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Phylogeny, ontogeny and adaptive radiation in the superfamily Tydeoidea (Acari: Actinedida), with a reappraisal of morphological characters

HENRI M. ANDRÉ FLS

Département de Zoologie, Musée royal de l'Afrique centrale, B-3080 Tervuren and Laboratoire d'Écologie et de Biogéographie, Université Catholique de Louvain, Place Croix du Sud 5, B-1348 Louvain-la-Neuve, Belgium

ALEX FAIN

Institut royal des Sciences naturelles de Belgique, 29 rue Vautier, B-1000 Bruxelles, Belgium

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The Tydeoidea as a whole (Tydeidae, Iolinidae and Ereynetidae) are analysed cladistically for the first time, based on a critical reappraisal of morphological characters. In addition to the chaetotaxy, solenidiotaxy and poroidotaxy, the following characters are considered: form of dehiscence line; number of eyes; presence of a posterior trichobothrium; number of discs on genital acetabula; breadth of cis-acetabulal area; sexual dimorphism (indicative of true mating); segmentation of legs and palps; presence and structure of ereynetal organ; shape of chelicerae and tarsus I; and number of calyptostases. Special attention is paid to a comparative study of the segmentation and chaetotaxy of the palp within the superfamily, as well as to the presence of prodorsal eye-spots, variations of the posterior sensilla and the segmentation of femur IV during ontogeny. Three types of phylogenetic analyses are employed: phenetic, cladistic and ontogenetic. The phenetic approach reveals that the current classification relies heavily on overall similarity between taxa, especially in adults, supplemented by ontogenetic peculiarities, such as the calyptostatic nymphs of Speleognathinae. The cladistic analyses lead to a reorganization of the Tydeoidea into four families. The Meyerellidae, characterized by the presence of three prodorsal eye-spots, include the Meyerellinae and Triophtydeinae, while the Tydeidae are restricted to Australotydeinae, Pretydeinae and Tydeinae. The remaining two families, Iolinidae and Ereynetidae, form the informal group Procurvata, characterized by the procurved dehiscence line. The family Iolinidae is enlarged to encompass the subfamilies Tydaeolinae, Pronematinae and Iolininae. The Ereynetidae, characterized by the ereynetal organ and double genital discs, include the Ereynetinae (senior synonym of Pseudotydeinae, transferred from the Tydeidae), Lawrencarinae and Speleognathinae. Minor discrepancies were found between the results for immatures and adults. These can be explained by ontogenetic trajectories that are not parallel and undergo a spectacular expansion into the character space as they extend. Within the Tydeoidea, diversification and adaptation have occurred through acceleration, with adult adaptations extending into earlier stases. Heterostasy is only expressed in the Speleognathinae, in which the nymphs are all calyptostatic. The monophyly of the Tydeoidea remains questionable, since the Meyerellidae might constitute a separate group, more closely related to the Eupodoidea. The Meyerellidae aside, the tydeoid mites seem to have originated from a group of free-living forms that colonized

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Note by the authors:
Proof corrections were not made to table 3 and the central dot of the second symbol in the legend of Fig. 13 was deleted after reading of proofs. Errata should be published in the Journal.

the soil and related habitats and underwent an early radiation, giving rise to three major lineages: the Tydeidae, Iolinidae and Ereynetidae. The Tydeidae are characterized by a low evolutionary rate combined with a high diversification indicative of a secondary adaptive radiation within the Tydeoidea. In contrast, the Iolinidae are characterized by a high evolutionary rate combined to a low diversification. The third lineage, the Ereynetidae, is highly diverse, showing high rates of evolution and speciation, linked to the adoption of endoparasitic habits. Different hypotheses to explain the success and diversification in Tydeidae and Ereynetidae are examined.

ADDITIONAL KEY WORDS:—Tydeidae – Ereynetidae – Iolinidae – Meyerellidae – systematics – cladistic analysis – heterochrony – ontogenetic trajectory – rates of evolution – diversification.

CONTENTS

INTRODUCTION

The mite superfamily Tydeoidea is worldwide in distribution, occurring from Antarctica to the tropics, from the seashore to alpine meadows, from the coldest areas to dry or hot deserts such as the Namib and the Chihuahuan. Its species have successfully colonized a wide range of habitats, from soil to the nasal cavities of mammals. The feeding habits of Tydeoidea exhibit a great diversity, as they include euryphagous species that feed on pollen, fungi and leaf tissues, predators that feed on arthropod eggs, other mites and nematodes, and highly specialized blood-sucking endoparasites. This diversity of modes of life is reflected in their morphology (e.g. stylet-like versus whip-like chelicerae, legs with no apotele I or with tarsi modified to conceal claws) and life-history strategies (mating vs. sperm transfer, arrhenotoky,

complex life cycle (CLC), multiple calyptostases, polymorphism, etc.). Tydeoidea thus appear to be an ideal group through which to outline and understand evolutionary processes.

In his review of the genera, André (1980) suggested the need for a broader appraisal of the superfamily, but no study has yet been devoted to the Tydeoidea as a whole. Moreover, the genera presently assigned to the component families—Tydeidae, Iolinidae and Ereynetidae—have never been submitted to any form of cladistic or other quantitative analyses. This work begins a line of research on the Tydeoidea that is aimed at elucidating the phylogenetic relationships of families and subfamilies on a worldwide basis. In this paper, we briefly review the history of studies on Tydeoidea and the ensuing classifications. A major part of our work consists of a critical evaluation and interpretation of the characters used in subsequent analyses. To understand the current classification and its underlying assumptions, and to test alternative classifications, the phylogenetic analyses are organized along three axes: phenetic, cladistic and ontogenetic. Evolutionary trends and the history of character changes are discussed, as well as their implications for the classification of the Tydeoidea.

History

The Tydeoidea, as used by André (1991) and André & Fain (1991), comprise three families, namely the Tydeidae Kramer, 1877, Ereynetidae Oudemans, 1931 and Iolinidae Pritchard, 1956. The Paratydeidae are sometimes included in the superfamily (Krantz, 1978), but are excluded here for the following reasons. Claparède organs, which are still well-developed in paratydeid larvae, do not persist in postlarval stases as in some Tydeoidea (André, 1991). Paratydeidae have a peritreme, an apomorphic character not shared by the Tydeoidea, and do not have the typical pad-like empodium found in all Tydeoidea. Their systematic position remains problematic, but according to Evans (1992), the Paratydeidae should be placed in another suborder, the Anystina, rather than in the Eupodina with the Tydeoidea.

The family Tydeidae was erected by Kramer in 1877. As Baker (1965: 96) rightly noted, the family is difficult to characterize, although easily recognized. Indeed, the detailed description of the family given by Baker (1965) lacks apomorphic characters and might equally apply to an *Ereynetes*, apart from the 'eye-spots'. The family was first reviewed by Thor (1933) and Baker (1965). In the latter revision, the family comprised only 15 genera. A new subfamily, the Pseudotydeinae, was created by Baker & Delfinado (1974) to accommodate a strange mite aptly named *Pseudotydeus perplexus*. It differed from other Tydeidae in having the genital and anal areas coalesced, invaginated and protruding posteriorly. Its status remains unclear since the types were tritonymphs and not females (André, 1980). Other major divisions were later proposed by André (1979, 1980) who distinguished seven subfamilies based on organotaxy (solenidiotaxy, chaetotaxy, and poroidotaxy), namely the Triophtydeinae, Meyerellinae, Australotydeinae, Pretydeinae, Tydeinae, Pronematinae and Tydaeolinae (see Table 2). Last, we should mention that two fossil species have been described by Dubinin (1962) and assigned to the family Tydeidae: *Paraprotacarus hirsti* and *Palaeotydeus devonicus*. However, the chaetotaxy of legs, especially that of tarsi, illustrated by Dubinin (1962: fig. 1346a,b; fig. 1347), is much richer than that found in Tydeidae and does not correspond to that of any of the subfamilies

treated hereafter. The two fossil species are thus excluded from the Tydeoidea and are tentatively assigned to Eupodoidea.

The family Ereynetidae was erected by Oudemans in 1931 to include two genera—*Ereynetes* Berlese, 1883 and *Riccardoella* Berlese, 1923—both characterized by the presence of posterior bothridia on the opisthosoma. Womersley (1936) described a new genus and species, *Speleognathus australis*, taken from moss in Australia. He designated this genus as the type of a new family, the Speleognathidae, which he placed in the Eupodoidea.

Fain (1957) reviewed the familial status of the Ereynetidae. The family Speleognathidae was lowered in hierarchic rank and considered to form part of the Ereynetidae, together with two other subfamilies, the Ereynetinae and the newly named Lawrencarinae. Most Ereynetinae are free-living or have been found in close association with snails or insects. They are characterized by the presence of genital acetabula and posterior bothridia on the opisthosoma. Both characters are missing in Speleognathinae, whereas Lawrencarinae are intermediate (presence of posterior bothridia and absence of genital acetabula). Lawrencarinae have been found in the nasal cavities of amphibians while Speleognathinae are nasal parasites of birds and mammals. This division into three subfamilies has remained unchanged (e.g. Fain, 1985a), but other diagnostic characters were subsequently added. Fain (1962a) stated that all Lawrencarinae had small perigenital discs that were lacking in Speleognathinae. Finally, Fain (1963) introduced ontogenetic development as a discriminant character. All stases, except the prelarva, are mobile in Ereynetinae, the tritonymph was thought to be missing in the Lawrencarinae whereas the Speleognathinae were characterized by the presence of three calyptostatic nymphs. The missing nymph of Lawrencarinae was, however, discovered later (André & Fain, 1991).

The status of the family Iolinidae was reviewed in detail by André (1984). It was created by Pritchard (1956) to receive an unusual mite, *Iolina nana* Pritchard, related to the Raphignathoidea but having a simple, single segmented palp and whip-like chelicerae. This family also included the genus *Proctotydaeus*, first placed in Tydeidae and then transferred to the Iolinidae by Baker (1965) and finally returned to the Tydeidae by André (1979, 1980) along with the genus *Anolina*, which was erected by Price (1972). Pritchard (1956) even created a new superfamily to receive the family Iolinidae, the Iolinoidea. The iolinids were lowered in hierarchic rank by Krantz (1978) and considered a part of the Tydeoidea. Their familial status was maintained by André (1984) pending a review of the superfamily.

This short overview shows that there has been some confusion between the three families of Tydeoidea, especially between the Iolinidae and Tydeidae (e.g. the transfer of the genus *Proctotydaeus* and its junior synonym *Anolina*). As for Ereynetidae and Tydeidae, it is enough to say that the first type of the genus *Ereynetes* selected by Berlese was *Tydeus polymitus* (for a detailed study of the type history, see Fain, 1964a). Finally, as we will explain later, the strange tydeid mite *Pseudotydeus perplexus* is actually closely related to the genus *Ereynetes*.

Aims and approaches

Three approaches will be used in this study and their results compared. First, we will refer to the so-called 'numerical taxonomy', better renamed the phenetic

approach. Following Sneath & Sokal (1973), we define phenetic clusters, i.e. polythetic groups comprising organisms that have the greatest number of shared character states. Phenetic clusters will thus be based on overall similarity.

In contrast, we also will use the cladistic approach as introduced by Hennig (1950, 1966), where monophyletic groups or clades are defined as an ancestor and all its descendants. Practically, a group of organisms is said to be monophyletic if it has a single most recent common ancestor that is not also an ancestor of organisms in the sample that are not included in the group (Maddison & Maddison, 1992). Different hypotheses of character evolution (e.g. Wagner versus Camin-Sokal parsimony) will be explored.

Lastly, an ontogenetic approach is also developed in light of the theory of age-dependent evolution proposed by Grandjean (1957) (see review by André, 1988a). It is based on previous approaches, but applied to all levels of development or stases, as well as on the ontogenetic trajectory method proposed by André (1988a).

With this threefold approach, we aim at revealing the hypotheses that implicitly underlie the present classification, outlining evolutionary trends with the subsequent classification, as well as describing the ontogenetic strategies developed by these mites.

MATERIAL AND METHODS

Material

Most of this work is based on type-material mounted on permanent slides and studied over many years by the authors. This approach allows correct identification of the material, but has some drawbacks. Depending on the quality of slides and the orientation of specimens, features such as the palpal solenidion or the lyrifissures may be difficult or even impossible to see.

To elucidate the chaetotaxy of the palp in *Ereynetes*, we had to dissect a specimen in a concavity slide. The palp was then mounted in a droplet of Hoyer's medium, covered with a coverslip, rolled under the microscope until an adequate position was found, and then heated prior to further study.

Character selection

Most of the characters used (Table 1) pertain to chaetotaxy and solenidiotaxy, i.e. to the distribution pattern and structure of setae and solenidia. Their form and size were deliberately ignored, even when important at the species level (Fain, 1963). Other meristic characters included the number of lyrifissures (poroidotaxy) and genital acetabula, and the presence of lenses.

The shape of the body and that of some organs are often difficult to code, unless sophisticated biometry techniques are used. Yet, the shape of an organ may contribute to the recognition of a taxon, e.g. the four-segmented palp which is typically shaped in Tydeidae (see Baker, 1965). This character becomes more important as the palp undergoes drastic changes in some parasitic species, such as in the ereynetid subfamily Speleognathinae or the Iolinidae. To simplify this character, only the number of segments constituting the palp was used.

TABLE 1. List of characters. Ancestral condition is coded '0'. Estimated ancestral state at the outgroup node is given in column 'A'. + indicates characters used in the basic matrix (B) and in different subsets related to stases (Ad: adult; Ny: nymph; La: larva). The number of changes (c) and reversals (r), estimated after analysis of the basic matrix, are given under hypotheses 1 (c1, r1) and 2 (c2, r2).

Characters	No.	States	A	B	Ad	Ny	La	c1	r1	c2	r2
Prodorsum	1	Recurved [0] or procurved [1]	0	+	+	+	+	1	0	1	0
Eye spots median	2	Pigment present [0] or absent [1]	1	+	+	+	+	2	0	2	0
lateral	3	Pigment present [0] or absent [1]	0	+	+	+	+	1	0	1	0
Lens	4	Present [0] or absent [1]	0	+	+	+	+	3	0	4	1
l2	5	Seta present [0] or absent [1]	1	+	+	+	+	1	0	2	0
l4	6	Seta normal [0] or bothridial [1]	0	+	+	+	−	3	1	3	0
ia	7	Lyrifissure present [0] or absent [1]	0	+	+	+	+	1	0	1	0
im	8	Lyrifissure present [0] or absent [1]	0	+	+	+	+	1	0	1	0
ip	9	Lyrifissure present [0] or absent [1]	0	+	+	+	+	3	0	3	0
ih	10	Lyrifissure present [0] or absent [1]	0	+	+	+	+	1	0	1	0
ge	11	Genital setae present [0] or absent [1]	0	+	+	+	−	1	0	1	0
eu ♂	12	Eugenital setae present [0] or absent [1] in ♂	0	+	+	−	−	4	2	5	0
eu ♀	13	Eugenital setae present [0] or absent [1] in ♀	0	+	+	−	−	1	0	1	0
Genital −1	14	Protonymphal acetabula present [0] or absent [1]	0	+	+	+	−	1	0	1	0
acetabula −2	15	Deutonymphal acetabula present [0] or absent [1]	0	+	+	+	−	1	0	1	0
CO	16	Claparède organ present only in larvae [0] or also in postlarval stases [1]	0	+	−	−	−	2	0	2	0
UR	17	Genital acetabula and Claparède organ with one [0] or two [1] discs	0	+	+	+	+	1	0	1	0
CIS−	18	Cis-acetabulal area normal [0] or reduced [1]	0	+	+	+	+	2	0	2	1
CIS+	19	Cis-acetabulal area normal [0] or enlarged [1]	0	+	+	+	+	1	0	1	0
Sexual dimorphism	20	Sexual dimorphism indicative of true mating absent [0] or present [1]	0	+	+	−	−	1	0	1	0
3d	21	Seta present [0] or absent [1]	0	+	+	−	−	2	0	2	0
4c	22	Seta present [0] or absent [1]	0	+	+	+	−	4	0	4	0
Apotele I	23	Present [0] or absent [1]	0	+	+	+	+	1	0	1	0
Chaetotaxy of tarsus I	24	Tarsus I with only fundamental setae (8 or less) [1] or richer (up to 12 setae) [0]	0	+	+	+	+	2	0	2	0
Shape of tarsus I	25	Usual shape with orthotrichous chaetotaxy [0] or segment modified with chaetotaxy usually not orthotrichous [1]	0	+	+	+	+	1	0	1	0
φ I	26	Solenidion present [0] or absent [1]	0	+	+	+	+	4	1	5	0
k″	27	Famulus associated with *l″* (cluster) [1] or not [0]	0	+	+	+	+	2	1	2	1
φ I	28	Solenidion recessed [1] or not [0]	?	+	+	+	+	3	0	3	0
φ II	29	Solenidion present [0] or absent [1]	?	+	+	+	+	2	0	2	0
ge III>ge IV	30	Chaetotaxy of genus III richer [0] or poorer than that of genus IV [1]	0	+	+	+	−	2	1	2	1
GE II to IV	31	Genus II to IV nude [1] or with at least one seta [0]	0	+	+	+	+	1	0	1	0
Femur IV	32	Femur IV divided [0] or not [1]	0	+	+	+	−	4	1	4	3
tr II	33	Seta present [0] or absent [1]	0	+	+	+	−	5	2	5	0
tr III	34	Seta present [0] or absent [1]	0	+	+	+	−	2	0	2	0
tr IV	35	Seta present [0] or absent [1]	?	+	+	−	−	2	0	2	0
Palp step 1	36	Palptarsus entire [0] or divided [1]	0	+	+	+	+	1	0	1	0
regression step 2	37	Terminal segment of tarsus present [0] or lost [1]	0	+	+	+	+	2	0	2	0
step 3	38	Femorogenu fused to tibia [1] or not [0]	0	+	+	+	+	3	0	3	0
step 4	39	Femorotibia fused to trochanter [1] or not [0]	0	+	+	+	+	3	1	3	0
step 5	40	Tarsus fused to form a single palpomere [1] or not [0]	0	+	+	+	+	3	0	3	0
Chelicerae	41	Stylet-like [0] or whip-like [1] movable digit	0	+	+	+	+	1	0	1	0
Protonymph	42	Stase mobile [0] or calyptostatic [1]	0	+	−	+	−	1	0	1	0
Deutonymph	43	Stase mobile [0] or calyptostatic [1]	0	+	−	+	−	1	0	1	0
Tritonymph	44	Stase mobile [0] or calyptostatic [1]	0	+	−	+	−	1	0	1	0
Rhagidial organ	45	Present [0] or absent [1]—used for outgroup comparison		+	−	−	−				

Similarly, the number of leg segments was also included. For instance, the absence of apotele I and the development of tarsus I observed in Pronematinae was considered, but merely coded as a presence/absence character.

Was also considered the shape of the dehiscence line, which is related to the distribution of prodorsal setae. The line was coded as a 2-state character, procurved versus recurved. In contrast, characters, such as the striation pattern of the integument in Tydeidae (e.g. in *Tydeus*) and the presence of a prodorsal scutellum in some ereynetids, were neglected.

Many characters observed in Ereynetidae have been reinterpreted or do not agree with those published in the literature. Therefore, further description and discussion of the characters used in the analysis are part of the results and will be dealt with below.

Ontogenetic data

Our first idea was to select only characters for analysis that were stable throughout the ontogeny. This is true for many of the characters used, such as the presence of lyrifissures. However, some others are variable. This is obviously the case with the genital acetabula, which are absent from the prelarva and larva and are represented by only one pair in the protonymph. Another character directly related to ontogeny is the number of calyptostases observed during the development. The prelarva is calyptostatic in all Tydeoidea, but the three nymphs are also calyptostases in the subfamily Speleognathinae (Fain, 1972).

Rather than discarding the immatures and thus acknowledging the traditional prejudice that only mature individuals are important for classification, it was considered necessary to include characters that change during ontogeny. Two approaches to coding ontogenetic information for mites may be used, namely a 'stase by stase' approach, based on Grandjean's concept of age-dependent evolution, and a method using transformation patterns (Klompen & OConnor, 1989). In the latter method, the transformation patterns themselves are treated as characters, a methodology based on work by de Queiroz (1985), who claimed that characters do not transform during ontogeny but rather that ontogenetic transformations are the characters. For example, there are only three transformation patterns of epimeral setae in Tydeidae (André, 1981), namely:

(1) Lv(3-1-2)—PN(3-1-2-0)—DN(3-1-3-2)—TN(3-1-3-3),
(2) Lv(3-1-2)—PN(3-1-3-0)—DN(3-1-4-2)—TN(3-1-4-3) and
(3) Lv(3-1-2)—PN(3-1-2-0)—DN(3-1-3-2)—TN(3-1-4-2).

In the 'stase by stase' approach, which we have chosen to use, the states of a given character are only compared between homologous stases. In other words, there are as many data subsets as there are stases. The risk is that incongruency may result between classifications based on different stases. To overcome this problem, the different subsets can be pooled to form a single matrix. An alternative solution is the ontogenetic trajectory method (André, 1988a), which involves plotting points representing the stases in an *n*-dimensional character space and connecting the points representing the successive stases of a species. Principal component analysis (PCA) is used to project the *n*-dimensional trajectories into a space of two or three dimensions, in which bundles of trajectories may be easily identified.

Taxa

Because of limitations with comprehensive search algorithms (exhaustive and branch-and-bound), it was not feasible to include all the genera of the Tydeoidea. Given the set of characters selected, we include as many taxa as necessary to cover all the combinations of characters observed in the superfamily. This led us to include the 35 tydeoid taxa listed in Table 2.

Some genera or subgenera were selected because of their peculiarities. The case of *Ereynetes (Huntereynetes) scutulis* is illustrative. This species was described in 1964 by Hunter as *Ereynetoides scutulis*. The same year, Fain (1964a) in a small addendum to his study of Berlese's types, commented on Hunter's description and, based on it, created a new subgenus, *Huntereynetes*, within the genus *Ereynetes*. The new subgenus was defined by the regression of adanal suckers and the size of the prodorsal scutellum. When we re-examined the types (male, female, nymphs and larva), we were unable to see lyrifissures *ia* and *im*, an unusual deficiency found only in endoparasitic ereynetids such as *Boydaia*.

Another example is the '*Tydeus* with 3 eyes' which was collected from trees in Sicily by Dr V. Vacante. It is typical of the genus *Tydeus* in every respect, except that it has three eye-spots. This 'atavistic' character is usually found only in Triophtydeinae and Meyerellinae.

The genus *Caleupodes*, described in detail by Baker (1987), was selected as an outgroup for analysis of the Tydeoidea. This eupodid genus belongs to the Eupodina, the cohort in which the Tydeoidea are traditionally placed (Krantz, 1978; Evans, 1992). [Traditionally, the Eupodoidea are considered the sister group of Tydeoidea. Norton *et al.* (1993) suggested that the Eriophyoidea are the sister group of Tydeoidea, and that, combined together, these two superfamilies form the sister group of the Eupodoidea. In a recent review, Lindquist (1998) acknowledged that the rationale given for a sister relationships between Eriophyoidea and Tydeoidea within the cohort Eupodina was persuasive, but not conclusive.] The genus *Caleupodes* is unique in that it retains primary opisthosomal segmentation. The only drawback with its use as an outgroup is that its immatures are unknown.

Some families will be rearranged at the end of this study. To avoid confusion, we will not refer to family names (except Ereynetidae) in the results section, but rather to the subfamilies.

Data matrices

The basic matrix BM (Table 3) was assembled using MacClade 3.01 (Maddison & Maddison, 1992). Missing data were entered as '?' and the ancestral state of characters was entered as '0'. Multistate characters were recoded as binary (0,1) characters using FACTOR (PHYLIP; Felsenstein, 1993). As may be seen from Table 3, BM was composed of 35 taxa and 44 characters. Different subsets of 4, 8, 12, and 20 species were also used to test MIX in comparison to PENNY (see below). The largest reduced taxa data set submitted to PENNY was composed of Ereynetidae as a whole (except *Pseudotydeus* for which too many characters are not certain).

Other data subsets, relating to stases were derived from the basic matrix. The adult data set (ADS) was a 34 taxa × 39 character matrix (the adult of *Pseudotydeus* is not known, and characters no. 42 to 44 do not refer to adults and were thus

TABLE 2. List of taxa with, for each, the stases known and the corresponding taxonomic range. The current classification is followed. The number of species described (synonyms and dubious cases excluded) are given in parentheses for each subfamily. SA: stase available (L: larva; P: protonymph; D: deutonymph; T: tritonymph; A: adult)

No.	Taxa	SA	Corresponding range
	EREYNETIDAE		
	Speleognathinae (94)		
1	*Speleognathus*	L-A	*Speleognathus* and other Speleognathinae with a 1-segmented palp
2	*Neoboydaia* 2	L-A	Species of *Neoboydaia* with a 2-segmented palp and no trochanteral II (e.g. *merops*)
3	*Neoboydaia* 1	L-A	Species of *Neoboydaia* with a 2-segmented palp and with a trochanteral II (e.g. *philomachi*)
4	*Psyttaboidaia*	L-A	Subgenus *Psyttaboidaia* and other Speleognathinae with a 2-segmented palp (*Neoboydaia* excluded)
5	*Boydaia* 2	L-A	Species of the genus *Boydaia* with no trochanteral II (e.g. *nigra*)
6	*Boydaia* 1	L-A	Species of the genus *Boydaia* with a trochanteral II (e.g. *sturni*)
7	*Astrida*	L-A	Subgenus *Astrida* and other Speleognathinae with a 3-segmented palp (*Boydaia* excluded)
	Lawrencarinae (18)		
8	*Lawrencarus* 2	L,D-A	Species of *Lawrencarus* with eugenitals in males (most species)
9	*Lawrencarus* 1	L,D-A	Species of *Lawrencarus* with no eugenitals in males (e.g. *lechriodi*)
10	*Batracarus*	L-A	*Batracarus*
11	*Xenopacarus*	L-P,T-A	*Xenopacarus*
	Ereynetinae (57)		
12	*Hydranetes*	A	*Hydranetes*
13	*Huntereynetes*	L-A	*Ereynetes (Huntereynetes)*
14	*Riccardoella*	L-A	*Riccardoella (Riccardoella)*
15	*Proriccardoella*	L-A	*Riccardoella (Proriccardoella)*
16	*Ereynetes*	L-A	*Ereynetes (Ereynetes)*
17	*Anereynetes* 2	A	Undescribed species from Dem. Rep. Congo (Butare)
18	*Anereynetes* 1	L-A	*Ereynetes (Anereynetes)* (except the species above)
19	*Gymnereynetes*	L-A	*Ereynetes (Gymnereynetes)*
	IOLINIDAE		
	Iolininae (2)		
20	*Idiolina*	P-A	*Idiolina*
21	*Iolina*	L-A	*Iolina*
	TYDEIDAE		
	Pseudotydeinae (1)		
22	*Pseudotydeus*	T	*Pseudotydeus perplexus*
	Tydaeolinae (40)		
23	*Tydaeolus*	A-L	Genus *Tydaeolus* and other Tydaeolinae
	Pronematinae (55)		
24	*Proctotydaeus*	L-A	Genus *Proctotydaeus* and other pronematines with a femur IV divided
25	*Pronematus*	L-A	Genus *Pronematus* and other pronematines with a single femur IV and one pair of genital acetabula
26	*Apopronematus*	T-A	Genus *Apopronematus* and other pronematines with a single femur IV and no genital acetabula
	Tydeinae (298)		
27	*Tydeus* (with 3 eyes)	A	Undescribed *Tydeus* species from Italy having three 'eyes'
28	*Tydeus*	L-A	Genus *Tydeus* and other Tydeinae (except the species above)
	Pretydeinae (15)		
29	*Prelorryia*	L, A	Genus *Prelorryia*
30	*Pretydeus*	L-A	Genus *Pretydeus* and other Pretydeinae
	Australotydeinae (1)		
31	*Australotydeus*	T, A	*Australotydeus kirstenae*
	Triophtydeinae (44)		
32	*Triophtydeus*	L, A	*Triophtydeus*
33	'Triomeyerella'	P, A	Undescribed taxon, collected from leaf domatia in Queensland
	Meyerellinae (4)		
34	*Pseudotriophtydeus*	L-A	*Pseudotriophtydeus*
35	*Meyerella*	P-A	*Meyerella*

TABLE 3. The basic matrix (BM). The first line indicates the ancestral state while the second refers to the parsimony method applied to each character (?: Wagner; S: Sokal–Camin). Characters are coded as listed in Table 1

A	01010	00000	00000	00000	00000	00000	00000	00000	0000
Mixed	????5	?5555	555??	?????	5555?	5??5?	5?555	?????	????
Speleognathinae	11111	01111	01100	01010	11001	00110	01011	11111	0111
Neoboydaia 2	11111	01111	01100	01010	11001	00110	01111	11110	0111
Neoboydaia 1	11111	01111	01100	01010	11001	00110	01011	11110	0111
Psyttaboldaia	11101	01111	01100	01010	11001	00110	01011	11110	0111
Boydaia 2	11101	01111	01100	01010	11001	00110	01111	11100	0111
Boydaia 1	11101	01111	01100	01010	11001	00110	01011	11100	0111
Astrida	11101	01111	00100	01010	11001	00110	01011	11100	0111
Lawrencarus 2	11111	11111	00100	01010	11001	00110	01111	11111	0000
Lawrencarus 1	11111	11111	01100	01010	11001	00110	01111	11111	0000
Batracarus	11111	11111	0?100	01010	11001	00110	01111	11110	0000
Xenopacarus	11111	01111	01100	01010	11001	00110	01111	11100	0000
Riccardoella	11111	10000	00100	01000	01001	01110	00011	11100	0000
Proriccardoella	11111	10000	00100	01000	01001	01110	00001	11100	0000
Hydranetes	11111	01111	0?100	01??0	01001	00110	00001	11000	0000
Ereynetes	11101	10000	00100	01000	00001	01110	00001	10000	0000
Aneyrenetes 2	11111	10010	00100	01000	00001	01110	00001	10000	0000
Aneyrenetes 1	11111	10000	00100	01000	00001	01110	00001	10000	0000
Gymnoereynetes	11111	10000	00100	01000	00001	00110	00001	10000	0000
Huntereynetes	11101	11100	00100	01000	00001	00110	00001	10000	0000
Pseudotydeus	11111	00000	0???00	010?0	00001	01110	0?001	10000	0000
Tydaeolus	11111	00000	00100	10100	00000	00010	01001	00000	0000
Proctotydaeus	11111	00000	11111	10101	01110	00010	00001	00000	0000
Pronematus	11111	00000	11110	10101	01110	00010	01001	00000	0000
Apopronematus	11111	00000	11111	10101	01110	00010	01001	00000	0000
Idiolina	11111	00000	11111	10101	01110	00010	01001	00111	1000
Iolina	11111	00000	11111	10101	01110	10010	01101	00111	1000
Tydeus (with 3 eyes)	00011	00010	00100	00100	01010	10010	01101	00000	0000
Tydeus	01011	00010	00100	00100	01010	10010	01101	00000	0000
Prelorryia	01011	00010	00100	00100	00010	10010	11001	00000	0000
Pretydeus	01011	00010	00100	00100	00010	00110	11001	00000	0000
Australotydeus	0??10	00000	00?00	00100	00000	10010	01001	00000	0000
Triophtydeus	00011	00000	00000	10000	10000	10010	00001	00000	0000
'Triomeyerella'	00011	00000	00000	10000	10000	00011	00001	00000	0000
Pseudotriophtydeus	00011	00000	00000	10000	10000	00001	00001	00000	0000
Meyerella	00011	00000	00000	10000	10000	00001	00000	00000	0000

discarded). Similarly, other subsets were derived for the tritonymph (TDS, 34 taxa × 39 character matrix), deutonymph (DDS, 32 taxa × 34 character matrix), protonymph (PDS, 32 taxa × 31 character matrix), and larva (LDS, 32 taxa × 24 character matrix). Pooling the subsets gave a 35 taxa × 167 character ontogenetic matrix (OM).

Data analysis

Cladistic analyses were run on a Macintosh 520C and Power Macintosh 7200 and 7600 computers using the programs MIX, PENNY and CONSENSE (Versions 3.2 and 3.572 of PHYLIP; Felsenstein, 1993). PENNY examines all possible trees by using a comprehensive search algorithm (exhaustive and branch-and-bound searches), and finds all the most parsimonious trees from a data matrix. The major drawback of this approach is that it is very slow and time-consuming for large data

First 3 lines of table 3 should read:

A	01010	00000	00000	00000	00000	00000	00000	00000	0000
Mixed	????S	?SSSS	SSS??	?????	SSSS?	S??S?	S?SSS	?????	????
Speleognathus	11111	01111	01100	01010	11001	00110	01011	11111	0111

sets. MIX is a much faster program than PENNY and carries out heuristic Wagner and Camin–Sokal parsimony methods in mixture. MIX was used with the multiple Jumble option. With this option, multiple searches are made with random input orders of species, and the trees found are those that are tied for best among all of those found by all these runs. Because MIX does not handle polytomies correctly, all analyses were duplicated using heuristic searches with PAUP 3.1 (Swofford, 1993).

We used a traditional approach, estimating ancestral states using outgroup analysis, and then resolving the ingroup given the ancestral states. Although this two-step procedure examines the outgroup and ingroup separately, it finds the cladograms that are most parsimonious (Maddison *et al.*, 1984).

Cladistic analyses were carried out under two different basic assumptions, Wagner and mixed parsimony. In the latter, Camin–Sokal parsimony (Camin & Sokal, 1965) was applied to chaetotaxy (presence/absence of setae), solenidiotaxy and poroidotaxy. Losses were treated as irreversible—this implies that when a seta, solenidion or lyrifissure disappears in a lineage, it is unlikely to reappear. This assumption is based on extensive comparative analyses of mite ontogeny and the harmony laws proposed by Grandjean (1947, 1951, 1957) (see review by André, 1988a). It is probably no coincidence that the Camin–Sokal parsimony method was proposed by an acarologist.

As immatures of the outgroup are unknown, the analyses by stase were carried out on the ingroup species only. The character-state polarities defined in previous analyses were used in the input data.

Other analyses were run using the *R* package (Legendre & Vaudor, 1991). The program PnComp was used to perform Principal Component Analyses (PCA) and to project the *n*-dimensional ontogenetic trajectories into a space of two or three dimensions where bundles of trajectories are easily identified. Phenetic clusters were obtained using K-MEANS, a program that relies on a variable centred classification algorithm developed by MacQueen (1967). Although the algorithms of this family, also called partitioning techniques, are usually considered as non-hierarchical clustering methods, they may serve to detect—and not to impose—a hierarchical structure in the data (André, 1988b). Both programs were used with the default options.

RESULTS

Characters

Prodorsum

The chaetotaxy of the prodorsum of Tydeoidea is noteworthy in being constant except in some parasitic species. The pair (*vi*) is only missing in the genera *Batracarus* and *Lawrencarus* (Lawrencarinae) as well as in *Meropiboydaia merops* and *Speleochir aitkeni* (Speleognathinae). Its disappearance seems to be announced by its bisynthesis as noticed in specimens of *Tydaeolus tenuiclaviger* (Tydaeolinae), *Proctotydaeus schistocercae* (Pronematinae), *Ereynetes papuanus* (Ereynetinae), *Xenopacarus africanus* (Lawrencarinae) and *Boydaia zumpti* (Speleognathinae). A vertition of *vi* was also observed in a paratype of *Astrida parrae* (Speleognathinae). In few species, the pair (*ve*) is missing [in *Parapronematus acaciae*, *P. citri* (Pronematinae), *Lawrencarus domrowi* (Lawrencarinae),

Boydaia clavata, *Meropiboydaia merops* and *Speleognathopsis galli* (Speleognathinae)]. The disappearance of (*ve*) seems to be preceded by its reduction [*Parapronematus geminus* (Pronematinae) and *Boydaia aratingae* (Speleognathinae)]. Last, the pair (*se*) is absent in the genera *Lawrencarus* and *Batracarus* (Lawrencarinae) and in *Speleognathopsis galli*, *Astrida parrae* and *Neoboydaia philomachi* (Speleognathinae). As these disappearances were infrequent and observed in different taxa scattered among Tydeoidea, they were not included in the analysis.

The first character of the data matrix (Tables 2, 3) is the shape of the dehiscence line, δ. As reviewed by Norton and Kethley (1994), mites exhibit a variety of ecdysial cleavage lines likely to be useful in phylogenetic analyses. This character was introduced by André (1981) in his revision of Tydeidae. It does not vary during the course of ontogeny and is of the prodorsal type *sensu* Coineau (1974) or prodehiscent *sensu* Norton and Kethley (1994). The dehiscence line is recurved in Meyerellinae, Triophtydeinae, Tydeinae and Pretydeinae and is procurved in all other tydeoid subfamilies.

Some tydeoids possess aggregates of silver granules forming two (Tydeinae, Pretydeinae) or three (Meyerellinae, Triophtydeinae) spots under the prodorsal integument. They are traditionally regarded as being eye-spots (Thor, 1933; Baker, 1965; André, 1981; Kazmierski, 1989b) but, surprisingly, they are not associated with a lens such as that found in Ereynetidae. In teneral specimens, the granules form a hollow sphere (Fig. 1A); later on, they are more compact but, in any case, they are clearly separate from the posterior end of the podocephalic canal (Fig. 1B). The absence of cornea does not preclude a photosensitive function since a median eye without cuticular differentiation has been proved histologically to be present in some Bdellidae, a related family (Alberti, 1975). However, the pigments tend to disappear when the specimens are cleared and mounted and there is doubt concerning their presence in some taxa, e.g. in *Australotydeus*. This multiple state character (3, 2 or 0 spots) has been recoded as two binary characters in the data matrix (see Table 1).

In contrast, we have never seen an *Ereynetes* having cornea backed by pigments. Thor (1932) erected a new genus, *Opsereynetes*, to receive an ereynetine species with so-called eye-spots. Thor's types are lost, but we studied types of *Opsereynetes simplexus*, a species described later by Baker (1945) and compared it to other Ereynetidae. The ereynetid pigment is quite different in colour and texture from that found in Tydeinae: it is greyish and composed of globules of various sizes. It is not visible in all specimens, but has been observed in both Ereynetinae and Speleognathinae (Fig. 1C). In all cases, it was found to be close to the posterior end of the podocephalic canal (Fig. 1C). This suggests that the two spots of Ereynetidae are nothing more than the secretions of glands discharging into the podocephalic canal. These glands would be part of the podocephalic gland complex described in Bdellidae by Alberti and Storch (1977). Depending on the physiological state of the mites, and probably also on the mounting conditions of specimens, these secretions may or may not be visible (Fig. 1D).

The presence of lenses or ocelli in some Ereynetidae is the fourth character of the matrix.

Dorsal face of the opisthosoma

The chaetotaxy of the tydeoid opisthosoma is orthotactic with a maximal number of (2, 2, 1, 2, 2, 3, 2) pairs of setae, the first five pairs being designated *d1-l1* to

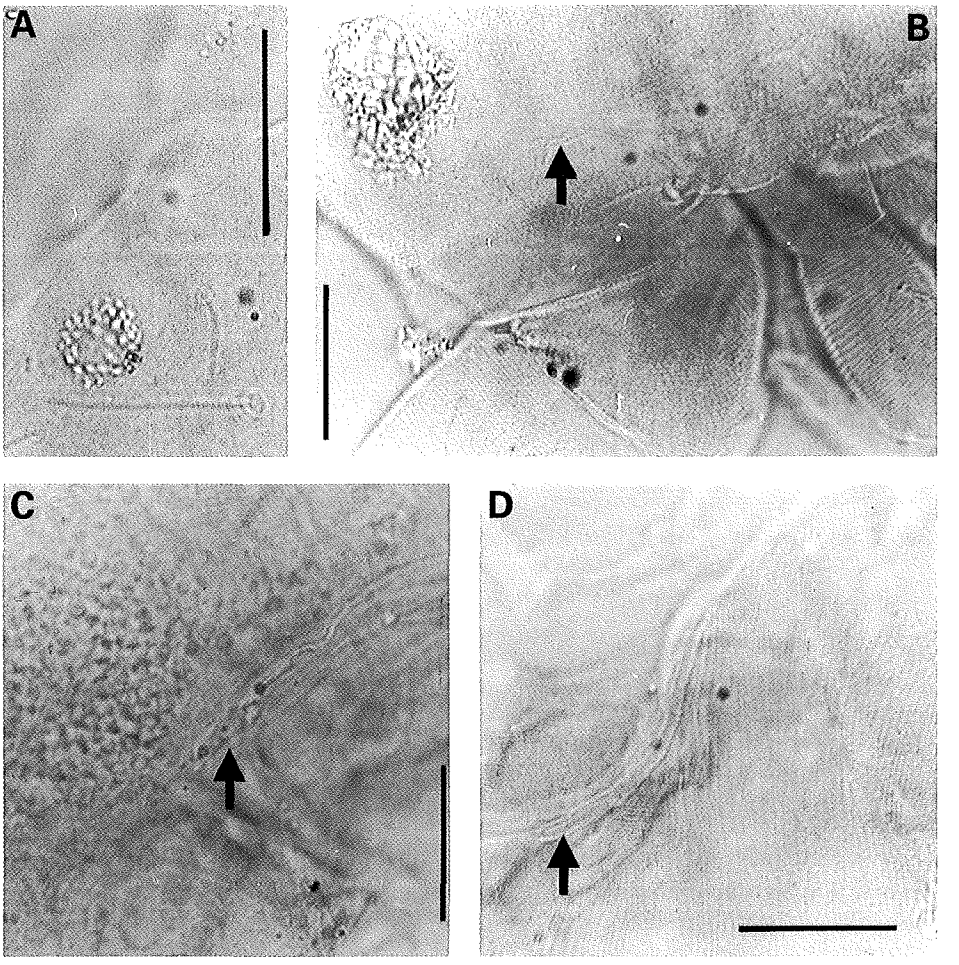


Figure 1. Prodorsal 'spots' in Tydeinae (A,B) and Ereynetidae (C,D). (A) Eye-spot in a teneral larva of *Orthotydeus* sp.; (B) eye-spot and posterior end of podocephalic canal (arrow) in a female of the same species; (C) glandular globules and posterior end of podocephalic canal in *Speleognathus schoutedeni* (Speleognathinae); (D) posterior end of podocephalic canal with no globules visible in *Ereynetes macquariensis* (Ereynetinae). Scale bars = 10 μm.

d5-l5. The fifth character is the presence of *l2*, which is absent in all genera except in *Australotydeus*. Most posterior setae, *h* and *ps*, which tend to disappear in several different taxa, were not included in the analysis. Neotrichy is rare among Tydeoidea: the only case seems to be that of setae *h* in *Lawrencarus ewori*.

The so-called posterior sensillum (character no. 6) is the opisthosomal seta *l4*, which arises from a bothridium and, most often, takes the same filiform shape as the prodorsal sensillum (Fig. 2E, F). The ereynetid posterior sensillum is different from that observed in the sister-group Eupodoidea, which corresponds to *d4* (Grandjean, 1939b). Fain (1957) regarded the posterior sensillum as a key character of Ereynetinae and Lawrencarinae. Later, Fain *et al.* (1969) expanded the concept of Lawrencarinae to include a new genus, *Xenopacarus*, which lacks the posterior

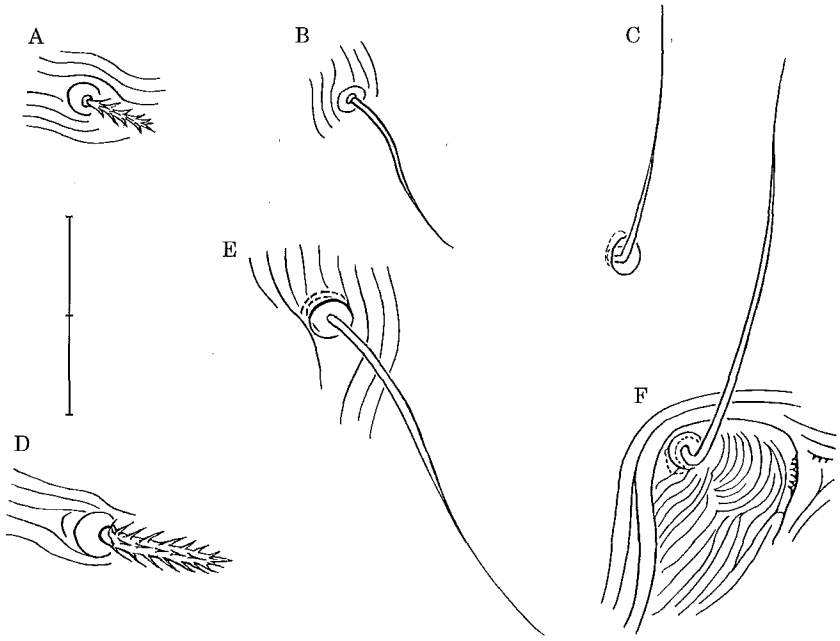


Figure 2. Opisthosomal setae and trichobothria in the larva (A–C) and adult (D–F) of *Lawrencarus hylae afrixali* Fain (Lawrencarinae) [paralectotype larva and lectotype female]; (A,D) normal seta *d4*; (B,E) seta *l4* with (E) or without (B) bothridium; (C,F) prodorsal trichobothria. Scale bar = 20 μm.

sensillum. Similarly, the concept of Ereynetinae was enlarged by Kethley (1971) to include a new genus, *Hydranetes*, with no posterior sensillum.

The presence of the posterior sensillum varies through ontogeny. In those ereynetid species whose ontogeny we have studied (*Ereynetes (A.) papuanus*, *E. (G.) macquariensis*, *E. (H.) scutulis*, *Riccardoella oudemansi*, *Lawrencarus eweri*, *L. hylae*), *l4* becomes a trichobothrium only at the protonymphal stase. However, the situation in the larva is intermediate between a true trichobothrium and a normal seta. For instance, the larva of *Lawrencarus eweri eweri* has a long and slightly spiny setae *l4*, similar to the prodorsal trichobothria and quite distinct in shape from the other opisthosomal setae, but there is no bothridium at its base (Fig. 2B). The same similarity in shape between a seta *l4* devoid of bothridia and the prodorsal trichobothria was also observed in larvae of other species (*Lawrencarus hylae afrixali*, *Riccardoella*).

Character nos 7 to 10 describe the idiosomal poroidotaxy, which basically consists of four pairs of lyrifissures. They are all present in Meyerellinae, Triophtydeinae, Tydaeolinae, Pronematinae, Iolininae, and most Ereynetinae, but lyrifissure *ip* is missing in Tydeinae and Pretydeinae (André, 1981). In the subgenus *Anereynetes*, all four lyrifissures generally are present except in one undescribed species where *ip* also is missing as in Tydeinae and Pretydeinae. This suggests that lyrifissure *ip* is the most easily lost. However, the loss of lyrifissures might be more complex. Indeed, in *Ereynetes* (*A.*) *meliponae* the three anterior lyrifissures seem to be vestigial (they have no funnel and look like scars devoid of striations), and only lyrifissure *ih* seems to be complete and functional. In the subgenus *Huntereynetes*, the prodorsal shield extends backwards to setae *d3* resulting in the disappearance of lyrifissures *ia* and

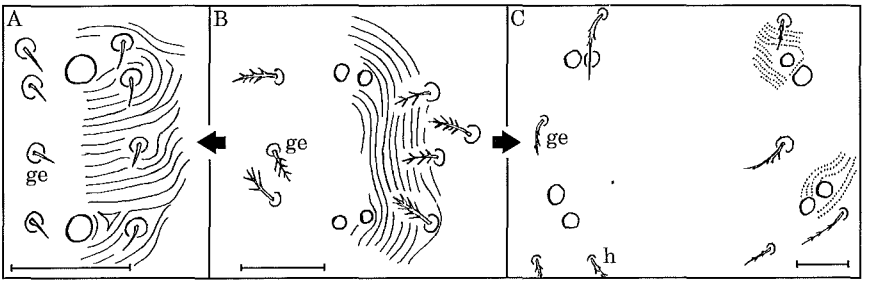


Figure 3. Evolution of genital area in nymphs of Tydeoidea, from the plesiomorphic form (B) to a reduction of the cis-acetabulal area with a bisynthesis of genital discs (A) or to an enlargement of the cis-acetabulal area combined with duplication of genital discs (C); (A) tritonymph of *Orthotydeus* sp. (Tydeinae); (B) tritonymph of *Pretriophtydeus tilbrooki* (Strandtmann) (Triophtydeinae); (C) deutonymph of *Lawrencarus eweri* (Lawrence) (Lawrencarinae). Scale bars = 10 μm.

im. Lastly, there is no lyrifissures at all in *Hydranetes* as well as in the two subfamilies, Lawrencarinae and Speleognathinae, composed of endoparasitic species.

Genital area

In Tydeidae, the genital chaetotaxy consists of three series of setae: the aggenitals, genitals and eugenitals (André, 1981). This notation also applies to Ereynetidae.

Aggenital setae are always present, at least in adults. Genitals (character no. 11) tend to disappear and are absent in Pronematinae and Iolininae (André, 1981, 1984). Eugenitals exist only in adults and their number depends on the sex. In males, they are missing in Pronematinae and Iolininae (André, 1981, 1984), as well as in Lawrencarinae and Speleognathinae (character no. 12). There are, however, two exceptions. Among Lawrencarinae, *Lawrencarus eweri* and *L. hylae*, contrary to other species of the genus, have two eugenitals in males, hence the presence of a taxon '*Lawrencarus* 2' in the data matrix. The second exception is found in the genus *Astrida* (Speleognathinae) in which males have a single eugenital. In females, eugenitals are observed only among Triophtydeinae and Meyerellinae (character no. 13). This character is not coded for *Australotydeus*, since the female is unknown.

Most Tydeoidea have two genital acetabula, one protonymphal and the other deutonymphal (character nos 14, 15). Genital acetabula are reduced to one or absent in Pronematinae and Iolininae (André, 1981, 1984).

In Ereynetidae, the genital area undergoes drastic changes not noted in previous reviews. First, genital acetabula have two small discs easy to observe in adults of *Ereynetes* and *Riccardoella*. The so-called double genital discs of André (1991) also are visible in nymphs (Fig. 3C). Likewise, duplication occurs in Claparède organs, which are homologous with genital acetabula (André, 1991). The presence of double genital discs corresponds to character no. 17. It must be emphasized that the double genital discs are large and easy to observe in Lawrencarinae but, contrary to Fain's (1962a) statement, they are also present (although sometimes inconspicuous) in Speleognathinae, together with double Claparède's organs. Lastly, double genital discs are present in the tydeid *Pseudotydeus perplexus*, contrary to all other Tydeidae, which have simple genital discs.

Furthermore, the genital acetabula of Lawrencarinae and Speleognathinae are reduced and move outside the progenital chamber of adults to form what Fain

(1962a) calls perigenital discs. This migration corresponds to an enlargement of the cis-acetabulal area (character no. 19). This enlargement is easy to observe in the nymphs (Fig. 3C) and adults of Lawrencarinae, but it is less marked and sometimes difficult to observe in the adult Speleognathinae, since the genital discs are sometimes inconspicuous and located along the border of the progenital opening (it is not, of course, visible in the nymphs of Speleognathinae, since they are calyptostatic). Surprisingly, such a migration is also seen in the tritonymph of *Pseudotydeus perplexus*, which separates this species from the Ereynetinae.

The enlargement of the cis-acetabulal area is counter to the trend observed in Australotydeinae, Tydeinae, Pretydeinae, Pronematinae and Iolininae, in which a reduction of this area is easily observed in nymphs (character no. 18). In these groups, each element of the pairs of genital discs moves onto the sagittal plane where they merge into one simple structure (Fig. 3A). As this trend is difficult to confirm in the progenital chamber, it was not coded for adults.

Considering the differences in location of the progenital aperture in males and females, the presence of an aedeagus in males and a dorsal process on male femur IV, André (1979) suggested that true mating might occur among Pronematinae and Iolininae. This hypothesis was confirmed by Knop (1985), who observed the mating in *Homeopronematus anconai* and described the role of male organs during coupling. Direct sperm transfer is a highly advanced strategy when compared to reproduction by means of spermatophores, a strategy that has been observed in Tydeinae (Schuster & Schuster, 1970). The presence of an aedeagus in males and associated features form character no. 20 and are considered indicative of mating.

Coxisternal area

Claparède's organ is homologous with the genital acetabula and may be simple or double, as already stated in the previous section (character no. 17). They were considered to be present only in larvae, until André (1991) observed that they were also present in postlarval stases of Australotydeinae, Pretydeinae, Tydeinae and Ereynetidae (character no. 16).

Two setae, *3d* and *4c*, are also of interest. *3d* (character no. 21) is absent in Meyerellinae and Triophtydeinae (Tydeidae) as well as in Lawrencarinae and Speleognathinae (Ereynetidae). Seta *4c* (character no. 22) is absent in Tydeinae, Pronematinae, Iolininae, Lawrencarinae and Speleognathinae, together with the genus *Riccardoella* (Ereynetinae). These characters vary during the course of ontogeny. For instance, *4c* only appears in the tritonymph and adult of *Ereynetes malayi*.

Legs

Of most interest is the reduction and loss of apotele I in Pronematinae and Iolininae (character no. 23) (Fig. 4D). A similar loss, combined with a substantial lengthening of tarsal eupathidia, was already described in Staurobatidae, an oribatid family, by Grandjean (1966), who referred to it as a 'palpian evolution'. Some of these mites are fast-moving and run on legs II to IV, tapping the substrate rapidly with the first pair of legs in a similar way to insect antennae (Knop & Hoy, 1983).

Tarsus I is subject to two apparently antagonistic evolutions (Fig. 4). It either undergoes a reduction in chaetotaxy (character no. 24) as observed in the Pretydeinae, Tydeinae, Pronematinae and Iolininae, or undergoes modifications of shape as in Ereynetidae (character no. 25). In the former case, all setae retain their normal

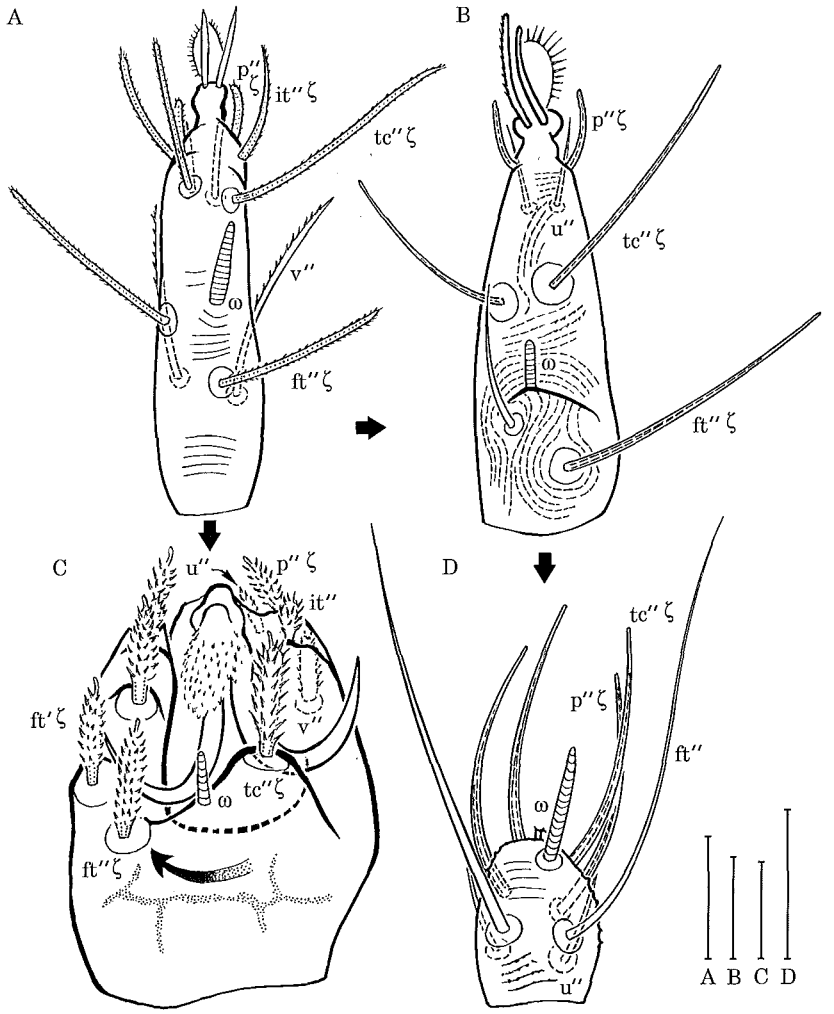


Figure 4. Evolution of tarsus I in Tydeoidea, from plesiomorphic state (holo- and orthotrichy, presence of apotele I) observed in Meyerellinae (A). (A) *Meyerella marshalli* (Meyerellinae); (B) *Tydeus* sp. (orthotrichy, apotele I; Tydeinae); (C) *Boydaia sturni* (holotrichy, apotele I; Speleognathinae); (D) *Idiolina augustae* (orthotrichy; Iolininae). Orthotrichy is not respected in (C), mainly due to a translocation of seta *ft''*. Scale bars = 10 μm.

location (orthotaxy) but are reduced to the eight fundamental setae, namely (*ft*), (*tc*), (*p*) and (*u*) (Fig. 4B). In the latter case, tarsus I presents a distal cavity or grooves within which the claws may be retracted. This modification of shape is often accompanied by important migrations of setae, including disjunction, anabasis, permutation with the solenidion, translocation (Fig. 4C). A more detailed description of these movements is given elsewhere (André, in prep.). The paradox is that, despite the setal movements, all ereynetid species have kept at least 10 setae rather than 8 on tarsus I, even in the larva (Fain, 1963). In most Ereynetidae, tarsus I is holotrichous (12 setae).

Solenidion φI (character no. 26) is lost in Triophtydeinae, Australotydeinae and

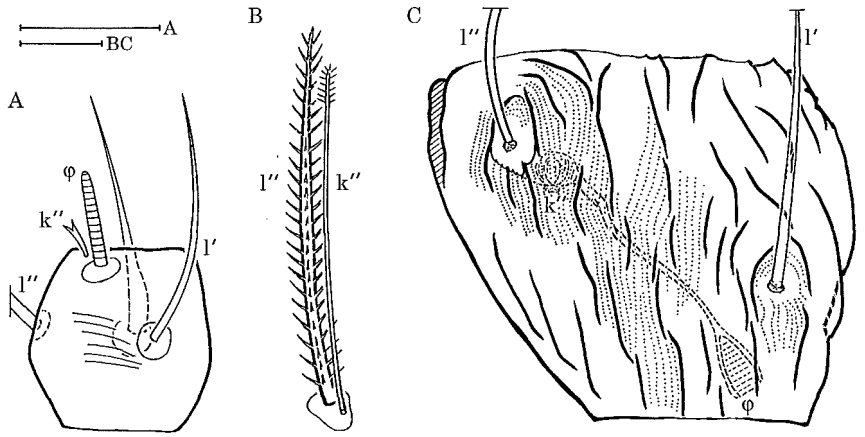


Figure 5. Situation of famulus *k''* in Tydeoidea. (A) isolated (*Idiolina augustae*, Iolininae); (B) associated with *l''* to form a cluster (*Ereynetes* (*Gymnereynetes*) sp., Ereynetinae); (C) deeply recessed to become part of ereynetal organ (*Neoboydaia philomachi*, Speleognathinae). Scale bars = 10 μm.

Tydeinae, as well as in the genera *Prelorryia* and *Iolina*. It tends to be recessed (character no. 28) in *Pretydeus* and in *Pseudotydeus*, as well as in all Ereynetidae where it forms the 'ereynetal organ' (Grandjean, 1939b; Fain, 1962b, 1964b). The ereynetal organ varies in complexity depending on the species; the solenidion is deeply recessed and may be associated with the famulus, *k''* (Fain, 1985b) (Fig. 5C). In Ereynetinae, however, the famulus is separate from the ereynetal organ and may form a cluster with seta *l''* (character no. 27) (Fig. 5B). This cluster, first described by Grandjean (1939b), was also found in *Pseudotydeus perplexus* (see André, 1980) and is a diagnostic character that discriminates the subgenera within the genus *Ereynetes* (see Fain & Camerik, 1994). The cluster may be difficult to see, especially in permanent slides, and may be impossible to see in dorsal view. Solenidion φII (character no. 29) is present only in the two meyerelline genera, *Meyerella* and *Pseudotriophtydeus*.

Usually, there is a gradient of chaetotaxy from the most setose leg, leg I, to the least setose, leg IV. Exceptions are rare. In *Meyerella*, *Pseudotriophtydeus* and *Triomeyerella*, genu III is more setose than genu IV (character no. 30): Another noteworthy chaetotaxy is that of Pretydeinae, in which genua II to IV are nude (character no. 31).

In some genera, the adult femur IV is composed of a basi- and telofemur (character no. 32). This is the case in the Meyerellinae, Triophtydeinae, Ereynetinae and some Pronematinae. However, femur IV of Tydeoidea is subject to what Grandjean (1954b) called an ontogenetic bipartition (André, 1985). For example, femur IV of *Triophtydeus* is undivided in the protonymph, whereas it is divided in the deutonymph and subsequent stases (André, 1985). This phenomenon—already known in several actinedid families (Bdellidae, Cunaxidae, Pachygnathidae, etc.)—has not previously been described in Ereynetidae. In the Ereynetinae, ontogenetic bipartition is delayed until the tritonymphal stase.

Finally, trochanter II is nude (character no. 33) in Tydeinae and Lawrencarinae, as well as in *Iolina* and some species of Speleognathinae. Trochanter III is nude (character no. 34) in Lawrencarinae, Speleognathinae and in the genus *Iolina*. Only

the adult and tritonymph of *Meyerella* have a seta on trochanter IV (character no. 35).

Palp

The four-segmented palp is typically shaped in Tydeidae (see Baker, 1965) and comprises four palpomeres identified as the trochanter, femorogenu, tibia and tarsus (Grandjean, 1938; Baker, 1965; André, 1981). Identification of the four palpal articles relies on a comparative study of the chaetotaxy (Grandjean, 1938) and on the ontogenetic bipartition of the femorogenu observed in other families of Actinedida such as Caeculidae (see Coineau, 1974). However, a striking exception is provided by *Pseudotydeus perplexus*, with a five-segmented palp, not four-segmented as mentioned by Baker & Delfinado (1974) and André (1980).

In Ereynetidae, the literature on palpal segmentation is unclear on some points. The maximum number of palpal segments recorded is five in the genus *Ereynetes* (see Fain, 1963, 1964a). This number was considered a key character to distinguish *Ereynetes* from *Riccardoella*, which has only three segments (Fain, 1964a; Hunter & Cross, 1968). Surprisingly, the number of palpal segments of *Ereynetes* was considered to be four by Fain & Van Goethem (1986) and some *Ereynetes* species have also more recently been described as having only four palpal segments (e.g. *Ereynetes meliponae* and *E. exilis*). This confusion arises from the presence of a minute segment appended at the end of the palp of *Ereynetes* that may be differently interpreted by authors. Three major interpretations may be advanced. Two are new and proposed by the authors who disagree in their interpretations.

The first interpretation was advanced by Booth (1984) who recognized five palpal segments he named the trochanter, femur, genu, tibia and a minute tarsus. This interpretation does not accord with that prevailing for Tydeidae, since Booth's femur corresponds to the tydeid femorogenu and his genu to the tydeid tibia. Further, Booth's hypothesis implies that the palp solenidion is located on the tibia and not on the tarsus, as usually observed in other actinedid families. Finally, his interpretation does not hold when the chaetotaxy is compared with that of Tydeidae, as discussed below.

Fain's interpretation also is predicated on recognizing five palpomeres, namely the trochanter, femorogenu, tibia, tarsus and a minute terminal segment that can only be the apotele. The minute segment bears apically what Booth (1984) called a claw-like structure, nude in the distal half, finely barbed or feathered in the proximal half. Internally, a short extension suggesting a tendon issues from the basis of the claw-like structure.

André's interpretation supposes that the palptarsus is secondarily divided into two segments, a large basal segment and a minute apical segment. This type of secondary division of the tarsus into 'false' articles is well-known in some mites and was described in detail in the genus *Tarsolarkus* (erythracarine Anystidae) by Grandjean (1952, 1954a). Such false articles differ from true articles in the absence of joints and proper muscles and their functioning is thus different. A comparative study of the *Ereynetes* palp shows that the chaetotaxy of the two terminal segments corresponds to that of the tydeid tarsus (Fig. 6A,B).

The claw-like structure corresponds to the strong ventral seta, *v*, observed in Tydeinae (and also in Eupodidae). The penultimate segment of the palp bears the solenidion and three setae which correspond to setae *l′*, *l″* and *d* in *Tydeus* (Fig. 6A,

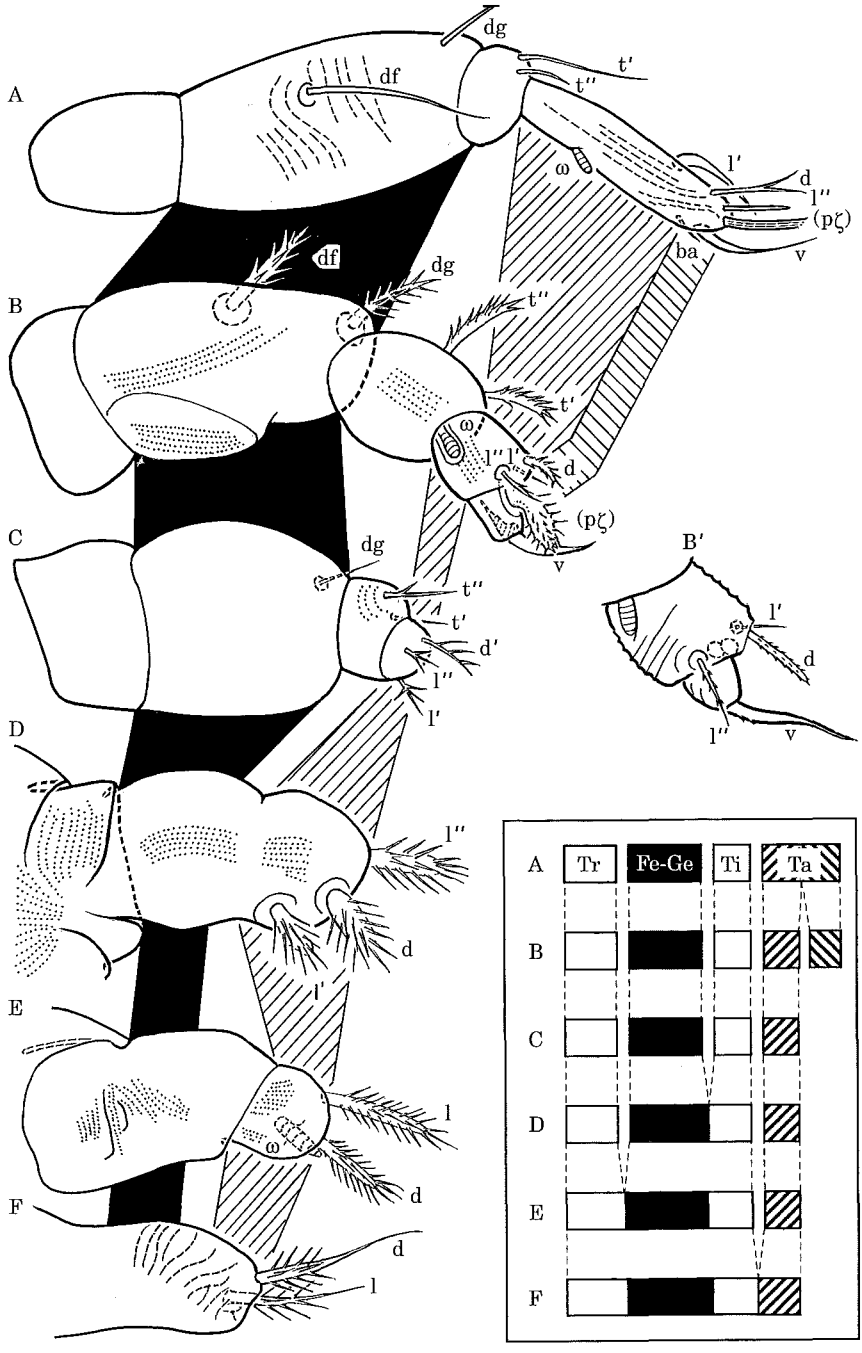


Figure 6. Evolution of the palp from Tydeinae to Ereynetidae. (A) *Tydeus* sp. (Tydeinae); (B) *Ereynetes* (*Gymnereynetes*) sp. (Ereynetinae); (B′) *idem* with prorals broken (dissected specimen); (C) *Hydranetes tropisternus* (Paratype; Ereynetinae); (D) *Boydaia clavata* (Holotype; Speleognathinae); (E) *Xenopacarus africanus* (Lawrencarinae); (F) *Lawrencarus hylae afrixali* (lectotype; Lawrencarinae). Antiaxial (A–C), ventral (D) and dorsal (E–F) views. Palpomeres are identified by patterns detailed in insert. Abbreviations in insert: Tr, trochanter; Fe-Ge, femorogenu; Ti, tibia; Ta, tarsus or, alternately a combination of the tarsus and apotele, depending on the interpretation (see text for further explanation).

B). The seta *ba*, minute in *Tydeus* but well-formed in more primitive genera, would be missing or vestigial in *Ereynetes* depending on the species. The penultimate segment bears also a dorsal eupathidia corresponding to the tydeine double eupathidia (*p*). In the *Anereynetes* illustrated in Figure 6B and in *E. macquariensis*, the dorsal eupathidia is a complex structure seemingly made of two elements, one leaf-like, and the other spoon- or fanlike, covering the tip of the palp. In a dissected palp the dorsal eupathidia of which was broken, we were able to distinguish the double base of (*p*) (Fig. 6B′); the double base seems to be located internally, at the tip of the penultimate segment, within the joint fold. In other species, the eupathidia is simply barbed or ciliate as other setae and may seem to arise from the intermediate area joining the two terminal segments. We do not rule out that the seta lost its eupathidial character in some more evolved *Ereynetes* prior to the loss of the terminal segment.

If the third hypothesis is accepted, the genus *Ereynetes* may be practically described as having a five-segmented palp but it should be remembered that the two terminal segments form only one true article or palpomere, namely the tarsus. It must be emphasized that the comparative study of chaetotaxy underlying hypothesis 3 does not necessarily preclude hypothesis 2. A fourth hypothesis would retain the homologies of setae outlined in Figure 6 but assume that the terminal segment of Tydeinae represents a composite made of the palptarsus and the apotele. The two segments would recover their identity in *Ereynetes* prior to the loss of the apotele.

Whatever the hypothesis chosen, all *Ereynetes* species (even those described as having four palpal segments, such as *E. meliponae*) and *Pseudotydeus perplexus* thus have five palpal segments. This number is four in all other Tydeidae and in the ereynetid genus *Hydranetes*. However, even if they have the same number of palpomeres, the palp of *Hydranetes* is not entirely comparable to that of Tydeinae. The palptarsus of *Hydranetes* is minute and much shorter than the palptibia, whereas the tarsus is at least as long as the tibia in Tydeinae. Its chaetotaxy is drastically reduced compared to that of Tydeinae (only three setae). If we compare the palptarsus of *Hydranetes* to that of *Ereynetes*, the former corresponds to the proximal palptarsus of the latter (Fig. 6). This suggests that the evolution from the type found in *Ereynetes* to that of *Hydranetes* involved the loss of the minute terminal segment, which represents the distal part of the palptarsus or the apotele. The palptarsus of *Hydranetes* is only homologous with the proximal part of the palptarsus of Tydeinae.

Further evolution in Ereynetidae involved a reduction in the number of palpomeres with fusion between the femorogenu and the tibia, a situation found in *Riccardoella*, *Xenopacarus* and *Boydaia*. This was followed by a fusion between the femorotibia and the trochanter, as observed in *Batracarus* and *Neoboydaia*. Finally, a complete fusion of all segments occurred in some Lawrencarinae (*Lawrencarus*) and Speleognathinae (*Speleognathus*). This evolution is gradual as shown in *Xenopacarus africanus*, which has a well-formed palp comprising two free articles and two others that are incompletely fused. The number of segments does not vary during the ontogeny of Tydeoidea and no case of ontogenetic bipartition has been reported.

The number of palpal segments in Ereynetidae was first coded as an ordered character following the trend outlined in Figure 6 and recoded as five two-state characters (characters 36–40 in Table 1).

The Iolininae have also undergone a regression of the palp, since it comprises only one article. Unfortunately, no intermediate form with more than one palpomere is known in this subfamily. The scenario leading to such a regression might be different from that of Ereynetidae, since the palp still bears a terminal eupathidia

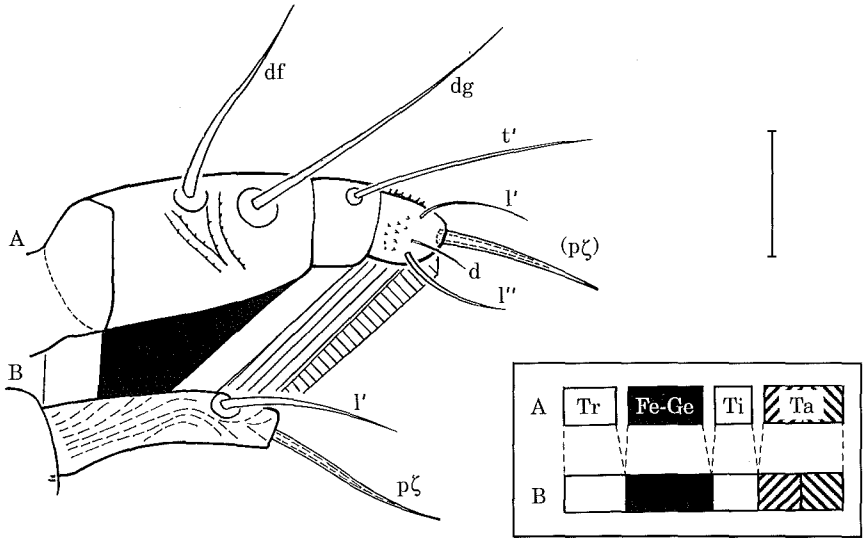


Figure 7. Evolution of palp from Pronematinae to Iolininae. (A) *Proctotydaeus schictocercae* (Pronematinae); (B) *Iolina nana* (Iolininae). Palpomeres are identified by same patterns as in Figure 6. Setae *l'* and *d* are especially thin in *Proctotydaeus* and are probably missing on palp of Iolininae. Dorsal views. Scale bar = 10 μm.

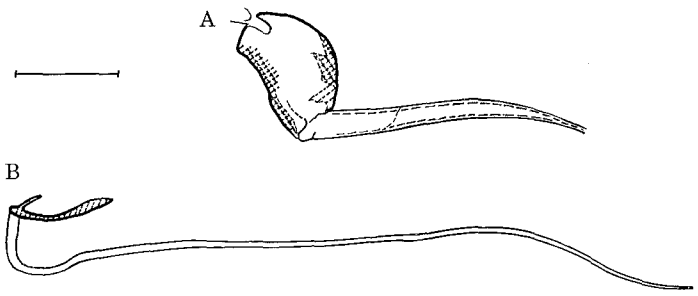


Figure 8. Evolution of movable digit of chelicerae, from stylet-like (A) to whip-like (B) type digit. (A) *Proctotydaeus schistocercae* (Pronematinae); (B) *Iolina nana* (Iolininae). Antiaxial views. Scale bar = 10 μm.

as in Tydeinae and Pronematinae and not the three setae, *l'*, *l''* and *d* which usually are observed in Ereynetidae with a regressed palp. A comparative study with the *Proctotydaeus* palp (Fig. 7) suggests that the iolinine palp regression may have followed the trend outlined in Figure 6 but skipped the first two steps, namely the division of the terminal segment and the loss of its distal part. Characters 36–40 were coded accordingly.

Chelicerae

The movable cheliceral digit (character no. 41) is stylet-like in all tydeoid subfamilies except in Iolininae, where it extends and becomes whip-like as in the Tetranychoidea (Fig. 8).

Number of calyptostases

The next three characters (42–44) refer to the presence of calyptostatic nymphs in the ontogeny. Fain (1963) thought that the tritonymph was missing in the Lawrencarinae, but all three nymphs of *Batracarus hylaranae* were discovered in the type-series and described by André & Fain (1991). A comparative study of the type material of *Xenopacarus africanus* reveals that it contains tritonymphs, characterized by the presence of 12 setae on tarsus I and 3–4 aggenitals, and protonymphs characterized by having only five tarsal setae on tarsus IV and lacking aggenitals. In *Lawrencarus ewerí*, a similar study shows that there are trito- and deutonymphs in collections. A tritonymph of *L. afrixali*, with four aggenitals, was described by Fain (1961) but misidentified as a deutonymph. In conclusion, we know all the nymphs of the genus *Batracarus* but are missing the deutonymph in *Xenopacarus*, and the protonymph in *Lawrencarus*. Therefore, we may reasonably assume that all nymphs are present as mobile forms in the ontogeny of Lawrencarinae contrary to Speleognathinae, in which they are all calyptostatic. Each nymph is coded separately for calyptostasy, since any one of them is likely to become calyptostatic independently of the others (Grandjean, 1957; André, 1988a).

Claparède's organ and rhagidial organ

The last character was only used for outgroup comparison. Members of the Eupodoidea, the outgroup, are characterized by having a rhagidial organ (character no. 45) which is missing in Tydeoidea.

Phenetic clusters

Based on the characters studied, two major clusters are identified; the Tydeidae together with the Iolinidae, and the Ereynetidae (Fig. 9). A second partition divides the Ereynetidae into two groups, the Ereynetinae on the one hand and the two other subfamilies on the other. Further partitionings lead to the successive recognition of several subgroups within the first major cluster, first the Meyerellinae and Triophtydeinae, then a cluster composed of the Tydeinae, Pretydeinae and Australotydeinae; finally, the Pronematinae are separated from Iolinidae. Partitioning into seven clusters divides the Ereynetidae into the three subfamilies after the relocation of the genus *Hydranetes*. This relocation seems to indicate that the family Ereynetidae is composed of three major groups rather than two.

Cladistic analyses

Ancestral states

Outgroup analysis estimates the state of a character in the most recent common ancestor of the ingroup and outgroup. Results of the outgroup analysis are given in Table 1.

Testing the basic assumptions

If the genus *Pseudotydeus* is disregarded, four most parsimonious trees are found with the Wagner parsimony method (length 83, CI 53, RI 89). If *Pseudotydeus* is

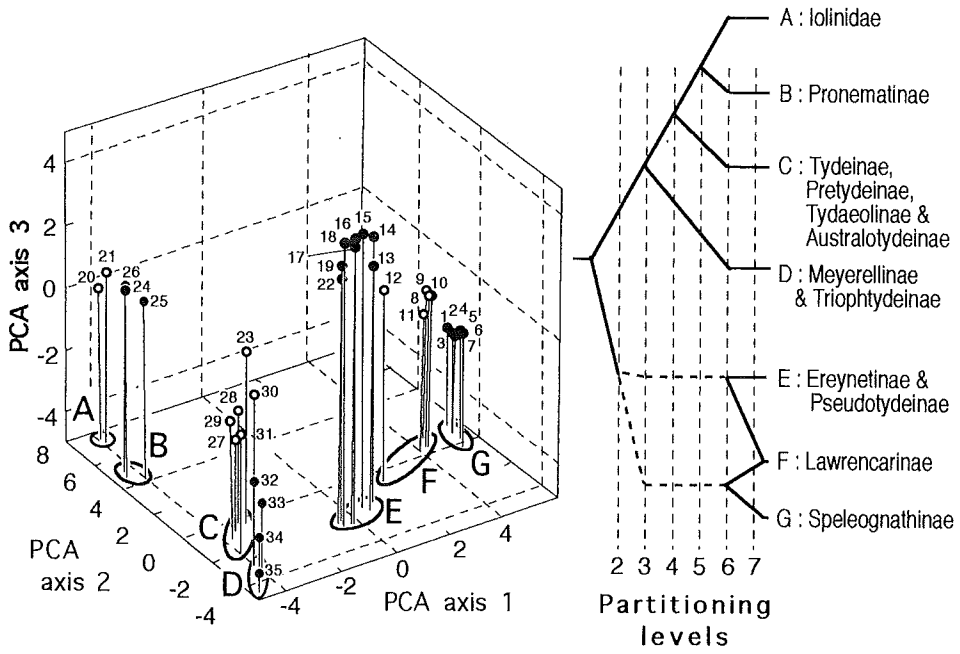


Figure 9. The first three axes of a PCA applied to the Basic Matrix (BM) with clusters recognized by *k*-means partitioning method (A) and hierarchical structure of data (B). The small numbers in (A) refer to the taxa numbers given in Table 2.

included, then 24 most parsimonious trees of 84 steps are found (length 85, CI 52, RI 88), since the genus may be placed in many different positions, just before, just after or within other Ereynetinae. The semi-strict consensus tree is given in Figure 10A.

Most tydeid subfamilies may be easily identified and combined with a sister-subfamily to form distinct clades. There are, however, two exceptions: Iolinidae cluster with Tydaeolinae and Pronematinae, while *Pseudotydeus* emerges together with the Ereynetinae. Last, the family Tydeidae appears to be paraphyletic.

In contrast, Ereynetidae are monophyletic but, within the family, only Speleognathinae appear to be so. Indeed, the genus *Hydranetes* is not placed with other Ereynetinae, and *Xenopacarus* and *Batracarus* are not grouped with *Lawrencarus*.

Some characters follow unexpected transformation patterns (Table 1). For instance, setae *l4* (character no. 6) becomes again bothridial in some Lawrencarinae after becoming normal in *Hydranetes* and *Xenopacarus*. Male eugenitals (character no. 12) undergo several reversals. While they are ancestrally present in the Ereynetinae, they disappear in most Lawrencarinae and Speleognathinae, only to reappear in *Lawrencarus* 2 and *Astrida*. Femur IV (character no. 32) follows the same pattern, being divided in the ancestor, becoming simple in Tydeinae and Pronematinae and then becoming divided again in *Proctotydaeus*. Trochanteral II (character no. 33) follows a similar pattern, with five changes and two reversals (it reappears in Speleognathinae after being absent in Lawrencarinae and disappears again in *Boydaia* 2). Solenidion φI (character no. 26) disappears in most Tydeinae and Pretydeinae to reappear in *Pretydeus*.

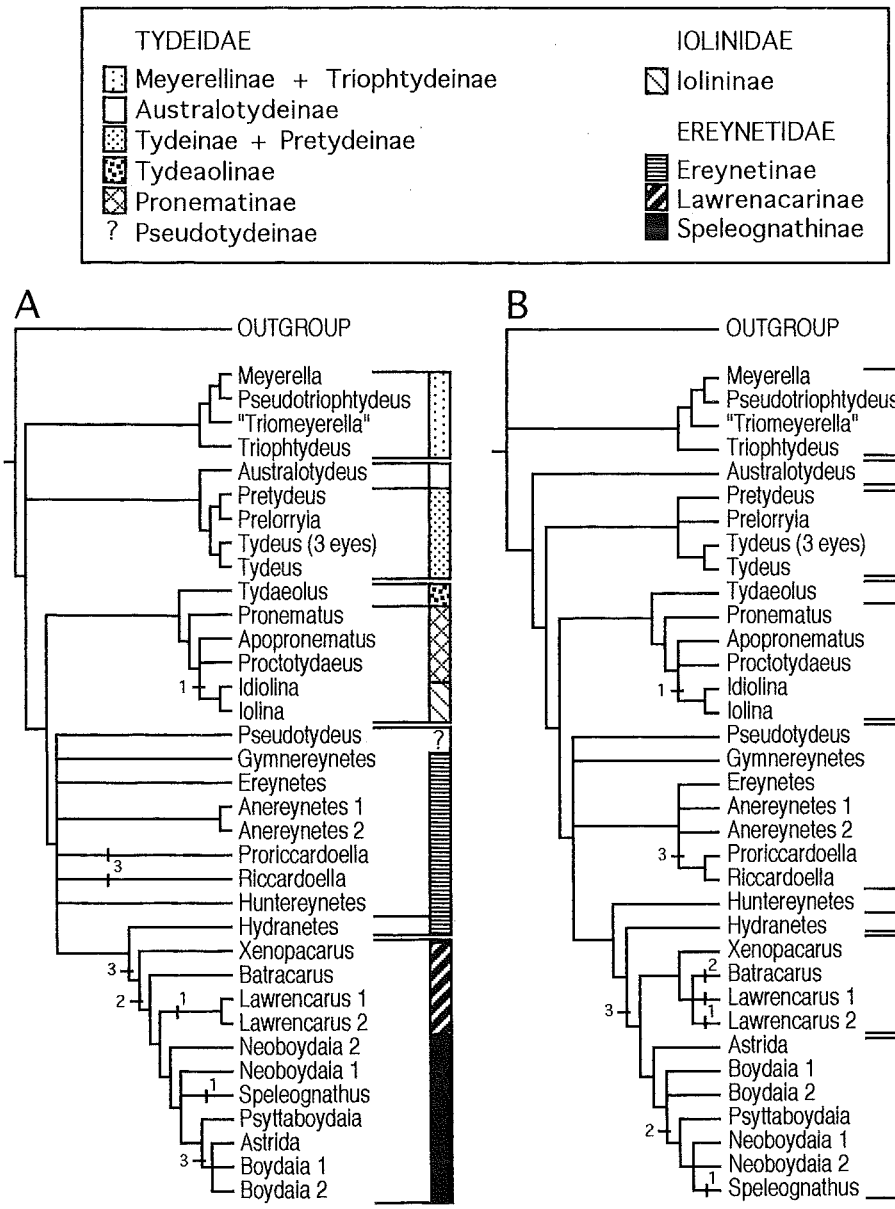


Figure 10. Semi-strict consensus trees for the Basic Data matrix (BM) under Wagner (A) and mixed (B) parsimony assumptions. Under the mixed assumption, the Camin–Sokal parsimony method was applied to phanerotaxy and poroidotaxy. Numbers indicate the number of palpomeres present in a clade beyond the dash. All subfamilies are identified by a corresponding pattern. The family classification of the legend follows the traditional presentation.

However, the most surprising evolution implied by cladogram in Figure 10A is that of the palp. The number of palpomeres is equal to or greater than four, unless indicated otherwise along the branches of the cladogram. The terminal group at the bottom of cladogram comprises three taxa, *Astrida*, *Boydaia* 1 and *Boydaia* 2, all

of which have a 3-segmented palp. Reconstructing the palpal evolution shows that this clade derives from an ancestor with a 2-segmented palp. In other words, the cladogram of Figure 10A implies that the fusion of palpomeres would be reversible.

If Camin–Sokal parsimony is applied to phanerotaxy (chaeto- and solenidiotaxy) and poroidotaxy (hypothesis 2, mixed parsimony), and if the genus *Pseudotydeus* is disregarded, the number of most parsimonious trees amounts to 8 (length 86, CI 51, RI 88), corresponding to $2 \times 2 \times 2$ permutations (permutations involve the position of *Prelorryia*, *Gymnereynetes* and *Batracarus*). When included, the different positions of *Pseudotydeus* are the same as under previous hypothesis. Trees are longer than those found under the Wagner parsimony (length 88, CI 50, RI 91). However, all permutations are of minor importance and do not affect the composition of major clades (Fig. 10B). The Tydeidae are still paraphyletic, but *Australotydeus* forms a clade distinct from the set Tydeinae-Pretydeinae. Among the Ereynetidae, both Lawrencarinae and Speleognathinae form distinct clades. Although the new set of hypotheses does not involve the palpal evolution, the new cladograms differ from previous ones by the progressive fusion of palpomeres in four separate clades and the absence of reversals (Fig. 10B).

Character evolution

The phylogram shown in Figure 11 is derived from a cladogram found under assumption 2 (Camin–Sokal parsimony method applied to phanerotaxy and poroidotaxy). This is only one of the possible scenarios, due to ambiguity in some characters. The number of state changes varies from 1 to 5 (Table 1). The characters that change most often are the presence/absence states involving eugenital setae in males (character no. 12), seta *tr II* (character no. 33), and solenidion φI (character no. 26). Characters with only one state change include the shape of the dehiscence line δ (character no. 1); duplication of genital acetabular discs (character no. 17); extension of the cis-acetabular area (character no. 19); presumed mating (character no. 20); deformation of tarsus I (character no. 25); nude genua (character no. 31); division of terminal palp segment (character no. 36); calyptostatic nymphs (character nos 42–44); and loss of lateral eye-spots (character no. 3), lyrifissures *ia*, *im* and *ih* (character nos 7, 8, 10), setae *ge* (character no. 11), *eu* in females (character no. 13) and *tr III* (character no. 34), genital acetabula (character nos 14, 15) and apotele I (character no. 23).

Simple character state reversals occur six times in the analysis and multiple reversals occur only once. Femur IV (character no. 32) is divided at the base of the phylogram, becomes simple before the node separating the Australotydeinae, is again divided in *Proctotydaeus* and in Ereynetinae, and finally fuses again in Lawrencarinae and Speleognathinae.

Ontogenetic approach

The partitioning method previously used with the basic matrix (BM) can be applied to any stase, such as larvae (Fig. 12A) and adults (Fig. 12B). The dendrogram for larvae recalls that of Figure 9B regarding the distinction between the Ereynetidae and other Tydeoidea, but differs in that Iolininae and Pronematinae are clearly separated from the other Tydeidae. Minor discrepancies occur between classifications

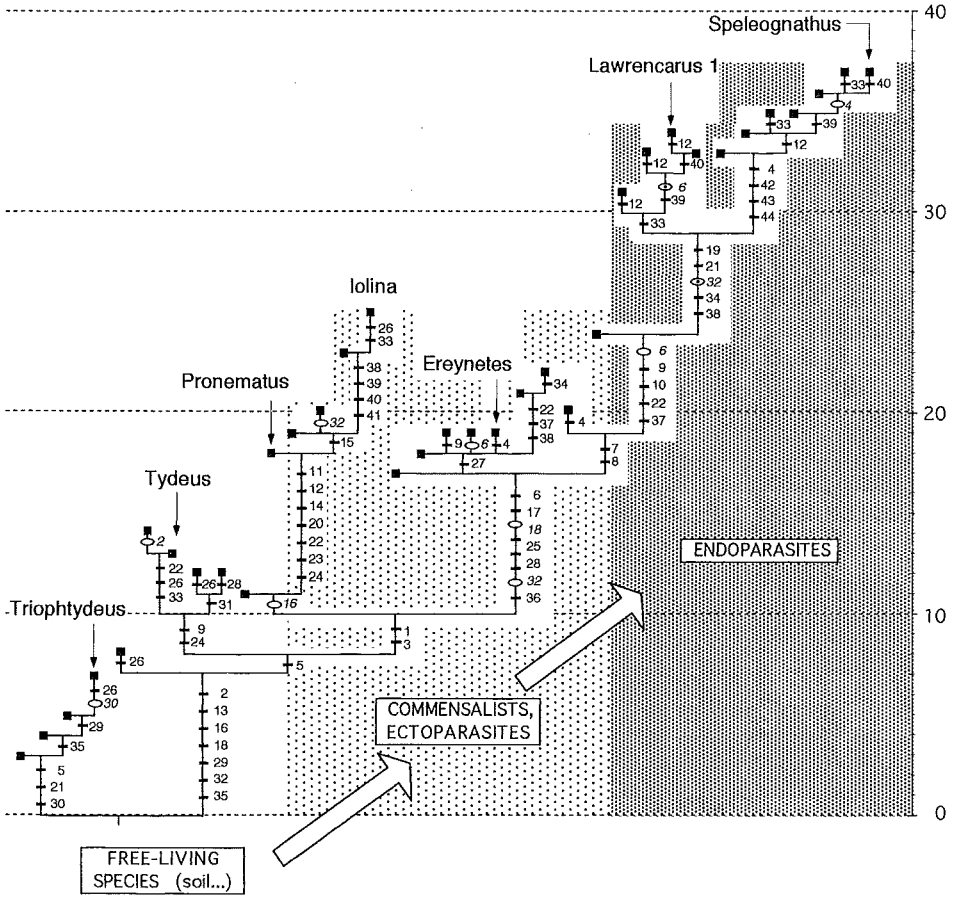
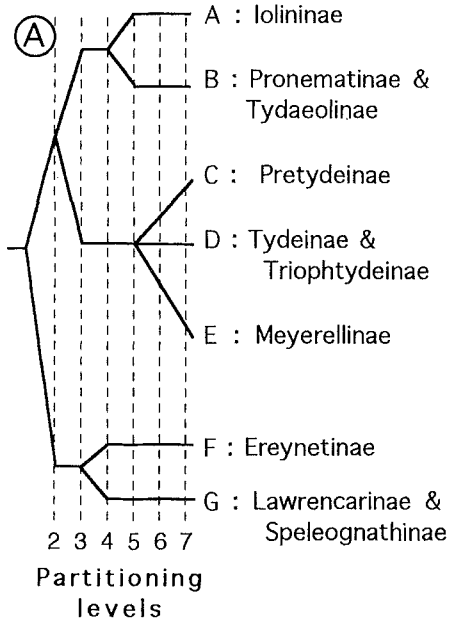
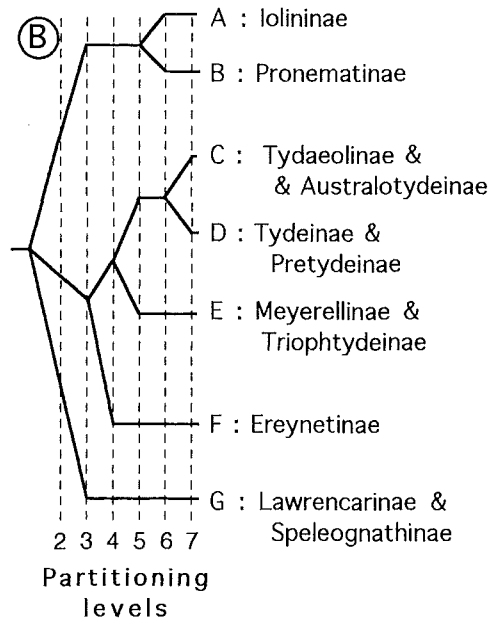


Figure 11. Phylogram derived from a cladogram found under the Camin–Sokal parsimony assumption applied to phanerotaxy and poroidotaxy. Numbers refer to characters listed in Table 2; figures in italics indicate reversals. Dashes indicate character state changes, while open and dotted ellipses designate first and subsequent reversals, respectively.

based on larvae (Fig. 12A) and adults (Fig. 12B), involving the position of Tydaeolinae, Triophtydeinae and Ereynetinae. These differences may be explained through the study of ontogenetic trajectories (Fig. 13). Tydaeolinae follow a special trajectory, intermediate between those of Tydeidae and Pronematinae-Iolinidae and are thus difficult to classify precisely. The discrepancy concerning the Triophtydeinae, in which the larvae are most similar to Tydeinae, but the adults are closer to those of Meyerellinae (Fig. 12A,B) is easy to understand, since the trajectory of *Triophtydeus* does not parallel those of the two subfamilies but jumps from one bundle to another. Lastly, the curvature of ereynetine trajectories is more pronounced than those of Lawrencarinae and they tend to curve inward towards the Tydeidae.

Minor discrepancies between classifications based on larvae and adults are due to the 'explosion' of ontogenetic trajectories. Trajectories all start from the same point, but undergo a spectacular expansion into the character space as they extend. This expansion may be evaluated for each stase through a dispersion index around





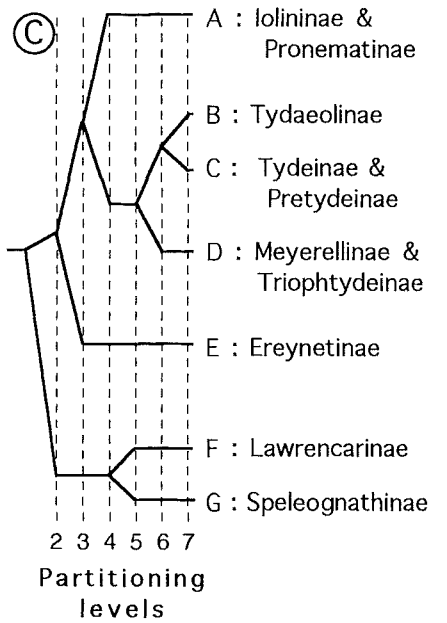


Figure 12. Phenetic clusters resulting from *k*-means partitioning method applied to larvae (A), adults (B) and the set of all stases handled as a combined matrix (OM) (C). Minor discrepancies between classifications A and B involve the position of Tydaeolinae, Triophtydeinae and Ereynetinae. The four major clusters recognized in C correspond to the four major bundles of ontogenetic trajectories outlined in Figure 13.

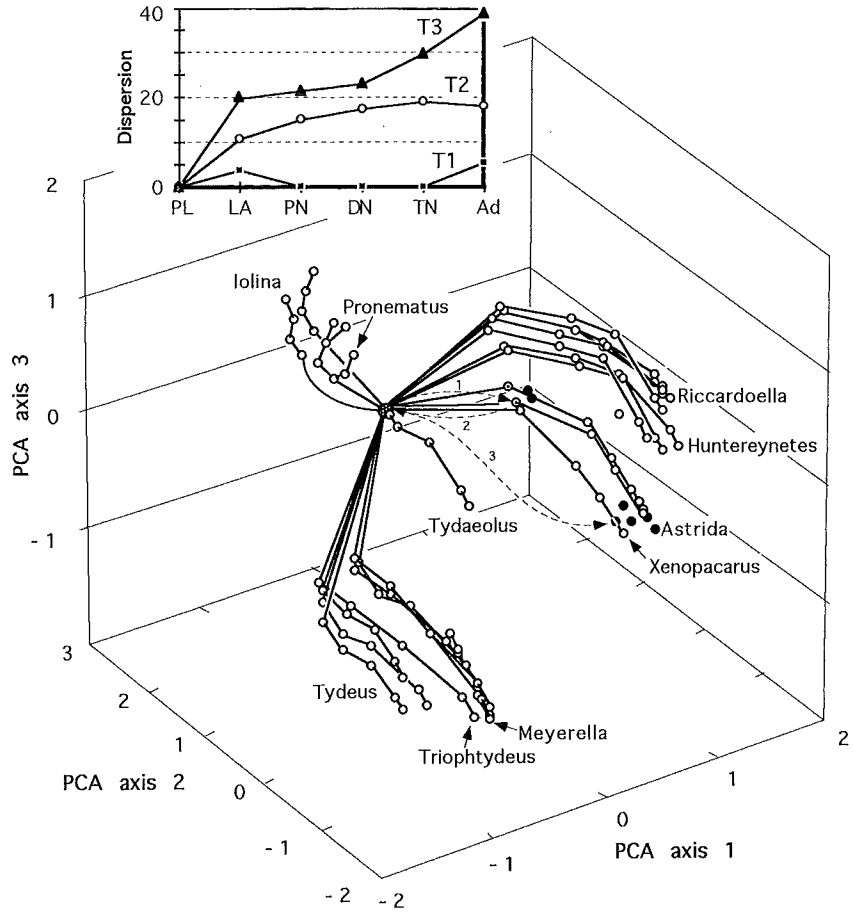


Figure 13. Ontogenetic trajectories of Tydeoidea resulting from a PCA applied to the original 41-dimensional character space. Small numerals along the dotted lines indicate the complex trajectory of the taxon *Speleognathus*. (●) stases of Speleognathinae; (⊙) points common to both Speleognathinae and Lawrencarinae. The insert shows the dispersion of stases around the bundle axis in Speleognathinae (T1), the other Ereynetidae (T2) and the other Tydeoidea (T3). Dispersion index was measured by the mean of squared distance of each taxon to the centroid of its group.

the centroids of bundles and, except in Speleognathinae, the degree of dispersion increases with the level of ontogeny (insert in Fig. 13).

To overcome these discrepancies, the *k*-means partitioning method was applied to the ontogenetic trajectories themselves (Fig. 12C) and led to the recognition of the four major bundles of trajectories outlined in Figure 13: (1) the Lawrencarinae and Speleognathinae, (2) the Ereynetinae, (3) the Iolininae and Pronematinae, and (4) the other subfamilies. The other subfamilies may be divided into three subgroups: the Tydaeolinae, the Tydeinae and Pretydeinae, and the Meyerellinae and Triophtydeinae.

The ontogenetic trajectories of Speleognathinae deserve special comment because they are not straight or slightly curved like those of other Tydeoidea. Instead, they draw a 'Z' as suggested by the dotted lines in Figure 13. Even if their shape, length

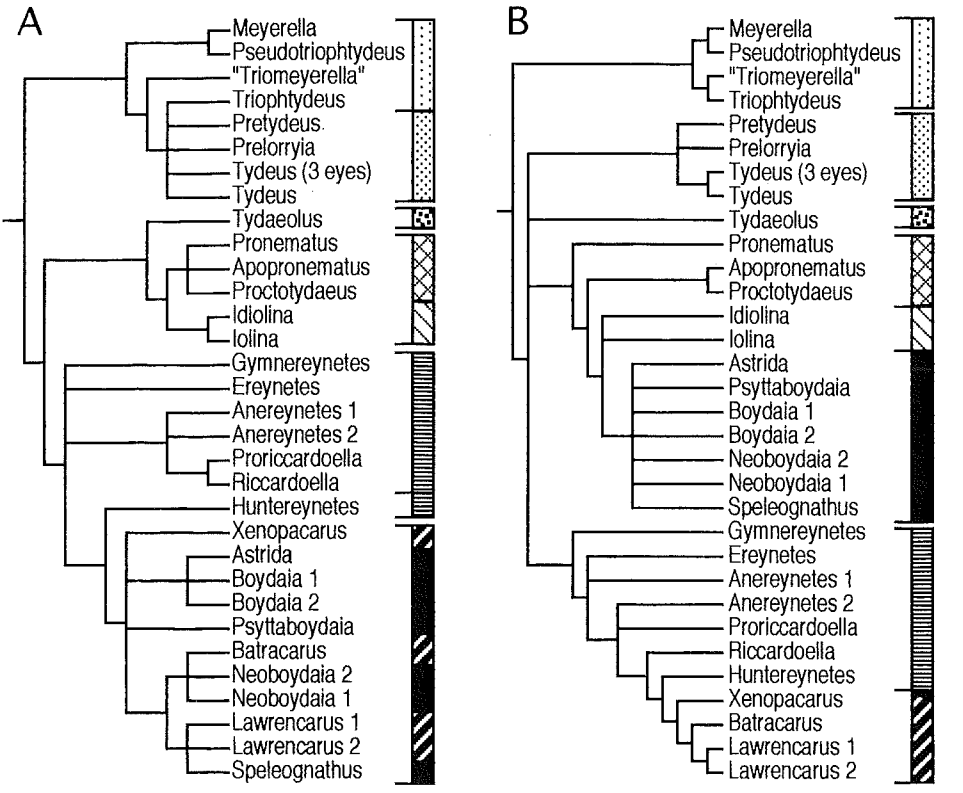


Figure 14. Semi-strict consensus trees for larvae (A) and deutonymphs (B) under the Camin–Sokal parsimony assumption applied to phanerotaxy and poroidotaxy. All subfamilies are identified by a corresponding pattern, as in Figure 10.

and complexity are different or greater than those of other Tydeoidea (see discussion in André, 1991), they remain in the vicinity of the trajectories of Lawrencarinae, hence the two subfamilies are closely related. The presence of three calyptostatic nymphs in Speleognathinae explains the special shape of their ontogenetic trajectories and the lack of increase of the dispersion index with the level of ontogeny (T1 in the insert of Fig. 13).

All stase subsets also were subjected to cladistic analyses under assumption 2 (Camin–Sokal parsimony method applied to phanerotaxy and poroidotaxy). In the absence of an outgroup, character-state polarities were considered to be the same as those obtained from previous analyses. The consensus cladogram (Fig. 14A) obtained from the analysis of LDS (Larva Data Subset) presents some differences from that of Figure 10B. The first clade identified near the root is composed of Meyerellinae, Triophtydeinae, Tydeidae and Pretydeinae. Next, endoparasitic larvae, namely Lawrencarinae and Speleognathinae, are confused.

The analysis of deutonymphs (matrix DDS) yields a more consistent result when the Speleognathinae are excluded from DDS. As in the global analysis, Triophtydeinae and Meyerellinae form a monophyletic group, as do Pretydeinae and Tydeinae, Pronematinae and Iolinidae, and Lawrencarinae. Only the Ereynetinae are split into many clades. When the Speleognathinae are included, they are considered

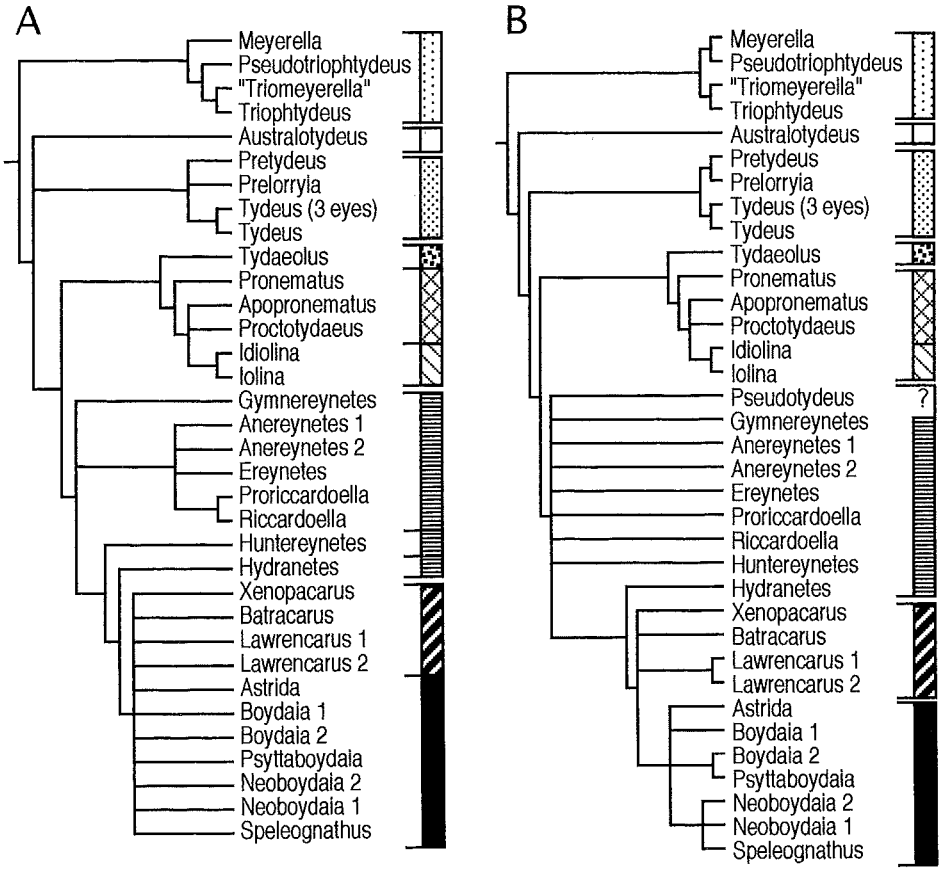


Figure 15. Semi-strict consensus trees for adults (A) and the set of all stases handled as a combined matrix (matrix OM, 35 taxa × 169 characters) (B) under the Camin–Sokal parsimony assumption applied to phanerotaxy and poroidotaxy. All subfamilies are identified by a corresponding pattern, as in Figure 10.

the sister-group of the genus *Iolina* (Fig. 14B). This result is not surprising: speleognathin mites are calyptostatic and present forms that are deprived of characters (e.g. no setae, no lyrifissures); they are thus logically classified close to the group poorest in setae, lyrifissures and palpomeres.

The analysis of adults yields cladograms that are close to the traditional classification and practically identical to cladograms based on the BM. The major difference between the semi-strict consensus tree for adults (Fig. 15A) and that based on BM (Fig. 10B) is that Speleognathinae are mixed with Lawrencarinae.

Strictly speaking, there is no real opposition between cladograms based on larvae (Fig. 14A) and adults (Fig. 15A). Discrepancies concern only the monophyly of the clade Meyerellinae–Triophtydeinae–Pretydeinae–Tydeinae, which was found in larvae but not in adults. To refine our approach and possibly overcome these discrepancies, a final cladistic analysis was applied to the overall 35 taxa × 169 character matrix (OM). The consensus cladogram (Fig. 15B) is close to that of Figures 10B and 15A and does not involve any confusion between Speleognathinae and Lawrencarinae. Still questionable is the monophyly of Lawrencarinae.

DISCUSSION

Character-state polarity

The character-state polarities defined after the outgroup analysis mostly agree with the ancestral state coded *a priori* (see Table 1). The evolution of organotaxy (chaetotaxy, etc.) follows the same trends as those observed in other mites such as Oribatida (Travé *et al.*, 1996), Actinedida (e.g. Coineau, 1974) and Gamasida (Chant, 1993; Sabelis *et al.*, 1994). The only discrepancies concern the median 'eye-spot' (character no. 2) and seta *l*2 (character no. 5).

Based on outgroup analysis, the plesiomorphic state of character no. 2 would be the absence of an eye-spot in the ancestor of Tydeoidea, yet the primitive mites had three pairs of eyes, comprising two laterals and one median (Grandjean, 1958; Coineau, 1974). This implies that the median eye would have first disappeared in the tydeoid ancestor, and subsequently reappeared in Meyerellinae and Triophtydeinae. This scenario with multiple reversals is clearly supported by the reappearance of a median eye-spot in a Sicilian population of *Tydeus*.

As for the second discrepancy, the absence of *l2* as the ancestral condition completely contradicts the trends outlined above and our hypothesis 2 (Camin–Sokal parsimony, applied to chaetotaxy). In this context, the reappearance of seta *l2* in *Australotydeus* may be interpreted as an autapomorphy.

From phenetics to phylogenetic taxonomy

The current classification of Tydeoidea involves three families and 12 subfamilies (Table 2). Whatever the approach chosen, two major changes emerge from our analyses. First, the subfamily Pseudotydeinae, comprising the single species *Pseudotydeus perplexus*, must be transferred to the family Ereynetidae. Indeed, the genus *Pseudotydeus* has an ereynetal organ, a five-segmented palp, the duplex *k*″-*l*″ on tarsus I as in the genus *Ereynetes*. Due to the presence of seta *d* on tibia I which has been lost in all other Ereynetidae, and the absence of posterior trichobothria, it is probably more primitive than the genus *Ereynetes*.

The second major change concerns the two subfamilies Pronematinae and Iolininae, which are sister-groups according to all the analyses performed. Both share the palpian evolution of leg I, a regression of the genital area (reduction of genital setae and acetabula), and morphological features in males indicative of mating. Currently, the two subfamilies are placed in two different families (Pronematinae within the Tydeidae and Iolininae within the Iolinidae), a situation that is no longer acceptable.

These two major differences apart, the results produced by the phenetic approach reflect the current classification, especially that based on the Basic Data Matrix. In other words, the present classification relies on the overall similarity between taxa, especially that between adults, supplemented by ontogenetic peculiarities such as the calyptostatic nymphs of Speleognathinae. However, the current classification does not obey the new paradigm underlying the cladistic approach. Indeed, whatever the hypothesis selected, the extant family Tydeidae appears to be a paraphyletic assemblage of early derivative tydeoid mites. In this context, Baker's (1965) statement that Tydeidae are difficult to characterize is quite meaningful. This situation parallels

that of Oribatida, which gave rise to the Astigmata (OConnor, 1984; Norton, 1994), and is likely to recur in the future whenever a cladistic approach is applied to a group of mites. It should be emphasized that the paraphyly of Tydeidae would have been overlooked if the Ereynetidae had not been included in the analysis.

In contrast, the Ereynetidae form a monophyletic group derived from an ancestral tydeid stock and are well characterized by their ereynetal organ, as already suggested by Fain (1962b, 1964b), and double genital discs. Within the Ereynetidae, the Speleognathinae also represent a monophyletic group, at least when a global analysis is carried out and their calyptostatic nymphs are taken into account. Lawrencarinae are their sister-group and, depending on the analysis, also form a monophyletic group. In contrast, Ereynetinae appears to be paraphyletic in all the cladistic analyses performed.

Naming of higher groups

If paraphyletic families are to be rejected, the current classification of Tydeoidea has to be rearranged. As already stressed in the previous section, the genus *Pseudotydeus* is close to the genus *Ereynetes*. The Pseudotydeinae are thus considered a junior synonym of Ereynetinae.

The family Iolinidae including only two genera, *Iolina* and *Idiolina*, share most of the apomorphic characters of Pronematinae (palpian evolution, etc.) and belong to the same lineage. From a traditional point of view, the Pronematinae might be merely considered a junior synonym of Iolinidae. However, in terms of phylogenetic relationships, the Iolinoidea as described by Pritchard (1956) are defined monophyletically by two synapomorphic characters not shared by other Pronematinae: the whip-like chelicerae and one-segmented palps. The Iolinoidea appear to be a highly specialized lineage derived from a pronematin ancestral stock, and deserve to be recognized as such. Under apomorphy-based definitions (de Queiroz & Gauthier, 1990, 1992), the Iolinidae and Pronematinae are not synonymous and we suggest that the Iolinoidea be again lowered in hierarchic rank and considered a subfamily close to the Pronematinae.

Based on the cladistic analyses (Figs 10, 14, 15), we present a new classification of the 11 remaining subfamilies into four families (Fig. 16). All families, except the Tydeidae, are monophyletic and characterized by an apomorphy, usually unique to them. Most characters used to identify the families are observable on any mite and on any mobile stase (thus excluding the calyptostases). Two subfamilies—Pronematinae and Ereynetinae—appear to be paraphyletic, but their nomenclatural status is maintained, pending a detailed analysis of their respective genera.

The Meyerellidae include the Meyerellinae and Triophtydeinae. These mites have few apomorphic characters. They are, however, unique in having three eyespots, due to the reappearance of a median element. The loss of epimeral seta *3d* in free-living forms is infrequent and, the Meyerellinae apart, has been observed only in endoparasitic Lawrencarinae and Speleognathinae. The present division into two subfamilies should be confirmed through future cladistic analyses. The family Tydeidae is characterized by the loss of eugenitals in females and a reduction of the cis-acetabular area. It comprises the Australotydeinae, Pretydeinae and Tydeinae and, due to the inclusion of the Australotydeinae, is paraphyletic (at least, under hypothesis 2).

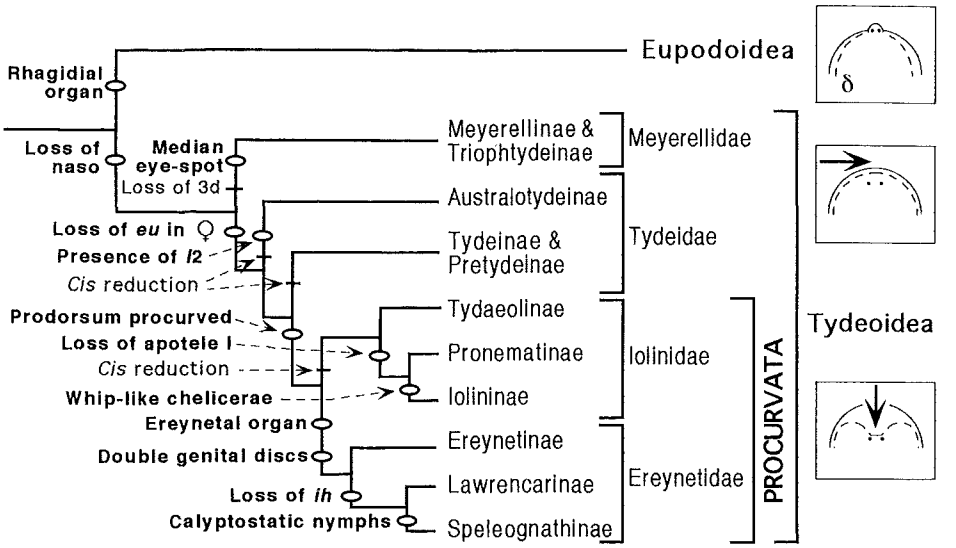


Figure 16. Cladogram of tydeoid subfamilies with corresponding apomorphic traits and the resulting classification. Open ellipses and bold text designate apomorphic traits with only one character change. The three schemes at the right show the evolution of the shape of the dehiscence line, δ, and the position of prodorsal setae *ve*, from the Eupodoidea with a naso (top) to the Procurvata with a procurved dehiscence line, passing through the intermediate prodorsum with a recurved line and no naso.

The remaining Tydeoidea, designated as the Procurvata in Figure 16, are characterized by a procurved prodorsum. The family Iolinidae is enlarged to encompass the three subfamilies Tydaeolinae, Pronematinae, and Iolininae, characterized by a reduction of the cis-acetabular area. Furthermore, the subfamily Pronematinae is characterized by the loss of apotele I while Iolininae are characterized by the whip-like chelicerae and one-segmented palp, as proposed by Pritchard (1956).

The family Ereynetidae is characterized by the ereynetal organ (Fain, 1962b, 1964b), and by double genital discs. As explained in the introduction, the subfamilies Ereynetinae and Lawrencarinae had to be enlarged to include species with no posterior bothridia. This character can no any longer be used to discriminate the subfamilies, and the Lawrencarinae are now characterized by the loss of lyrifissure *ih*. Lastly, the Speleognathinae are unique in having three calyptostatic nymphs.

If we compare the Tydeoidea to its sister-group, the Eupodoidea (Fig. 16), there is a trend from the Eupodoidea with a naso on the prodorsum to the Procurvata which have a procurved dehiscence line, passing through an intermediate prodorsum with a recurved line and no naso. [Schiess (1981) used the term 'naso' to designate the part of the prodorsum overlying the gnathosoma in some Tydeinae. As already noted by Kazmierski (1989a), this is inconsistent with normal usage.] If we suppose that the presence of a naso is a plesiomorphic character in Actinedida, as discussed by Coineau (1974), then this trend consists of a backwards movement of the prodorsal integument, resulting in the disappearance of the naso, the deformation of the dehiscence line and the posterior migration of setae *ve* towards the furrow *das*. To confirm this hypothesis, it will be necessary to enlarge the scope of this study to include related superfamilies.

We would like to stress that characters selected in Figure 16 are key-characters, which may be supplemented by others. For instance, it is possible to recognize the four families by observing only tarsus I and the combination of three characters outlined in Figure 4. Each of tarsi illustrated in Figure 4 corresponds to a family.

Ontogeny, heterochrony and heterostasy

Cladograms derived from the study of larvae are less resolved than that for adults. Several groups are polytomous (e.g. *Proctotydaeus–Pronematus–Parapronematus* and *Xenopacarus–Astrida–Boydaia 1–Boydaia 2*). Next, several subfamilies are merged together, as is the case for Triophtydeinae, grouped with Pretydeinae and Tydeinae, and for Lawrencarinae combined with Speleognathinae (Fig. 14A).

Cladograms based on adults give the 'best' results in the sense that most of the traditional subfamilies are recognized or associated with only one sister-subfamily. The Triophtydeinae are combined with the Meyerellinae, the Pretydeinae with the Tydeinae, and the Lawrencarinae with the Speleognathinae. The only 3-subfamily clade is that formed by Tydaeolinae, Pronematinae and Iolininae (Fig. 15A).

Combining all stase subsets gives the consensus cladogram illustrating in Figure 15B. Most clades correspond to subfamilies or pairs of subfamilies. The only exceptions are the Ereynetinae and Pronematinae, which appear to be paraphyletic. The result is surprisingly better than would have been expected from the conclusions of Klompen & OConnor (1989).

Discrepancies between cladograms based on different stases are also observed when a phenetic approach is applied (Fig. 12). These discrepancies result from ontogenetic trajectories (Fig. 17) which are not parallel (the case of *Triophtydeus* is exemplary, with a larva close to the genus *Tydeus* and an adult close to *Meyerella*). The problem of congruency between classifications based on insect larvae and adults was investigated early by Lenz (1926) and Emden (1927, 1957). Emden's (1927) statement that genuine incongruencies between both classifications are rare and indicate that one of the system concerned is unnatural does not hold, since it implies that ontogenetic trajectories would be necessarily parallel, an assumption clearly refuted by our data.

It appears that, within the Tydeoidea, diversification and adaptation proceeded by acceleration *sensu* Gould (1977). This is supported by the dispersion index, which increases as ontogeny proceeds (Fig. 12) and can be illustrated by several examples. The first concerns seta *l4*: When *l4* is bothridial, it is so in adult and nymphs, but never in larvae. This clearly parallels the *Camisia*-type trichobothrial regression observed in oribatid mites (Grandjean, 1939a) but in reverse. A second example is given by the ontogeny of the ereynetal organ, the solenidion of which is usually more recessed in the adult than in the larva. A third example is offered by the palpian evolution of leg I in Pronematinae and Iolininae, which have lost apotele I in all stases. However, in a few species, apotele I still persists in the larva as a vestigial segment. In other words, what started as an adult adaptation apparently flowed through into the earlier stases. In this context, it is expected that larval cladograms will be less resolved than for adults. The acceleration observed in Tydeoidea, including the parasitic Ereynetidae, contradicts the traditional view that parasites are marked by paedomorphosis (e.g. Giard, 1887; Gould, 1977; Holm,

1985). Although host resistance and immunological responsiveness have been demonstrated in many parasitic relationships (Kennedy, 1984), paedomorphosis in parasites is sometimes correlated with a protective environment and a lack of environmental selection (Holm, 1985). The acceleration observed in Tydeoidea should not be generalized to all mites. Indeed, in chigger mites (Trombiculidae), the classification is based on larvae, and their importance has been stressed to such an extent that they are considered the 'repository' of phylogeny and taxonomy by Vercammen-Grandjean (1969a), who later introduced the term nepophylogeny to describe this phenomenon (Vercammen-Grandjean, 1969b; Vercammen-Grandjean *et al.*, 1973).

Heterostasy in Tydeoidea is only expressed in the Speleognathinae, in which all nymphs are calyptostatic and not omitted as misunderstood by Matsuda (1979). In other words, there are no missing stases in Tydeoidea. The so-called 'missing' stases reported in the literature (Fain, 1963; Kuznetzov, 1980) simply reflect a failure to observe certain stases (see full discussion in André, 1992). As already outlined by Fain (1972), the succession of three calyptostatic nymphs can be used as a key character to distinguish Speleognathinae from all other Tydeoidea.

Evolutionary processes

The monophyly of all four tydeoid families as a whole remains questionable as the Meyerellidae might constitute a separate group closer to Eupodoidea than to other Tydeoidea. Enlarging the scope of this study will be the only way to resolve this problem.

That question aside, the tydeoid mites seem to have originated from a group of free-living forms that colonized the soil and related habitats (Fig. 11). Combining the phenetic and cladistic approaches makes it possible to reconstruct the history of the group and distinguish anagenesis from cladogenesis (Fig. 17). Cladogenesis is directly related to the number of species, s, described within each major clade. Anagenesis refers to the evolutionary rate, classically defined as the rate of morphological changes which is estimated here by the distance, d_m (maximum distance), measured in the character space between the early radiation point (asterisk in Fig. 17) and the terminal taxa of major clades. Because the characters used are discrete and are supposed to be independent, d_m was estimated using the Manhattan metric. From a primitive stock (asterisk in Fig. 17) were derived three major diverging lineages, the Tydeidae, Iolinidae and Ereynetidae. Tydeids form a large, homogeneous group with few apomorphic characters (in contrast to the two other clades), no remarkable specializations and a low evolutionary rate ($d_m = 10$). Many of them are soil-dwellers. Some, however, colonize plants, an example being the genus *Orthotydeus*, which is well-known on cultivated plants (e.g. grape, citrus, apple tree, tea). There may be a close association between species of this genus and their plant hosts as, in Oregon, three distinct species were collected from three different plants (P. Pratt, unpublished data). The cosmopolitan genus *Tydeus* also has been recorded from soil, but is also known from plants, rodent and bird nests, on rodents themselves and insects, and

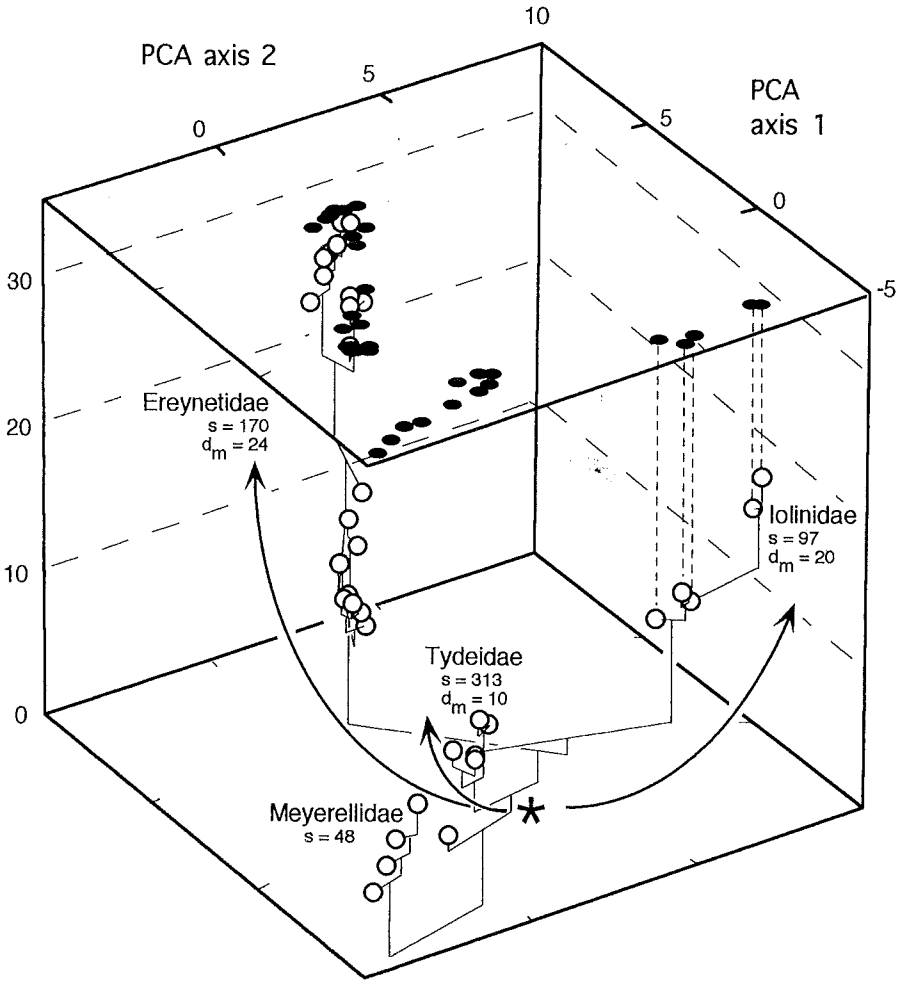


Figure 17. Diagram illustrating both cladogenesis and anagenesis in Tydeoidea. The phylogram of Figure 11 has been redrawn in a 3-dimensional space, such that the projection (dotted lines drawn for Iolinidae) of each point onto the top surface correspond to its coordinates on the first two axes of the PCA of Figure 9. The asterisk designates the early radiation zone from which the three major lineages, Tydeidae, Iolinidae and Ereynetidae, diverge. The number of component species (s) is shown for each family, along with its evolutionary rate, estimated through d_m. d_m (maximum distance is the Manhattan distance between the terminal taxon of major lineages and the early radiation point (*), measured in the character space.

in bee-hives. Tydeids are particularly drought-resistant and several species co-exist in the Namib and Chihuahuan deserts.

Early radiation within the Tydeoidea (asterisk in Fig. 17) gave rise to a second lineage, the Iolinidae, ending up with the genus *Iolina*. This lineage is characterized by the palpian evolution of leg I, the loss of genital acetabula and genitals, and by the acquisition of mating and arrhenotoky. These species are free-living on plants, in bee-hives or are associated with, or phoretic on, insects.

The third lineage to emerge from this radiation was the Ereynetidae. Ereynetinae

mostly comprise free-living forms or ectoparasites on molluscs, insects and crustaceans. This lineage extends into a clade comprising only endoparasitic forms, either in the nasal cavities of batracians (the Lawrencarinae: see review by Fain, in press) or those of birds and mammals (the Speleognathinae). It remains to be seen whether this transition to parasitism was facilitated by phoresy or other mutualistic relationships, as argued by Houck and Cohen (1995) for acaridid mites. The Ereynetidae seem to be restricted to humid or wet habitats, whether they be the nasal cavities colonized by endoparasitic species, the elytra of aquatic insects, or the soils of temperate or tropical regions. In Lubumbashi (Dem. Rep. Congo) soils, Ereynetidae are much less numerous than Tydeidae and are five times more abundant during the rainy than the dry season (Noti, 1991). Unlike Tydeidae, ereynetids have not been recorded from dry deserts.

Like that of other parasitic mites (see Fain, 1979, 1988, 1994), the evolution of Ereynetidae follows two opposite patterns. On the one hand, some structures have become increasingly complex and specialized, such as the ereynetal organ, which became progressively more recessed into the tibia and involved first the solenidion and then the famulus. This is also the case for the duplication of the genital discs and the modification of tarsus I, which becomes deformed with grooves and cavities into which claws are retracted. On the other hand, the regression of external structures, such as chaetotaxy and solenidiotaxy, is of utmost importance in endoparasites to prevent immunological reactions of the host. The regression of the ereynetid palp offers a remarkable example of this (Fig. 6).

The function of the ereynetal organ, which is unique to Ereynetidae, remains unclear. The recessed solenidion is simply a sensillus with wall pores, considered to be an olfactory receptor (Altner, 1977; Altner & Prillinger, 1980). Since Ereynetidae are restricted to humid and wet habitats, it has been suggested that the ereynetal organ might also be a hygroreceptor (Fain, in press). Finally, the ereynetal organ appears in Ereynetinae with a terminal palp segment that divides prior to the loss of the distal part. This suggests that the evolutionary specialization of the ereynetal organ compensates for the regression of the palp and that the functions usually performed by the palp eupathidium are taken over by the recessed solenidion and associated structures. In this context, the ereynetal organ would indicate a palpian evolution of leg I, quite different from that already observed in Iolinidae.

The family Ereynetidae is the sister-group of Iolinidae. Although both families show high evolutionary rates (Fig. 17) and are, to some extent, convergent in terms of palpal regression, they differ markedly in their specializations, ontogenetic trajectories (Fig. 14) and diversity. The Ereynetidae includes some known 170 species versus only 97 in Iolinidae. Such a high diversity may be explained by the adoption of parasitic habits. Obviously, the nasal cavity of vertebrates served as an empty adaptive zone wherein Ereynetidae speciated and radiated to attain their present diversity. Adaptive radiation in Ereynetidae, especially in Lawrencarinae and Speleognathinae, may also be driven by improved adaptations to cope with biotic interactions with hosts and their immunological responses. Our data support the prediction, based on an extension of Ehrlich and Raven's (1964) 'escape and radiation model' which concludes that parasites as a whole should have diversified more rapidly than groups retaining older habits. An alternative, though complementary, explanation is provided by Price (1980), who suggested that parasites might speciate more rapidly than predators or saprophages as a result of their

TABLE 4. Habitat shifts and evolutionary rates between successive groups along the three major lineages in Tydeoidea

Lineage	Mean $d \pm$SD	Habitat shift and description
Ereynetidae		
Lawrencarinae→Speleognathinae	6.32 ± 1.02^{ab}	− nasal cavities
Ereynetinae→Lawrencarinae	13.82 ± 0.50^{a}	+ soil and various hosts→nasal cavities
*→Ereynetinae	12.43 ± 1.72^{b}	+ soil→soil and various hosts
Iolinidae		
Pronematinae→Iolininae	5.67 ± 1.41^{c}	− plants and insects
Tydaeolinae→Pronematinae	8.00 ± 1.00^{c}	+ soil→plants and insects
*→Tydaeolinae	6.00	− soil
Tydeidae		
*→Tydeinae	9.25 ± 0.50	+ soil→plants and insects

For each pair within a lineage, the evolutionary rate was estimated by mean *d*, i.e. the mean of the distances measured between each taxon of the derived group and the centroid of the first. Distances were estimated using the Manhattan metric. The genera *Pseudotydeus* and *Hydranetes* (Ereynetinae) were not included.

* Refers to the early radiation point (asterisk on Fig. 17).

Signs + and − indicate, respectively, the presence or absence of habitat shift between two successive groups.

Superscripts designate values that are significantly different (^{a,b} at level $P<0.01$, ^{c} at level $P=0.06$).

typically extreme ecological specialization and their unusually fragmented population structure, due to the discrete and patchy distribution of hosts.

The combination of strong diversification and a high evolutionary rate (Fig. 17) in the Ereynetidae offers remarkable support for Mayr's view (1942) that groups searching for a new adaptive peak may undergo rapid evolution, after which evolution may begin to stagnate. The more pronounced the habitat shift between two successive groups in a lineage, the higher is the evolutionary rate. Depending on the presence of a habitat shift, the evolutionary rate in Ereynetidae, and the Tydeoidea as a whole, was found to be greater or lower than 7 (Table 4).

There is, however, another secondary adaptive radiation within the Tydeoidea, that of Tydeidae. The Tydeinae, with the cosmopolitan genus *Tydeus*, numbers nearly 300 species, while the number of Pretydeinae increased from 9 to 15 species in a recent study (Kazmierski, 1996). However, the Tydeidae comprise typical predatory or saprophagous species and the mechanisms invoked to explain the diversification of Ereynetidae cannot account for that of Tydeidae. Tydeidae live in the soil or on cultivated plants where they are easily sampled, contrary to parasitic Ereynetidae, which require special collecting methods. This raises an important question: Is the number of described species representative of the number of extant species? Gaston (1991) showed that large species tend to be described earlier than small species and explained that larger species are more likely to have been collected than smaller ones because they tend to be both more conspicuous and easier to obtain using non-specialist techniques. These explanations about small species apply directly to parasites. Farrell and Mitter (1993) stated that, since sister-groups are by definition of equal age, differences in their diversity must reflect different rates of diversification. In practice, the real diversity of a group is unknown and we only have an estimate. Farrell and Mitter's statement supposes that the sampling effort and probability of capture is the same for both sister-groups, conditions which obviously are not met when the diversity of Ereynetidae is compared to that of Tydeidae. Nevertheless, beyond the difficulty in establishing quantitative comparisons between the two groups, both the Tydeidae and Ereynetidae are successful groups

that have diverged morphologically and ecologically through different evolutionary strategies.

An alternative hypothesis for the diversity of Tydeidae could involve phytophagy. This is clearly a well-established strategy among Actinedida (Krantz & Lindquist, 1979; Lindquist, 1998) and is one of a number of strategies employed by Tydeidae. However, the doubts expressed by Mitter *et al.* (1988) concerning relationships between phytophagy and the diversity of insects could also apply to mites. Walter and O'Dowd (1995) observed that plants provided mites with many microhabitats and suggested that mite-plant associations may promote mite biodiversity. Indeed, the Tydeidae are well-represented in the mite fauna observed on plants, both on the phylloplane (leaf surface) (Walter *et al.*, 1994) and trunk (André, 1986). The diversification in Tydeidae might also be explained by the diversity of their strategies (saprophagy, predation and phytophagy, numerous (>10) eggs in gravid females in the genus *Orthotydeus* as opposed to few eggs in *Tydeus*).

In contrast to other Tydeoidea, the third lineage, Iolinidae, notwithstanding peculiar adaptations (e.g. mating, arrhenotoky, polymorphism between males) seem to be less successful in terms of diversity. The more specialized insect-associated subfamily Iolininae includes only two described species. The Iolinidae presents intermediate characters between the Tydeidae and Ereynetidae, insofar as they tend to leave the soil, are frequent on plants, or are found associated with insects. In contrast to the Ereynetidae, iolinids apparently have not found an adaptive zone in which to diversify. To some extent, they might be seen as a dead end of some kind, or, alternatively, as a first attempt at diversification through the colonization of plants and insects, prior to the emergence of the Ereynetidae.

Conclusions

For the first time, the Tydeoidea as a whole have been analysed and subjected to a cladistic analysis. The major phylogenetic conclusion is the paraphyly of the traditional family Tydeidae. To replace the former classification based on overall similarity between taxa, a new phylogenetic classification into four families is proposed. The new classification seems to be robust. Indeed, the undescribed taxon '*Anereynetes* 2' was discovered late in the course of this study, after analyses had begun. Introducing the new taxon into the analyses, despite its differences from other *Ereynetes*, did not affect the cladograms obtained.

This study was designed to provide a frame of reference for future work. Future revisions on tydeoid systematics may be orientated in one of two ways: either downward to the generic and specific levels or upward to suprafamilial levels. In the former case, the subfamily definitions will be tested (e.g. Tydeinae versus Pretydeinae, Triophtydeinae versus Meyerellinae and the paraphyly of Pronematinae and Ereynetinae) and the generic relationships rearranged after cladistic analyses of the entire organotaxy. In the latter case, relationships with the sister-group Eupodoidea will be investigated and the position of Meyerellidae will be reassessed within a larger framework. Because the Eupodoidea include many highly specialized soil-inhabiting species, both endogean (down to −80 cm below the soil surface) and cavernicolous, their study, combined with that of Tydeoidea, will provide a wider spectrum of forms, varying from typical soil-dwellers (supposed to represent the ancestral lifestyle) to highly derived endoparasites.

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