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RECONSTRUCTION OF STEM SPECIES PATTERN AS A STRATEGY TOWARDS INTEGRATED PHYLOGENETIC SYSTEMATICS AND TAXONOMY, APPLIED TO EARLY-DERIVATIVE PORONOTA (ORIBATIDA)

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ABSTRACT — The stem species concept is a modified method of phylogenetic systematics which uses not only apomorphies of taxa but also plesiomorphic character states for the assessment of phylogenetic interrelations. In a theoretical section the concept is outlined, and differentiated criteria on the homology of character states are presented on a background of conceptual models on epigenetic control of phenotypical characters. The method is exemplified with families of the early-derivative Poronota of oribatid mites. The superfamily Oribatelloidea is placed in the early-derivative Poronota, for which group a phylogenetic cladogram is proposed. As a result of the analyses, the problem of family diagnoses is discussed, resulting from the issue that 'classical' diagnostic characters are evolved partly within the evolution of the included genera and are not stem species characters of the family.

KEYWORDS — Acari; oribatid mites; cladistic phylogeny; evolutionary reversals

INTRODUCTION

In several important publications, Grandjean (1954, 1965b, 1969) elaborated a higher taxa concept of oribatid mites which arranged the genera described up to the middle of the last century into families by phenotypic similarities of the adults and aspired to be phylogenetically substantiated, e.g. by using characters of immatures.

But nowadays, it is more and more difficult to survey the increasing number of genera in oribatid mites. Since 1950, more than 80% of the approximately 10.000 known species of oribatid mites were described. More than 80% of about 1.500 described genera and more than 70% of families (now more than 200) were proposed after 1950 (Schatz 2002,

2005; cf. Subías 2004), partly based on newly described species, partly by splitting older genera and families. In several cases, the splitting seems to be questionable and is not substantiated with phylogenetical arguments. Balogh and coworkers (Balogh 1972; Balogh and Balogh 1992, 2002) repeatedly remarked in their important compilation books that their provisional classification must not be regarded as phylogenetic. Such classifications often use single conspicuous characters, or some combination of characters, whose value for assessing phylogenetic relations is questionable, or at least not examined or discussed. Nevertheless these classifications are used by acarologists.

Within oribatid mites, morphological characters often seem to have a mosaic distribution, as Woos

(1986, 1990) stated, and he concluded that oribatid mites were not suitable for analysis with cladistic methods following Hennig (1966). Yet in my opinion, cladistic systematics is still the best method to analyse phylogenetic interrelations based on morphological data, given that the common theory of evolution is accepted in that supra-specific categories of classification should reflect that closely related descent communities are monophyletic and thus descended from a presumed real historical stem species.

With this contribution I discuss whether modern comparative-morphological criteria are suitable to evaluate supra-specific groups of mites and to describe their phylogenetical interrelations. The families of the early-derivative Poronota (Achipteriidae, Oribatellidae, Phenopelopidae, Tegeribatidae and Unduloribatidae) are chosen as examples. For this purpose, the stem lineage concept (Ax 1985) will be applied, differentiated criteria on the homology of character states will be presented, conceptual models on epigenetic control of phenotypical characters will be discussed, and regarding the mosaic-like distribution of character states, alternative explanations will be presented in addition to homoplasy. None of these theoretical aspects is new, but this article might encourage consideration of phylogenetical theory regularly when a supra-specific taxon is proposed.

THEORETICAL SECTION

The stem species concept

Based on Hennig's phylogenetic systematics, Ax (1985) proposed a stem lineage concept in which he precised the terminology of Hennig (1966), e.g. synapomorphy, autapomorphy and others, and reflected on the relations between 'real supra-individual units in nature', 'taxa in the phylogenetic system' and 'categories of conventional classification'. In a phylogenetic system a 'taxon species' represents an 'evolutionary species', whereas each supra-specific taxon is an equivalent of a 'closed descent community', i.e. a monophylum which is "represented by one stem species and all of its descendants as the historical product of phylogenesis"

(Ax 1985). The reflections of Ax on taxonomy and classification will not be discussed in detail in the following. A concise paper from a modern viewpoint on the integrative possibilities of this view of taxonomy is Valdecasas *et al.* (2008).

The term 'stem species pattern' was first used by Sudhaus and coworkers (Lieven and Sudhaus 2002; Sudhaus 2004). In acarology it has been applied by Wirth (2002), in phylogenetic papers on vertebrates by Frahnert and Ade (2001), Carter and Mess (2007) and others. A term with about the same meaning is groundpattern or 'groundplan', the latter used by Kukalová-Peck (2008; critically commented by Béthoux *et al.* 2008) in a comprehensive paper on insect phylogeny which refers to the concept of Hennig (1981).

The **stem species pattern** (SSP) consists of all apomorphies and plesiomorphies of the stem species (Sudhaus 2004; Wirth 2002). The apomorphies are characters or character states evolved in the direct stem lineage (after Ax 1985) of the 'closed descent community' – i.e. the monophyletic group reflected by a clade in a cladogram – which is represented by the stem species. The SSP is the set of character states of the stem species, and this is the last common ancestor of a set of related species, i.e. a taxon. These apomorphies are autapomorphies of the monophylum and are regarded as synapomorphies of the first subsequent sister-clades (or sister-taxa) within the monophylum. The apomorphies on this phylogenetical level become plesiomorphies on the next lower level if not transformed to homologous new apomorphies. In a practical phylogenetical analysis, one will not list all possible plesiomorphic character states of a SSP but only those with relevance for the analysis: these are character states which are transformed within subsequent lower taxa (or clades) of the respective clade and those characters which are used for outgroup comparisons within the cladistic procedure.

The stem species pattern concept modifies the Hennigian procedure of cladistic systematics (= phylogenetic systematics) in being not only based on apomorphies of taxa but additionally plesiomorphies in the phylogenetic analysis. It is no problem if we are not sure at the outset which character state

is an apomorphy or a plesiomorphy: we include it into the SSP. The same is done with possible 'homoplasious characters'. We may start with a more or less substantiated cladogram which is to be confirmed or modified within the cladistic procedure. The main goal in each cladistic procedure is to appoint monophyletic groups in a hierarchical cladogram cluster which may be arranged in a first provisional design partly with unproven similar characters, partly with presumed homologies. We have to decide whether similarities are more probably homologies or the result of homoplasy. In a section below, different types of homology are discussed briefly. For all possibly relevant homologous characters and character states in the taxa, the polarity must be assessed, i.e., whether the character state is apomorphic or plesiomorphic. The determination of the character polarities as also the reconstruction of a phylogenetic cladogram is an iterative process of character evaluations from high to low systematic levels and conversely.

The stem species as the representative of a monophyletic group with at least two species represents the hypothetical last common ancestor of members of the monophyletic group, characterized by the stem species pattern of characters and character states. An autapomorphy of the stem species is determined by assessing the respective presumed synapomorphy of the direct descendants, as illustrated in figure 1 for the taxa B and C. Likewise symplesiomorphies of the descendants provide the probability of the respective plesiomorphy postulation for the stem species character. More problematic is the case when sister-taxa differ in the character state of a homologous structure, assuming that the sister relation is supported by other synapomorphies. The respective character state of one sister-taxon can be presumed as autapomorphic, the character state of the other may remain plesiomorphic: this character state is shared then with the stem species (in figure 1: taxon A and stem species y). The polarity presumption should be assessed by comparison with the presumed closest relative; the same should be done if both sister-taxa have different apomorphic character states. In such cases, the SSP construct is advantageous for detecting the

character polarities and the first appearance of an apomorphy, it is the nodal point for character comparison between ancestors and descendants.

A problem arises if one sister-clade (or taxon) shows confirmed autapomorphies but the other clade has only corresponding plesiomorphies. We can find such cladistic patterns in the literature (e.g. Haumann 1991) and also in the special section of this paper (in figure 4, the sister-clade of Phenopeloidea is without any proved autapomorphic character state). Such a clade is characterized by the lack of the autapomorphies of the sister-clade and as such is an existing remainder-group. This problem of possible paraphyly will not be discussed here.

Homology and character transformations

Most phylogenetic analyses based on morphological structures use homologies as arguments for phylogenetic relations between taxa. With the progress of biological knowledge, especially in molecular and developmental biology, the theoretical and operational content of the term 'homology' has changed. It is not possible and not intended to refer to the vast literature on homology. But the following is a short outline of the different facets of homology on which this paper is focussed.

At first, homology was mainly a descriptive term, based on similarity. "Darwin gave homology a historical meaning: *Organs of two organisms are homologous if they have been inherited (and perhaps modified) from an equivalent organ in the common ancestor.*" (statement and citation from Futuyma, 1998: 122). This definition includes the possibility of more or less dissimilar features being homologous. For practical character evaluation within comparative morphology, Remane (1952) formulated criteria of homology which among others should distinguish homologies from homoplasies. Hennig (1966, 1981) developed his phylogenetic systematics with the important differentiation of homologies into apomorphies and plesiomorphies, and he gave reasons for the predominant role of apomorphies in establishing monophyletic groups and taxa.

The spectacular progress of knowledge on gene controlled character expression and fundamen-

FIGURE 1: Illustration on the stem lineage concept. A, B, C: related taxa; – y, z: hypothetical stem species; C1: plesiomorphic state of character 1; – C1a: apomorphic state of character 1.

tal understanding of developmental processes allow homology and character transformation to be viewed from a new functional perspective. From gene-control models, as e.g. elaborated in *Drosophila* genetics and development research, we know about the complex genetic background of phenotype characters in arthropods, with hierarchical gene control in the course of ontogenetic development and gene blocking by other genes and several more (Futuyma 1998; Davidson 2006).

A modern definition of homology must take into account also the genetic aspects, as presented by Dohle (1989): *Homologous features are those characteristics whose similar structure can be traced back to a common origin, thus eventually to a primarily identical genetic information and an identical epigenetic differentiation* (translated from German). The linkage between evolutionary and developmental processes ("evo-devo research", see e.g. Goodman and Coughlin 2000) has become a central aspect to modern biological disciplines. Even if taxonomists deal with comparative-morphological data, they should consider the processes from genetic information to phenotypic character states and aspects of epigenetic differentiation. Such reflections can influence the

assessment of characters as homologies and their polarity as apomorphic or plesiomorphic.

As special case of homology, an **evolutionary reversal** of a character state constitutes a return from a "derived" character state to a more "ancestral" state (cf. Futuyma 1998: 110). Such an atavistic character state of a homologous feature is more or less identical with that found in farther relatives, and we can presume therefore homologous genetical information for the character expression. Already Hennig (1966: 116) discussed the possibility of so-called 'retrograde evolution' (here termed 'evolutionary reversals'): "The fact that almost any organ that once appeared in a transformation series as a new apomorphic character may later be reduced to the point of complete disappearance shows that retrograde evolution can take place. However, the possibility that characters that have disappeared may reappear again is probably often underestimated."

In literature, few remarks can be found on atavistic reversals in oribatid mites. Examples with reference to the special section below are: (i) Norton and Behan-Pelletier (1986) report an unusual presence of seta *d* on tibia IV in Phenopelopidae, which is presumed an atavistic reversal (details below in

the section "characters of legs"). (ii) Weigmann (2010) reported individual abnormal reappearance of additional notogastral setae in Scheloribatidae and other families with normally ten pairs, which show the setal pattern of taxa with generally higher number of setae. This phenomenon is discussed as reappearance of an ancestral character state, caused by reactivation of a previously suppressed genetic information – an explanation which may fit also to the various taxa in brachypylinae Oribatid mites (e.g. Oppiidae: *Ramusella* – *Multioppia*) with alternatively high or reduced notogastral setation. (iii) There are several families and even genera in poronotic Oribatida which have members with porose areas in the notogastral 'octotaxic system' as well as other members with sacculi in the same positions (cf. Norton and Alberti 1997). Obviously, a change between the two phenotypes of porose organs occurred independently within different taxa, a phenomenon which can be explained by a morphogenetic switch between a derived character state (porose areas) within Poronota to an atavistic reversal (sacculi). Such an evolutionary reversal represents a regressive plesiomorphic character state. Details and the hypothesized phylogenetic polarities are discussed below in the sections on 'opisthonotal and humeral characters', 'stem species patterns' and 'regressive and homoplasious characters...').

Finally, **serial homologies** occur in the setation and other characters of legs in Arthropods. A specific segment, e.g., the tibia, has the same (or identical) homologous character states in more than one leg; or in other respect, the segments of one leg, as genu and tibia, have the same homologous character states. This can be explained as morphogenetic character expression by one and the same gene complex in different units of segmented body parts, but in each at the respective place. An example may be the coupled appearance of a solenidion with a normal seta dorsally on segments of legs I–IV in members of the families Damidae and Phthiracaridae (Norton 1977, 1979; Niedbala 1992; Miko 2006). Such a coupling is observed on tibia and genu, and we find more or less related taxa with or without coupled setal organs in the same position and we can find both character states in the same species

on different positions. We may presume a morphogenetic switch between the two phenotypical characters, coupled or separated, both of which should have a genomal disposition.

SPECIAL SECTION

Character analysis

In the following, an advanced cladistic concept is demonstrated which adopts the main principles of Hennig's phylogenetic systematics, especially the character evaluation as apomorphic and plesiomorphic (Hennig 1966, 1981) and the reconstruction of 'stem species patterns' for taxa of the family levels (groups of superfamilies to families). Further on, the detection of regressive characters is illustrated, characters which may be suspected convergently evolved as apomorphies, but which can be explained better as atavistic reversals, i.e. regressive plesiomorphies inherited from ancestors, as discussed in the last section. The systematic group of 'early-derivative Poronota' (Norton and Alberti 1997) is chosen as example for this attempt, a group including Achipterioidea, Phenopeloidea and possibly Oribatelloidea which is discussed in the respective section. This superfamily-group descends most probably from poronotic members of the Licneremaeoidea (sensu Norton and Behan-Pelletier 2009) whose internal phylogenetic structure is unsolved but is not the subject of this article. This study hopes to contribute towards a phylogenetical concept of Poronota, yet a revision of the early-derivative Poronota is not intended and is not possible without further studies on the systematics e.g. of several genera of Achipteridae, Tegoribatidae and others which are not described and defined sufficiently and are positioned provisionally. Rather, this article focusses on basal characters within genera, families and higher taxa to elaborate the respective stem species patterns. Diverse out-group and sister-group comparisons are necessary to hypothesize the polarity of character states as apomorphic, plesiomorphic, regressive plesiomorphic or homoplasious (convergent).

The most important sources for the character evaluations in the context of the early-derivative

TABLE 1: Codes of the morphological structures and their character states

Immatures		ff opisthonotal characters	
I1	nymph opisthonotum folded or plicate	O3	no conspicuous anterior not. tectum
I1a	no plication	O3a	with conspicuous anterior not. tectum
I2	nymph apherodermous	O4	pteromorph present, immovable
I2a	apopherodermous	O4a	pteromorph movable (long or short hinge)
I3	nymph notogaster laterally carinate	O5	octotaxic system with saccules
I4	nymph with humeral organ	O5a	octotaxic system with 4 pairs of porose areas
I4a	humeral organ absent	O5b	octotaxic system reduced or lost
I5	nymph with 15 pairs of notogastral setae	O6	octotaxic organs not associated with setae
I6	nymph notogastral setae homomorph	O6a	octotaxic organs each associated with seta
I6a	notogastral seta da specialized	O6b	porose area A_1 associated with $lp + h_3$
Adult – prodorsal characters		O6c	A_1 associated with lp only
P1	cusps of lamella medium sized, $\pm$ triangular	O6d	A_1 associated with h_3 only
P1a	cusps large, with lateral and medial tooth	O7	cerotegument thin, inconspicuous
P1b	cusps large, asymm. with distinct lateral tooth	O7a	thick cerotegument
P1c	cusps broad, without lateral and medial teeth	O8	humeral porose area Ah present
P1d	cusps fused to large prodorsal shield	O9	pteromorph without knife-like projection
P1e	cusps small, acuminate	O9a	pteromorph with knife-like projection
P2	Translamella connecting cusps basally	Adult – gnathosomal characters	
P2a	Translamella absent, cusps with distance	G1	chelicera normal, chelate-dentate
P2b	Between cusps a median dens	G1a	chelicera forceps-like (pelopsiform)
P2c	Cusps fused in basal part	G2	palpal eupathidium acm free
P3	seta le centred at distal margin of cusp	G2a	palpal eupathidium acm attached to solenidion
P3a	seta le at medial margin of cusp	G3	axillary saccule of infracapitulum present
P3b	seta le at ventral side of cusp	G3a	axillary saccule of infracapitulum absent
P4	Tutorium present	Adult – ventral characters	
P5	genal tooth and genal incision present	V1	Discidium with custodium present
P5a	genal tooth reduced, incision small	V2	postanal porose area present
P5b	genal tooth and incision absent	V2a	postanal porose area absent
P5c	genal tooth associated with tutorium	V3	six pairs of genital setae
P6	Bothridium with spiral thickenings	V3a	more than six pairs of genital setae
P6a	Bothridium without spiral thickenings	Adult – leg and pedotectal characters	
P7	interlamellar seta normal, not broad	L1	solenidion Φ on TiIV present
P7a	interlamellar seta enlarged and broadened	L1a	solenidion Φ on TiIV absent
Adult – opisthonotal and humeral characters		L2	Tibia IV without seta d
O1	notogaster multideficient (10 pairs of setae)	L2a	Tibia IV with seta d
O1a	notogaster with (11-)15 pairs of setae	L3	Tibia IV with setiform seta l'
O1b	notogaster with 8 pairs of setae (p_2, p_3 lost)	L3a	Tibia IV with spine-like thick seta l'
O2	Notogaster with posterior tectum	L4	Pedotectum I without carina
O2a	Notogaster without posterior tectum	L4a	Pedotectum I with transversal carina

Poronota are Grandjean (1954), Alberti and Norton (1997), Norton and Behan-Pelletier (1986, 2009) and Behan-Pelletier (2001). Table 1 lists and codes the selected characters and character states, as evaluated for this contribution. As an example, code P1 represents the proposed plesiomorphic state of the lamellar cusp as present in ancestors of Poronota and some nonporonotic Brachypylina, codes P1a to P1e represent derived apomorphic states on the respective level of the first appearance in "early-derivative Poronota"; they become plesiomorphic states on subsequent lower systematic levels. The immature characters I1-I6 are separated from adult characters which are sorted as to body areas: Prodorsal (P), opisthonotal and humeral (O), gnathosomal (G), ventral (V), and concerning legs and pedotectal characters (L).

Characters of immatures (I1-I6)

Notogastral integument structures: Most immatures of early-derivative Poronota have a folded or plicate opisthonotal integument (figure 2a; coded as character I1 in tables 1-2 and figure 4) and the opisthonotum is carinated laterally (I3). In Oribatellidae the opisthonotum is carinated but not plicate; this presumed loss of plication may be linked with the apopheredermous character (I2), a phenomenon of immature Oribatellidae, where the scalp of the proceeding juvenile stage remains on the notogaster after moulting up to the tritonymph (Grandjean 1954); remaining scalps on the opisthosoma has been reported by Behan-Pelletier (2001) for *Tegoribatibates americanus*. But as far I know, all other species of Tegoribatidae do not bear any juvenile scalps and are thus apopheredermous (Grandjean 1954). In apopheredermous species, the scalp is not closely fixed to the respective stage but attached with a distance only with more or less specialized notogastral setae *da* (I6a) (cf. *Oribatella canadensis* in Behan-Pelletier and Eamer 2010) whereas in some nonporonotic families of so-called eupheredermous Brachypylina the scalps are fixed with a special secretion-stick ("la tache Z" of Grandjean 1965a).

Plicate integument of immatures is apparently a plesiomorphic state of the Poronota (Norton and Behan-Pelletier 1986) which is still present

in some nonporonotic Brachypylina families (e.g. Cymbaeremaeidae, Ameronothridae, Tectocephidae, Eremaozetidae, Limnozetidae, Hydrozetidae). Therefore the absence of opisthonotal plication (I1a) in Oribatellidae is regarded as apomorphic. The carinate lateral border of the flattened opisthosomal dorsum (I3) can be observed in the Scutoverticidae (Licneremaeoidea) and in the nonporonotic Tectocephidae. Therefore the carinate opisthosoma is regarded as plesiomorphic.

The **humeral organ of immatures** (coded as I4) mostly is a papilliform porose organ ('humeral vesicle', Norton *et al.* 1997: 10), an invaginated sacculus with the central part evaginated to the surface in some superfamilies of higher Poronota. Exceptionally, the humeral organ is a porose area in immature *Ceratozetoides* (Behan-Pelletier and Eamer 2009). Within the early-derivative Poronota, the humeral organ is present only in the Oribatelloidea (if as presumed, the Oribatellidae do not belong to the higher Poronota).

The homologous structure of adults is the humeral porose area *Ah* in the same humeral position, one porose area of the humerosejugal series, as discussed in Norton *et al.* (1997), who report the existence of *Ah* already in some poronotic Licneremaeoidea (*Passalozetes*, *Adhaesozetes*). The appearance of the humeral organ in immatures of Poronota (Oribatellidae, Ceratozetoidea, Galumnoidea) but never in immatures of poronotic representatives of Licneremaeoidea (sensu Norton and Behan-Pelletier 2009) is therefore presumed as an apomorphic character of the stem species of early-derivative and higher Poronota – possibly a caenogenetic character transformed from the porose area *Ah* of the adults (cf. Norton and Alberti 1997: 132, 134); and it is re-transformed within the ontogenetic development to the adult from a sacculus-like structure to a porose area, following this argumentation. Exceptionally, for adults of Poronota, e.g. in some species of *Eupelops* a humeral vesicle (see Norton *et al.* (1997: 10/11), in *Ceratozetes* and *Ceratozetoides* (see Behan-Pelletier and Eamer 2009: 296) a sacculus instead of porose area *Ah* is reported. This fact indicates the morphogenetic ability in early-derivative Poronota to express both homologous phenotype

FIGURE 2: (a) – Habitus of an achipteriid nymph with plicate integument; (b-o) – different types of the lamellar complex: (b) – short basal type of a lamellar complex of *Poronota*, schematic; (c) – enlarged type, schematic; (d) – basal type in *Austrachipteria*, *A. grandis*; (e) – *Achipteria* type; (f) – *Cerachipteria* type; (g) – *Oribatella reticulata*, with translamella; (h) – *Oribatella quadricornuta*, with median dens; (i) – *Anachipteria sacculifera*; (k) – *Unduloribates undulatus*; (l) – *Propelops canadensis*; (m) – *Peloptulus* type; (n) – *Eupelops* type; (o) – *Tegoribates* type. (a: after Seniczak 1977; d: after Hammer 1967; i: after Root *et al.* 2008; l: after Norton and Behan-Pelletier 1986; f-h, k, m-o: after Weigmann 2006)

FIGURE 3: Notogastral characters of Poronota. (a) – sacculus in transection and dorsal aspect, schematic; (b) – porose area in transection and dorsal aspect, schematic; (c) – setation pattern of the unideficient type (15 pairs); (d) – setation pattern of the multideficient type (10 pairs); (e) – porose areas (*Aa*, *A1*–*A3*) of the octotaxic system on a multideficient notogaster; (f) – pattern of porose areas and setae of the *Eupelops* type.

character states, and secondly it indicates the existence of genetic information which normally transforms a sacculus-like organ of the immatures into a porose area of the adults. If a humeral organ is present in the immatures of a species, the adult always possesses *Ah*, in the form of a porose area or 'vesicle' (Norton and Alberti 1997: 134).

The **notogastral setation** of the nymphs of poronotic Brachypylyna is unideficient (coded as I5), i.e. regularly there are 15 pairs of setae with more or less equal shape (I6) which are plesiomorphic states of Poronota, as observable in most Brachypylyna.

Characters of adults

Prodorsal characters (P1–P7)

The **lamellar complex** (P1–3) of Poronota is highly diverse as it is in nonporonotic Brachypylyna. A

likely groundplan (figure 2b) includes the presence of the lamella (*lam*) with protruding cusp (*cus*), at the anterior part of the cusp bearing the lamellar seta (*le*), the cusps basally connected by a translamella (*trl*). Lamella with cusp and translamella are blade-like structures, which can be reduced to a carinate line or which can be lost totally. In most early-derivative Poronota, especially the **cusp of the lamella** is large and broad, protecting most of the lateral and anterior parts of the prodorsum, whereas in most representatives of higher Poronota the cusp is distinctly smaller (most Ceratozetoidea) or even lost (Galumnoidea, diverse Oripodoidea).

The correspondence of cusp types (P1–P1e in Tab.1) to systematic groups is somewhat speculative; nevertheless, I try to present a possible trend of phylogenetic polarity of cusp types. The pre-

sumed plesiomorphic character state of the cusp (code P1; figure 2b), developed moderately sized with more or less triangular shape, is present e.g. in some poronotic Licneremaeoidea (Scutoverticidae) and in higher Poronota (several Ceratozeitoidea). As apomorphic stem species character of early-derivative Poronota (cf. figure 2d,g,h) a broad lamella with a long, broad cusp, distally with a lateral and a medial tooth (P1a) is presumed, forming a rounded indentation in between, bearing the lamellar seta centred at the distal margin of the cusp (P3, plesiomorphic), with a short **translamella** (P2, plesiomorphic). In each superfamily of early-derivative Poronota we find representatives with a short and backwards convex translamellar edge or line (Oribatelloidea: *Oribatella*, *Ophidiotrichus*, *Tectoribates*; Achipterioidea: some *Austrachipteria*; Phenopeloidea: *Unduloribates*, *Eupelops*, *Peloptulus*; cf. figures 2d,g,k,n). This special translamellar shape is presumed additionally as stem species character of early-derivative Poronota, but the evidence is not strong because of uncertain phylogenetic relationships within Oribatellidae and Achipteriidae.

Most species of Oribatellidae have this lamellar cusp type distally with lateral and medial teeth, with the lamellar setae centred (codes P1a, P3; figures 2g, h). This pattern is present also in several *Austrachipteria* species (Achipteriidae), and therefore it is proposed as stem species character of the clade Oribatelloidea+Achipterioidea (figure 4). Several *Oribatella* species have a basally rounded interspace between the cusps, with a distinct short translamellar blade or only a translamellar ridge (plesiomorphic character state as coded P2; figure 2g); but in a group of species, we observe a median dens instead of the translamella, regarded as intrageneric apomorphic character state (code P2b; figure 2h). A similar median dens in some Liacaridae (Gymnonota) is regarded as convergent). Other oribatellid genera, as *Tectoribates* and *Ophidiotrichus*, differ in cusps being basally fused (code P2c), a character state which is presumed to be convergent to similar conditions in some Achipteriidae.

Within the species-rich genus *Austrachipteria* (cf. Balogh and Balogh 2002) we find a high diversity of

the lamellar complex with regard to the distal teeth (partly present: P1a; partly lost: P1c), the position of the lamellar seta (partly centred: P3; partly medial: P3a) and the translamellar structure (partly complete: P2; partly interrupted: P2a), which might be explained by phylogenetic radiation of this mainly Australian genus, which needs revision. In several achipteriid genera the medial tooth of the cusp is lost whereas the lateral tooth is still present (P1b), and the lamellar seta is positioned on the medial edge of the cusp (P3a); this configuration is presumed to be derived within Achipteriidae, e.g. in *Anachipteria*, *Achipteria*, *Parachipteria*. Most representatives of these three genera (and others) have basally fused cusps instead of a translamella (P2c), a character state which is regarded as derived and synapomorphic for these genera. But there are exceptions within some genera: e.g. *Anachipteria sacculifera* Root, Kawahara et Norton, 2008, has a short translamella which can be presumed as plesiomorphic (P2) and a regressive character state as it is present in the hypothetical stem species of the family. *Anachipteria geminus* Lindo, Clayton and Behan-Pelletier, 2008, shows separated cusps without translamella (P2a), which is observed also in few *Austrachipteria* (see above) and which is characteristic also for the genus *Cerachipteria*: this character state is presumed as convergent in the genera.

Also for the stem species pattern of Phenopeloidea, the plesiomorphic character state with large lamellar cusp and distal teeth is presumed (P1a), with a lamellar seta centred on the distal margin (P3), because this configuration is observed in three of five *Unduloribates* species; a different lamellar cusp with scarcely indented anterior margin and without distinct lateral and medial teeth (P1c) is present in *U. undulatus* (Berlese, 1914); *U. hebes* Aoki, 1965, lacks any indentation and teeth, a character state regarded as apomorphic within *Unduloribates*. In all genera of Phenopelopidae, the lamellar seta is inserted on the ventral side of the cusp (P3b). In *Propelops* and *Peloptulus* the lamella remains broad and the cusp long (figures 2l-m); in *Eupelops* we find an apomorphic size reduction, a narrow lamella and mostly a small cusp (P1e; figure 2n). Norton and Behan-Pelletier (1986) hypoth-

esize this reduction in context with the extremely enlarged interlamellar setae in *Eupelops*, which instead of the lamella can protect the retracted legs I.

As an apomorphic character state of the lamellar complex, in most Tegeribatidae the cusps are totally fused in the medial area as a shield covering the prodorsum, with the lamellar setae at the anterior margin (P1d; figure 2o).

Some other characters of the prodorsal shield are of phylogenetic interest. The **tutorium** (*tut*; code P4) is a lateral blade on the prodorsum, which likely protects legs I and II, when withdrawn to the body surface. This structure is present in several nonporonotic Brachypylna and therefore is a plesiomorphic character of all early-derivative Poronota. It is partly or fully reduced in Licneremaeoidea and some higher Poronota. Most Poronota have a **genal tooth** on the lateral edge of the prodorsal shield (P5) behind a short oblique incision. This structure is regarded as a plesiomorphic character of the stem species of the early-derivative Poronota, modified differently as independent apomorphic character states (i) in Unduloribatidae as an abnormal narrow incision with no genal tooth (code P5a) (Norton and Behan-Pelletier 1986); (ii) in Tegeribatidae (lack of any incision; code P5b) (Behan-Pelletier 2001); (iii) in *Peloptulus* (Phenopelopidae) where the genal tooth is associated with the tutorium (code P5c) (described by Norton and Behan-Pelletier 1986). Most early-derivative Poronota share spiral thickenings in the **bothridium** (P6) with Scutoverticidae and some nonporonotic Brachypylna (Behan-Pelletier, pers. comm.); therefore this character is plesiomorphic for its stem species. But there is a convergent reduction (P6a) in Tegeribatidae and Oribatellidae (cf. Norton and Behan-Pelletier 2009).

Opisthonotal and humeral characters

In Brachypylna, the adults have at most 15 pairs of **notogastral setae** (figure 3c; 'unideficient': i.e. the 16th seta f_1 present in "lower Oribatida" is lost normally in Brachypylna), apart from few exceptions. But in many families of non-poronotic and poronotic Brachypylna (= Poronota) we can observe similar reductions of setae, often regarding

the centrodorsal setae da , dm and dp and the anterior setae c_1 and c_3 (Grandjean 1934, 1949; cf. Seniczak *et al.* 1990) giving 10 pairs of setae (figure 3d-f; 'multideficient'). In poronotic Brachypylna, the superfamilies Ceratozetoidea and Oripodoidea of the higher Poronota include both unideficient and multideficient taxa. Seniczak *et al.* (1990) described for the ceratozetid genera *Melanozetes* and *Fuscozetes* different degrees of setal loss within the genera and also "great lability of setae da and dm in *F. setosus*". Thus, the phenotypic expression of some notogastral setae in adults can be blocked in species or even individuals. All superfamilies of the early-derivative Poronota have generally unideficient adults (i.e. plesiomorphic with 10 or 11 pairs of notogastral setae: code O1). Two extreme exceptions with more than this setation (O1a) shall be mentioned here. (i) *Oribatella bromeliarum* Behan-Pelletier and Paoletti, 1993, from forests in Venezuela, has 15 pairs of notogastral setae, the additional setae da , dm , dp , c_1 and c_3 , as compared with the normal adult oribatellid setation, are in the same positions as in other unideficient taxa of Poronota and in the same positions as in the normally unideficient nymphs of most Poronota. For this species and two further *Oribatella* species, Subías (2004) proposed a new subgenus *Multioribatella*. (ii) The second exception is a population of an unnamed *Eupelops* species from France, partly with normal notogastral setation of 10 pairs, partly with increased setation up to 15 pairs (Lions 1970); all additional setae are the same as the additional ones in *O. bromeliarum* and in the same positions. There is no other species in Phenopeloidea or in Achipterioidea with more than 10 pairs of notogastral setae in the adults. Such phenomena of unusually high setation in multideficient Poronota species are discussed by Weigmann (2010) for genera of Scheloribatidae and others, hypothesized as atavistic appearance of these setae, which have been present normally in adults of unideficient ancestor species and whose morphogenetic disposition is still present cryptically in multideficient species (see discussion below); this cryptic presence in adults is a fact because their nymphs have generally all 15 pairs of notogastral setae. The loss of notogastral setae p_2 and p_3 in adult *Peloptulus*, resulting in 8 pairs of se-

tae only, is a special apomorphic character of the genus (O1b).

Porose integumental organs of oribatid mites with respiratory or secretory functions in diverse body parts (compiled in Alberti and Norton 1997) probably are developed as porose areas (figure 3b), primarily. From case to case in several oribatid taxa, these organs are represented as saccules which are invaginated porose integumental organs with a narrow opening to the surface (figure 3a). We know little about the compounds and the functional aspects of the secretory porose glands. But we can imagine a functional reason for the character state of secretory porose organs: gelatinous or semi-fluid secretates may be excreted better by superficial porose areas, fluid or volatile secretory compounds better by saccules (see Alberti *et al.* 1997: figures 14, 15). I propose that both morphological types of secretory porose organs are predisposed genetically in poronotic Oribatida (= Poronota), from case to case a species or higher taxon may express either saccules or porose areas.

The monophyletic group of Poronota is characterized by the '**octotaxic system**' (Grandjean 1954) on the notogaster of adults, represented by four pairs of porose organs of unsolved phylogenetic or epigenetic origin (Norton and Alberti 1997). From a phylogenetic view, the octotaxic system is firstly developed in adult poronotic representatives of Licneremaeoidea as a series with maximally four pairs of gastronomic secretory organs. The octotaxic system is likely represented by porose areas (O5a), being an apomorphic character state of the stem species of early derivative Poronota (Weigmann 2010) in contrast to saccules as plesiomorphic character state (O5) in an assumed licnodamaeoid ancestor (Norton and Alberti 1997). There are arguments for this proposed phylogenetic polarity of the octotaxic character states in Poronota:

(1) Within some superfamilies of Poronota both character states of the octotaxic system are represented, either as saccules or porose areas (poronotic Licneremaeoidea, Achipterioidea, Oribatelloidea, Ceratozetoidea, Oripodoidea). In some families or genera the presence of saccules is exceptional (e.g. in *Trichoribates*, *Peloptulus*, *Anachipteria*; see below;

cf. Norton and Alberti 1997). It is hard to assume multiple convergent evolution of sacculiform octotaxic organs from superficial porose areas, or the other way round. Thus we can assume a basic morphogenetic ability to develop both character states or even to reduce the octotaxic system from case to case (in 'gymnonotic' Poronota, in the terminology of Balogh 1972).

(2) The asymmetric presence of a single saccule, as described by Weigmann (2010) in an abnormal specimen of *Peloptulus phaenotus* (C. L. Koch, 1844) with porose areas in all other octotaxic positions, demonstrates the ability of the octotaxic system to find its expression as well in porose areas as in saccules. The abnormal occurrence of a saccule must be atavistic and thus the plesiomorphic character state. Also the exceptional species *P. sacculiferus* Weigmann, 2008, the single known representative with saccules in all octotaxic positions within the species-rich family Phenopelopidae, confirms the presumption of a cryptic genetic disposition in taxa with porose areas to develop notogastral saccules.

In conclusion, these and similar phenomena of exceptional saccules within a genus or family of Poronota are explainable by an appearance of the regressive and atavistic character state with saccules (code O5), i.e. the respective plesiomorphic character state of a hypothetical ancestor, the presumed Poronota stem species within Licneremaeoidea.

Within Phenopelopidae, the porose areas of the octotaxic systems are associated with notogastral setae each (O6a), which can be regarded as apomorphic character of the family; the details are discussed below in the section on the familial and generic characters. Another family-typical character is a protruding anterior **notogastral tectum** (O3a) which likely is evolved convergently in genera of Mycobatidae (Ceratozetoidea). A thick, blocky, birefringent **cerotegument** (O7a) is an apomorphic character of Phenopelopidae (Norton and Behan-Pelletier 1986).

The **pteromorphs** are more or less large humeral blades of the notogaster in Poronota, which serve as protection for retracted legs III and IV. These structures seem to be preformed in several non-

poronotic families of Brachypylina with smaller humeral protuberances whose homology with pteromorphs is questionable. Poronotic families within Licneremaeoidea lack this structure, which occurs in all other superfamilies of Poronota and therefore may be regarded provisionally as apomorphic character of the early-derivative Poronota stem species (code O4) which is secondarily reduced in some derived taxa. Families with distinct pteromorphs but without octotaxic system, as Limnozetestidae and Microzetidae, are regarded as non-poronotic Brachypylina (Norton and Behan-Pelletier 2009); the systematic position of these families is not clearly solved. In several lines of Poronota pteromorphs are hinged (O4a; figure 3f) with the ability to move (for better protection of legs?). There are no good arguments to reject the presumption of convergently movable pteromorphs; but the moving-mechanisms and hinge structures are not studied sufficiently in detail to propose a phylogenetical implication.

Gnathosomal characters

The **chelicera** in Poronota is normally of chelate-dentate type (code G1; as in most Oribatida). A specialized forceps-like chelicera ("pelopsiform": G1a) can be found in the phenopelopid genera *Eupelops* and *Peloptulus*, but not in *Propelops*, as discussed in detail by Norton and Behan-Pelletier (1986). This apomorphic character state has been evolved within the family and not as basal familial stem species character.

Two further gnathosomal characters seem to be typical for Poronota: (i) the so-called **double-horn on the palpal tarsus**, which is formed by attachment of the palpal eupathidium *acm* with a solenidion; (ii) an **axillary saccule of the subcapitulum** at the base of the palp. Both characters can be observed in Licneremaeoidea (e.g. in Dendroeremaeidae, cf. Behan-Pelletier *et al.* 2005) and therefore are regarded as plesiomorphic stem species characters (G2a; G3) of early-derivative Poronota. Norton and Behan-Pelletier (1986) presented an overview on the distribution of the axillary saccule within Poronota: it is present in all superfamilies but Achipterioidea and Oripodoidea, where the axillary saccule is regarded as lost (G3a) secondarily and convergently.

Ventral characters

Poronota have evolved a **discidium with custodium** latero-ventrally between the insertions of legs III and IV. The discidium is a small longitudinal blade, often with an acuminate anterior tip, the custodium (the latter reduced in some derived taxa). These structures are absent in all Licneremaeoidea (Norton and Behan-Pelletier 2009), but a discidium is present within all other superfamilies of Poronota. We can regard the discidium with custodium as apomorphic stem species character of the early-derivative Poronota. A **postanal porose area** seemed to be a typical character of Ceratozetidae, but it has been found also in Tegeribatidae, Galumnoidea and partly in Oribatelloidea (Norton and Behan-Pelletier 1986, 2009; Behan-Pelletier 2001; Behan-Pelletier and Eamer 2010); these authors report its absence in Scutoverticidae (Licneremaeoidea), in Phenopelopodoidea, Achipterioidea and Oribatulidae (Oripodoidea), but in Dendroeremaeidae (Licneremaeoidea) it is present (Behan-Pelletier *et al.* 2005). The mosaic-like occurrence in poronotic families indicates in all probability a first apomorphic character evolution in poronotic Licneremaeoidea; in the stem species of early-derivative Poronota it is plesiomorphic (V2) and the disappearance (V2a)- e.g. in Achipterioidea and Phenopelopodoidea – is probably convergent. Nearly all representatives of early-derivative Poronota have six pairs of **genital setae**, regarded as the plesiomorphic number. Within the genus *Unduloribates*, some species show an apomorphic increase of up to 10 pairs of genital setae (Behan-Pelletier and Walter 2009).

Characters of legs

The chaetotaxy of the **legs** is very complex in oribatid mites and is subject of several general publications (e.g., Grandjean 1940, 1942, 1946a) and of publications regarding systematics of Poronota (especially in the context of this contribution: Norton and Behan-Pelletier 1986, 2009; Behan-Pelletier 2001). As outlined in the theoretical section of this contribution, chaetotaxic characters of legs often show serial homology. As an example cited from Behan-Pelletier and Walter (2009) for *Undu-*

loribates diana: Setae *l''* on genu and tibia of leg II are spine-like and similar in shape – a serial homology in segments; Setae *l'* on genu and tibia of leg IV also are spine-like and similar in shape and therefore regarded as mutual serial homology (but different in shape from non-homologous setae *l''* of leg II). The spine-like seta *l'* of tibia IV is used as argument for systematic relations between Unduloribatidae and Phenopelopidae (see also Norton and Behan-Pelletier 1986) and is regarded as apomorphic character state (L3a). Similar spine-like setae on tibia IV have been observed in *Hypozetes* and a *Lepidozetes* sp. (Tegoribatidae; Behan-Pelletier 2001), in *Oribatella quadridentata* (Oribatellidae; own observation), but neither in Achipteridiidae (Behan-Pelletier 2001) nor in *Lepidozetes singularis* (Tegoribatidae; own observation). We need information on seta *l'* of tibia IV of more species of early-derivative Poronota for a phylogenetic evaluation of this character state.

Norton and Behan-Pelletier (1986) discuss a special character for the **tibia IV** in Phenopelopidae and related families, specifically: "The most distinctive leg character of the Phenopelopidae is the very unusual absence of solenidion Φ on tibia IV (Grandjean 1936, 1964) and the presence of seta *d* on the same segment. Typically this solenidion is present and seta *d* is absent, as in both *Propelops* and Ceratozetoidea. Solenidial presence is clearly plesiomorphic and absence of *d* is probably so in these taxa, associated with solenidial-induced regression (Grandjean 1946b). The unusual presence of seta *d* in Phenopelopidae, a seta that is absent from the adult (and usually immatures) of other poronotic Brachypyliina, may involve an atavistic reversal associated with a need for at least some sensory capacity in the dorsal area of tibia IV, given the absence of solenidion Φ ." In *Scutovertex* and other Licneremaeoidea, we observe the plesiomorphic character states, on tibia IV the solenidion Φ being present (code L1) and the seta *d* absent (L2). These character states are shared by the stem species of early-derivative Poronota obviously. Within the early-derivative Poronota, the alternative character states, solenidion Φ absent (L1a) and seta *d* present (L2a) on tibia IV, are described

only for the clade *Eupelops*+ *Peloptulus* (Norton and Behan-Pelletier 1986) and for *Hypozetes* (Tegoribatidae; Behan-Pelletier 2001); the presumption of two independent atavistic reversals to the character states of a common ancestor is the best explanation.

DISCUSSION

Reconstruction of stem species patterns

The hypothetical stem species pattern of a systematic clade includes all basic apomorphic and all plesiomorphic characters of phylogenetical relevance. The reconstruction of the stem species pattern requires careful evaluation of the character states of the members of the clade as well as comparisons with presumed sister clades and ancestors. Table 2 lists the selected stem species characters of the families and higher taxa, evaluated as apomorphic or plesiomorphic character states for the respective systematic level. The cladograms (figures 4 and 5) are focussed on the respective apomorphic characters. For sister-clades, the plesiomorphic characters which correspond with the indicated apomorphic characters are presented additionally.

The stem species pattern of early-derivative Poronota (I)

There are seven apomorphic characters (I4, P1a, O4, O5a, V1, V2, L3a) which are part of the stem species pattern of the early-derivative Poronota (clade I: figure 4; tab. 2). Four of these characters are regarded as newly evolved (I4: the nymphal humeral organ; O4: the true pteromorphs; V1: a discidium with custodium; V2: a postanal porose area). Three of these characters (P1a: a large lamellar cusp with distinct lateral and medial tooth; O5a: an octotaxic system on the notogaster with four pairs of porose areas; L3a: a spine-like thick seta *l'* on tibia IV) are present in apomorphic states each in the hypothetical stem species of all early-derivative Poronota and their plesiomorphic homologies can be found in the presumed ancestor taxon Licneremaeoidea. All relevant plesiomorphic character states of the early-derivative Poronota are listed in table 2 (for codes see table 1).

TABLE 2: Stem species patterns in systematic groups of early-derivative Poronota. I: Characters of immatures; – P: prodorsal characters; – O: Opisthonotal and humeral characters; – G: Gnathosomal characters; – V: Ventral characters; – L: leg and pedotectal characters. – For code numbers see Table 1, for stem species relations figure 4.

Stem sp. I: early-derivative Poronota						
Apomorphic:	I:4	P:1a	O:4,5a		V:1-2	L:3a
Plesiomorphic:	I:1-3,5-6	P:2-7	O:1-3,6-8	G:1-3	V:3	L:1-2,4
Stem sp. II						
Apomorphic:						
Plesiomorphic:	I:1-6	P:1a,2-7	O:1-4,5a,6-8	G:1-3	V:1-3	L:1-2,3a,4
Stem sp. III: Phenopeloidea						
Apomorphic:	I:4a		O:2a,3a,7a		V:2a	
Plesiomorphic:	I: 1-3,5-6	P:1a,2-7	O:1,4,5a,6,8	G:1-3	V:1	L: :1-2,3a,4
Stem sp. IV: Achipterioidea						
Apomorphic:	I:4a					
Plesiomorphic:	I: 1-3,5-6	P:1a,2-7	O:1-4,5a,6-8	G:1-3	V:1-3	L:1-2,3a,4
Stem sp. V / VI: Oribatelloidea / Oribatellidae						
Apomorphic:	I:1a,2a,6a	P:6a				
Plesiomorphic:	I:3-5	P:1a,2-5,7	O:1-4,5a,6-8	G:1-3	V:1-3	L:1-2,3a,4
Stem sp. VII: Achipteriidae						
Apomorphic:				G:3a	V:2a	
Plesiomorphic:	I:1-3,4a,5-6	P:1a,2-4,6-7	O:1-4,5a,6-8	G:1-2	V:1,3	L:1-2,3,4
Stem sp. VIII: Tegeribatidae						
Apomorphic:		P:5b,6a				
Plesiomorphic:	I:1-3,4a,5-6	P:21a,-5,7	O:1-4,5a,6-8	G:1-3	V:1-3	L:1-2,3a,4
Stem sp. IX: Unduloribatidae						
Apomorphic:		P:5a	O:5b			
Plesiomorphic:	I:1-3,4a,5-6	P:1a,2,3,4,6-7	O:1,2a,3b,4,6,7a,8	G:1-3	V:1,2a,3	L:1-2,3a,4
Stem sp. X: Phenopelopidae						
Apomorphic:		P:3b	O:4a,6a,6b			L:4a
Plesiomorphic:	:1-3,4a,5-6	P:1a,2,4-7	O:1,2a,3a,5a,7a,8	G:1-3	V:1,2a,3	L1-2,3a

The higher Poronota, with the superfamilies Ceratozetoidea, Galumnoidea and Oripodoidea, are not analysed explicitly within this study. They likely share some stem species characters with the early-derivative Poronota and thus are suspected to be a sister taxon. But until further research, the systematic relationship remains unsolved and will be discussed only in context of the stem species pattern of Oribatelloidea in the following.

The stem species pattern of the Oribatelloidea+Achipterioidea clade (II)

This clade II of early-derivative Poronota has no autapomorphies and thus is regarded as more similar to the hypothetical stem species of early-derivative Poronota in relation to the sister-clade Phenopeloidea (III) which in contrast is characterized by several autapomorphic stem species characters. The apomorphic character states of early-derivative Poronota remain characteristic for this clade (II), characters which are regarded as inherited plesiomorphic character states on this systematic level.

The stem species pattern of the Phenopeloidea (III)

Five autapomorphic character states define this clade (III) - I4a: absence of the humeral organ in immatures; O2a: notogaster without posterior tectum; O3a: presence of a distinct anterior tectum of notogaster; O7a: a thick conspicuous, birefringent, cerotegument layer on notogaster; V2a: absence of the postanal porose area.

The stem species pattern of the Achipterioidea (IV)

There is only one apomorphic stem species character (I4a) but three plesiomorphic characters (I1, I2, I6) of this superfamily (clade IV) in contrast with the Oribatelloidea (clade V) as presumed sister-taxon. The character I4a (absence of the humeral organ in immatures) is not an argument of high importance because it is a loss, which also occurs in Phenopeloidea and other clades. Nevertheless, the lack of the apomorphic stem species char-

acters of Oribatelloidea supports the differentiation of both superfamilies.

The stem species pattern of the Oribatelloidea (V, VI)

The Oribatelloidea includes only Oribatellidae as sole family. In this passage and in figure 4 those characters with corresponding differences in Achipterioidea are regarded as superfamilial characters (V) and other characters, corresponding with differences either in Achipteriidae or Tegoribatidae, are indicated as familial characters (figure 4: stem species pattern VI) which all are plesiomorphic, but the apomorphic character state P6a, spiral thickenings of bothridium reduced (Norton and Behan-Pelletier 2009). The characteristic features of the Oribatelloidea (clade V) refer to characters of the immatures, which are unique within Poronota as well as within the other Brachypylina: the plesiomorphic character I4, the apomorphic character states I1a, I2a and I6a. The latter three characters may be correlated with each other: the opisthonotum without plication (I1a) may be caused by the apopheredermous character (I2a) bearing a scalp on the dorsal surface, which is fixed in some distance by specialized notogastral setae *da* (I6a).

The presence of the humeral organ (I4) in oribatellid immatures is exclusive within early-derivative Poronota, but the organ is found also in Galumnidae and in most Ceratozetoidea, both belonging to the higher Poronota. This may be a good argument for considering Oribatelloidea one of the higher Poronota superfamilies (Norton and Alberti 1997: 124). The facts are ambiguous; as reported above in the passage on the humeral organ, this is homologous with the humeral porose area *Ah* of adult Poronota, which first evolved in poronotic Licneremaeoidea, from which both groups, the early-derivative Poronota and higher Poronota, likely descend. The porose area *Ah* as well as the homologous realization in immatures is most likely a stem species character of the both Poronota groups.

However, Oribatelloidea show characters which are not present in higher Poronota: (i) the carinate immatures (I3), (ii) the lack of any opisthono-

FIGURE 4: Cladogram with stem species (I-X) and their characteristic apomorphies, plesiomorphies and regressive plesiomorphies of the families of early derivative Poronota. – Explanation of codes in table 1; – ‘div.’: diverse more plesiomorphies listed in table 2.

tal sclerites or plates in immatures which are typical for Galumnoidea and Ceratozetoidea, (iii) the large lamellar complex with a lateral and a medial tooth, which is not present in that configuration in higher Poronota. The ambivalence of the morphological characters requires more phylogenetic studies for a conclusive answer on the systematic position of Oribatelloidea. Unfortunately molecular data are also inconclusive: Maraun *et al.* (2004) clustered several oribatid species, basing on data of the D3 region of the 28S rDNA, and they found different positions of *Oribatella*, depending on the clustering method: in one case *Oribatella* species clustered near *Eupelops* species, in another case *Oribatella* near *Galumna* (Galumnoidea), in both cases achipteriid species were distant from other Poronota. Based on the ribosomal 18S region, Domes *et al.* (2007) found a close relationship of *Achipteria* with *Eupelops* (*Oribatella* was not included in this analysis).

The stem species pattern of the AchipterIIDae (VII)

The family AchipterIIDae (clade VII) is well separated from its sister-taxon Tegoribatidae (clade VIII) by two apomorphic character states (G3a, V2a) and six plesiomorphic character states (P1a, P3, P5, P6, O4, L3). The loss of the axillary saccule of the subcapitulum (G3a) is unique within the families of early-derivative Poronota; the absence of the postanal porose area (V2a) in AchipterIIDae contrasts with its presence in Tegoribatidae, and therefore the loss is regarded as homoplasious with that in Phenopelopoidea and some Oribatellidae (cf. Norton and Behan-Pelletier 2009). The plesiomorphic character states concerning the lamellar complex, P1a (cusp of lamella large with a lateral and a medial tooth), and P3 (lamellar seta *le* centred at distal margin of the cusp) are basal characters within the family as found in some *Austrachipteria* (figure 2d), and this character state is modified in some more derived genera, as *Anachipteria*, *Achipteria*, *Parachipteria* and others, to the configuration P1b (cusp large, asymmetric with lateral tooth only) and P3a (lamellar seta at the medial margin of the cusp). In consequence, this commonly known 'typical lamellar complex' of AchipterIIDae (figure 2e) is

an apomorphic one within the family (see also respective section on prodorsal characters above).

The stem species pattern of the Tegoribatidae (VIII)

The family conception became complicated with the inclusion of *Hypozaetes* Balogh, 1959, as a member of Tegoribatidae by Behan-Pelletier (2001) based on some convincing arguments. *Hypozaetes* lacks characters which so far have been regarded as familial characteristics, especially the undivided large shield above the prodorsum, formed by the fused lamellar cusps in all other genera. Behan-Pelletier (2001) discussed several characters of *Hypozaetes* and possible relations but did not offer a phylogenetic cladogram for the family. The unique occurrence of the undivided prodorsal shield (P1d; figure 2o) in all genera of Tegoribatidae but *Hypozaetes* is most likely an autapomorphy within the family (e.g. in *Lepidozaetes*, *Tegoribates*, *Scutozaetes*) and therefore no basal stem species character. The lamellar complex of *Hypozaetes* is similar to that of several Ceratozetoidea, with moderately sized lamella and lamellar cusp, which is triangular, bearing the lamellar seta centred and distally (cf. figure 2b; codes P1, P3), with or without translamella in the species. This type of lamellar complex is not like that postulated within this study as characteristic for the stem species of Achipterioidea, with large cusps and lateral and medial tooth (cf. figure 2d; code P1a). It is open for speculations whether the lamellar complex of *Hypozaetes* is an apomorphic character state of the genus, homoplasious with the ceratozetoid type, or an atavistic regression to the plesiomorphic character state of basal Poronota. As a precaution, the first alternative is preferred with the consequence that the plesiomorphic character state of the lamellar complex within Achipterioidea (P1a in the cladogram figure 4) remains a stem species character of Tegoribatidae.

There are two stem species characters regarded as apomorphic (P5b, P6a) and five character states as plesiomorphic (P1a, P3, O4, G3, V2, L3a) for the whole family, in contrast with the respective character states in AchipterIIDae (figure 4). The absence of the genal incision (P5b) is unique within early-

FIGURE 5: Cladogram with selected characters and species of *Eupelops* and *Peloptulus*. – Explanations see figure 4.

derivative Poronota. The loss of spiral thickenings in the bothridium (P6a) is regarded as homoplasious with the same character in Oribatellidae and as an apomorphic character state; spiral thickenings are still present in poronotic Licneremaeidae (*Scutovertex*) and in most early-derivative Poronota. The immovable pteromorphs (O4) in *Hypozetes* is a plesiomorphic stem species character shared with Achipteridae and Oribatellidae, whereas the movable pteromorphs (O4a) in most other genera of Tegoribatidae is presumed a synapomorphic character, homoplasious in Phenopelopidae and several taxa in higher Poronota.

The stem species pattern of the Unduloribatidae (IX)

The family is well-founded as member of Phenopeloidea (Norton and Behan-Pelletier 1986). Within this study, two apomorphic character states (P5a, O5b) and three plesiomorphic character states (P3, O4, L4) are relevant in contrast with

Phenopelopidae (figure 4). The small genal incision without the genal tooth (P5a) is a unique character, whereas the loss of the octotaxic system on the notogaster occurs in some poronotic taxa convergently (Norton and Alberti 1997). The plesiomorphic stem species character state (P1a), cusp with lateral and medial tooth, is modified in some *Unduloribates* species, as discussed in the section on the prodorsal characters above.

The stem species pattern of the Phenopelopidae (X)

The family includes three well-known genera, and the phylogenetic relationships are analysed by Norton and Behan-Pelletier (1986), as partly interpreted in figure 4. Five apomorphic (P3b, O4a, O6a, O6b, L4a) and two plesiomorphic stem species character states (P5, O5a) define the family in contrast with Unduloribatidae (figure 4). The lamellar seta is inserted at the ventral side of the cusp (P3b), which is regarded as a stem species character as

also the movable pteromorph (O4a) and the association of each octotaxic organ with at least one notogastral seta (O6a). All the three genera, *Propelops*, *Peloptulus* and *Eupelops*, have different configurations of the lamellar complex (figure 5), presumed to be evolved independently, and therefore the plesiomorphic cusp type (P1a) is presumed for the stem species pattern of the family, having no better arguments. As basal stem species character – present in *Propelops* and some *Eupelops* species, the association of the porose area A_1 with both setae lp and h_3 is postulated (O6b; figure 3f). The large pedotectum I has a transversal carina (L4a), an autapomorphic character of all Phenopelopidae.

Characters of the genera. The basal genus *Propelops* has one apomorphic (P1c) and seven plesiomorphic character states (P5, P7, O1, O6b, G1, L1, L2) compared with the sister-taxon Phenopelopinae (*Eupelops* + *Peloptulus*), which was established by Norton and Behan-Pelletier (1986). In *Propelops*, the lamellar cusp is broad, without a lateral and a medial tooth (P1c). The Phenopelopinae stem species is mainly characterized by the apomorphic pelopisiform chelicerae (G1a) and also by a loss of the solenidion Φ (L1a) on tibia IV, instead of which the setae d is present (L2a): Following the presumption of Norton and Behan-Pelletier (1986), the presence of solenidion Φ suppresses the seta d at the same dorsal position on tibia IV, and the loss of solenidion Φ may involve an atavistic reversal of seta d , which clearly must be a reactivation of a previously suppressed genetic information.

Apomorphic stem species character states of *Eupelops* are: a small, acuminate lamellar cusp (P1e) and a very large and broad interlamellar seta (P7a; see figure 5). Apomorphic stem species character states of *Peloptulus* are: A large asymmetric lamellar cusp (P1b; the similarity with some Achipteridae is regarded as homoplastic), association of the genital tooth with the tutorium (P5c), loss of the notogastral setae p_2 and p_3 in adults (O1b), the association of the porose area A_1 with the notogastral seta h_3 (O6d).

Regressive and homoplasious characters in selected genera and species

Genera of Phenopelopidae

The octotaxic system in *Peloptulus* species is present as porose areas (O5a) as it is in Phenopelopidae, generally. But in a single species, *Peloptulus sacculiferus* Weigmann, 2008, we observe sacculi (O5; figure 5). This phenomenon is discussed in the section on 'opisthonotal and humeral characters' with the most likely explanation of a regressive plesiomorphic character state, i.e. an atavistic reversal to the character state of a basal poronotic ancestor, which had the character state of notogastral sacculi.

In *Eupelops*, we know two species groups with different notogastral characters regarding the association of porose area A_1 with setae: Type A, represented by *E. torulosus* (C. L. Koch, 1839) in figure 5, has the typical phenopelopid pattern as A_1 associated with lp and h_3 (O6b; see figure 3f), the plesiomorphic character state within the genus. Type B, represented by *Eupelops acromios* (Hermann, 1804) in figure 5, has an apomorphic character state as A_1 associated with lp only (O6c). Weigmann (2010) described rare specimens of *E. acromios* with an atavistic reversal on one side only to the character state (O6b), which is the evidence of the cryptic disposition to the plesiomorphic phenotype A in species from type B, normally. This and similar aberrations in poronotic Oribatida help to decide the polarity of character states.

Lions (1970) reported on a population of an unnamed *Eupelops* sp. with partly aberrant increase of the notogastral setae number up to 15 pairs, as discussed in the respective section above: this case may be another example of atavistic reversal within a family with normally 10 pairs of notogastral setae to the character state with 15 pairs (O1a) of ancestors. This plesiomorphic character state is the same as present in the nymphs of *Eupelops*, which allows an alternative hypothetical interpretation: the additional notogastral setae are normally suppressed in the adult by a special gene; if this gene is blocked the phenotypical appearance of the additional setae is reactivated. Again, we can postu-

FIGURE 6: Cladogram with selected characters and species of Achipteridae. – Explanations see figure 4.

late the cryptic disposition to express plesiomorphic characters.

Genera of Achipteridae

One of the conspicuous characters of most Achipteridae is a knife-like pointed projection on the anterior margin of the pteromorph (O9a; figure 2e); yet this is no stem species character of the family but is apomorphic for a group of some derived genera, as e.g. *Achipteridae*, *Cerachipteria*, *Parachipteria* and *Pseudachipteria*. Within the family (figure 6), the genera *Anachipteria* and *Austrachipteria* represent presumably the plesiomorphic character state of the pteromorph without such a projection (O9).

The stem species pattern of the family likely includes porose areas as character state of the octotaxic system (O5a). In both two groups of genera in figure 6, we find taxa with the octotaxic system represented as saccules (O5): in all species of *Achipteridae*, in two among several *Anachipteria* species (*A. dubia* Weigmann, 2001, and *A. sacculifera* Root, Kawahara and Norton, 2008); in most *Austrachipteria* species, wherefore saccules are presumed as stem species

character state of the latter genus. The presence of saccules of the octotaxic system in different clades of Achipteridae is regarded as independent cases of the same atavistic reversal, i.e. regressive plesiomorphic.

In both two groups of genera, we find representatives without discernible porose areas or saccules (O5b), within the *Achipteridae*-group in the genus *Pseudachipteria* (but see remark in Norton and Alberti 1997), within the *Anachipteria*-group in *Austrachipteria lamellata*. These reductions of the octotaxic organs are regarded as homoplastic.

Oribatella and *Tectoribates* (Oribatellidae)

A notogaster with 10 pairs of setae (O1) and with porose areas (O5a) is regarded as characteristic for the stem species of Oribatellidae. Whereas *Oribatella* and other genera have porose areas (O5a) without known exceptions, *Tectoribates* shows notogastral saccules instead (O5), a further case of regressive plesiomorphic (figure 7). The same is presumed for the unique species within the genus, *Oribatella bromeliarum*, with 15 pairs of notogastral se-

FIGURE 7: Cladogram with selected characters and species of Oribatellidae. – Explanations see figure 4.

tae (O1) (cf. section on 'opisthonotal and humeral characters').

GENERAL REMARKS

As a result of the stem species reconstructions, a contrast between classical family diagnoses and the stem species patterns of the early-derivative Poronota families is remarkable. Characters regarded as typical for a family evolve partly within the family as apomorphic character states and not basally in its stem species lineage. This result becomes evident e.g. by an early-derived genus with the respective character in a different and plesiomorphic state. Examples for this assessment are Phenopelopidae, Achipteriidae and Tegeribatidae.

Following the systematical analysis of Norton and Behan-Pelletier (1986), *Propelops* most likely belongs to the family Phenopelopidae. Nevertheless it has a lamellar complex different from that in *Eupelops* or *Peloptulus* and it lacks the typical 'pelopoid' chelicera which consequently cannot be a stem species character of the family neither a diagnostic character of Phenopelopidae in toto. Comparably, *Austrachipteria* does not correspond well with the typical phenotype of an achipteriid genus. Yet

Behan-Pelletier (2001) gave good reasons to shift *Austrachipteria* into Achipteriidae. In *Austrachipteria* the lamellar complex is distinctly different from that in the nominal genus *Achipteria* and others, moreover it is highly variable within the genus. Therefore the lamellar complex and the cusp character states of the *Achipteria* type cannot be regarded as unequivocal family character neither a character state of the stem species of Achipteriidae. In Tegeribatidae, the prodorsal shield formed by totally fused lamellar cusps is commonly regarded as typical familial character. But Behan-Pelletier (2001) gave several arguments to transfer *Hypozetes* into Tegeribatidae, a genus without such prodorsal shield. Therefore we can presume that this character evolved within the family and is no stem species character of Tegeribatidae.

The stem species pattern method induces a researcher in systematics to think about the polarity of character states and to make a decision for apomorphy or plesiomorphy. This is advantageous for phylogenetic systematics and taxonomy. At the same time diagnoses of taxa, e.g. genera up to superfamilies, may become more problematic. Obviously in some cases, a classification into ranked categories reflects poorly defined phylogenetic inter-

relations. This may not be a surprise when taking into account the common theoretical opinion that evolution makes only small steps, with the result that presumed 'family-typical character combinations' should evolve step by step, not being present completely in basally derived members of the family. In consequence, diagnoses of families and other higher categories may include alternative character states besides commonly known apomorphic characters (cf. Norton and Behan-Pelletier 2009).

The frequency of evolutionary reversals of homologous characters is likely underestimated, as still assumed by Hennig (1966) and as may be deduced from the examples discussed in this contribution. In cases of presumed homoplasious character states within a systematic analysis, the possibility of regressive plesiomorphies should be taken into account more often. But it is of high importance to present reasonable arguments for a proposal of a regressive atavistic character state.

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REFERENCES

- Alberti G., Norton R.A., Adis J., Fernandez N.A., Franklin E., Kratzmann M., Moreno A.I., Weigmann G., Woas S. 1997 — Porose integumental organs of oribatid mites (Acari, Oribatida). 2. Fine structure — *Zoologica*, 48: 33–114.
- Alberti G., Norton R.A. 1997 — Porose integumental organs of oribatid mites (Acari, Oribatida) — *Zoologica*, 48: 1–143.
- Ax P. 1985 — Stem species and the stem lineage concept — *Cladistics*, 1: 279–287.
- Balogh J. 1972 — The oribatid genera of the world — Budapest: Akad. Kiadó. pp. 188 + 71 tables.
- Balogh J., Balogh P. 1992 — The Oribatid mites genera of the world — Budapest: Hung. Nat. Mus. Press. vol. 1+2. p. 263, 375.
- Balogh J., Balogh P. 2002 — Identification keys to the oribatid mites of the Extra-Holarctic regions — Miskolc: Well-Press Publ. vol. 1+2. p. 453, 504.
- Behan-Pelletier V.M. 2001 — Phylogenetic relationships of *Hypozetes* (Acari: Tegeribatidae) — In: Halliday R.B., Walter D.E., Proctor H.C., Norton R.A., Colloff M.J. (Eds). *Acarology: Proceedings of the 10th International Congress*; Melbourne: CSIRO Publ. p. 50–57.
- Behan-Pelletier V.M., Eamer B., Clayton, M. 2005 — *Dendroeremaeidae* n. fam., from forest trees in Western North America (Acari: Oribatida: Licneremaeoidea) — *Acarologia*, 46 [2004]: 321–339.
- Behan-Pelletier V.M., Eamer B. 2009 — *Ceratozetes* and *Ceratozetoides* (Acari: Oribatida: Ceratozetidae) of North America — *Can. Entomol.*, 141: 246–308.
- Behan-Pelletier V.M., Eamer B. 2010 — The first sexually dimorphic species of *Oribatella* (Acari, Oribatida, Oribatellidae) and review of sexual dimorphism in the Brachypylina — *Zootaxa*, 2332: 1–20.
- Behan-Pelletier V.M., Walter D.E. 2009 — *Unduloribates* from North America (Acari, Oribatida, Unduloribatidae) — *Zootaxa*, 2294: 47–61.
- Béthoux O., Kristensen N.P., Engel M. 2008 — Henningian phylogenetic systematics and the 'Groundplan' vs. 'Post-Groundplan' approaches: a reply to Kukalová-Peck — *Evol. Biol.*, 35: 317–323.
- Carter A., Mess A. 2007 — Evolution of the Placenta in Eutherian Mammals — *Placenta*, 28: 259–262.
- Davidson E.H. 2006 — The regulatory genome: gene regulatory networks in development and evolution — Amsterdam: Elsevier Acad. Press. pp. 289.
- Dohle W. 1989 — On the problem of homology of ontogenetic structures — *Zool. Beitr. (n.s.)*, 32: 355–389. (German)
- Domes K., Althammer M., Norton R.A., Scheu S., Maraun M. 2007 — The phylogenetic relationship between Astigmata and Oribatida (Acari) as indicated by molecular markers — *Exp. appl. Acarol.*, 42: 159–171.
- Frahnert, S. and Ade, M. (2001): Why do we reconstruct stem species patterns? *Zoology, Supplement*, 4: 69.
- Futuyma D.J. 1998 — *Evolutionary biology* — 3. ed. München: Spektrum. p. 763.
- Goodman C.S., Coughlin B.C. 2000 — The evolution of evo-devo biology — *PNAS*, 97: 4424–4425.
- Grandjean F. 1934 — La notation des poils gastronomiques et des poils dorsaux du Propodosoma chez les Oribates (Acariens) — *Bull. Soc. zool. France*, 59: 12–44.
- Grandjean F. 1936 — Les Oribates de Jean Frédéric Hermann et de son père (Arachn. Acar.) — *Ann. Soc. Ent. France*, 105: 27–110.
- Grandjean F. 1940 — Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates (2e partie) — *Bull. Soc. Zool. France*, 45: 32–44.

- Grandjean F. 1942 — La chaetotaxie comparée des pattes chez les Oribates (2e série) — Bull. Soc. Zool. France, 67: 40-53.
- Grandjean F. 1946a — Les poils et les organes sensitifs portés par les pattes et le palpe chez les Oribates. 3e partie — Bull. Soc. Zool. France, 71: 10-29.
- Grandjean F. 1946b — La signification évolutive de quelques caractères des acariens (1er série) — Bull. biol. France Belg., 79: 297-325.
- Grandjean F. 1949 — Formules anales, gastronomiques, génitales et aggénitales du développement numérique des poils chez les Oribates — Bull. Soc. Zool. France, 74: 201-225.
- Grandjean F. 1954 — Essai de classification des Oribates (Acariens) — Bull. Soc. Zool. France, 78: 421-446.
- Grandjean F. 1965a — *Fosseremus quadripertitus* nom. nov. (Oribate). — Acarologia, 7: 343-375.
- Grandjean F. 1965b — Complément à mon travail de 1953 sur la classification des Oribates — Acarologia, 7: 713-734.
- Grandjean F. 1969 — Considérations sur le classement des oribates leur division en 6 groupes majeurs — Acarologia, 11: 127-153.
- Grandjean F. 1964 — La solénidiotaxie des Oribates — Acarologia, 6: 529-556.
- Hammer M. 1967 — Investigations on the oribatid fauna of New Zealand, Part II — Biol. Skr. Dan. Vid. Selsk., 15,4: 1-64, 40 Tables.
- Haumann G. 1991 — Zur Phylogenie primitiver Oribatiden (Acari: Oribatida) [Phd Thesis] — Graz: dbv-Verlag Technische Univ. Graz. pp. 237.
- Hennig W. 1966 — Phylogenetic systematics — Urbana: University of Illinois Press. p. 263.
- Hennig W. 1981 — Insect phylogeny — New York: Wiley. pp. 514.
- Kukalová-Peck J. 2008 — Phylogeny of higher taxa in Insecta: Finding synapomorphies in the extant fauna and separating them from homoplasies — Evol. Biol., 35: 4-51.
- Lieven A. Fürst von, Sudhaus W. 2002 — Comparative and functional morphology of the buccal cavity of Diplogastrina (Nematoda) and a first outline of the phylogeny of this taxon — J. Zool. Syst. Evol. Res., 38: 37-63.
- Lions J.-C. 1970 — La chaetotaxie gastronomique chez un Pelopsidae (Oribate) — Acarologia, 12: 612-622.
- Maraun M., Heethoff M., Schneider K., Scheu S., Weigmann G., Cianciolo J., Thomas R.H., Norton R. 2004 — Molecular phylogeny of oribatid mites (Oribatida, Acari): evidence for multiple radiations of parthenogenetic lineages — Exp. appl. Acarol., 33: 183-201.
- Miko L. 2006 — Damaeioidea — In: Weigmann G. Hornmilben (Oribatida). Die Tierwelt Deutschlands, vol. 76. Keltern: Goecke and Evers. pp. 520.
- Niedbala W. 1992 — Phthiracaroida (Acari, Oribatida), systematic studies — Amsterdam: Elsevier. pp. 612.
- Norton R.A. 1977 — A review of F. Grandjean's system of leg chaetotaxy in the Oribatei and its application to the Damaeidae — In: Dindal D.L. (Ed.). Biology of oribatid mites. New York: SUNY Coll. Environ. Sci. Forestry Syracuse. p. 33-62.
- Norton R.A. 1979 — Generic concepts in the Damaeidae (Acari Oribatei). Part 2 — Acarologia, 21: 496-513.
- Norton R.A., Alberti G., Weigmann G., Woas S. 1997 — Porose integumental organs of oribatid mites (Acari, Oribatida). 1. Overview of types and distribution — Zoologica, 48, 1-31.
- Norton R.A., Alberti G. 1997 — Porose integumental organs of oribatid mites (Acari, Oribatida). 3. Evolutionary and ecological aspects — Zoologica, 48, 115-143.
- Norton R.A., Behan-Pelletier V.M. 1986 — Systematic relationships of *Propelops*, with a modification of family-group taxa in Phenopeloidea (Acari: Oribatida) — Can. J. Zool., 64: 2370-2383.
- Norton R.A., Behan-Pelletier V.M. 2009 — Suborder Oribatida — In: Krantz G.W., Walter D.E. (Eds). A manual of acarology, 3. edit. Lubbock: Texas Tech University Press. p. 430-564.
- Remane A. 1952 — Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und Phylogenetik — Leipzig: Geest and Portig. pp. 400.
- Root H.T., Kawahara A.Y., Norton R.A. 2008 — *Anachipteria sacculifera* n. sp. (Acari: Oribatida: Achipteridiidae) from arboreal lichens in New York State — Acarologia, 47 [2007]: 173-181.
- Schatz H. 2002 — Die Oribatidenliteratur und die beschriebenen Oribatidenarten (1758-2001) - Eine Analyse — Abh. Ber. Naturkundemus. Görlitz, 74,1: 37-45.
- Schatz H. 2005 — Diversity and global distribution of oribatid mites (Acari, Oribatida) - evaluation of the present knowledge — Phytophaga (2004), 14: 485-500.
- Seniczak S. 1977 — The systematic position of moss mites of the genus *Anachipteria* Grandjean, 1935 (Acarina, Oribatei) in the light of ontogenetic studies — Acarologia, 18: 740-747.
- Seniczak S., Behan-Pelletier V.M., Solhøy T. 1990 — Systematic value of losses of some notogastral setae in adult Sphaerozetinae (Acari: Oribatida: Ceratozetidae) in the light of ontogenetic studies — Acarologia, 31: 395-400.

- Subías L.S. 2004 — Lista sistematico, sinonimico y biogeografico de los Acaros Oribatidos (Acariformes, Oribatida) del mundo (1758-2002) — Graellsia, 60 (num. extra.): 1-305.
- Sudhaus W. 2004 — Radiation within the framework of evolutionary ecology — Organisms Div. Evol., 4: 127-134.
- Valdecasas A.G., Williams D., Wheeler Q.D. 2008 — 'Integrative taxonomy' then and now: a response to Dayrat (2005) — Biol. J. Linn. Soc., 93: 211-216.
- Weigmann G. 2006 — Hornmilben (Oribatida) — In: Dahl (ed.). Die Tierwelt Deutschlands, vol. 76. Keltern: Goecke and Evers. p. 1-520.
- Weigmann G. 2010 — Anomalies of notogastral structures in poronotic oribatid mites (Oribatida: Poronota) interpreted as cryptic ancestral characters modulated by regulatory genes — In: Sabelis M.W., Bruin J. (Eds). Trends in Acarology; Dordrecht: Springer. p. 17-22.

- Wirth S. 2002 — The stem species pattern of Histiostomatidae (Acari) and description of *Histiostoma palustre* n.sp., a mite with two types of males — Acarologia, 42: 257-270.
- Woas S. 1986 — Beitrag zur Revision der Oppioidea sensu Balogh, 1972 (Acari, Oribatei) — Andrias, 55: 21-224.
- Woas S. 1990 — Die phylogenetischen Entwicklungslinien der Höheren Oribatiden (Acari). 1. Zur Monophylie der Poronota Grandjean, 1953 — Andrias, 7: 91-168.

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