Acarologia is proudly non-profit, with no page charges and free open access

Please help us maintain this system by encouraging your institutes to subscribe to the print version of the journal and by sending us your high quality research on the Acari.

Subscriptions: Year 2020 (Volume 60): 450 €
http://www1.montpellier.inra.fr/CBGP/acarologia/subscribe.php

Previous volumes (2010-2018): 250 € / year (4 issues)
Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France
ISSN 0044-586X (print), ISSN 2107-7207 (electronic)

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d’avenir » programme (Labex Agro: ANR-10-LABX-0001-01)

Acarologia is under free license and distributed under the terms of the Creative Commons-BY-NC-ND which permits unrestricted non-commercial use, distribution, and reproduction in any medium, provided the original author and source are credited.
A GENERIC REVISION OF THE FAMILY TYDEIDAE
(ACARI : ACTINEDIDIDA)

III. ORGANOTAXY OF THE LEGS *

by Henri M. ANDRÉ **

PHANEROTAXY
TYDEID LEG
ANABASIS

SUMMARY: The phanerotaxy of each leg segment is analyzed in depth, particularly from the standpoint of variation. A designation system is presented for all segments but the tarsus where a notation system is possible. The degree of fusion and muscle relationship of the interfemoral joint on leg IV is given special attention.

PHANÉROTAXIE
PATTE DE TYDEIDAE
« ANABASE »

RÉSUMÉ : La phanérotaxie de chaque segment de patte est étudiée en détail, notamment du point de vue de ses variations. Un système de désignation est proposé pour chacun des segments à l’exception du tarse auquel un système de notation peut s’appliquer. Le degré de fusion et la musculature de l’articulation de la patte IV sont également étudiés.

Legs generally comprise six segments in Tydeidae. These are the trochanter, femur, genu, tibia, tarsus and apotele 1. In some genera, femur IV is composed of a basi- and a telofemur. Following the introductory statements to this section, a paragraph will be devoted to each leg segment, beginning with the most distal.

The setiform organs of the legs are idionymic but different migrations of the setae make difficult the establishment of homologies. Therefore a designation system—or descriptive nomenclature—is considered appropriate for all segments but the tarsus where a notation system is possible. Two basic concepts will be applied to this data:

1° GRANDJEAN’s parallel homology law and conformity to this law,
2° the verticil theory.

GRANDJEAN (1961: 216) made a distinction between the parallel homology law which is an hypothesis based on an archetype (i.e. on a primitive position where each segment is supposed to be identical on the four legs), and the conformity to this law, which deals with the evolution i.e. with derived characters. The conformity may be entire or partial, it does not matter. From some of the preliminary observations, it might be worthwhile to study the conformity to the law proposed by GRANDJEAN as it applies to the

* This is a part of a thesis submitted to the Graduate School of the Oregon State University (Corvallis, OR 97331, U.S.A) in partial fulfillment of the requirement of the degree of Master of Science.

** Present address: Laboratoire d’Ecologie générale et expérimentale, Université Catholique de Louvain, Place de la Croix du Sud, 5, 1348 Louvain-la-Neuve, Belgium.

1. According to VAN DER HAMMEN (1977), Actinotrichida do not have coxae.

Acarologia, t. XXII, fasc. 2, 1981.
Tydeidae. For instance, genera II, III and IV of Pretydeinae are nude. This parallel regression is a good sign of conformity.

The second concept is based on the assumed presence of five setal whorls or verticils on the legs of Tydeidae. The designations used (one dorsal, $d$; two laterals, $l'$ and $l''$; two ventrals, $v'$ and $v''$) imply this assumption which, however is debatable. The setae found in a given segment of a tydeid leg could belong to different primitive verticils, as clearly indicated at least for the femora.

A. APOTELE (Figure 1).

The apotele is a free segment comprising a basal sclerite which represents the remnant of the body of this segment, two claws and an empodium (comprising at times a third unpaired claw) which are nothing more than specialized setae (Grandjean, 1941), and muscles originating in the preceding segment, i.e. the tarsus.

The basal sclerite may be located by means of three adjacent well sclerotized structures. Two are lateral and constitute the cotyloid cavities (cot) which are connected with the condylophores (k.ph.). The third is found proximal and ventral to the empodial root.

Because of their setal derivation, lateral claws and the empodium which are nothing more than specialized setae (Grandjean, 1941), and muscles originating in the preceding segment, i.e. the tarsus.

Two are lateral and constitute the cotyloid cavities (cot) which are connected with the condylophores (k.ph.). The third is found proximal and ventral to the empodial root.

Because of their setal derivation, lateral claws and the empodium which are nothing more than specialized setae (Grandjean, 1941), and muscles originating in the preceding segment, i.e. the tarsus.

In Meyerella, they are setiform and look serrate. The third unpaired element becomes what is usually called an empodium, i.e. a padlike structure with ventral rows of very thin filaments. The empodium has a root from which arises a rather large excrescence which expands into a real claw in some genera or species like the "true" claws; it is birefringent.

The cotyloid cavities are connected with two condylophores which are very much developed in Pronematinae. These condylophores are less distinctive in the other tydeid subfamilies. The basic structure coincides with that of Caeculidae (Coi, 1974) or Camisia segnis (Grandjean, 1941) and is the same on each leg except in Pronematinae. Pronematinae are interesting because apotele I is very much reduced or even lost. Such a phenomenon is known in some other actinotid families and has been studied extensively by Grandjean (1966) in two species of Staurobatidae (Oribatida). As in the latter family, two steps in regression of the apotele have been observed in Tydeidae. The first step is seen in some adults of the genera Naudea, Pausia and Pronecupulatus as well as in larvae of Metapronematus and Homeopronematus. Only the larva of Homeopronematus was studied in depth because it alone was prepared in lactic acid. The size of the apotele is reduced but the empodium remains obvious. A close study shows that, in addition to the empodium, every element of a normal apotele is present: the two lateral claws which are vestigial, the basilar sclerite, and even the condylophores. Therefore, as in the oribatid Staurobates schusteri, the apotele is assumed to have retained its mobility. The major difference when compared to the usual leg I of tydeids is the great development of the tarsial eupathidia, exactly as in Staurobatidae. The second step in regression of the apotele is the complete disappearance of the segment. This is associated with the disappearance of the condylophores belonging to tarsus I as in Stauroroma cephalotum. The tarsal eupathidia are again more slender than usual.

Grandjean (1966) advanced an interesting hypothesis dealing with the phenomenon of regression. He referred to it as "palopian evolution". Where the apotele drops out, no new organ seems to appear on tarsus I, but a substantial lengthening of the existing eupathidia is noticed. According to Grandjean (1961).

GRANDJEAN (1966) advanced an interesting hypothesis dealing with the phenomenon of regression. He referred to it as "palopian evolution". Where the apotele drops out, no new organ seems to appear on tarsus I, but a substantial lengthening of the existing eupathidia is noticed. According to Grandjean (1961),
FIG. 1: Apotele. *Proctotydaeus schistocerca*: lateral (A) and dorsal (B) views of apotele IV of a male, dorsal view of apotele II of a tritonymph (C). *Pretydeus lwioensis*: lateral (D) and dorsal (E) views of apotele I of a tritonymph.
to Grandjean, this lengthening precedes and even "causes" the loss of the apotele, which becomes quite unable to assume its usual function.

Lastly, the few immatures known suggest that the regressive evolution of the apotele is of a descendant harmony type (figure 1B in the first part).

B. TARSUS (figure 2).

The phanerotaxy of the tarsus is the most complex of all the leg segments particularly that of tarsus I. However, the homologies are easy to establish at the adult stage since each setiform organ retains its fixed location.

The adult chaetotaxy of tarsus I includes as many as 12 setae, of which eight may be eupathidial. The most primitive pattern is found in Meyerella which has 12 setae, of which eight are eupathidia. The 12 other chaetotactic formulae for tarsus I are summarized in table I.

It may be seen in table I that setae (it) are eupathidial in formulae 1 to 4. These formulae, as well as formula 6 characterize the subfamilies Meyerellinae and Triophtydeinae. The priority list for tarsus I is:

\[(f_t', (c), (p), (u)), f_t'', ((ii), v''), v' (1)\]

Some exceptions to this priority list do occur; e.g. formulae 9 and 10 which represent Austratoideus kirstenae, Aestheteydeus setsukae and Tynapedus eloquens. The problem arises because (it) and (v) do not obey the same regression type. The latter are eustatic and the former amphistatic (see paragraph on ontogeny). Once again, ontogenetic data are necessary to understand these exceptions.

The chaetotaxy of tarsi II-IV is straightforward in that every seta keeps its location throughout ontogeny. Therefore, the homologies are clear. A metameric priority list may be drawn up from table I as follows:

\[(f_t', (p), (u)), t_c'', t_c', f_t'', ((ii), v''), v' (2)\]

### Table I. - Chaetotactic Formulae of Tarsi (Adult).

<table>
<thead>
<tr>
<th></th>
<th>(f_t)</th>
<th>(c)</th>
<th>(p)</th>
<th>(u)</th>
<th>(v)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>1. E E E E E E E E N N N N</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>2. E E E E E E E E N N N N</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>3. E E E E E E E E N N N N</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>4. E E E E E E E E N N N N</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>5. E E E E E E E E N N N N</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>6. N N E E N N E E N N N N</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>7. N E E E N N E E N N N N</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>8. N N E E N N E E N N N N</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>9. N E E E --- --- --- ---</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>10. N N E E --- --- --- ---</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>11. N E E E --- --- --- ---</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>12. N N E E --- --- --- ---</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>13. N E E E --- --- --- ---</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>PF 100 99 100 100 40 40 100 100 100 100 22 40</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td></td>
<td>ESF 11 84 100 100 11 11 100 100 --- ---</td>
<td>100</td>
<td>99</td>
<td>100</td>
<td>100</td>
</tr>
</tbody>
</table>

| II | 1. N E --- --- --- N E N N | 100 | 99  | 100 | 100 |
|    | 2. N N* --- --- --- E N N N | 100 | 99  | 100 | 100 |
|    | 3. N N --- --- --- N E N N N | 100 | 99  | 100 | 100 |
|    | 4. N N N N --- --- --- E N | 100 | 99  | 100 | 100 |
|    | 5. N N N N --- --- --- N N | 100 | 99  | 100 | 100 |
|    | 6. N N N N --- --- --- N N | 100 | 99  | 100 | 100 |
|    | 7. N N* --- --- --- N N N N | 100 | 99  | 100 | 100 |
|    | PF 100 100 26 36 --- --- --- --- --- | 100 | 99  | 100 | 100 |
|    | ESF 7 --- --- --- 2 12 --- --- --- | 100 | 99  | 100 | 100 |

| III-IV | 1. N N N N --- --- --- N N N N | 100 | 99  | 100 | 100 |
|        | 2. N N N N --- --- --- N N N N | 100 | 99  | 100 | 100 |
|        | 3. N N N N --- --- --- N N N N | 100 | 99  | 100 | 100 |
|        | 4. E --- --- --- N N N N | 100 | 99  | 100 | 100 |
|        | PF 100 --- 33 41 --- --- --- --- --- | 100 | 99  | 100 | 100 |
|        | ESF 6 --- --- --- --- --- --- --- --- | 100 | 99  | 100 | 100 |

| IV | 1. N N N N --- --- --- N N N | 100 | 99  | 100 | 100 |
|    | 2. N N N N --- --- --- N N N | 100 | 99  | 100 | 100 |
|    | 3. N N N N --- --- --- N N N | 100 | 99  | 100 | 100 |
|    | 4. E --- --- --- N N N N | 100 | 99  | 100 | 100 |
|    | PF 100 --- 33 38 --- --- --- --- --- | 100 | 99  | 100 | 100 |
|    | ESF 6 --- --- --- --- --- --- --- --- | 100 | 99  | 100 | 100 |

**Symbols:** E: eupathidial setae; N: normal setae; ---: setae absent; *: undersized; PF: presence frequency (in %) based on 81 species; ESF: eupathidial state frequency (in %).

This latter list is more precise than that for tarsus I but contains a contradiction regarding the relative strengths of \(f_t''\) and \((c)\).

A list of eupathidial priorities may also be built from the data summarized in table I.

\[p'', p', (tc), f_t'', f_t', (it) (3)\]

It will be seen that this list does not coincide with lists (1) and (2). For instance, \(f_t'\) is more persistent than \(f_t''\) but this seta is more often eupathidial. The strength of the eupathidial character does not necessarily imply that the setae itself is strong.

Table I also prompts other comments about eupathidia. The eupathidial character of \((it)\)
Fig. 2: Leg segment phanerotaxy in Tydeidae. Diagram of a leg segment phanerotaxy in dorsal view (archetype) (A); antiaxial view of tarsus I of *Meyerella marshalli* (tritonymph) (B).
seems stronger in Meyerellinae and Triophydeinae than in other groups. Either proral may be eupathidial on tarsus II, which means that, prim­
itively, the pair had to be eupathidial. Men­
tion should also be made of the presence of eupa­
thidia on tarsi which have already lost one or 
several setae. This suggest heretore unobserved 
eupathidial on tarsus 11, which means that, prim­
itively, the pair had to be eupathidial. Men­
than in other groups. Either proral may be 
thidia on tarsi which have already lost one or 
ition should also be made of the presence of eupa­
them having

setal conditions may exist. On the other hand, most formulae for tarsus I are paired, one of 
them having $ft^*$ eupathidial, the other $ft^*$ normal. The loss of the eupathidial character has 
been observed in several very different genera (Tydeus, Apopronematus, Lasiotydeus...) and is 
thus a secondary character. Lastly, table I suggests that the eupathidial condition is more fre­
rquent in antiaxial than in paraxial setae, although 
additional information will be necessary to verify 
this point.

The larval chaetotaxy of tarsus I is more 
difficult to interpret for the setae assume various 
positions. When tarsus I of the larva of Pre-
lorryia indionensis is observed for the first time, 
six setae are obvious and seem easy to name: 
$(ft)$, two large tectal eupathidia $(tcT)$ and $(p)$. 
On the other hand, the fundamental chaetotaxy 
of tarsus I of Tydeus seems very strange and 
could be interpreted at first sight as being: $(ft)$, 
$te^*s$, $p^*s$, $(v)$. Both interpretations are wrong.

The solution of the problem is found in the larva of two species of Metatriophydeus. Two 
large eupathidia exist as in Tydeus; the more 
distal one is $p^*$ and occupies the usual location, 
while the other is situated at the typical position 
of $te^*$. In addition, a distal pair of setae is 
found on the ventral side and another pair, $(ft)$, 
on the dorsal side apparently completes the count. 
Closer study, however, shows that there are two 
additional setae, rather small and slender, and 
inserted near the eupathidium occupying the loca-
tion of $te^*$. These two setae have to be named 
and the only consistent formula becomes:

$$(ft), (tc) \text{ both undersized, } (p^*s), (u).$$

In this interpretation, all the strongest setae of 
the priority list are present and accounted for 
and the eupathidia may be identified as the pro-
rais, which is the established rule (figure 3). 
However, the strange location of $p^*$ must be 
explained. A backward and upward setal migra-
tion must be assumed, a type of movement already 
seen in several families by Grandjean (1944) and 
in a Caeculidae by Coineau (1964). As noted 
by Coineau (1974), such a migration is more than 
a mere disjunction. This phenomenon is herein 
referred to as “anabasis” 4.

The position of the dorsal setae in Metatriophy-
tydeus is only the first step of a more important 
process involving the reduction and eventual 
loss of $(tc)$. The tectals are undersized in Meta-
triothydeus and keep their own insertion. A 
Further step is met in Pretydeus kevani and 
Tydeus spp., where both tectals are vestigial and 
the insertion of $te^*$ begin to amalgamate 
with the insertion of $p^*s$. The next phase is the ana-
basis of $p^*s$ as in Prelorryia indionensis or Ty-
daeolus: $(tc)$ are vestigial but both share the 
same insertion with $(p^*s)$. The last step involves 
the complete disappearance of $(tc)$. This may 
be the case in Homeopronematus vidae whose $(tc)$ 
could not be found 5. In any case there is a 
substitution for the tectals (which are weak setae 
but apparently have an important role) by the 
prorals which are stronger than the tectals. 
This process is a typical case of anhomologous 
tautergy, a common phenomenon among mites 
(Grandjean, 1962, 1964). The tautergy is anho-
mologous only between the larva and proto-
nymph; subsequently, it is homologous.

4. From ευρε, meaning both upward and backward, and βαπελ, to go, to walk.

Anabasis may occur on tarsus I or II, as in several genera of the family Stigmaeidae. It may be simple or double depending 
on whether only one or both prorals emigrate. It may be inside as in Aparstigmaeus navicella (figure 5 of Grandjean, 1944) 
where the prorals are situated between the tectals or outside of them as in Tydeidae. Lastly, a simple anabasis may be prime 
(which was the only case known until now and observed in Raphignathoidea, Cheyletidae, Erythraeidae, Bdellidae and Caecu-
lidae) or second as in Tydeidae.

5. To be sure, it would be enough to check if $(tc)$ are eupathidial or normal in the protonymph (since eupathidia first appear 
as normal setae through ontogeny). Unfortunately, the protonymph was not available for study.
Table II summarizes data on fundamental chaetotaxy of each tarsus.

**TABLE II. — FUNDAMENTAL CHAETOTAXY OF TARSI.**

<table>
<thead>
<tr>
<th>Tarsus</th>
<th>(1p)</th>
<th>(2p)</th>
<th>(3p)</th>
<th>(4p)</th>
<th>(5p)</th>
<th>(v)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>NN N</td>
<td>N* N*</td>
<td>N* N*</td>
<td>E E</td>
<td>N N</td>
<td>N N</td>
</tr>
<tr>
<td>II</td>
<td>N N</td>
<td>N* N*</td>
<td>N* N*</td>
<td>E E</td>
<td>N N</td>
<td>— N</td>
</tr>
<tr>
<td>III-IV</td>
<td>N N</td>
<td>N* N*</td>
<td>E E</td>
<td>N N</td>
<td>— —</td>
<td>— —</td>
</tr>
</tbody>
</table>

**III**

<table>
<thead>
<tr>
<th>Tarsus</th>
<th>(1p)</th>
<th>(2p)</th>
<th>(3p)</th>
<th>(4p)</th>
<th>(5p)</th>
<th>(v)</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>PF 100</td>
<td>50</td>
<td>7</td>
<td>7</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>II</td>
<td>ESF</td>
<td>— —</td>
<td>25</td>
<td>29</td>
<td>— —</td>
<td>— —</td>
</tr>
</tbody>
</table>

Symbols: the same as in the previous table.

### Ontogeny of the setae

As far as is known, the fastigials become eupathidial at the deutonymphal stage. Seta $ft^*$ disappears in Apolorryia congoensis, a loss which is preceded by a reduction in setal size in protonymphs and larvae of several species (*Microtydeus* sp., *Tydeus bedfordiensis*, *Proctotydeus schistocercæ*...). Seta $ft^*$ becomes eupathidial on tarsus II in the tritonymph and on tarsi III and IV in the adult. There is, therefore a metameric delay in the acquisition of the eupathidial state from leg I to IV. These setae seem to be eustatic which is the usual state of fundamental setae (Grandjean, 1942: 238).

The tectals become eupathidial on tarsus I of the protonymph. Seta $tc'$ appears on tarsus II at the tritonymphal stage in *Meyerella marshalli* and *Proctotydeus schistocercæ* while both tectals, $(tc)$, appear together in the deutonymph of *Paratydaeolus* and *Tydaeolus frequens*, and in the tritonymph of *Paratriophtydeus*. Setae $(tc)$ exist on tarsus III and IV at the adult stage in *Microtydeus* and *Tydaeolus* but not in the deutonymph (unfortunately, their tritonymphs are unknown). In *Coccotydaeolus*, $(tc)$ appear at the deutonymph stage on tarsus III but are delayed to the tritonymph on tarsus IV. The unpaired tectal seta, $tc'$, is formed at the deutonymphal stage on tarsus III of *Homoeopronematus* but only in the adult on tarsus IV. The tectals are thus amphistatic.

Iterals are typically amphistatic. Four iteral formulae are known for tarsus I from the protonymph to the tritonymph: $(N N) - (\xi N) - (\xi ^\prime N) - (\xi ^\prime ^\prime N) ; (- -) - (N N) - (\xi N) - (\xi ^\prime N) ; (\xi ?) - (?) - (N N) - (\xi N) - (\xi ^\prime N)$ (page 168), this arrangement permits more precision in arriving at eupathidial priorities:

$$p^*, p', (tc), ft^*, ft', it', it^* (4)$$

The ventral setae $(v)$ are a special case in that they are eustatic from the larval stage.

Both regression types, i.e. eustasy and amphistasy, are found on tarsus I of tydeids. Tectals and iterals are amphistatic while fastigials and ventrals are eustatic, which helps explain the difficulties encountered in building a setal priority list.

### Parallel homology

Parallel homology in tydeid leg chaetotaxy and the degree of conformity to this may be approached by table III.

Formula 8 is the most complete and may be considered as being paleotrichious for the Tydeidae. In sorting all the other formula, two trends may be distinguished. Either the depilation relative speed of tarsus I is high (left part of table III), or this relative speed is slow following fast depilation of the other tarsi (right part of the table III). The latter trend characterizes the Meyerellinae and Triophtydeinae, while the former is met in the other subfamilies.

**TABLE III. — TARSAL CHAETOTACTIC FORMULAE.**

<table>
<thead>
<tr>
<th>Tarsus</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>7</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>8</td>
<td>11</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>12</td>
<td>11</td>
<td>10</td>
</tr>
<tr>
<td>II</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>7</td>
<td>7</td>
<td>8</td>
<td>8</td>
<td>7</td>
<td>7</td>
<td>6</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>III</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>6</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>IV</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>6</td>
<td>7</td>
<td>7</td>
<td>7</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
</tbody>
</table>

**Solenidiotaxy** of tydeid legs is simple and entails only one solenidion $(\omega)$ on tarsi I and II. Solenidion $\omega I$ is present in every species and, as far as ontogenies are known, is eustatic from the larva; $\omega I I$ is missing in a few species of Tydeinae.

**Some special features** or particular adaptations of the tarsal chaetotaxy must be pointed out. The eupathidia of tarsus I are very long and slender in Pronematinae, a feature which
is related to the disappearance of apotele I. However, this lengthening does not affect the eupathidial strength of the setae. As in the other subfamilies, $ft''$ tends to lose its eupathidial character. In *Apopronematus*, $ft''$ is a normal setae and is no longer than $ft'$. The subfamily Pronematinae displays another special condition which has been observed in three different species (*Proctotydaeus pyrohippeus*, *Metapronematus leucohippeus* and *Homeoprone­matus vidae*). The second fastigial $ft''$, on tarsus II and the prime fastigial, $ft'$, on tarsi III and IV are always the most proximal. They have a smaller root than do the other setae and are slender. The meaning of this observation is unclear, but the condition is useful for recognizing which setae persist on tarsi with the minimum of five setae.

There is often a second disjunction of the fastigials on tarsus I, which usually is slight, but which is extreme in *Pseudotydeus perplexus*. The eupathidium $ft''$ is situated on a conical protuberance, well ahead of $ft'$. The migration is such that the tectals are displaced forward to the tip of the tarsus while the iterals are displaced to the sides. However, the most surprising development is the tarsal cluster which includes $\omega I$ and $ft'$. Such a pairing has already been

---

**Fig. 3**: Anabasis. Tarsus I of larva of *Metatriophtydeus* sp. (A), *Orthotydeus* sp. (B) and *Pelorria indionensis* (C).
described in an Ereynetes species by Grandjean (1939). However, in that species, the cluster characterizes tarsus I of the male only, while it is observed at least starting with the tritonymph in Pseudotydeus.

C. Tibia.

The study of the tibia is more difficult than that of the tarsus because the relative locations of the tibial setae often are poorly defined. The archetype (figure 2) includes five normal setae of which one may be eupathidial, a famulus $k^\prime$ and a solenidion $\varphi$.

If only the normal setae are taken into account, the chaetotactic formula for the tibia is $(d, l', l'', v', v'')$, signifying a typical five setae verticil. If such a verticil is supposed to have existed on each of the four tibiae, and if we assume that at least one seta always occurs on a segment and that the setae are quite independent, then the number of different possible formulae describing the four legs rises to 625. If the above assumptions are followed, the number of possible formulae between the two observed extremes: $(5-3-2-2)$ and $(2-1-1-1)$ (table IV), is still high: 48. With the inclusion of one additional assumption; i.e. that a segment may not carry more setae than a more anterior segment, the number of possibilities drops to 25. However, formula 8 of table IV cannot be included in the set. A last assumption may be added here: there is a priority between the setae, simple (i.e. amphistasy and eustasy do not coexist) and absolute. The number of possible formulae is then reduced to eight.

Of these eight formulae, one has not been observed and is missing in table IV, (3-2-2-1) while formulae 8 and 9 do not belong to the set of eight. This mathematical exercise shows clearly that setal loss on the tibiae is not a stochastic phenomenon.

However a leg setal tabulation\(^6\) may be dangerous and lead to errors. Indeed, the four setae of tibia I of Metatriophtydeus are not the same as the four setae of tibia I of Tydaeolinae; i.e. they are not homologous. Figure 4 depicts the homologies and chaetotactic regression of the tibial five-setae verticil. In the case of tibia I, the designation used at starting may be interpreted as a notation; for tibiae II-IV, however, designation still remains the only means of defining a seta.

TABLE IV. — CHAETOTACTIC FORMULAE OF THE FOUR TIBIAE.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>5</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>II</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>III</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>IV</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

The first element of formula 1 of table IV refers to tibia I of Meyerella (figure 4, A) which have five setae, one of which is eupathidial (l"$\zeta$). The seta v" appears in the deutonymph. The first step in setal regression of tibia I occurs in Metatriophtydeus (B), where v" first appears in the tritonymph. Seta v" is thus amphistatic. Likewise, a seta disappears from the lateroparaxial area at each stase. However, the missing setae is d rather than l' as might be expected. Figures 4 A' and A" explain this circumstance and refer respectively to Ereynetes (GRANDJEAN, 1939) and to Pseudotydeus perplexus. A' is similar to A except that v" is delayed to the tritonymph. A" differs from A' in that d is reduced. Seta d may consequently be supposed to become unable to assume its role because of its reduced size, and in light of the movement of l"$\zeta$, which seemingly is usurping its location. Seta l" in Pseudotydeus is easily recognized since it is eupathidial. Inasmuch as there is no more logical way to name the five setae, the interpretation calling for seta l"$\zeta$ to substitute for d seems consistent. In fact, each normal seta moves slightly and in such a way that their insertions are situated at right angles to one another. In Metatriophtydeus (figure 4 B), the same assumption may be made for d, but in this case seta d completely disappears and l' substitutes for it. Theoretically, the substitution of d by l' is as likely as by l"$\zeta$. Moreover, such a substitution has been observed as will be described in the following paragraph.

---

6. This term is taken from Vercammen-Grandjean (1971).
Fig. 4: Schematic regressive pattern in tibial chaetotaxy in Tydeidae. Roman figures refer to the four legs.
Figure 4 C depicts another regressive step: the complete absence of \( v'' \) from all stases, but with setae \( d \) still present. Such a pattern is found in *Coccotydaeolus, Microtydeus*, and *Tydaeolus...* However, one species, *Tydaeolus frequens* (Grandjean, 1938) shows, once again, the reduction of \( d \) (figure 4 C'). Here again, movement of a lateral seta is observed, but in this case, it is seta \( l' \) which moves to the dorsal face while \( l'' \) retains its typical position in relation to \( v' \). To go from figure 4 C' to D requires only the loss of seta \( d \). Figure 4 D depicts tibia I of most Pronematinae, which have three setae of which one is dorsal and another, antiaxial. However, seta \( d \) is missing and the formula is \( (l', v', l'') \). There are also three setae in *Tydeus* but the lateral seta is paraxial (figure 4 E). A final supposition assumes the substitution of \( d \) by \( l'' \). The most regressive chaetotaxy is found, for instance, in *Parapronematus*, which has only two setae on tibia I. The ventral seta is likely \( v' \) while the setae on the dorsal face should be a lateral one (figure 4 F).

In tibia II, the richest formula includes three setae whose designations are \( l', v', v''N2 \) (figure 4 G). To homologize \( v''II \) with \( v''I \) is tempting as both are amphistatic. However such an hypothesis needs more support. Seta \( v'' \) is found to disappear (figure 4 H) and, lastly, \( l'' \) drops out (figure 4 I). Tibiae III and IV are similar except that the setae of leg III are already present in the larval stase whereas the setae of the leg IV are formed first in the deutonymph (figure 4 J, K, L, M). Both tibiae III-IV lose the setae situated on the dorsal face.

Among the normal setae, \( k'' \) deserves special attention. This seta is hollow and is present in every species and stase. It is likely a famulus and should be homologous to \( k'' \) in the family Caeculidae. The seta is situated dorsoantiaxially but is slightly more antiaxial and a bit more distal than solenidion \( \varphi I \). In *Pseudotydeus perplexus*, seta \( k'' \) forms a cluster with \( l'' \) as in *Ereynetes* as described by Grandjean (1939); it is slender and lies side by side with the setae except at the tip, so that it is difficult to see.

The solenidiotaxy of the tibiae indicates only two solenidia, \( \varphi I \) and \( \varphi II \). The latter exists only in Meyerellinae and is recessed. Solenidion \( \varphi I \), on the other hand, is found in several subfamilies. It may be external as in Meyerellinae and Tydaeolinae, partially recessed as in Pretydeinae, or completely recessed within the segment as in *Pseudotydeus*. Solenidial recession is typical in mites and sometimes precedes their disappearance. However, such a phenomenon could also be adaptive as Zacharda (1979) hypothesizes for the Rhagidiidae.

D. GENU.

The genu is more difficult to interpret than the tibia since there are only four setae present with no other reference point. Table V summarizes the genual chaetotactic formulae. It may be seen that the richest is \( (4-4-3-1) \) and the most regressive are \( (2-0-0-0) \) and \( (1-1-0-0) \). If the previous mathematical treatment is again applied to genu, there are 160 possible formulae between the above-mentioned extremes if the regression is stochastic. However, if a genual segment is considered not to carry more setae than a more anterior segment, and if there exists a simple and absolute priority, the number is reduced to 52. The relatively high number of formulae reveals that the regression is a less simple phenomenon than observed on the tibia. This diversity, plus the lack of reference points and the absence of variation throughout ontogeny, makes interpretation difficult. The only positive feature seems to be the disappearance of \( v'' \) on the first genu. However, this should be considered only as a designation since setal migrations similar to those observed on the tibiae are likely also on the genua.

Formula 4 of table V refers to the genua of Meyerellinae and Triophtydeinae; as with tibia III in those genera, genu III is the most regressive of the genua.

7. However, an exception is known in the generic unit T1 where these positions are reversed.
TABLE V. — Genual chaetotactic formulae.

<table>
<thead>
<tr>
<th>I</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>10</th>
<th>11</th>
<th>12</th>
<th>13</th>
<th>14</th>
<th>15</th>
<th>16</th>
<th>17</th>
<th>18</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>II</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>III</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>IV</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

E. FEMUR (figure 2).

The femur is special in that it consists of two primary segments: a basi- and a telofemur, which usually are fused following a proregressive evolution (Grandjean, 1952, 1954). Van der Hammern (1970) draws the same inference on the basis of his study of different types of joints. The division of femur IV in Tydeidae is a commonly generic character, but it has not been thoroughly studied. Observations have revealed that the joint between basi- and telofemora IV is vanishing, even in Meyerellinae and Triophtydeinae. In these subfamilies, there is a degree of flexibility at each leg joint except for the interfemoral junction where flexion does not appear to occur. If strong pressure is exerted on leg IV, then it is possible to elicit flexion even at the interfemoral joint. However, the flexion is less pronounced than at other joints. This difference in degree of flexibility is easy to understand when leg segment musculature is studied.

Each joint from the tarsus to the basifemur is monovalent as explained by Van der Hammern (1970). Several muscles originate from the ventral and proximal area of a segment and are proximally attached to the dorsal face of the two (or more) preceding segments. The need for several muscles at a single point is easily understood if muscle orientation with regard to line of action of the articulation is taken into account. Specifically, the further distally a muscle is inserted, the closer to the line of action is the muscular force vector, and the larger is its projection onto the line of action. Thus, the muscle has a maximum force when its force vector becomes coincident with the line of action. At this point, a limit is reached beyond which the motion may not continue. Here, another muscle, more proximally inserted, may take up the action with minimum stress.

It may also be stated that, the more proximal the joint, the greater the stress that it must endure. This implies that the leg musculature efficiency becomes more and more crucial as one moves proximally to the femur. In Eotydeus, the major stress joint is situated between the femur and genu (i.e. the primitive telofemur-genu joint). The position is the the same in Meyerella: the major joint is located between the telofemur and genu and not more proximally between the telo- and basifemur. The interfemoral joint is served by only one muscle which originates from the ventral side of the telofemur and is ventrally attached to the basifemur. Such a system is inefficient for two reasons:

1°) its orientation with regard to the line of action of the joint is disadvantageous,

2°) the muscle is regressive and much thinner than other leg muscles.

The inefficiency of this arrangement is all the more important in that the joint is proximal and should be a major stress point. The joint is thus vanishing. In Eotydes, the interfemoral muscle has dropped out entirely. The migration to the ventral side of the telofemur and the resulting regression of the joint is likely to be related to the backward migration of all the muscles innervating the genu (i.e. the main joint).

In the absence of muscles, the interfemoral

8. Or, respectively, a femur 1 and a femur 2 after the nomenclature of Van der Hammern (1970).
9. The musculature of three specimens was studied: an Eotydeus adult and a Meyerella adult in cavity slide and a paratype of Apatriophydeus wilkesi in permanent slide. Only leg IV was examined closely.
10. The tendons could not be seen. In any case, their attachments must be more distal than the distal end of their muscles.
11. More precisely, what is briefly called "line of action" refers to the line of action of the useful component of the muscular vector force.
12. The trochanter is unimportant in this context since its joint with the femur is bivalent and devoted to forward and backward movement.
13. Except when the angle of flexion is null or close to zero.
joint may be located by the presence of the dor­
sal condyle as observed, for instance, in Procto­
tydaeus pyrohippeus. The presence of a joint
membrane with no striation also aids in its loca­
tion. The disappearance of the joint is likely
gradual following reduction of the joint membrane,
with the subsequent coalescence and finally the
fusion of the two femora.

Table VI summarizes the femur chaetotactic
formulae. The richest is (6-4-3-2) and the most
regressive is (2-2-1-1). Once again, the mathe­
atical approach to the tarsus and tibia may be
applied here. Between the two extreme formulae,
noted above, there are 135 possible setal combina­
tions on the femora if the regression is random,
52 if a given segment is supposed not to carry more
setae than a more anterior segment, and lastly
only 10 formulae if there exists a simple and
absolute priority.

**TABLE VI. — FEMORAL CHAETOTACTIC FORMULAE.**

<table>
<thead>
<tr>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>5</td>
<td>6</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td>9</td>
<td>10</td>
<td>11</td>
<td>12</td>
</tr>
<tr>
<td>13</td>
<td>14</td>
<td>15</td>
<td>16</td>
</tr>
<tr>
<td>17</td>
<td>18</td>
<td>19</td>
<td></td>
</tr>
</tbody>
</table>

Several observations must be made here. First,
the femoral chaetotaxy is independent of the fusion
of the basi- and telofemora. The fused femur IV
has fewer setae than the single femur of leg I.
As for the tibiae and genua, femur III is often
poorest in Triophtydeinae and, in one case,
femur II is the poorest (Apotriophtydeus). Austra­
lotydaeus kirstenae also has the minimum number
of setae on the third femur. This is in oppo­
sition to the general pattern, where legs are more
and more regressive from the first to the fourth.

A basi- and telofemoral verticil may be found
on each femur. The distal verticil is telofemoral
and may consist of as many as four setae on
femur I. The proximal basifemoral verticil keeps
only two setae. Ontogenic study provides no
information on setal derivation in the distal
verticil, but the dorsal setae of the proximal
verticil of femur IV are found in the tritonymph
of Meyerella and Metatriophtydeus lebruni. The
same setae would appear in the tritonymph of
Metatriophtydeus lebruni on femur I, but the
homology is not clear. In general, femoral
setal homologies are as difficult to establish as
those of the genu. Only the proximoventral setae,
pv, seems to be easy to recognize. This seta is
the strongest on leg IV and among the strongest
on the other legs.

All the setae of femur IV are formed in the deu­
tonymph, as are those of genu and tibia IV. This
sudden appearance of all the setae at the same
stage is surprising. It implies that all the setae
are delayed in appearance as eustatic setae or,
conversely, that the setae are eustatic at the deuto­
nymphal stage. Neither explanation seems sati­
sfactory, since such a regularity in the behavior
of the setae of all the species observed is unlikely.
An explanation based on the phenomenon of defi­
ciency (GRANDJEAN, 1951) would be more cogent.
The protonymphal level of Tydeidae may be re­
garded as being deficient with regard to femo­
ral, genual and tibial chaetotaxy. GRANDJEAN
(1946) pointed out this denudation of the proto­
nymphal leg IV in mites and interpreted it as a
precursory sign of the disappearance of the leg.

Lastly, sexual dimorphism is observed on fe­
mur IV of adult Pronematinae. The males bear
a dorsal spinoform excrescence at the distal edge
of the femur which is absent in the female.

**F. TROCHANTER.**

Table VII summarizes the data regarding the
trochanteral chaetotactic formulae. Of the total
of 16 possible formulae, only six are known to
exist. This means that a priority list based on
table VII may be induced. This list is (tr III,
tr I, tr II, tr IV). It must be pointed out that
formula 4 does not fit with this list. The differ­
et ontogenies reveal that the setae are all amphi­
static. The seta tr III always appears first except
after the disappearance of seta tr II; then, tr I
seems to become a strong as tr III.
It must be pointed out that setae do not normally appear at the adult stage; they are formed at the latest in the tritonymph. This is a part of a more general phenomenon: the tritonymphs of Tydeidae have the same organotaxy as the adult except, of course, in the genital area.

**BIBLIOGRAPHY**


**GRANDJEAN (F.), 1961b. — Nouvelles observations sur les Oribates (1re série). — Acarologia, 3 : 206-231.**

**GRANDJEAN (F.), 1962. — Au sujet des Hermanniellidae, 1re partie. — Acarologia, 4 : 237-273.**

**GRANDJEAN (F.), 1964. — Nouvelles observations sur les Oribates (3e série). — Acarologia, 6 : 170-198.**


**HAMMEN (L. VAN DER), 1970. — La segmentation des appendices chez les acariens. — Acarologia, 12 : 11-15.**

**HAMMEN (L. VAN DER), 1977. — The evolution of the coxa in mites and other groups of Chelicerata. — Acarologia, 19 : 12-19.**


---

15. Two exceptions are known, (tc) III and IV are formed in the Meyerella bifurcatus adult as is tc* IV in Homepronematus vidae.