy since the first observation of this mode of sperm transfert in Oribatida by PAULY (1952).

MATERIAL AND METHODS

The reader is referred to part I of our study (FERNANDEZ *et al.*, Acarologia, vol. XXXII, fasc. 3, 1991, pages 261-286).

RESULTS AND DISCUSSION

All spermatophores known from Oribatida (Cryptostigmata) belong to the "droplet type" as judged superficially from the general shape constituted by a stalk and a more or less spherical head. The head includes the sperm package and the head matrix.

The spermatozoa are located within the sperm package (or sperm sac). It is found basally and ring shaped surrounding a part of the stalk which inserts into a composed central region of the sperm package in all oribatids investigated so far ultrastructurally except for Phthiracaridae (KÜMMEL and DOBNER

1986, present study/part I), *Hermannia gibba* (present study/part I) *Punctoribates punctum* (KÜMMEL and DOBNER 1986), and *Eupelops acromios* (present study/part I). In the Phthiracaridae the sperm package is in a subequatorial position and also ring-shaped whereas in *Punctoribates* and *Eupelops* the sperm package is formed like an inverted bowl located in the upper part of the head. In *Hermannia gibba* the centre of the sperm package is represented by a simple column; no specific package wall is present and the stalk does not protrude into the head.

The sperm package is separated by a genuine cover (Phthiracaridae) or distinct package wall from the head matrix with the exceptions of *Hermannia gibba*, *Punctoribates punctum* (KÜMMEL and DOBNER 1986) and *Eupelops acromios*. The sperm package of *Damaeus clavipes* and other Belboidea (KÜMMEL and DOBNER 1986) and *Hermannia gibba* as well as *Scutovertex sculptus* are only partly covered by an umbrella-like structure resting on a column or central region respectively. Whereas in *Hermannia* this umbrella is rather irregular in outline, it is a specific structure in Belboidea with a thick peripheral fringe. In *Scutovertex*, part of the umbrella-material peripherally turns apically and continues into a peripheral zone covering the head matrix. In these taxa (*Hermannia*, Belboidea, *Scutovertex*) the package is latero-basally exposed to the surrounding air, at least to some extent (*Hermannia*, *Scutovertex*). When the peripheral umbrella edge (where umbrella-material turns into peripheral zone) approaches the stalk insertion, the latero-basal opening of the sperm package is more or less closed. In species such as *Liacarus subterraneus*, *Adoristes ovatus*, *Oppia nitens*, *Hermannella punctulata*, *Achipteria quadridentata*,

and *Parachipteria punctata*, the sperm package is only basally open. The extension of the circular "gap" between the wall and the stalk varies in different species. In *Oppia* it is rather wide whereas in e.g. *Hermanniella* it is rather narrow (KÜMMEL and DOBNER 1986, present study/part I). This gap is possibly a disclosure zone from which the spermatozoa may be released in the female. A special case is demonstrated by *Euzetes* in which the plate-like enlargement of the stalk further narrows this "gap". We distinguish this specific structure from the less clearly defined apical thickenings of the stalk which are often seen (e.g.) in *Scutovertex sculptus*, *Hermanniella punctulata*, *Oppia nitens*, *Achipteria quadridentata*, *Parachipteria punctata*; KÜMMEL and DOBNER 1986, present study). Probably a structure similar to that of *Euzetes globulus* has also been observed by WOODRING and COOK (1962a) in *Ceratozetes cisalpinus* ("lateral support") and *Scheloriabates laevigatus*. Evidently, in *Euzetes* this region provides a preformed zone of disruption.

Within the sperm package dense particles of varying size and structure usually can be seen between the sperm cells. The secretions in which the spermatozoa are embedded contain proteinaceous components.

The head matrix in itself demonstrates a high degree of complexity with different types of secretions arranged rather specifically. Most obvious are large bodies (LB) or large secretions (LS), often subsumed under the term "spherical bodies" (SHEREEF 1972, 1977, TRÁVNÍČEK 1979, KÜMMEL and DOBNER 1986). The present study confirms the previous statement (KÜMMEL and DOBNER 1986) that their structure is very different from one another. The "spherical bodies" can show similarities possibly hinting at relationships. So only the representatives of the Achipteriidae possess a homogeneous large body. It is peripherally surrounded by an intricate reticulate or honey-comb structure, which is in a coarser appearance also present in *Adoristes*. In *Euzetes* this body is surrounded by layers of "membrane-like structures" as can evidently also be recognized in *Punctoribates punctum*. Similar layers are apparent in *Scutovertex*, *Hermanniella* and — to a lesser extent — in *Eupelops*.

Finally the "spherical bodies" of the three Belboidea examined until now electron microscopically exhibit certain concordances too (KÜMMEL and DOBNER 1986). All these taxa belong to the "higher oribatids". In contrast no such zone was observed in *Hermanniella*. Only in *Punctoribates punctum* and *Eupelops acromios* the "spherical body" is located beneath the sperm package, otherwise it is situated apically above the sperm package. Most often one large body is present composed of several subunits. These may disintegrate (convergently) to form several isolated bodies (e.g. *Liaccarus subterraneus*, *Euzetes globulus*, *Parachipteria punctata*; TRÁVNÍČEK 1979, KÜMMEL and DOBNER 1986, present study/part I). "Spherical bodies" do obviously not occur in all oribatid spermatophores. They are surely absent in all Phthiracaridae investigated, and they could not be seen in *Oppia nitens* (KÜMMEL 1982, KÜMMEL and DOBNER 1986, present study). However, in his light microscopical study SHEREEF (1972) has observed the structure in several other species of Oppiidae. According to FERNANDEZ (1981) the spermatophores of *Epilohmannia maurii* also seem to be devoid of this structure.

In those species investigated histochemically it always gave positive evidence for lipids.

In addition to the "spherical bodies" there are further structures immersed in the ground substance. Membrane-like structures as in *Achipteria*, *Parachipteria* and *Euzetes* shall be specially mentioned. *Parachipteria* and *Achipteria* demonstrate their close relationships by a further peculiarity which they have in common. Only in these two species more or less dense particles in the periphery of the head orientated against the center of the head are present. A distinct peripheral zone, which differs widely in the details, is developed in most oribatid spermatophores. In *Punctoribates punctum* and *Eupelops acromios*, however, no such zone is recognizable (KÜMMEL and DOBNER 1986, present study/part I).

In all species studied, mucopolysaccharides are present in the head matrix.

The stalk length differs according to the species. Thus the head is maintained in a definite position over the substrate. There are three types of stalks with respect to shape: straight stalks present in most

species and stalks with an inflection or wavy part, respectively, next to the head. The latter types have been found in Belboidea (wavy part, often with a "knee") (PAULY 1952, 1956, TABERLY 1957, SCHLIWA 1965, SHEREEF 1972, KÜMMEL and DOBNER 1986), *Pelops* sp. (TABERLY 1957), and *Eupelops acromios* (inflection). A slight inflection was also depicted in the spermatophore of *Granuloppia* sp. (Oppliidae) by SHEREEF (1972), whereas other Oppliidae have straight stalks (SHEREEF 1972, KÜMMEL, 1982). The case of *Granuloppia* could be an artifact due to ageing since the sperm head was covered by numerous spines, presumed by us to indicate fungus infection (an assumption also made by TRÁVNÍČEK 1979).

Ultrastructurally the stalk is composed of a heterogeneous material. In some species it presents a specialized region with longitudinal elements next to the head (*Parachipteria*, *Achipteria*). In *Eupelops* distinct dense inclusions are a conspicuous component in the stalk. It was possible to demonstrate areas containing proteins alternating with areas in which no reaction with the applied dye occurred. These most likely contain lipids since in *Liaccarus* the apical part of the stalk reacted very strongly with Sudan Black.

The area of contact between stalk and head demonstrates characteristic peculiarities. In the Phthiracaridae, *Hermannia gibba*, *Punctoribates punctum*, and *Eupelops acromios* (KÜMMEL and DOBNER 1986, present study) this apical region of the stalk is a more or less flat portion to which the spermatophore head is attached. However, there are differences: The extension in Phthiracaridae is formed like a bowl on which the sperm head rests, whereas in the remaining species the stalk material is toothed into the head matrix. In *Hermannia* a distinct column is based on the flat apical portion. In other species the stalk protrudes more or less into the head ("ampoule" according to SHEREEF 1972). The appearance of the material of the stalk protrusion is often different from that of the free stalk. Together with other structures (package wall, ground substance), thus a centre is formed, around which the sperm package is situated (composed central region). In *Achipteria* and *Parachipteria* the ground substance extends into the apical part of

this central region. In *Euzetes* it even reaches the base of the central region. In *Adoristes* the apical portion of the stalk is characteristically swollen.

The distinctly different composition of head and stalk may give some information about the formation of spermatophores. In contrast to Actinedida in which the male genital system possesses elaborate glandular structures (see e.g. ALBERTI 1974, WITTE 1975) oribatids only exhibit an extensive glandular part of the testis and a small stalk or accessory gland (WOODRING and COOK 1962b, SCHLIWA 1965, WOODRING 1970). The original assumption of WOODRING and COOK (1962b) that this gland is producing the stalk material was doubted by SCHLIWA (1965). The author argued that the gland is too small in relation to the amount of secretions needed to produce a complete stalk. This view was adopted by WOODRING (1970). According to the results obtained from *Chamobates borealis* (see part I) it seems reasonable to assume that most of the spermatophore material comes from the glandular part of the testis (seminal vesicle in WOODRING and COOK 1962b, WOODRING 1970; see also SCHLIWA 1965, ALBERTI 1980b). It is most likely that the spermatophore is formed upon its deliverance as suggested by SCHLIWA (1965) and WOODRING (1970) and that it is not partly preformed as e.g. in several actinedids (ALBERTI 1974, WITTE 1975). SCHLIWA (1965) suggested that the accessory gland may add a component which could induce separation of components (stalk and head material). However, such a separation must also occur during formation of the complex head, the components of which are obviously produced in the glandular part of the testis. Probably a fine structure study of the accessory gland could reveal its role in spermatophore (stalk?) formation. Apparently the assumed (self-) organization of the components is not always perfect since sometimes components are found within the "wrong place" (e.g. spermatozoa within the stalk material protruding into the central region; see *Archipteria quadridentata*; part I).

Presently only speculations are possible on the functions of the various secretory components involved in the spermatophore formation: protection against desiccation by covers, prevention from

desiccation by “hygroscopic” components, attraction of females (pheromones), prevention of further fertilization by plugging the female (to secure sperm priority) etc. (WOODRING 1970, MANN 1984, THOMAS and ZEH 1984, WITTE 1984, 1991, KÜMMEL and DOBNER 1986). The observations of microorganisms in a distinct position (i.e. within the peripheral zone) (*Hermanniella punctulata*; see part I) may also indicate that this stratum serves as a barrier against microbial or fungal infection, at least for some time.

The different extension of the package wall is certainly of functional significance. It could be that the spermatophores with nearly completely enclosed package (e.g. *Achipteria*, *Euzetes*) maintain their contents of spermatozoa functional (fertile) over a longer period than other species. This would be of advantage in less dense populations. Further, the number of spermatophores produced by one male could be reduced, since the probability to be picked up by a female increases with the extension of this period. Or, these specialized spermatophores are adapted to be deposited in less humid microhabitats. Though these ideas need to be confirmed by experiments it seems evident that spermatophore structure is closely related to autecological demands and conditions (population density, patchy or even distribution, microclimate, attractiveness of spermatophores to the female etc.). It should be remembered in this context that pair formation is only exceptionally encountered within oribatids in *Collohmanna gigantea*, a member of the “lower oribatids”, in which stalked spermatophores never have been observed (SCHUSTER 1962). The problem whether pair formation in taxa with indirect spermatophore transfer is a derived character or not seems still to be under discussion (ALEXANDER 1964, SCHALLER 1979, WEYGOLDT and PAULUS 1979, MANN 1984, THOMAS and ZEH 1984).

In all oribatids investigated so far the spermatozoa are found as individual cells arranged apparently at random within the sperm package. Generally spermatozoa of moss mites are lens-shaped/discoidal (Phthiracaridae, ALBERTI 1980b, KÜMMEL and DOBNER 1986) or spherical/ovoid/ellipsoid (ALBERTI 1980b, KÜMMEL 1982, KÜMMEL and DOBNER 1986, WAITZBAUER 1983). However, *Liacarus*, *Adoristes*,

and also *Hafenrefferia* (WITALINSKI 1982) all included in the Liacaridae, have elongate sperm cells. With regard to the Liacaridae this was already indicated by the comprehensive light microscopical study of TRÁVNÍČEK (1979). *Liacarus subterraneus* is further remarkable as it represents the only case within oribatids in which spermatozoa are aggregated. Comparable small groups have in Acari only been found in testes of certain representatives of the actinotrid family Bdellidae by ALBERTI and STORCH (1976). The light microscopical observations of WOODRING and COOK (1962b) of clusters of sperm in *Ceratozetes* was later referred to by WOODRING (1970) as being incorrect.

In general, the spermatozoa of oribatids are covered by a secretory sheath which may represent a protective coating according to the suggestion of ALBERTI (1980b) since it is only present in actinotrid mites producing spermatophores deposited on the ground. This sheath appears to be rather simple, though stratified in probably all species. In some species the substructure seems to be more complex comprising fine granules in the periphery (e.g. *Phthiracarus*, *Scutovertex*). Most remarkable is *Adoristes ovatus* in this context, however (c.f. part I).

The sperm cell contains a chromatin body which generally occupies most of the cell. Usually this body is electron dense and homogeneous. Only in *Hermannia gibba* a paracrystalline pattern has been observed until now, a peculiarity which was not always recognizable, however. In nearly all oribatid sperm cells a bowl body (first termed “dense body”; ALBERTI 1980b) is present (KÜMMEL and DOBNER 1986, present study). Phthiracarids certainly represent an exception in this respect. Also in this taxon a system of fine “canaliculi” had been observed (KÜMMEL and DOBNER 1986). Similar “canaliculi” have now been also found in *Hermannia* and *Euzetes*. Their significance is not known. In *Oppia nitens* the presence of a bowl body could not be assured because of the poor preservational state of the sperm cells (KÜMMEL and DOBNER 1986). The presence of the bowl body is also not evident from the description of the spermatozoa of *Hafenrefferia gilvipes* (Tenuialidae, Liacaridae) given by WITALINSKI (1982). However, it is most likely that it is a basic (synapomorphic?) structure common to all

Circumdehiscentiae and the Hermanniidae, a character thus supporting the classifications of BALOGH (1972), LEE (1984), and WOOLLEY (1988). In most species the bowl body is a single structure which reaches nearly the dimensions of the chromatin body. In some taxa the bowl body apparently is divided into several subunits (*Eupelops*, *Galumna*) or appears to be segmented (*Chamobates*) (see below).

Mitochondria are regularly present in oribatid sperm. In all Phthiracaridae investigated they are deeply embedded into the chromatin body, whereas in *Parachipteria*, *Achipteria*, *Euzetes*, *Punctoribates*, *Chamobates*, and *Galumna* the mitochondria are obviously completely but only superficially embedded (ALBERTI 1980b, KÜMMEL and DOBNER 1986, present study/part I). Hence this character applies for all Poronotae investigated except *Eupelops acromios*. However, in this species mitochondria are often attached to thin extensions of the chromatin body, an arrangement which gives a rather similar aspect. Evidently such a position is also found in some but not in all Liacaroidea (WITALINSKY 1982, present study/part I). In all other oribatid species mitochondria lie also close to the chromatin body, either they are slightly indented (*Damaeus*, *Metabelba*, *Hermanniella*) or they are at least adjacent to it (*Hermania*, *Scutovertex*; in *Oppia* the situation is not fully understood) (ALBERTI 1980b, KÜMMEL 1982, WAITZBAUER 1983, KÜMMEL and DOBNER 1986, present study/part I). Thus it appears that the close spatial relationship of the mitochondria to the chromatin body is a basic character of all oribatids (c.f. KÜMMEL and DOBNER 1986). In many cases the mitochondria no longer have the typical aspect, e.g. cristae are often not recognizable (see also WITALINSKI 1982). The results now on hand show, however, that there are also quasi normal mitochondria in certain species (e.g. *Scutovertex sculptus*, *Euzetes globulus*, *Eupelops acromios*).

The widespread occurrence of microvilli-like protrusions is also of interest in this respect, but cannot be interpreted easily on the basis of the available material.

The application of electron microscopy has extended the knowledge about spermatophores and spermatozoa of Oribatida considerably demonstra-

ting that former interpretations of these structures as "simple" are not correct. In this paper (part I) rather simple histochemical observations similarly demonstrated the complexity of the spermatophores of moss mites (see also SCHLIWA 1965, WOODRING, 1970). In fact, a true "stalked droplet type" of spermatophore, i.e. simply a droplet of sperm fluid on a stalk (MANN 1984, SCHALLER, 1971, 1979, WEYGOLDT 1966), has not been found within Oribatida until now. In contrast it may be present within the Actinedida (see ALBERTI 1974, EHRSBERGER 1977, 1988, SCHUSTER and SCHUSTER 1977, WITALINSKI 1985, WITTE 1984). In snout mites (Bdellidae) and Erythraeidae (both Actinedida) species-specific spermatophores of different complexity are found within the same family (WALLACE and MAHON 1972, 1976, ALBERTI 1974, WITTE 1975, 1977, TURK 1988). It is remarkable that the sperm package is exposed to the surrounding air over wide areas in *Hermannia gibba* ("lower oribatids"), Belboidea, *Scutovertex sculptus*, *Punctoribates punctum* and *Eupelops acromios* ("higher oribatids"). The spermatophores of *Punctoribates* and *Eupelops acromios* are those which are closest to the classical droplet type. However, it presently seems most likely that they represent derived types.

So the data of this paper confirm the impression gained from earlier light microscopic studies and from the recent papers of KÜMMEL (1982) and KÜMMEL and DOBNER (1986) that spermatophore ultrastructure could be usefully applied in phylogenetic or systematic considerations in a similar way as sperm ultrastructure (see BACCETTI 1985 for general informations, ALBERTI 1980a, b, and 1991 with regard to Acari). Unfortunately, from the 145 oribatid families which are presently distinguished according to JOHNSTON (1982) several are entirely reproducing parthenogenetically (NORTON *et al.* 1988) and those from which spermatophores have been described are mainly from the Circumdehiscentiae ("higher oribatids"). This is regarded as a monophyletic taxon since the studies of GRANDJEAN (see for ref. GRANDJEAN 1954, 1965, 1969, KRANTZ 1978, BALOGH 1972, JOHNSTON 1982, LEE 1984, MARSHALL *et al.* 1987, WOOLLEY 1988). The results on *Phthiracarus* and *Steganacarus* (ALBERTI 1980b, KÜMMEL and DOBNER 1986, present study/

part I) demonstrate the taxonspecificity of the spermatophore including the spermatozoa in a restricted taxon (Phthiracaridae) even on the ultrastructural level and with respect to geographically very distant representatives. Clear congruences are also found in the investigated species of Belboidea (KÜMMEL and DOBNER 1986). The representatives of Liacaroida examined ultrastructurally until now (WITALINSKI 1982, present study) are characterised by the special form of their spermatozoa (more or less elongate). In all inspected Poronotae (with the slight exception of *Eupelops*; see above) the mitochondria appear completely but only superficially embedded into the chromatin body. Furthermore both species belonging to the Achipteridae correspond highly in their spermatophore structure. Table I and II sum up some of the characteristics found in both, spermatophores and spermatozoa, which we think may be of systematical value.

Summarizing the available data, 5 types of spermatophores may be distinguished :

1) *Phthiracarus*-type with subequatorial ring-shaped sperm package completely surrounded by a specific package wall (or cover) including the ring-structure and inward spiral. No spherical body. *Phthiracarus*, *Steganacarus*.

2) *Hermannia*-type with basally located ring-shaped sperm package surrounding a central column which extends into an irregular "umbrella". The head matrix partly covers the sperm package, which thus is partly open laterobasally. No genuine package wall. Spherical body present, but not delimited from the ground substance by special structures. *Hermannia*.

3) *Damaeus*-type with basally located ring-shaped sperm package surrounding a central region into which the stalk protrudes. Composed central region. The apical part of this region extends into an umbrella with a thick peripheral fringe. No peripheral zone. A spherical body is present, delimited by a distinct and complex wall. The sperm package is freely exposed laterobasally. The stalk is (always?) provided with an apical wavy portion. *Damaeus*, *Metabelba*.

4) *Achipter*-type with basally located ring-shaped sperm package surrounding a composed central

region including the stalk prolongation. The spherical body is usually present (*Oppia nitens* may be an exception) and is surrounded by a specific wall. *Scutovertex* obviously differs from the remaining taxa and is tentatively placed within this type. Peripheral zone present and continuous with a distinct package wall. The package wall covers the sperm package laterobasally to different extents : *Scutovertex* — *Oppia* — *Hermannella*/*Achipter*/*Parachipter*/*Liacarus*/*Adoristes*-*Euzetes*. At least in the last taxa a preformed disclosure/disruption zone is present around the stalk insertion. *Scutovertex*, *Oppia*, *Hermannella*, *Liacarus*, *Adoristes*, *Achipter*, *Parachipter*, *Euzetes*.

5) *Punctoribates*/*Eupelops*-type with apically located sperm package and basally located spherical body. There is no package wall. Within the pelopids the stalk has an apical inflection. *Punctoribates*, *Eupelops*.

It is strongly evident that the *Phthiracarus*-type deviates from all the others reflecting the remote systematical position ("lower oribatids", Ptyctima, Euptyctima, Mixonomata, Mesomixonomata) (GRANDJEAN 1954, 1969, BALOGH 1972, JOHNSTON 1982, LEE 1984, MARSHALL *et al.* 1987, WOOLLEY 1988). In contrast, the remaining types are rather close to each other with the remarkable exceptions of *Punctoribates* and *Eupelops*.

Interestingly, spermatophores of *Epilohmannia* (another representative of the "lower oribatids"; GRANDJEAN 1969, BALOGH 1972, LEE 1984, MARSHALL *et al.* 1987, WOOLLEY 1988) appear to occupy an "intermediate position" between those of Phthiracaridae and of *Hermannia* according to the detailed light microscopical investigations of FERNANDEZ (1981).

With regard to the *Hermannia*-, *Damaeus*-, and *Achipter* (*Scutovertex*!)-types the similarity of the spermatophores (apical large body, ring-shaped sperm package) is remarkable as the systematic position of Hermannioidea and Belboidea is problematic. According to GRANDJEAN (1954) the Hermannidae are member of the Nothroidea within the "lower oribatids" in contrast to the Belbidae which belong to the Circumdehiscentiae ("higher

oribatids"). Similarly did JOHNSTON (1982) place the Hermanniidae within a taxon Nothronata separate from the Circumdehiscentiae. MARSHALL *et al.* (1987) similarly separated both taxa by placing the Hermannioidae within a taxon Desmonomata and the Belboidea with the Brachypylina (= "higher oribatids"). In contrast is the suggestion by BALOGH (1972) who positioned both within the Brachypylina. Similarly, LEE (1984) included both in the Holosomatina and WOOLLEY (1988) united the Nothroidae (and several other including the Belboidea) with the remaining Circumdehiscentiae in a large taxon Nothronata. Apparently both Hermannioidae and Belboidea have a special position close to the basis of the "higher oribatids".

In contrast, the position of the Hermanniellidae close to the Belboidea as suggested by LEE (1984) is not substantiated by the spermatophore structure.

The spermatophores subsumed under the *Achipteria*-type are rather different. Thus three subtypes could be distinguished represented by *Scutovertex*, *Oppia* and the remaining taxa (including *Hermanniella*!). This arrangement is in concordance with the placement of *Oppia* in a separate taxon (Oppioidea, Pycnonota/Pycnonoticae; GRANDJEAN 1954, BALOGH 1972, WOOLLEY 1988). However, *Scutovertex* is placed together with the remaining species within the Poronotae/Poronoticae by the same authors and by LEE (1984). Taking into account the quite different spermatophores of *Punctoribates* and *Eupelops* it is evident that the Poronotae/Poronoticae represent a rather heterogeneous assemblage with regard to spermatophore structure.

Moreover, according to GRANDJEAN (1954) Pelopidae are systematically related with the Scutoverticidae and Achipteriidae, whereas the Mycobatidae (to which *Punctoribates* belongs) is brought close to the Euzetidae, Chamobatidae, and Galumnidae. This arrangement would not fit with the similarities/differences observed in the spermatophores.

Eupelops and *Galumna* have a divided bowl body in common (for *Galumna* see ALBERTI 1980b). Unfortunately, the spermatophores of *Galumna* are only poorly known. ROCKETT and WOODRING (1966) depicted the presence of three supporting arms, presumably elongations of the stalk in *Perga-*

lumna omniphagus. Apparently there is no central region!

There are at least two possibilities to explain these above mentioned discordances. Either are the suggested relationships within the Poronotae/Poronoticae based on the wrong characters or the spermatophore structures have evolved convergently in several of the poronote groups defined by GRANDJEAN (1954). However, the rather identically structured spermatophores of the Phthiracaridae and Belboidea respectively (see also the light microscopical investigations in the latter!), do demonstrate that spermatophores may be rather stable structures within these taxa.

The spermatophores of *Punctoribates* and *Eupelops* clearly deviate far more from the *Achipteria*-type than is reflected in the several proposed classifications. Further, they are more different from the *Scutovertex*/*Achipteria*/*Euzetes*-spermatophores than those of *Oppia* and also Liacaroidae; both the latter are, however, not placed with the other into the Poronotae/Poronoticae, but in the Pycnonota/Gymnonota/Pycnonoticae (GRANDJEAN 1954, BALOGH 1972, LEE 1984, WOOLLEY 1988).

Since the taxon Poronotae/Poronoticae is based in part on the presence of notogastral "area porosae" it is remarkable that these structures turned out to be no respiratory organs as was previously thought (GRANDJEAN 1959) and sometimes is still pretended by recent publications (BALOGH and MAHUNKA 1983; WOOLLEY 1988), but have been shown to present dermal glands (WOODRING and COOK 1962b, ALBERTI *et al.* 1981). Probably this character should be reevaluated.

More detailed statements on relationships between higher taxa would be highly speculative in view of the up to now still only fragmentary knowledge. Further investigations should be awaited.

ACKNOWLEDGMENTS

The authors are grateful to the Deutsche Forschungsgemeinschaft which financially supported this study (Al 138/2-3). Further we wish to acknowledge a grant from the Deutscher Akademischer Austauschdienst to N.A.F., which made this coope-

ration possible. We are also indebted to Dr. Ch. HARTNIGK-KÜMMEL (Karlsruhe) for her stimulating contributions and her assistance with the English version of the manuscript. The French résumé were kindly provided by Dipl. Dol. Ch. BASTIAN (Heidelberg). Thanks are also due to Dipl. Biol. M. KRATZMANN (Heidelberg) for various helpful remarks. For skilful technical assistance we wish to

thank Mrs. G. ADAM, Mrs. R. MUMMERT, and Mrs. I. RANKER (Heidelberg). Last but not least we want to express our gratitude to Prof. Dr. N. Paweletz (DKFZ, Heidelberg) for his kind permission to use the SEM and Prof. Dr. J. TRAVÉ (Banyuls sur Mer) as well as Prof. Dr. G. WEIGMANN (Berlin) for their valuable advice.

TABLE I : Characters of spermatophores according to results obtained by light and electron microscopy.
Abbr. : + = character present, — = character absent according to source, ? = state of character not clear from source, character ? = character assumed to be present/absent, confirmation is needed.

	position of sperm package	large body	stalk/head attachment	central portion column, region	form of package wall	basal gap peripheral zone	shape of stalk	reference
PHTHIRACAROIDEA								
<i>Phthiracarus</i> sp.	subequatorial ring	—	distinct bowl	central portion	ring structure inward spiral	— —	straight	present study
<i>Phthiracarus piger</i>	subequatorial ring	—	distinct bowl	central portion	ring structure inward spiral	— —	straight	KÜMMEL & DOBNER 1986
<i>Steganacarus magnus</i>	subequatorial ring	—	distinct bowl	central portion	ring structure inward spiral	— —	straight	KÜMMEL & DOBNER 1986
EPILOHMANNIOIDEA								
<i>Epilohmannia maurii</i>	basal ring	—	bowl ?	central portion ?	arched wall ?	? ?	straight	FERNANDEZ 1981
HERMANNIOIDEA								
<i>Hermannia gibba</i>	basal ring	apical	stalk plate	column	irr. umbrella no pack. wall	wide —	straight	WAITZBAUER 1983 present study
LIDOIDEA								
<i>Poroliodes farinosus</i>	?	?	stalk plate ?	?	?	? ?	straight	TABERLY 1957
BELBOIDEA								
<i>Damaeus onustus</i>	basal ring	apical	stalk prolongation	comp. central region	umbrella	wide ?	wavy with knee	PAULY 1952, 1956 SCHLIWA 1965
<i>Damaeus crispatus</i>	?	?	?	— ?	?	? ?	wavy no knee	TABERLY 1957
<i>Damaeus kulczyński</i>	?	?	?	comp. central region ?	?	? ?	wavy with knee ?	TABERLY 1957
<i>Damaeus clavipes</i>	basal ring	apical	stalk prolongation	comp. central region	umbrella fringe	wide —	wavy with knee	KÜMMEL & DOBNER 1986
<i>Damaeus riparius</i>	basal ring	apical	stalk prolongation	comp. central region	umbrella fringe	wide —	wavy with knee	KÜMMEL & DOBNER 1986
<i>Damaeus quadrihastatus</i>	?	?	stalk prolongation ?	comp. central region ?	?	? ?	— with knee	CANCELA DA FONSECA 1969
<i>Epidamaeus plumosus</i>	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy with knee	SHEREEF 1972
<i>Epidamaeus grandjeani</i>	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy ?	SHEREEF 1972
<i>Epidamaeus kamaensis</i>	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy ?	SHEREEF 1972

	position of sperm package	large body	stalk/head attachment	central portion column, region	form of package wall	basal gap peripheral zone	shape of stalk	reference
<i>Epidamaeus</i> sp.	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy ?	SHEREEF 1972
<i>Spatiodam. sub- verticillipes</i>	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy ?	SHEREEF 1972
<i>Belba meridionalis</i>	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy ? with knee	SHEREEF 1972
<i>Belba rossica</i>	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy ?	SHEREEF 1972
<i>Porobelba spinosa</i>	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy ?	SHEREEF 1972
<i>Metabelba pallipes</i>	basal ring	apical	stalk prolongation	comp. central region	umbrella fringe	wide —	wavy with knee	KÜMMEL & DOBNER 1986
<i>Metabelba rara</i>	basal ring	apical	stalk prolongation	comp. central region ?	umbrella ?	wide ?	wavy ?	SHEREEF 1972
PASSALOZETOIDEA								
<i>Scutovertex sculptus</i>	basal ring	apical	stalk prolongation	comp. central region	umbrella patches	wide +	straight	present study
LIACAROIDEA								
<i>Ceratoppia bipilis</i>	?	?	stalk prolongation	comp. central region ?	?	? ?	straight	TABERLY 1957
<i>Liacarus coracinus</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall	narrow ?	straight	TABERLY 1957 TRÁVNÍČEK 1979
<i>Liacarus subterraneus</i>	basal ring	apical several units	stalk prolongation	comp. central region	arched wall	narrow +	straight	TAB. 1957, TRÁVNÍČEK 1979, pres. stud.
<i>Liacarus nitens</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	narrow ? ?	straight	TRÁVNÍČEK 1979
<i>Liacarus xylariae</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	narrow ? ?	straight	TRÁVNÍČEK 1979
<i>Dorycranosus infissus</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	narrow ? ?	straight	TRÁVNÍČEK 1979
<i>Dorycranosus moraviocus</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	narrow ? ?	straight	TRÁVNÍČEK 1979
<i>Xenillus tegeocranus</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	narrow ? ?	straight	TRABERLY 1957 TRÁVNÍČEK 1979
<i>Xenillus clypeator</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	narrow ? ?	straight	TRÁVNÍČEK 1979
<i>Adoristes ovatus</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall	narrow +	straight	present study
HERMANNIELLOIDEA								
<i>Hermanniella granulata</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	narrow ? ?	straight	SHEREEF 1972
<i>Hermanniella punctulata</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall	narrow +	straight	present study
CARABODOIDEA								
<i>Carabodes</i> sp.	basal simple ball ?	—	—	— ?	?	? ?	straight ?	SHEREEF 1972

	position of sperm package	large body	stalk/head attachment	central portion column, region	form of package wall	basal gap peripheral zone	shape of stalk	reference
OPPIOIDEA								
<i>Oppia concolor</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	? ?	straight	SHEREEF 1972
<i>Oppia</i> sp.	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	? ?	straight	SHEREEF 1972
<i>Oppia nitens</i>	basal ring	— ?	stalk prolongation	comp. central region	arched wall	intermediate +	straight	KÜMMEL 1982 KÜMMEL & DOBNER 1986
<i>Granuloppia</i> sp.	basal ring	apical	stalk prolongation	comp. central region	arched wall ?	? ?	inflection ?	SHEREEF 1972
ORIBATULOIDEA								
<i>Peloribates pilosus</i>	basal (ring ?)	apical	—	— ?	?	? ?	straight	SHEREEF 1972
<i>Xylobates souchnaiensis</i>	basal ring	apical	stalk prolongation	comp. central region ?	?	? ?	straight	SHEREEF 1977
<i>Schelorbates laevigatus</i>	?	apical *	st. prolong. lat. support	comp. central region ?	?	? ?	straight	WOODRING & COOK 1962a
CERATOZETOIDEA								
<i>Ceratozetes cisalpinus</i>	?	apical *	st. prolong. lat. support	comp. central region ?	?	? ?	straight	WOODRING & COOK 1962a
<i>Diapterobates numerosi</i>	basal (ring ?)	apical	—	— ?	?	? ?	straight ?	SHEREEF 1972
<i>Punctoribates punctum</i>	apical inverted bowl	basal	stalk plate	—	no package wall	— —	straight	KÜMMEL & DOBNER 1986
<i>Euzetes globulus</i>	basal ring	apical several units	st. prolong. lat. support	comp. central region	arched wall	narrow +	straight	TABERLY 1957 present study
PELOPOIDEA								
<i>Pelops</i> sp.	?	?	?	—	?	? ?	inflection	TABERLY 1957
<i>Eupelops acromios</i>	apical inverted bowl	basal	stalk plate	—	no package wall	— —	inflection	present study
ORIBATELLOIDEA								
<i>Plakoribates multicuspidus</i>	basal ring	+ ?	stalk prolongation	comp. central region ?	?	? ?	straight	SHEREEF 1977
<i>Parachipteria punctata</i>	basal ring	apical several units	stalk prolongation	comp. central region	arched wall	narrow +	straight	KÜMMEL & DOBNER 1986
<i>Achipteria quadridentata</i>	basal ring	apical	stalk prolongation	comp. central region	arched wall	narrow +	straight	present study
GALUMNOIDEA								
<i>Pergalumna omniphagus</i>	?	?	3 supporting arms	— ?	?	? ?	straight very short	ROCKETT & WOODRING 1966
incertae sedis								
<i>Pelokylla malabarica</i>	basal (ring ?)	— ?	Stalk prolongation	comp. central region ?	?	? ?	straight	HAQ & ADOLPH 1981

* In the original paper (WOODRING & COOK, 1962a) the region interpreted here as large body was described as sperm sac.

TABLE II : Characters of spermatozoa according to results obtained by electron microscopy.
Abbr. : + = character present, — = character absent according to source, ? = state of character not clear, character ? = character assumed to be present/absent, confirmation is needed.

	bundles	shape	sheath	position of mitochondria	bowl body/ dense body	microvilli/ protrusions	reference
PHTHIRACAROIDEA							
<i>Phthiracarus</i> sp.	—	discoidal	simple	deeply embedded	—	+	present study
<i>Phthiracarus piger</i>	—	discoidal	simple	deeply embedded	—	+	KÜMMEL & DOBNER 1986 present study
<i>Steganacarus magnus</i>	—	discoidal	simple	deeply embedded	—	+	KÜMMEL & DOBNER 1986 present study
HERMANNIOIDEA							
<i>Hermannia gibba</i>	—	spherical	simple	not embedded	+	—	WAITZBAUER 1983 present study
BELBOIDEA							
<i>Damaeus onustus</i>	—	ellipsoid	simple	partly indented	+	—	ALBERTI 1980b
<i>Damaeus clavipes</i>	—	ellipsoid	simple	partly indented	+	+	KÜMMEL & DOBNER 1986
<i>Damaeus riparius</i>	—	ellipsoid	simple	partly indented	+	+	KÜMMEL & DOBNER 1986
<i>Metabelba pallipes</i>	—	ellipsoid	simple	partly indented	+	+ ?	KÜMMEL & DOBNER 1986
PASSALAZETOIDEA							
<i>Scutovertex sculptus</i>	—	spherical	simple	not embedded	+	+ ?	present study
LIACAROIDEA							
<i>Hafenrefferia gilvipes</i>	—	elongate tadpole-like	simple ?	embedded	+ ?	—	WITALINSKI 1982
<i>Liacarus subterraneus</i>	+	elongate ribbon-like	simple	embedded	+	—	present study
<i>Adoristes ovatus</i>	—	elongate fusiform	complex	partly embedded	+	—	present study
HERMANNIELLOIDEA							
<i>Hermanniella punctulata</i>	—	spherical	simple	partly indented	+	?	present study
OPPIOIDEA							
<i>Oppia nitens</i>	—	ellipsoid	simple	?	+ ?	+	KÜMMEL 1982 KÜMMEL & DOBNER 1986
CERATOZETOIDEA							
<i>Punctoribates punctum</i>	—	ellipsoid	simple	compl./superf. embedded	+	+	KÜMMEL & DOBNER 1986
<i>Chamobates borealis</i>	—	ellipsoid	simple	compl./superf. embedded	segmented	+	present study
<i>Euzetes globulus</i>	—	spherical	simple	compl./superf. embedded	several units	+	present study

	bundles	shape	sheath	position of mitochondria	bowl body/ dense body	microvilli/ protrusions	reference
ORIBATELLOIDEA							
<i>Parachipteria punctata</i>	—	ellipsoid	simple	compl./superf. embedded	+	—	KÜMMEL & DOBNER 1986
<i>Achipteria quadridentata</i>	—	ellipsoid	simple	compl./superf. embedded	+	—	present study
PELOPOIDEA							
<i>Eupelops acromios</i>	—	spherical	simple	incompl./chrom. extension	several units	+	present study
GALUMNOIDEA							
<i>Galumna elimata</i>	—	ellipsoid	simple	compl./superf. embedded	several units	+	ALBERTI 1980b

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Paru en Décembre 1991.