AN ABSTRACT OF THE THESIS OF

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Title : APPLICATION OF THE STUDY OF ORGANOTAXY TO A

GENERIC REVISION OF THE FAMILY TYDEIDAE (ACARI :

ACTINEDIDA).

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Abstract approved : _____
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The organotaxy of the family Tydeidae is reviewed in
light of the fundamental paradigms of Grandjean. The
system of designation previously used to describe the
tydeid idiosoma is replaced by a notation system based
on chaetotaxy and poroidotaxy. A preliminary survey of
dorsal sigillotaxy also is included. The phanerotaxy of
each leg segment is analyzed in depth, particularly from
the standpoint of variation. The degree of fusion and
muscle relationship of the interfemoral joint on leg IV
is given special attention. The basic structure of
gnathosoma is summarized and an interpretation of the
palp phanerotaxy is presented.

Based on the results of these studies, 41 genera are
proposed. Proctotydaeus Berlese 1911 sensu Fain & Evans
1966 is returned to the Tydeidae. Two genera are defined
as new combinations (Proctotydaeus and Tydeus Koch 1835)
while 21 others are listed as new. The genera are
distributed in seven new subfamilies as follows :

Australotydeinae (Australotydeus Spain 1969) ;
Meyerellinae (Meyerella Baker 1968) ; Pretydeinae
(Pretydeus n. gen. and Prelorryia n. gen.) ; Pronematinae
(Apopronematus n. gen., Homeopronematus n. gen., Meta-
pronematus n. gen., Naudea Meyer & Rodrigues 1965,
Parapronematus Baker 1965, Pausia Kuznetzov & Livshits
1972, Proctotydaeus n. comb., Pronecupulatus Baker 1965,
Pronematulus Baker 1965, Pronematus Canestrini 1886 sensu
Baker 1965) ; Triophtydeinae (Apotriophtydeus n. gen.,
Metatriophtydeus n. gen., Pretriophtydeus n. gen. and
Teletriophtydeus n. gen.) ; Tydaeolinae (Aesthetydeus
n. gen., Coccotydaeolus Baker 1965, Lasiotydeus Berlese
1908 sensu Baker 1965, Metatydaeolus n. gen., Microtydeus
Thor 1931 sensu Baker 1965, Paratriophtydeus Baker 1966,
Paratydaeolus n. gen., Primotydeus n. gen., Pseudotydeus
Baker & Delfinado 1974, Tydaeolus Berlese 1910 sensu
Baker 1965, Tyndareus Livshits & Kuznetzov 1972) and
Tydeinae (Afrotydeus Baker 1970, Apolorryia n. gen.,
Eotydeus Kuznetzov 1973, Homeotydeus n. gen., Idiolorryia
n. gen., Krantzlorryia n. gen., Metalorryia n. gen.,
Neolorryia n. gen., Orthotydeus n. gen., Perafrotydeus
n. gen., Tydeus n. comb. and Tydides Kuznetzov 1975).

    Eight species are described : Meyerella marshalli,
Metatriophtydeus lebruni, Homeopronematus vidae,
Apopronematus bakeri, Paratydaeolus lukoschusi, Meta-
tydaeolus joannis, Paratriophtydeus coineaui, and Primo-
tydeus strandtmanni. The study concludes with a brief
discussion of the systematic position of the family.

Application of the Study of Organotaxy to a
Generic Revision of the Family Tydeidae
(Acari : Actinedida).

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CHAPTER I : INTRODUCTION

A. The nature and necessity of paradigms

"No natural history can be interpreted in the
absence of at least some implicit body of intertwined
theoretical and methodological belief that permits
selection, evaluation and criticism" (Kuhn, 1970 : 16).
In other words, as summarized by Bertalanffy, science is
not simply an accumulation of facts. Facts become
knowledge only when they are incorporated into a
conceptual system. This body of belief or this conceptual
system, called a "paradigm" by Kuhn, may be considered as
a basic feature of scientific activity. Kuhn analyzes
some consequences of the absence of a paradigm :
  - all the facts that could possibly pertain to the
    development of a given science are likely to seem
    equally relevant ;
  - early fact-gathering is a nearly random activity
    and is usually restricted to the wealth of data
    that is readily at hand ;

- this sort of fact-collecting produces a morass.

This above description by Kuhn is not unlike the situation that prevailed in acarology some years ago and that in fact is still appropriate in several taxa, including the family Tydeidae. Some examples from tydeid literature clearly illustrate Kuhn's remarks. The ornamentation of the cuticle is generally considered to be as relevant as chaetotaxy in distinguishing genera. The chaetotactic formula generally given for leg I of the tydeid subfamily Pronematinae is wrong ; only the eupathidia (which are very long) and an easily seen seta have been taken into account. However, a preliminary study of leg I of a variety of tydeids showed that, in addition, setae ($\underline{u}$) were always present, even in the Pronematinae. Such inconsistencies produce great confusion. As pointed out by Strandtmann (1967), it is sometimes difficult to know to what genus a species belongs. As a case in point, the genus Lorryia as defined by Baker (1965) illustrates several chaetotactic formulae, some of which are common to other genera.

Therefore, following a period of time devoted to accumulating materials, and after the first syntheses by Baker (1965) and Kuznetzov (1973), I felt it was time to review the Tydeidae. I decided that such a revision must be based on elaborate morphological observations ; since any description must be partial, the typical natural history study often omits just those details that later scientists find to be sources of important information (Kuhn, 1970 : 16). In addition, it was decided that such a revision must rest on established paradigms in order to avoid an unmethodical and fruitless approach. Before

defining these paradigms, it should be emphasized that a paradigm is not a rule and that scientists can agree in their _identification_ of a paradigm without agreeing on, or even attempting to produce, a full _interpretation_ or _rationalization_ of it. "Lack of a standard interpretation or of an agreed reduction to rules will not prevent a paradigm from guiding research" (Kuhn, 1970 : 44).

B. A fundamental paradigm

Evolution cannot be considered as a random phenomenon ; on the contrary, evolution is supposed to be governed by laws and to follow a strategy. This point of view is well expressed by the famous Simon's fable of the two watchmakers (1965). Briefly, two watchmakers, Hora and Tempus, make watches consisting of a thousand parts each. Hora assembles his watches part by part whereas Tempus puts together sub-assemblies of ten parts each, assembling these into a larger sub-assembly of a hundred units ; ten of these larger sub-assemblies make the whole watch. At each disturbance, the watch Hora tries to assemble falls to pieces and he has to start over again. On the contrary, if there is a disturbance, Tempus has to repeat at most nine assembling operations, and possibly none at all. At a ratio of one disturbance in a hundred operations, Hora will take 4000 times longer to assemble a watch than will Tempus. This fable illustrates the properties of hierarchial systems. These are the systems that have time to advance and are characterized by incomparably greater stability and resilience. Evolution follows such a strategy (Koestler, 1972).

The general properties of an element of such a
hierarchy - called holon by Koestler or integron by
Jacob (1970) - are closely developed by Koestler (1967).
Some of them are fundamental and deserve some comment here.

> "1. Functional holons are governed by fixed sets
> of rules and display more or less flexible
> strategies.
> 2. The rules - referred to as the system's
> canon - determine its invariant properties, its
> structures, configuration and/ or functional
> pattern.
> 3. While the canon defines the permissible steps
> in the holon's activity, the strategic selection of
> the actual step among permissible choices is
> guided by the contingencies of the environment.
> 4. The canon determines the rules of the game,
> strategy decides the course of the game.
> 5. The evolutionary process plays variations on
> a limited number of canonical themes. The
> constraints imposed by the evolutionary canon are
> illustrated by the phenomena of homology,
> homeoplasy, parallelism, convergence and the loi
> du balancement" (Koestler, 1967).

The goal of Grandjean was no doubt to try to
understand the canons, the laws which guide the evolution
of mites. In logic, such canons are expressed in terms
of relations. A relation between sets A_1, A_2, ...A_n, is
a subset of the cartesian product A_1 x A_2 x ... x A_n :

$$R_{1 < i < n} (A_i) \subseteq \mathbf{X}_{1 < i < n} A_i$$

A good example is offered in figure 5 (chapter II,
C). Set A_1 includes six aggenital elements and A_2
comprises six genital elements. Thus, the cartesian
product involves 36 possible combinations, among which
only a few really exist. Consequently, there is a relation
between these two sets which could be expressed as a law.
The work of Grandjean contains numerous observations which
lead to formulating such rules or canons.

The purpose of this work is to gain an understanding
of the rules governing the evolutionary behavior and
strategies of the holon called Tydeidae. Such an
undertaking is of course impossible without the help of
an adequate methodology, and without having recourse to
some of the concepts already expressed by Grandjean.

C. Methodology

Methodology in an acarological study essentially
consists of acute observation of the object under study in
three-dimentional view, and its eventual description by
graphic processes or by formulae. The iconographic
description of a mite should be devised as a drafting as
well as a drawing. "Orthographic projections are views of
an object taken at right angles to the object and
arranged in specific relative positions on the drawing"
(Bethune, 1977). Surely, it is not necessary to
describe a mite in such a way. However, from the six
possible orthogonal views of an object (front, top, bottom
right side, left side and rear views), three are usually
used : the top view (i.e. a dorsal view), the bottom view
(i.e. a ventral view), and a lateral view. These views
have to be orthogonal, which means that, in the case of
a dorsal view, the symmetry plane must be vertical or,
practically speaking, that a pair of homologous organs
must stay in the same horizontal plane. Even if the three
orthogonal views are not reproduced in the published
description, the study of a mite from these three points
of view (and sometimes from intermediate points of view)
remains the only way to understand a mite as a three-

dimensional object.

These three views are useful for understanding
the morphology of the body, but the study of appendages
is a bit more complex. In this case, one has to dis-
tinguished , in addition to the dorsal and ventral views,
the two side views. The right and left lateral views
are not homologous in that a leg is divided by a
pseudosymmetrical plane and the prime face (') may be
distinguish from the second face ("). The prime side is
the anterior aspect of the appendage when it is
perpendicular to the body. A given aspect of an appendage
or part of an appendage will also be spoken of as the
paraxial (π) or the antiaxial (α) face depending on
whether the side is towards the body or not. Lastly, as
a segment or a leg may be considered a cylinder, they
may be studied in end view. This allows one to know
exactly where the setal insertions lie. Indeed, it may be
difficult to decide whether a seta is antiaxial or
paraxial in lateral view. Moreover the end view is
sometimes the only way to know how many setae arise from
the end of minute terminal segments, such as the palp
tarsus.

It goes without saying that a description of the
type described above requires good examination techniques.
The observation of mites in cavity slides has been
described previously (Grandjean, 1949 ; Travé, 1965 ;
van der Hammen, 1972 ; Coineau, 1974). As emphasized by
Coineau (1974), this is the best method for morphological
studies with a microscope. The medium used is lactic acid,
which provides the advantages of low refraction index,
low volatily,reasonably good preservation qualities and
miscibility in water in any proportion. Permanent slides

present many disadvantages. Specimens flattened in
permanent mounts are often impossible to use in a critical
morphological study. It is difficult or even impossible
to understand a three-dimensional object when it is
observed only from one point of view. For example, the
paraproctal suckers of Tydeidae, which are sometimes very
well developed, have almost always been "forgotten" because
they are difficult to discern in dorsal or ventral views.
Furthermore, an ideal orientation for making valid
comparisons is rarely obtained in a permanent mount. In
fact, getting a good orientation even in a cavity slide
is sometimes difficult and it often takes more time to
put the specimen in the right position than to draw
it. Some details are visible only from a very special
angle ; e.g. the famulus of Pseudotydeus perplexus
(figure 25B). Lastly, some details are difficult to see in
permanent mounts even when the orientation is satisfactory.
For example, the palp solenidion of genus Meyerella
could not be discerned in a permanent slide, so that it
was necessary to transfer the specimen to a cavity slide.
The refraction index of the medium is very important here,
especially when working at the resolution limit of the
microscope. Some eupathidia also are difficult to see in
permanent slides, often because of poor orientation and
the transparency of the structure. Lastly, dissecting a
specimen is sometimes the only one way to check a feature.
For instance, the palp is difficult to study in end view
on a whole specimen because other appendages tend to
confuse the view.

Working with a light microscope was found to present
some difficulties during the course of this study. For
instance, it often was difficult to verify the presence

of vestigial setae with a light system. A better understanding may have been gained through use of the scanning microscope. This method was not used here for several reasons, the main one being that such a study would have to be considered secondary. Scanning microscopy is a fairly exotic technique which is not generally used for "routine" identification. For this reason, every observation reported in this work has been based on study with a light microscope equipped with phase contrast.

D. Some fundamental paradigms of Grandjean

Stase and ontogeny. The concept of stase is fundamental in the work of Grandjean (1938d, 1951, 1957, 1959). It differs in basic ways from the other ontogenic concepts, such as that of "instar", for instance. The terms "instar" and "stadium" refer to an animal or to a period of its life between two successive moltings (Jones, 1978). The difference between these terms is just a matter of convention. A problem arises because words are discrete units used to describe a continuum (1), the life of an animal.

A stase is one of the successive forms through which an animal passes, these forms being different from one another by the criterion of "all or none". The change in character is emphasized, not the change of skin. In other words, a stase is an animal at any level of its ontogeny.

(1) This continuum is sensed as a series of discrete units at a particular time resolution level : a butterfly is a nymph on one day, and an imago the next. But if a finer resolution level is chosen, the development is of course continuous.

As a consequence, a stase is always an instar, but not
the reverse. Logically, stase is a proper subset of the
set "instar".

There exists seven forms through which a mite passes
(2) : the egg, prelarva, larva, protonymph, deutonymph,
tritonymph and adult. By definition, all but the egg are
considered as stases (3). They are idionymic, which is
another fundamental difference between the concepts of
stase and instar.

Two particular stases were emphasized by Grandjean.
Elattostasis (1957) is a stase whose mouthparts are
reduced in such a way that the animal is unable to eat.
Calyptostasis (1951) differs from elattostasis in that
calyptostatic forms lose the appendages or at least their
use, particularly the legs (4). Calyptostasis is quite
common in the Insecta. A typical case is the chrysalid of
a butterfly.

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(2) In "mites", I include only the Actinotrichida or
Acariformes. The stases found among the Parasitiformes
are not homologous with the stases of Actinotrichida. In
other words, a larva of Gamasida does not belong to the
same ontogenic level as a larva of Tydeidae (Athias-
Henriot, 1975)

(3) Grandjean excluded the egg as a stase in 1957
(Remark 11) and in 1970. Most prelarva are calyptostatic
and have no chaetotaxy because they have lost their
setae. An egg has no setae either, not because the egg has
lost its setae but rather because chaetotaxy does not
exist at this level (otherwise, it should be considered as
a special calyptostasis). It is thus impossible to make
any real comparison between an egg and the other forms ;
therefore, the egg is not considered as a stase. As
pointed out by Grandjean (1957), a problem arises because
the term "absence" is ambiguous. Later, "absence" will be
shown to mean disappearance following presence.

(4) Once again, words are discrete units and some
particular cases fall somewhere "between" calypto- and
elattostasis.

The theory of "l'évolution selon l'âge". Stases,
therefore are steps through ontogeny characterized by
features which are discrete units, by characters of
"all or none". Grandjean was interested in the relation
between ontogeny (defined as a succession of steps) and
phylogeny, and advanced the idea that each level of
development has its own phylogeny. In other words, an
animal has as many phylogenies as stases, and it is
pointless to speak about THE phylogeny of a species. This
is nothing less than a scientific revolution sensu
Kuhn (1970) and upsets many existing interpretations.
Grandjean's stase concept is closely explained in two
detailed papers (1951, 1957) (5) ; and is summarized by
van der Hammen (1964) and Coineau (1974).

One of the features of mites which intrigued Grandjean
and led him to the theory of the "evolution selon l'âge"
is the occurence of calyptostasis at any level of mite
ontogeny. Calyptostatic inhibition occurs once or several
times throughout the ontogeny, seemingly at random,
between homeo- and heteromorphic stases. This special and
very advanced type of evolution seems thus a stochastic
process whose true meaning is not yet understood. The only
consistent explanation for calyptostasis is that this very
regressive state is a stase which followed its own
evolution ; it is not an intercalary or added state
allowing a metamorphosis. Thus, the chrysalid is not a
transition state between the caterpillar and the butterfly.
There are two (and not one) "metamorphoses" : one from
the caterpillar into the chrysalid and a second from the

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(5) These ideas had already been expressed in earlier
papers. However, these two references are essential to
understanding.

chrysalid into the adult. The old concept of a transition state between the caterpillar and the butterfly loses credence when one observes calyptostasis occuring between homeomorphic mite stases. This type of regression, or more precisely this type of inhibition (6), seems rather special and is called a "deficiency level" by Grandjean (1951).

It must be mentioned that independent phylogeny in a given stase describes a possibility, not an obligation. In other words, the phylogeny of a stase may be quite divergent from that of any other stase or the different phylogenies may be parallel and the stases homeomorphic. In any case, the conclusions will be the same, as seen below.

Ontogeny and phylogenies. The principle that "ontogeny recapitulates phylogeny" is a famous phylogenetic concept. Some biologists agree with it, some others do not. The following examples point out that the concepts of independent stase and of ontogenic recapitulation are essentially different.

Let P be a primitive character, i.e. a character which through phylogenic time $\underline{T}$, precedes a derived or secondary character, S. There is no intermediate step between P and S and they are exclusive. What happens through ontogenic time $\underline{t}$? A priori, these are three possibilities : P precedes S or P comes after S, or thirdly either P or S may be present through the entire ontogeny. The three situations are found among tydeid mites and are illustrated by ontophylogenic diagrams (Grandjean, 1957b) (figure 1).

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(6) Coineau (1974 : 110) prefers the term "inhibition" rather than "regression".
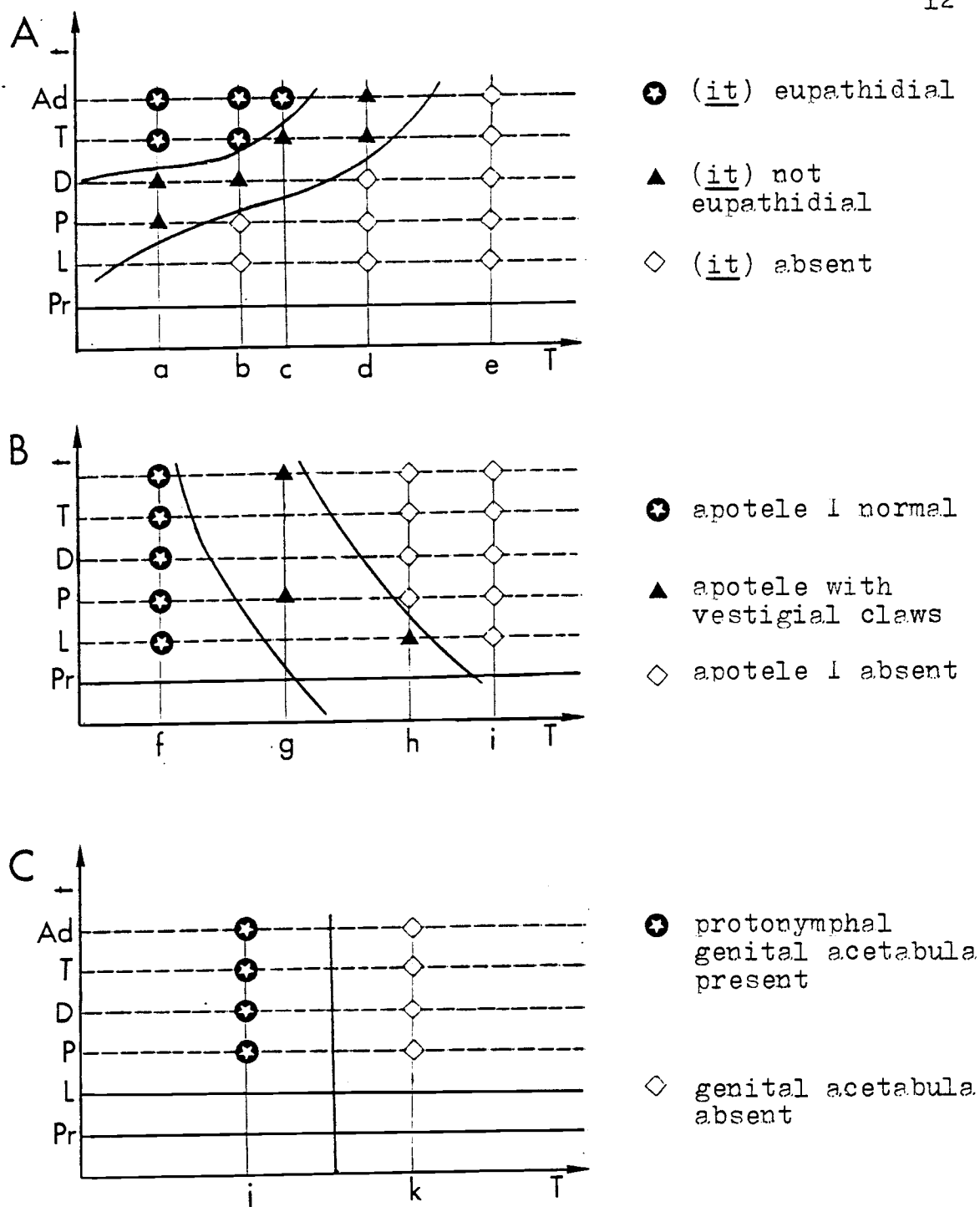
Figure 1 : Ascendent (A), Descendent (D) and Vertical harmony (C). T = phylogenetic time ; t = ontogenetic time ; a = Meyerella sp. ; b = Metatriophtydeus sp. ; c = Teletriophtydeus sp. ; d = Coccotydaeolus sp. ; e = Tydeus sp.; f = Tydeus ; g = Pronecupulatus sp. ; h : Homeopronematus ; i = Proctotydaeus sp. ; j = Tydeus sp. ; k = Proctotydaeus.

Diagram A refers to the tarsal setae (_it_) which are
sometimes eupathidial. The eupathidial character is
considered to be the most primitive state, while the
normal setae is the derived state ; the absence of the
setae is a character which is still more advanced. These
three states are plotted against ontogenic time, t, and
the phylogenic time, T. Lines may be drawn to separate the
three states. Plotting of this data results in what
Grandjean (1951) called an ascendent harmony or, since
it is a regression along time T, a retroprogression.
This means that, through ontogeny, the character S
precedes the character P or, briefly, that the larva is
"more advanced" than the adult in this respect. This
example negates the recapitulation theory of earlier
authors. Diagram B refers to another 3-state character.
P is represented by the presence of apotele I, the derived
state is the presence of vestigial claws, and the very
advanced state is the complete disappearance of the
apotele. The resulting diagram is the reverse of the
previous one, in that the separating lines are descendent.
This is a descendent harmony or, since it is a regression
along time T, a retroregression. The character P precedes
the character S both through ontogeny and phylogeny, and
the larva is "less advanced" than the adult in this
respect.

Diagram C refers to the third possibility, and deals
with the protonymphal genital acetabula. Either these
genital acetabula are formed in the protonymph (larva is
at a deficiency level in this respect, as is the prelarva)
and are present through the entire ontogeny, or the
acetabula do not appear in the protonymph, or in fact in
any of the later stases (i.e. the acetabula are eustatic).

This is called a _vertical harmony_ or, since it is a
regression, a vertical regression. Proving whether a
character state in Tydeidae is primitive or derived is
beyond the scope of this work. A global knowledge of mites
as a whole will be necessary to define the direction of
evolutionary changes. The Tydeidae, as emphasized by
Grandjean (1938) are well advanced mites and cannot be
expected to provide in themselves further information on
acarine evolution as a whole.

Grandjean was impressed by the fact that, given a
character, the ontogeny of a species, or the ontogenies
of a group, are cut only once by the line PS (except of
course when there is a dysharmony resulting from a
deficiency level) (7). If several ontogenies are studied
along time T and if there is no dysharmony, then the
harmony remains of the same type. Hence, the principle of
concordance in harmonic evolution which states that, if a
change occurs only once through any ontogeny, then it
occurs only in one way in the considered group.

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(7) There are a few apparent exceptions which are
explained by different orthogeneses : two different pro-
cesses acts at the same time and independently at two
different levels (for further particulars, see
Grandjean, 1951).

CHAPTER II : IDIOSOMA

A. Prodorsum (8) (figure 2)

The chaetotaxy of the prodorsum of Tydeidae is
noteworthy in being constant. There is one pair of
trichobothria ($\underline{s}$), and three pairs of setae identified as
$\underline{p1}$, $\underline{p2}$ and $\underline{p3}$ by Baker (1965). However, the insertions of
($\underline{p1}$), the most paraxial pair, vary from a position
anterior to ($\underline{p2}$) and ($\underline{s}$) to a posterior position between
and behind the bothridia. The same variation in position
also appears in Ereynetidae (Fain, 1970). This criterion
has never been used in systematic studies of Tydeidae.
However, this movement is more important than it appears,
in that it is related to the shape of the dehiscence line,
δ (the "Guirlande" of Thor, 1933 or the "garland" of
Marshall, 1970), a linear breach in the normal striation
pattern. The breach line extends around the three pairs of
prodorsal setae in the immatures and may extend beyond
the $\underline{das}$ furrow. When setae ($\underline{p1}$) are in an anterior
position, the line is recurved. However, when setae ($\underline{p1}$)
move posteriorly, the line follows the movement and
becomes procurved in its paraxial portion. In other words,
the prodorsum may be referred to as procurved or recurved
depending on this shape. Anyway, the dehiscence line of
Tydeidae is of prodorsal type (Coineau, 1974).

Only one anomaly was noticed in the prodorsal setation

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(8) This area is still referred to as the propodosoma by
several authors. However, following the theory of
Grandjean and his terminology, the term prodorsum is
preferred.
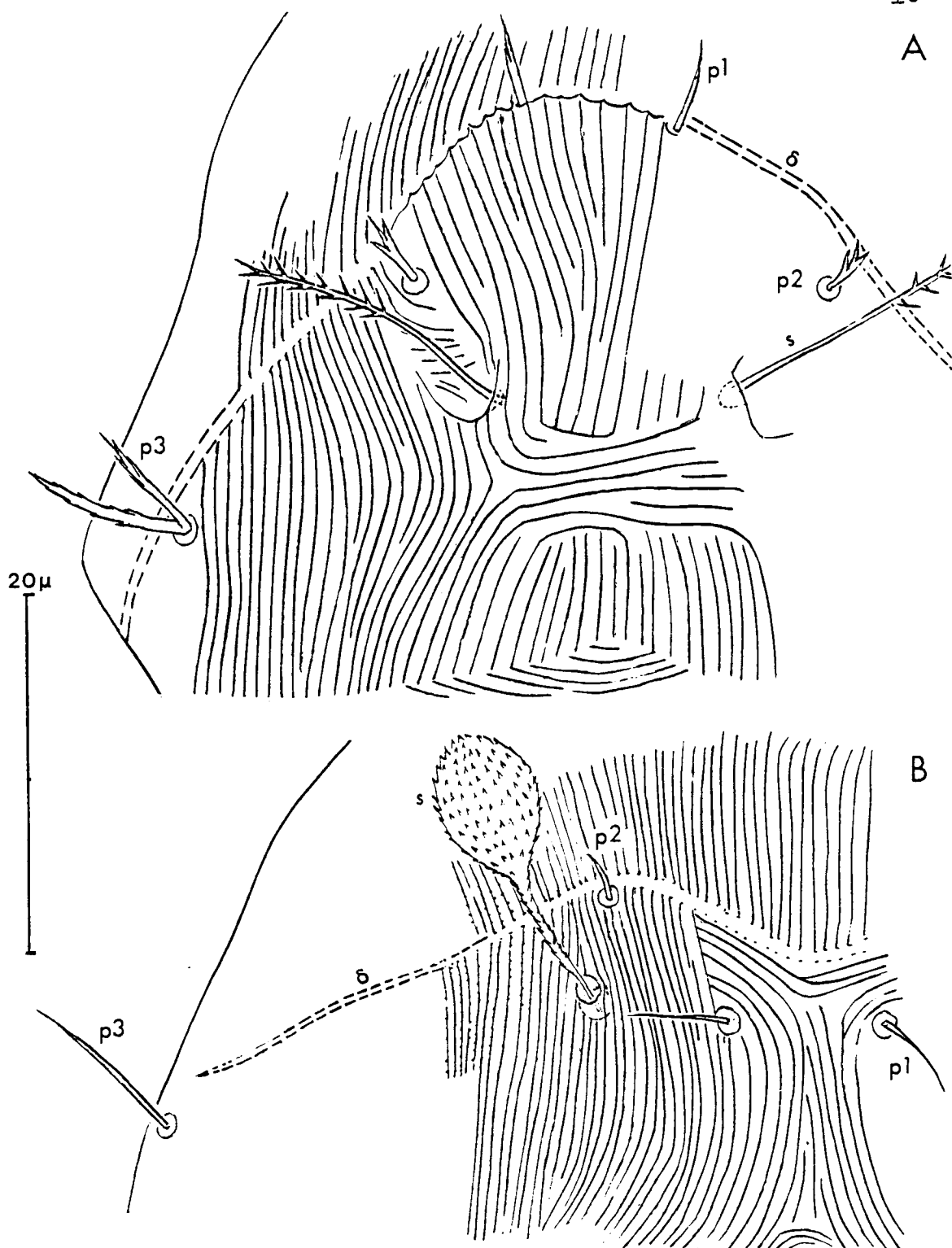
Figure 2 : Prodorsal types : Prodorsum recurved (A)
(deutonymph of _Meyerella marshalli_), and procurved (B)
(larva of _Paratydaeolus lukoschusi_).

In a _Proctotydaeus_ _schistocercae_ nymph, one setae p disappeared and the other moved just onto the sagittal plane. The striation which usually demarcates two clear circular areas around the setal insertions demarcates only one of them in this specimen. I will refer later to such a phenomenon (disappearance of a seta followed by the movement of the remaining element of the pair onto the sagittal plane) as a bisynthesis.

In some other cases, the pair (p2) disappears (_Parapronematus_ _acaciae_, _Parapronematus_ _citri_) or is reduced (9) (_Parapronematus_ _geminus_).

The shape of the bothridia may be more or less complex. In some cases, it is a mere pit (as in Triophtydeinae) ; on the other hand, the bothridia may present a more complex shape (as in _Coccotydaeolus_...). The trichobothridial setae may be simple, plumose, or clublike... (figures 20C and D ; 21D ; 23C).

Lastly, Tydeidae may have some eye-spots, generally silver (three in _Metatriophtydeus_ and _Meyerella_, two in _Tydeus_, _Lasiotydeus_...) or they may be absent (_Homeopronematus_). This character is little used as these "eyes" disappear when the specimens are cleared. The eye pigment is internal.

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(9) It is heuristic to distinguish the diminution of a seta ("amoindrissement" _sensu_ Coineau, 1974) which leads to a persistent state, from the reduction ("nanisme" _sensu_ Coineau, 1974) which leads to the relatively quick disappearance of a seta.

B. Dorsal face ($_{10}$) of the opisthosoma (figure 3)

Following Coineau's findings in the Caeculidae, the basic chaetotactic network of the dorsal face of a Tydeid should include ten pairs of dorsal setae plus the setae h and ps. Coineau found that Caeculidae have three lyrifissures ; however, the tydeid genus Australotydeus has four pairs of lyrifissures, nine setae on the dorsal side, plus one pair at the posterior tip and one pair in the anal area. To name the first lyrifissuresis easy and partly already done by Marshall (1970) : from front to back are successively met ia, im and ip.

If we compare the network comprised of the chaetotaxy and the poroidotaxy of Australotydeus, it is clear that a seta pair is missing between im and ip, i.e. the third pair of setae from the lateral series. Thus there are two pairs of anterior setae d1 and 11 ; the lyrifissures ia, d2 and 12, im, d3, ip, d4 and 14 and lastly d5 and 15 (11). Setae 13 are not present.

This interpretation is all the easier to advance as a lateral view shows that the setae have kept the primitive and theoretical alignment. Australotydeus is thus orthotactic.

If Australotydeus is compared to all the other Tydeidae, two features may be noted :

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(10) A difference is made between the dorsal side - which is the area visible from above, i.e. in dorsal view - and the dorsal face which is the superior area from the anus to the mouth parts. A part of the dorsal face may not be visible in dorsal view.

(11) The setal nomenclature is that of Baker (1965). Homologies with Coineau's system are easy to make.
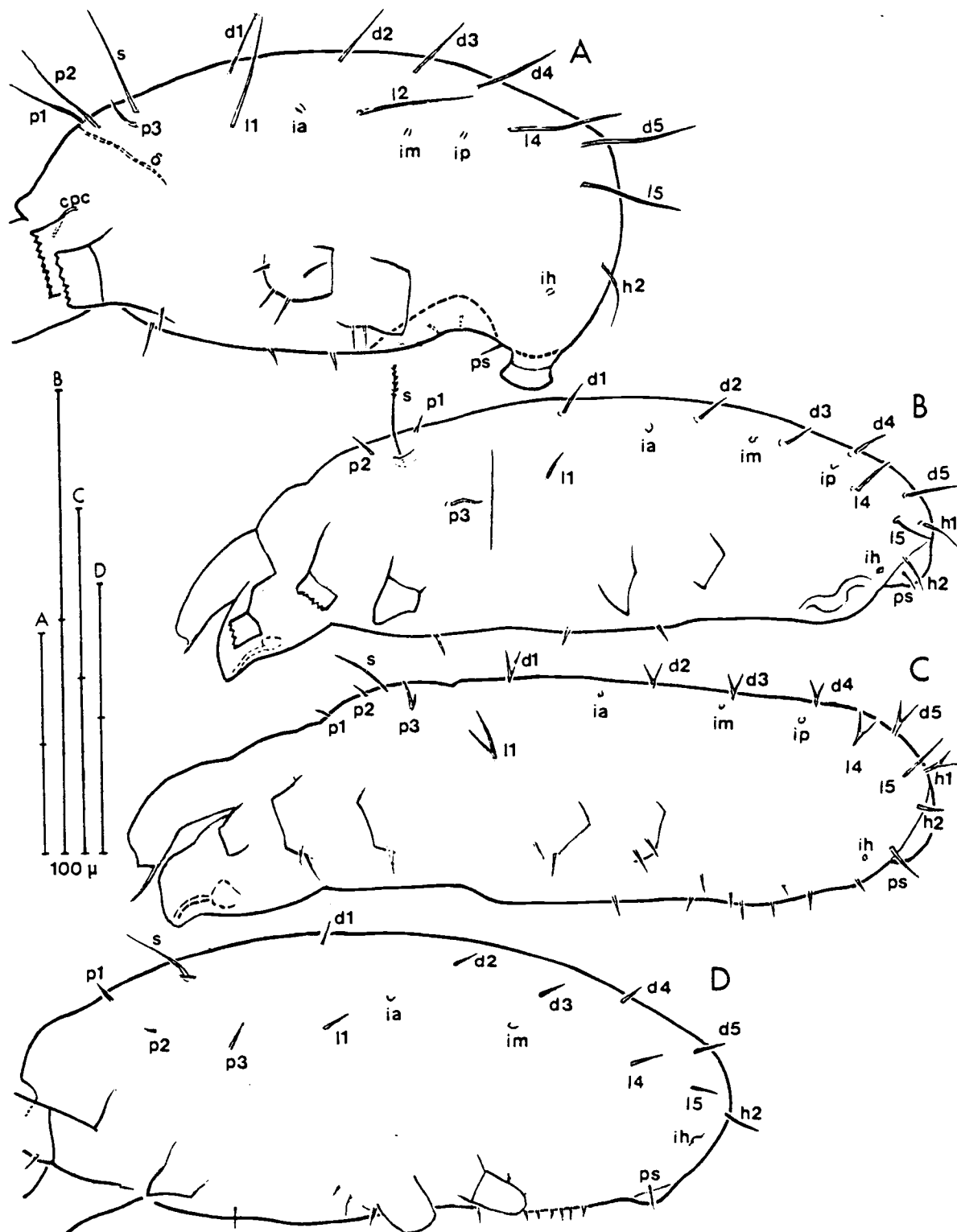
Figure 3 : lateral habitus of Tydeidae : _Australotydeus kirstenae_ (tritonymph) (A), _Microtydeus_ sp. (B), _Meyerella marshalli_ (tritonymph) (C), _Tydeus tridactylus_ (D). Some ventral setae are not represented.

1°) the disappearance of 12 in all genera except for
Australotydeus. Indeed, there are no setae
between ia and im, which are always present,

2°) the disappearance of ip in several genera
(Tydeus...).

Except for these two features, the organotaxy remains
remarkably constant throughout the family.

Only one pair of setae is found between d5-l5 and the
anal area in Australotydeus and certain other genera
(Tydeus...), while two pairs are seen in many other genera.
These setae may only be (hl) and (h2) of segment H. It
seems that (hl) are weak setae ; its bisynthesis has been
observed in a nymph of Proctotydaeus schistocercae (12). In
a few cases (Idiolorryia macouillani and cf. macouillani,
Apolorryia congoensis...) both (hl) and (h2) disappear.

The setae of the anal area often appear at the larval
stase, which means that they are not anal setae but, by
definition, pseudanal setae, (ps). In a few cases, these
setae are absent at the adult stase (Parapronematus) or
only at the larval stase (Proctotydaeus schistocercae)
(13). This leads to the question as to whether there is
another segment posterior to the pseudanal segment in
Tydeidae. When working on mites with heavy sclerites, the
answer to such a question may be obvious. Unfortunatelly,
the idiosoma of Tydeidae is without a shield and there
are no setae posterior to (ps). It is therefore difficult
to determine wether a new segment appears in the
protonymph.

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(12) This seems coincide with the opinion of Coineau
(1974) about the origin of hs in Caeculidae.

(13) This setae is present in the deutonymph,
unfortunatelly, the protonymph is still unknown.

Nevertheless, two elements provide a possible solution to
this question. The first is the presence of paraproctal
suckers in virtually all Tydeidae. These suckers are
particularly well developed in _Australotydeus_, _Procto-_
tydaeus schistocercae, and _Parapronematus_. They seem to
arise from the adanal segment, inasmuch as such suckers do
not exist in the larva. A fine example is provided by
Proctotydaeus schistocercae where, in the larva, the anal
aperture is ventral and bordered by two striated lips. In
the nymphs, the anal aperture is terminal and bordered by
the suckers. The presence of striated lips in the larva
and their substitution by suckers whose integument is thin
and smooth parallels the situation observed in _Apo-_
pronematus, _Paratydaeolus_, _Microtydeus_, _Metatriophtydeus_
and _Homeopronematus_. A more or less accentuated movement
toward the terminus of the idiosoma goes with this
substitution. The only known exception to this scenario
is the larva of _Proctotydaeus pyrohippeus_, which has
smooth anal lips. This suggests that the pseudanal segment
could participate in the formation of the suckers. The
other element of importance in determining whether a post-
pseudanal segment is present is the location of the setae
(_ps_). In the genus _Tydeus_, where paraproctal lips are
striated in every stase, (_ps_) of the larva are on the lips
themselves. At the protonymphal stase, a movement away
from the paraproctal lips is observed. Such a migration
also occurs in the other tydeid genera which have suckers.
The presence of paraproctal suckers, and the position of
(_ps_), suggest the presence of an adanal segment. According
to this interpretation, the regressive evolution of
Tydeidae is such that there would be a four-level
paraproctal atrichosy in most Tydeidae, with a five-level

atrichosy occuring in Proctotydaeus schistocercae.

The role of the lyrifissures is not clear. They are presently considered to be proprioreceptors (Krantz, 1978). Their structure in the Tydeidae has been particularly well studied in Australotydeus kirstenae, a large species, but is the same throughout the Tydeidae. Each lyrifissure consists of a small socket, oval at the surface, narrowing into a funnel and ending in a circle pore. The lateral aspects of the socket seem to be reinforced. Each integumental striation breaks down in neightborhood of a lyrifissure, demarcating at both ends of the lyrifissure a kind of channel with no striation. This could suggest an excretory role, but their position supports the hypothesis of a proprioreceptor as they are often located in folds (lyrifissure ia in a furrow smd of Tydaeolus is an example) or in an area which is easily folded when the mite is mounted. This sometimes makes it difficult to locate them. In addition the lyrifissures are oriented in the same direction as the integumental fold. The two "channels" which extend the lyrifissure, as well as the lyrifissure itself, could be interpreted as a weak line allowing a degree of folding and the concommitant perception of this movement.

Another noteworthy element of organotaxy is the sigillotaxy. Once again, the absence of sclerites poses a problem and makes such a study difficult. Nevertheless some sigilla are fairly obvious in some "Lorryia" and have been referred to as "rosettes" by Baker (1965) and by Marshall (1970). A pair of large sigilla is located near the das furrow anterior to dl : ma. This sigillum is connected with two large muscles which extend ventrally and a bit laterally to the venter. Two sigilla are found

between d1 and d2. The anterior one, mb1, is quite in-
distinct and bears only one muscle which is inserted on
the ventral side. The posterior sigillum, mb2, is a true
apodeme on which two large muscles originate. This
apodeme is the "rosette" of Baker (op. cit.), and usually
observed ; it extends paraxially into a scale. From there
originate three bundles of muscles extending anteriorly
to das and a second group of bundles extending posteriorly.
Another indistinct sigillum, mc, exists between d2 and d3.
An important sigillum, md, is located between d3 and d4
and is connected with two large muscles. The second
longitudinal bundles are attached in the sagittal area
mds, from which point a third pair extends posteriorly
to mes. This pair of sigilla is located almost sagittally
between d4 and d5 and also bears muscles extending to the
anal area. Another sigillum, me, is more antiaxial and is
connected with a muscle extending to a sclerite located
in the posterior area of the genitalia. These observations
have been carried out on a specimen of Tydeinae (genus
Eotydeus) in which muscles were preserved, and in some
other species where only sigilla were visible. The muscles
of a Meyerella specimen also were observed and were found
to exhibit some differences from the Tydeinae described
above. For example, a pair of muscle was observed between
d5 and h1 which had never been noted in the Tydeinae
(Eotydeus).

The posterior tip of the idiosoma may exhibit some
other features. There exists in Pseudotydeus perplexus
a kind of "tail" overhanging an inward fold where the
anus opens and where (ps) are located. This fold exhibits
some structures difficult to define and has been mistaken
for genitalia in the past. The same fold with the same

kind of structure has also been seen in Homeopronematus
but on a smaller scale. In Pausia magdalenae, the anal
area is located on a kind of terminal cone. In addition
to the two paraproctal suckers, there is a third one
located posteriorly at the tip of the anal cone. These
structures seem typical of the Pronematinae and likely
reflect some particular adaptation, which should receive
more attention in the future.

In summation, the dorsal idiosomal paleotaxy of
Tydeidae is as follows :

chaetotaxy : d1, l1, d2, l2, d3, d4, l4, d5, l5, h1,
h2, ps.

poroidotaxy : ia, im, ip, ih.

Hence, no tydeid mite is paleotrichial since
Australotydeus has only one setae h and l2 is missing in
every other known tydeid ; i.e. they are all PROTOTRICHIAL
The setae likely to be lost are l2, h1, h2 and ps. On the
other hand, most of the setae keep the same relative
location and therefore tydeids are ORTHOTRICHIAL. There is
no movement of l2 as previously imagined (Baker, 1965).
This is important in that the basic classification of the
family has previously been based on this character. The
only setae which migrate are (d3) which tend to move so as
to fill the gap following the disappearance of (l2) and
(l3). However this movement never goes beyond the
lyrifissure im and the setae d3 always remain behind it.

Regarding poroidotaxy, only ip is likely to be
lacking.

Lastly, it could be supposed that segment Ad still
exists. In this case, it shoud be a paraproctal atrichosy
derived from the protonymph or even from the larva. This
interpretation, however, is without experimental support
at present.

C. Ventral face of the opisthosoma

The vental face includes primarily the genital area and the inferior part of the podosoma.

The genitalia are complex and their study is beyond the field of this work. However several misinterpretations of the genital area must be corrected. The first of these concerns what is usually called the genital aperture. It is in fact the progenital aperture and its shape may vary considerably. The true genital aperture, also called eugenital aperture, is within the progenital chamber. The chamber is vanishing in Tydeidae. Generally it has quite disappeared in the nymphs. In *Australotydeus* there remains only a progenital depression in the tritonymph, and in *Meyerella* (deuto- and tritonymphs) and *Teletrioph-tydeus wadei* (trito-), a progenital groove (14) ; some signs of the anterior apex of the chamber also are visible in the tritonymphs of *Pretydeus lwiorensis* and *P. kevani*. As for the adults, the chamber is closed in Triophtydeinae males and the progenital aperture is longitudinal. The chamber tends to become less and less hermetic and opens at both ends. In this condition, the aperture has the shape of a recumbent letter H. In *Pausia*, the progenital aperture is longitudinal but there is a movement of the fore part of the genital area (from each corner of the aperture) backward and over the lateral lips which shrink ; this results in an aperture with five branches. If this

(14) This groove coincides exactly with Grandjean's theory on the formation of the progenital chamber (1969). It could be said that there remains only what Grandjean called the progenital ridges.
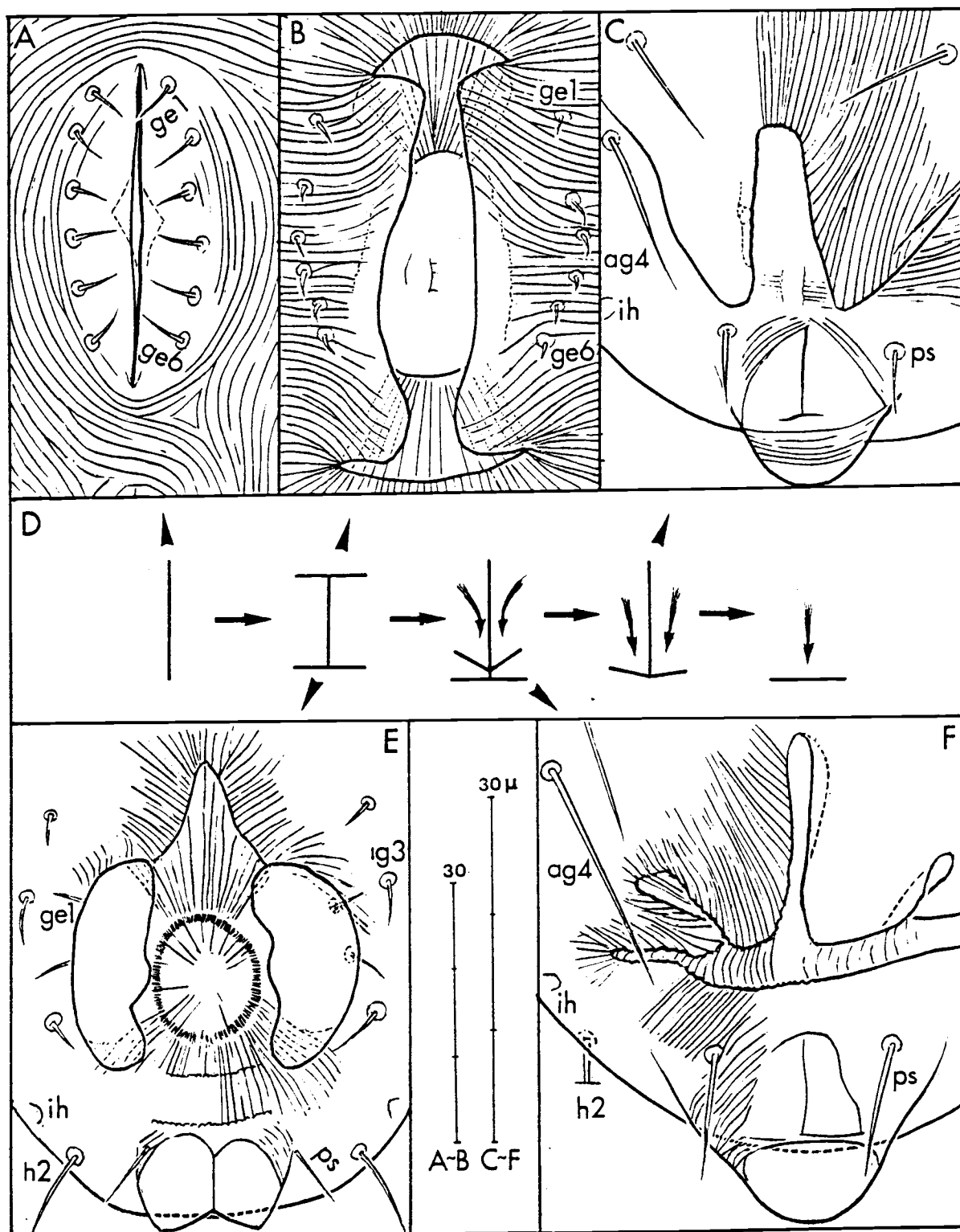
Figure 4 : Genital area of Tydeidae : *Tydeus tridactylus* ♂ (A) and ♀ (B) ; *Proctotydaeus pyrohippeus* ♀ (C); *Tydaeolus* sp ♀ (E) ; *Pausia magdalenae* ♀ (F). Figure 4D is a schematic diagram expressing the evolutionary trend in the shape of the progenital aperture.

movement is magnified, it creates a T-aperture (Procto-
tydaeus pyrohyppeus) , or even a completely transverse
aperture as in Proctotydaeus schistocercae (figure 4).

A progenital aperture does not exist in immature
tydeids as the progenital chamber has disappeared. This
means that the genital acetabula are external, with no
shelter. In fact, what is visible are not the genital
acetabula themselves but rather the diachile slots
(Grandjean 1938, 1969) of the invaginations within which
are located the genital acetabula. The genital acetabula
s. str. have been observed only in a Meyerella female
and are difficult to see. These invaginations may
sometimes be quite deep as in Australotydeus, but often
are no more than a slight depression. Generally there are
one pair of diachile slots in the protonymph and two in
the deuto- and tritonymphs. In several cases, the pairs
are fused into one simple aperture as in Tydeus. In
Metapronematus leucohippeus only one pair of diachile
slots may be seen. The number of genital acetabula - or
what are usually called genital acetabula - is of course
the same in the adult as the number of diachile slots in
the deutonymph and tritonymph, but they are small,
sheltered in the progenital chamber and not easy to see.

The genital chaetotaxy includes the eugenital (eu),
genital (ge) and aggenital (ag) setae. The eugenital
seate are special because they are, as usual, eupathidia
and the only setae of the cis-acetabulal area (Grandjean,
1969) (15). Their number is greatly reduced in most

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(15) There is however an exception. The genitals of
Pseudotydeus perplexus are cis-acetabulal as far as the
8-shaped structure drawn by Baker and Delfinado (1974)
are considered as genital discs.

Tydeidae and always smaller in females than in males. The
maximum is six.. The cis-acetabulal area seems to be
shriking in the adults, if chaetotaxy may be considered as
an indicator of its magnitude. In the nymphs this area is
certainly vanishing as the result of fusion of the
diachile slots in several genera.

The maximum of genital setae in Tydeidae is six, and
the maximum known number of aggenital setae, five.
However, it could not be surprising to find a tydeid with
six aggenital pairs. There exist only a small number of
genital setal formulae, and these are summarized in the
figure 5 . This figure shows that the decrease in genital
chaetotaxy is obviously not a random phenomenon in the
adults or in the immatures.

The left side of the figure deals with phylogeny ;
the right side concerns ontogeny.

First, let us consider the ontogeny formulae. Only
a few are known but nevertheless, a first interpretation
seems justified. In figure 5 , the formulae are ranked
from the richest in setal number to the poorest. Group A
includes successions starting with no genitals and only
one pair of aggenitals in the protonymph (0-1). Both
groups B and C start with (0-0) but group C is unique
in that aggenitals are absent throughout ontogeny.
special formulae are grouped in D.

Three preliminary statements on the ontogeny of
genital chaetotaxy may be made :

    1°) Not all ontogenies are initiated with one pair of
        aggenitals (0-1) ; some start with (0-0) in the
        protonymph.

    2°) Any setal number in an ontogenic succession is
        never higher than the homologous number following
        it.

Figure 5 : Left : combination of the number of genital and aggenital setae at
each stase (immatures designated by abbreviations L, P, D, T ; adult
represented by a square including the number of eugenitals in female and
male observed for each combination. Right : ontogenic formulae commencing
from the protonymph.

3°) The maximum value is six pairs of genitals and
five pairs of aggenitals (6-5).

A method developed by Grandjean (1961) may be used
to determine whether the regression of genital chaetotaxy
is eustatic or amphistatic. To apply this approach, the
genital and aggenital setae will be treated together as
a whole (i.e. 11 setae). If the setae are considered to be
independant, and if the three preliminary remarks noted
above are taken into account, it may be shown that there
are 572 possible formulae for genital chaetotaxy in
Tydeidae. The paucity of known formulae (see figure 5)
indicates that every genital or aggenital setae may not be
amphistatic. If, on the other hand, the starting
succession is the first one, and if the setae are assumed
eustatic and independent, then the number of possible
successions is reduced to 160. Following Grandjean (1961),
the more restrictive hypothesis must be chosen ; i.e. the
setae are assumed to be generally eustatic and there exists
a priority among them.

Is this hypothesis consistent with the observations ?
Grandjean (op. cit.) was working with ten pairs of
genital setae, and one of them was consistently present
from the protonymph. In the primitive Tydeidae there are
11 pairs, but a distinction between the genitals and the
aggenitals is often possible ; this is an advantage.

The first succession noted at the top of the figure
(A1) shows one pair of aggenitals in the protonymphal stase
(ag1) (16). In the deutonymph, three setal pairs appear :
one aggenital (ag2) and two genitals (ge2', ge2"). In the
tritonymph, four additional setae appear : two aggenitals

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(16) This is an ontogenic notation, and not a designation
      based on location.

(ag3', ag3") and again two genitals (ge3', ge3"). Lastly in the adult appear three new setae : one aggenital (ag4) and once again two genitals (ge4', ge4"). This succession is met only in Meyerellinae and in most Triophtydeinae.

The second succession (A2) is similar to the first, the only one difference being the disappearance of ag4 (which consequently should be considered the weakest pair).

The third succession (A3) differs from the second in the disappearance of ge2 (ge2' or ge2") Hence, ge2 is stronger than ag4 and the eustasy hypothesis is consistent with this group of three ontogenies (group A).

In group B, only one ontogeny is known in its entirety (B5). A stase is missing in formula B7 and B4 and three in B6. Setae ag1 disappear in group B, but there are two aggenitals in the deutonymph. One is ag2 and the second can only be ag1 which is thus delayed in appearance. The amphistasis hypothesis applies to ag1. Moreover, the second setae ge2 also disappears. The sequel of development is normal in the formula B4. The priority list becomes (ge2', ge2', ag4) with ag1 delayed to the deutonymph.

Formula B5 differs from B4 in the disappearance of one ge3. The priority list becomes (ge3', ge2', ge2", ag4) with ag1 delayed.

The last two formulae of group B unfortunately are incomplete. These formulae likely imply the disappearance of the second ge3 and lastly of one ag3. The priority list should be (ag3', ge3', ge3", ge2', ge2", ag4).

Group C is unique and quite homogenous. It is characterized by the complete disappearance of the genital setae followed by the loss of the aggenitals. All pronematine tydeids belong to this group.

Group D includes only special cases. Formula D11 is similar to formula A2, but the delay in appearance of one *ge2* and one *ge3* must be taken into account. Formula D12 is doubtful because *Pretydeus lwiorensis* has too many vertitions (cft. § about this genus). Formula D13 is obviously too poor to establish relationships.

In conclusion, the number of ontogenic successions in tydeid genital chaetotaxy is low, but it is likely that much remains to be discovered. However, it may be said that the chaetotaxy of the genital area is primarily eustatic ; some setae are amphistatic and only delayed in appearance. The complete disappearance of the genitals is noteworthy among Pronematinae. However, it is not surprising since the primitive pair of progenital lips on which genital setae are always located, are vanishing in this group. The shortening of the progenital lips appears to be a general phenomenon among Tydeidae and even seems to precede the disappearance of the genital setae. Shortened lips with a maximum of setae do exist, but not entire lips with few setae. On the other hand, it is premature at this time to finalize ontogenic priorities.

The left portion of figure 5 deals with phylogeny. It illustrates that, as a whole, eugenitals are the weakest (although they are eupathidia). The matrix shows two groups of formulae separated by a gap ((1-4) does not exist in adults). This breach separates Pronematinae (which lose all genital setae with the disappearance of the progenital lips) from the other Tydeidae in that other tydeids do not go through as drastic a regression of the progenital lips and genital setae. However, the aggenitals commonly illustrate a trend toward loss of the aggenitals, a situation approaching the primitive deutonymphal formula

The genital setae are likely idionymic, as are the
aggenitals. However, the homologies are difficult to
establish (17) although vertitions which are frequent in
this area may reveal some trends. An example is offered
by Paratriophtydeus coineaui. In this species, the nine
males studied have four pairs (4+4) of genital setae.
Among the 20 females studied, 14 specimens have three
pairs of genital setae (3+3), five have three pairs of
genital setae on one side and four on the other side
(4+3), and only one has four setae on each progenital
lip (4+4). This means that the appearance frequency of
four ge on a progenital lip of a female is 0.175. Hence,
it is easy to show that the frequency distributions of
the three formulae (4+4), (4+3) and (3+3) coincide with a
random distribution. This is a basic characteristic of a
vertition as defined by Grandjean (1972) who also
developed a probability approach to the phenomenon. In
females with a heterogenous formula, the two posterior
pairs of ge are opposite one another whereas the third
seta on a lip is on a level with the anterior pair of the
opposite lip. On one specimen, the two anterior setae of
a four setae alignment share the same basis and have a
common root, both of which are larger than usual (18). The
tritonymph of Pretydeus lwiorensis has only five ge ; the

(17) This is the reason why a designation system is used
to name the setae. Agl merely means that an aggenital
setae is the first of the alignment, and does not entail
any homology between different species or stases.

(18) This has also been observed in other species where
two genitals share the same basis but keep their own root.
With the shortening of the progenital lips, one may
imagine a sequence in which the genital setae converge and
share a common base, and finally share a common root.

unpaired element is anterior and very much undersized.
This suggests that the anterior pair of ge disappear
first. However, the process could be more complex ; in
Teletriophtydeus wadei male for instance, setae ge are
plumose except for the extreme anterior and posterior
pairs, which are smooth. This could be interpreted as a
sign of weakness in these setae.

As for the aggenital setae, the process seems to be
different. When a specimen with four (ag) is compared with
one having two (ag), the two missing pairs are obviously
the posterior ones. However, in a tritonymph of
Apopronematus, it was noted that there are only seven ag
because of a vertitionel absence of one of the four
anterior ag. This suggests that the priority list in the
aggenital alignment is different from the list of the
genital alignment.

As might be expected, the genital area offers the
primary characters for distinguishing males from females
(19). The shape of the progenital lips often varies
between sexes as does genital chaetotaxy. The eugenital
setae are always less numerous in females than in males.
The genital setae have a different shape in males and
females of Pretriophtydeus tilbrooki. There are three
pairs of genitals in female Paratriophtydeus and four in
males. However, based on observations on P. coineaui, this
evolution is vertitional. A different genital chaetotaxy
between females and males is also met in Homeopronematus.
Here, the females have four (ag) whereas males have only
one (ag). Such a regression entails a sexual dimorphism

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(19) Sexual dimorphism also is expressed in secondary
characters. Males usually are smaller than females and
may have an excrescence on femur IV or distinctively
shaped empodia and paraproctal suckers.

in the tritonymph which has either four (ag) (female
tritonymph) or only one (ag) (20).

The ventral side of the podosoma is difficult to
interpret. As no precise boundary exists between the
ventral or sternal area and the coxae, this area will be
called the coxisternal or epimeral area, and its setae
will be referred to as coxisternal or epimeral setae. The
paleotrichous formula of the tydeid venter is (3-1-4-3).
In the adults, there are only two other formulae : (3-1-
3-3) or (3-1-4-2). This means that either seta 3d or seta
4c is missing, but never both together. The 3-1-3-3
formula is found in Meyerellinae and Triophtydeinae, and
the 3-1-4-2 formula in Pronematinae and Tydeinae. The
basic chaetotaxy is (3-1-2-(0)) in every species studied.
From that, three ontogenies exist :

$$(3\text{-}1\text{-}2\text{-}0)\text{---}(3\text{-}1\text{-}3\text{-}2)\text{---}(3\text{-}1\text{-}3\text{-}3)\ (a)$$
$$(3\text{-}1\text{-}2)\diagup\text{---}(3\text{-}1\text{-}3\text{-}0)\text{---}(3\text{-}1\text{-}4\text{-}2)\diagdown\text{---}(3\text{-}1\text{-}4\text{-}3)\ (b)$$
$$(3\text{-}1\text{-}4\text{-}2)\ (c)$$

The first ontogeny (a) is unique because a suppression
exists on the third metameron from the protonymph to the
adult. The two other ontogenies (b and c) are quite
similar, differing only in the presence or absence of 4c
in the tritonymph and adult. The coxisternal area is also
the site for the paired Claparède organs in the larva.
These organs have been located in a Tydeus species and in
Proctotydaeus pyrohippeus. Each consists of a small and
obscure depression in the antiaxial area of the posterior
edge of the epimere I, near 1b. As organs have been seen
in the advanced subfamilies Tydeinae and Pronematinae it
may be supposed that they exist throughout the family.

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(20) In fact, the only one "male" tritonymoh observed
during the course of this study has only a single ag.

Another feature of the coxisternum are the "coxal organs"
found by Karg (1973) in several Tydeinae and likely to be
a specific character in that genus. Coxal organs exist in
all known Tydeinae, Prototydeinae and in Australotydeus,
as paired microprotuberances on epimere I. Such a
character has not been found in the other Tydeidae.

CHAPTER III : LEGS

Legs generally comprise six segments in Tydeidae.
These are the trochanter, femur, genu, tibia, tarsus and
apotele (21). 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 Tydeidae. For instance, genua II, III and IV

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(21) According to van der Hammen (1977), Actinotrichida
do not have coxae.

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, $\underline{d}$; two laterals, $\underline{l'}$ and $\underline{l''}$; two ventrals, $\underline{v'}$ and $\underline{v''}$) 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 6)

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 ($\underline{cot}$) which are connected with the condylophores ($\underline{k.ph.}$). The third is found proximal and ventral to the empodial root.

Because of their setal derivation, lateral claws (22) and the empodium are birefringent and have a root and a development (23) similar to that of a seta. The lateral

(22) The french word "ongle" used by Grandjean is trans-lated as "claw". The set of three "ongles" is called "griffe" by Grandjean. In french, a distinction is made between "griffe" (=claw) and "ongle" (=nail) depending on whether the structure is innervated by a muscle or not.

(23) The development of a claw has been followed in several larvae, beginning with their formation in the prelarval anoderm. Initially, they are, like a seta, very clear and
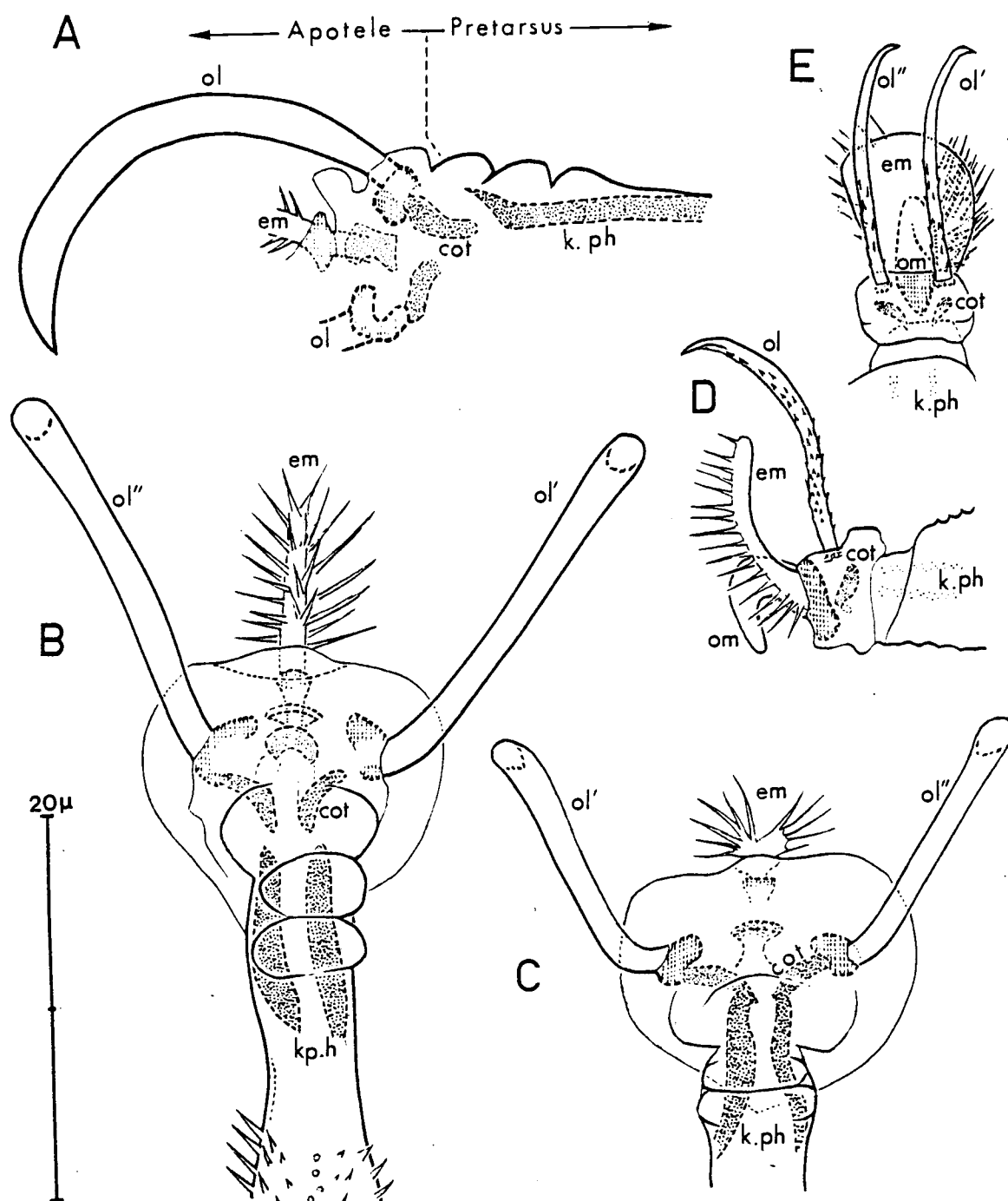
Figure 6 : Apotele. *Proctotydaeus schistocercae* : lateral (A) and dorsal views (B) of apotele IV of a male, dorsal view of apotele II of a tritonymph (C). *Pretydeus lwiorensis* : lateral (D) and dorsal views (E) of apotele I of a tritonymph.

claws are more or less hooked and often have small teeth
on the lower face. 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 wich 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 (Coineau, 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 actinedid 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

... with no root. In Oribatida, claws are subject to
vertitions (Grandjean, 1961).

Staurobates schusteri, the apotele is assumed to have
retained its mobility. Th 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
dissapearance of the condylophores belonging to tarsus I
as in Stauroma 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 "palpian evolution". Where the apotele drops out, no
new organ seems to appears on tarsus I, but a substantial
lengthening of the existing eupathidia is noticed.
According 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 descendent
harmony type (figure 1B).

B. Tarsus (figure 7)

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
stase 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
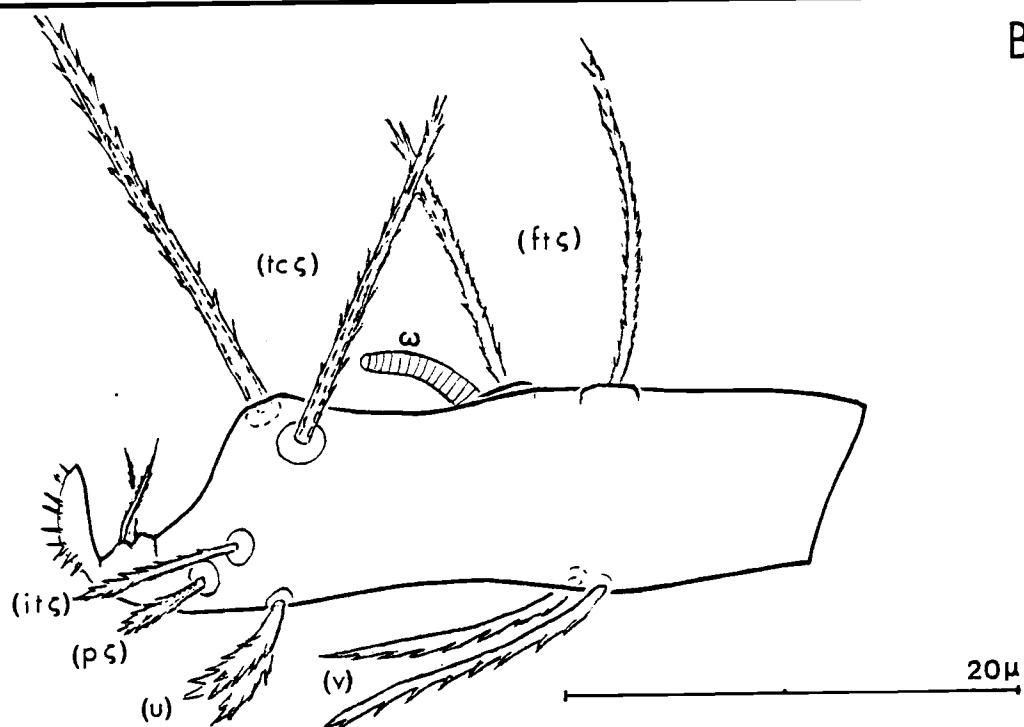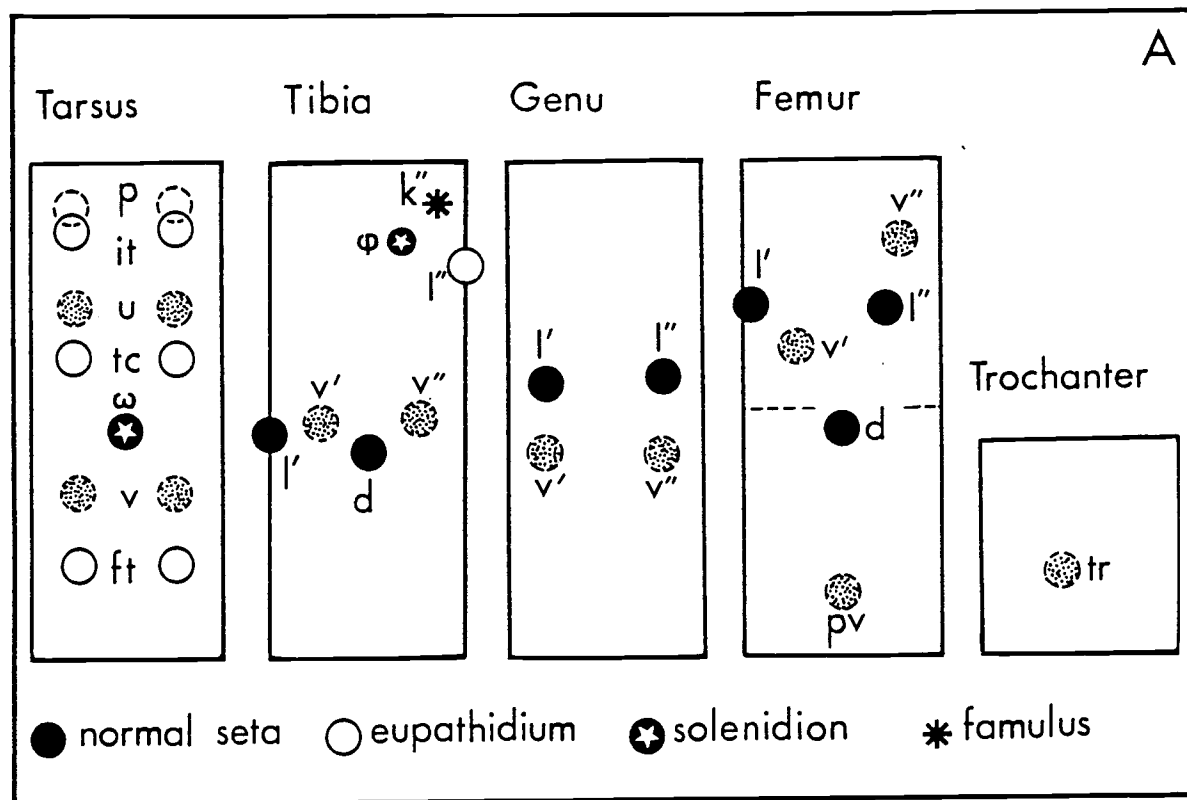
Figure 7 : Leg segment phanerotaxy in the Tydeidae.
Diagram of a leg segment phanerotaxy in dorsal view
(archetype) (A) ; antiaxial view of tarsus I of Meyerella
marshalli (tritonymph) (B).

formulae for tarsus I are summarized in table I.

It may be seen in table I that setae (<u>it</u>) 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 :

$$(\underline{ft}', (\underline{tc}), (\underline{p}), (\underline{u})), \underline{ft}'', ((\underline{it}), \underline{v}''), \underline{v}' \quad (1)$$

Some exceptions to this priority list do occur ; e.g. formulae 9 and 10 which represent <u>Australotydeus kirstenae</u> <u>Aesthetydeus setsukae</u> and <u>Tyndareus eloquens</u>. The problem arises because (<u>it</u>) and (<u>v</u>) 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 :

$$(\underline{ft}', (\underline{p}), (\underline{u})), \underline{tc}'', \underline{tc}', \underline{ft}'', ((\underline{it}), \underline{v}''), \underline{v}' \quad (2)$$

This latter list is more precise than that for tarsus I but contains a contradiction regarding the relative strengths of <u>ft</u>" and (<u>tc</u>).

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

$$\underline{p}'', \underline{p}', (\underline{tc}), \underline{ft}'', \underline{ft}', (\underline{it}) \quad (3)$$

It will be seen that this list does not coincide with lists (1) and (2). For instance, <u>ft</u>' is more persistent than <u>ft</u>" but this seta is more often eupathidial. The strengh 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 (<u>it</u>) seems stronger in

TABLE I.. CHAETOTACTIC FORMULAE OF TARSI (ADULT).

		(ft)		(tc)		(it)		(p)		(u)		(v)	
I	1.	E	E	E	E	E	E	E	E	N	N	N	N
	2.	E	E	E	E	E	E	E	E	N	N	-	N
	3.	E	E	E	E	E	E	E	E	N	N	-	-
	4.	E	N	E	E	E	E	E	E	N	N	-	-
	5.	N	E	E	E	N	N	E	E	N	N	N	N
	6.	N	N	E	E	N	N	E	E	N	N	N	N
	7.	N	E	E	E	N	N	E	E	N	N	-	N
	8.	N	N	E	E	N	N	E	E	N	N	-	N
	9.	N	E	E	E	-	-	E	E	N	N	N	N
	10.	N	N	E	E	-	-	E	E	N	N	N	N
	11.	N	E	E	E	-	-	E	E	N	N	-	-
	12.	N	N	E	E	-	-	E	E	N	N	-	-
	13.	N	-	E	E	-	-	E	E	N	N	-	-
	PF	100	99	100	100	40	40	100	100	100	100	22	40
	ESF	11	84	100	100	11	11	100	100	-	-	-	-
II	1.	N	E✶	-	-	-	-	N	E	N	N	-	-
	2.	N	N✶	-	-	-	-	E	N	N	N	-	-
	3.	N	N	-	-	-	-	N	E	N	N	-	-
	4.	N	N	-	N	-	-	N	E	N	N	-	-
	5.	N	N	N	N	-	-	N	N	N	N	-	-
	6.	N	N	-	N	-	-	N	N	N	N	-	-
	7.	N	N✶	-	-	-	-	N	N	N	N	-	-
	PF	100	100	26	36	-	-	100	100	100	100	-	-
	ESF	-	7	-	-	-	-	2	12	-	-	-	-
III-IV	1.	N	-	N	N	-	-	N	N	N	N	-	-
	2.	N	-	-	N	-	-	N	N	N	N	-	-
	3.	N	-	-	-	-	-	N	N	N	N	-	-
	4.	E	-	-	-	-	-	N	N	N	N	-	-
III	PF	100	-	33	41	-	-	100	100	100	100	-	-
	ESF	6	-	-	-	-	-	-	-	-	-	-	-
IV	PF	100	-	33	38	-	-	100	100	100	100	-	-
	ESF	6	-	-	-	-	-	-	-	-	-	-	-

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

Meyerellinae and Triophtydeinae than in other groups.
Either proral may be eupathidial on tarsus II, which
means that , primitively, the pair had to be eupathidial.
Mention should also be made of the presence of eupathidia
on tarsi which have already lost one or several setae.
This suggests heretefore unobserved 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 frequent 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 Prelorryia indionensis is
observed for the first time, six setae are obvious and
seem easy to name : (ft), two large tectal eupathidia
(tc⸮) 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), tc"⸮,
p'⸮, (v). Both interpretation are wrong.

The solution of the problem is found in the larva
of two species of Metatriophtydeus. Two large eupathidia
exist as in Tydeus ; the more distal one is p' and
occupies the usual location, while the other the other
is situated at the typical position of ft". 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 location
of ft". These two setae have to be named and the only
consistent formula becomes :

(ft), (tc) both undersized, (p$^\varsigma$), (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 prorals, which is the
established rule (figure 8). However, the strange
location of p" must be explained. A backward and upward
setal migration 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" (24).

The position of the dorsal setae in Metatriophtydeus
is only the first step of a more important process
involving the reduction and eventual loss of (tc). The
tectals are undersized in Metatriophtydeus and keep their
own insertion. A further step is met in Pretydeus kevani
and Tydeus spp., where both tectals are vestigial and the

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(24) From ανα, meaning both upward and backward, and
βαρειν, 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 Apostigmaeus 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, Erythraeidea, Bdellidae
and Caeculidae) or second as in Tydeidae.
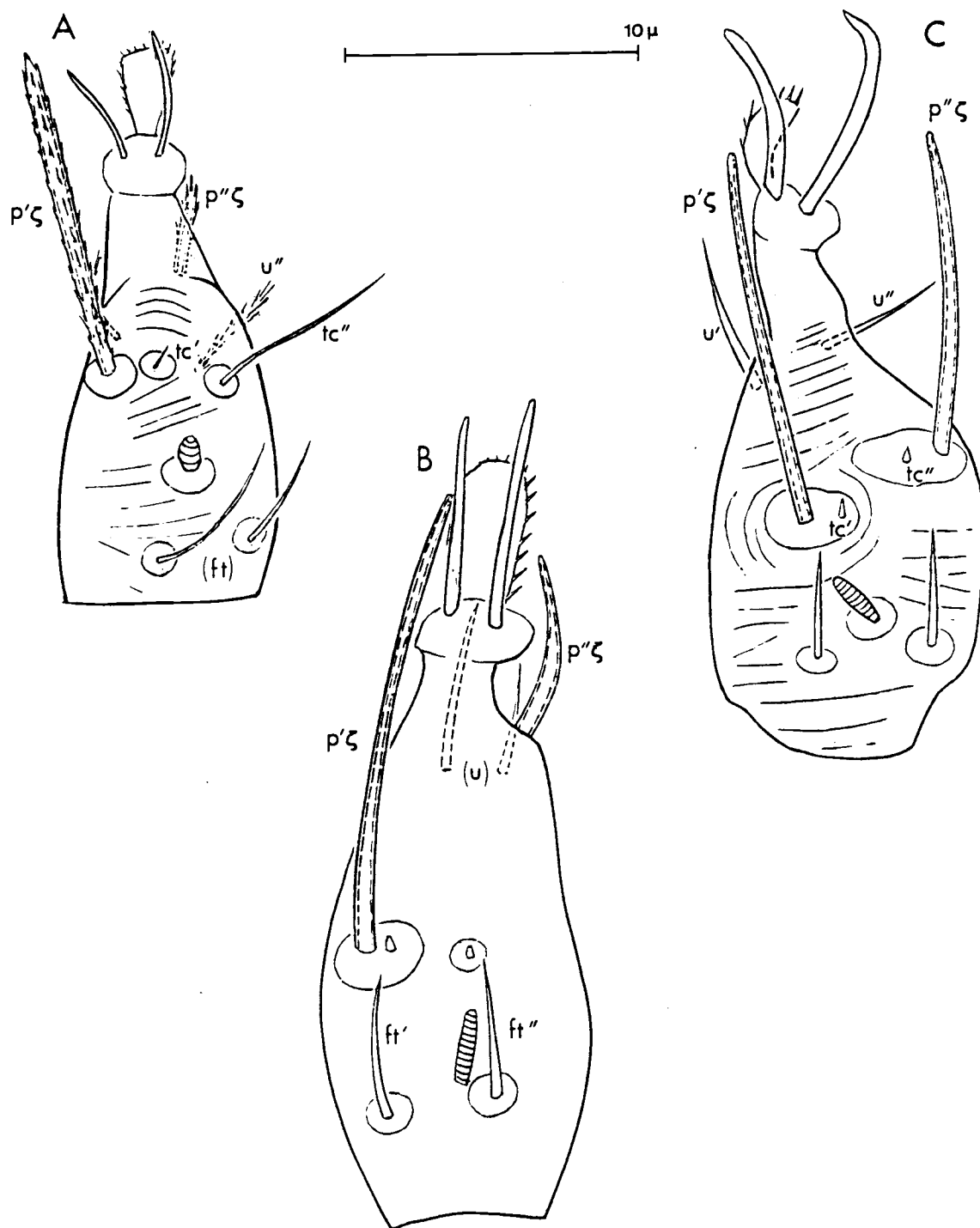
Figure 8 : Anabasis. Tarsus I of larva of Metatriophtydeus sp. (A), Tydeus sp. (B) and Prelorryia indionensis (C).

insertion of <u>tc</u>" begin to amalgamate with the insertion of <u>p</u>"⚲. The next phase is the anabasis of <u>p</u>'⚲ as in *Prelorryia indionensis* or *Tydaeolus* : (<u>tc</u>) are vestigial but both share the same insertion with (<u>p</u>⚲). The last step involves the complete disappearance of (<u>tc</u>). This may be the case in *Homeopronematus* vidae whose (<u>tc</u>) could not be found (25). 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 anhomologous only between the larva and protonymph ; subsequently, it is homologous.

Table II summarizes data on fundamental chaetotaxy of each tarsus.

TABLE II. FUNDAMENTAL CHAETOTAXY OF TARSI

		(<u>ft</u>)		(<u>tc</u>)		(<u>it</u>)		(<u>p</u>)		(<u>u</u>)		(<u>v</u>)	
I	1.	N	N	N^x	N^x	–	–	E	E	N	N	N	N
	2.	N	N	N^x	N^x	–	–	E	E	N	N	–	N
	3.	N	N	N^x	N^x	–	–	E	E	N	N	–	–
	4.	N	N	–?	–?	–	–	E	E	N	N	–	–
II	1.	N	N	–	–	–	–	N	E	N	N	–	–
	2.	N	N	–	–	–	–	N	N	N	N	–	–
III-IV	1.	N	–	–	–	–	–	N	N	N	N	–	–
	PF	100	50	7	7	–	–	100	100	100	100	4	7
	ESF	–	–	–	–	–	–	25	29	–	–	–	–

<u>Symbols</u> : the same as in the previous table.

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(25) To be sure, it would be enough to check if (<u>tc</u>) are eupathidial or normal in the protonymph (since eupathidia first appear as normal setae through ontogeny). Unfortunately , the protonymph was not available for study

Ontogeny of the setae. As far as is known, the
fastigials become eupathidial at the deutonymphal stase.
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, Proctotydaeus schistocercae...).
Seta ft" becomes eupathidial on tarsus II in the trito-
nymph 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 : 3).

The tectals become eupathidial on tarsus I of the
protonymph. Seta tc" appears on tarsus II at the trito-
nymphal stase in Meyerella marshalli and Proctotydaeus
schistocercae while both tectals, (tc), appear together
in the deutonymph of Paratydaeolus and Tydaeolus frequens,
and in the tritonymph of Paratriophtydeus. Setae (tc)
exist on tarsi III and IV at the adult stase in
Microtydeus and Tydaeolus but not in the deutonymph
(unfortunatelly, their tritonymphs are unknown). In
Coccotydaeolus, (tc) appear at the deutonymphal stase on
tarsus III but are delayed to the tritonymph on tarsus IV.
The unpaired tectal seta, tc', is formed at the
deutonymphal stase on   tarsus III of Homeopronematus
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 : (NN) - (ƧN) - (ƧƧ) - (ƧƧ) ; (--) - (NN) -
(ƧƧ) - (ƧƧ) ; (??) - (??) - (NN) - (ƧƧ) and (--) - (--) -
(NN) - (NN). From formula (3) (page 43), 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 eustasic from the larval stase..

   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 eustasic,
which helps explain the difficulties encountered in
building a setal priority list.

   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

	1	2	3	4	5	6	7	8	9	10	11	12	13
I	7	8	8	8	8	8	11	12	12	12	12	11	10
II	6	6	6	6	7	7	8	8	7	7	6	6	6
III	5	5	6	6	6	7	7	7	7	5	5	5	5
IV	5	5	5	6	6	7	7	7	7	5	5	5	5

Solenidiotaxy of tydeid legs is simple and entails
only one solenidion (ω) on tarsi I and II. Solenidion ωI
is present in every species and, as far as ontogenies are
known, is eustatic from the larva ; ωII 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 ωI and ft'. Such a pairing has already been 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. (figure 25)

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 7) includes five normal setae of which one may be eupathidial, a famulus k" and a solenidion φ.

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 in-dependent, 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.

TABLE IV. CHAETOTACTIC FORMULAE OF THE FOUR TIBIAE

	1	2	3	4	5	6	7	8	9
I	5	4	4	3	3	3	2	4	2
II	3	3	2	2	2	1	1	2	2
III	2	2	2	2	1	1	1	1	2
IV	2	2	2	2	1	1	1	2	2

However a leg setal tabulation (26) 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 9 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.

The first element of formula 1 of table IV refers to tibia I of Meyerella (figure 9 , A) which have five setae, one of which is eupathidial ($\underline{1}''\varsigma$). The seta $\underline{v}''$ appears in the deutonymph. The first step in setal regression of tibia I occurs in Metatriophtydeus (B), where $\underline{v}''$ first

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(26) This term is taken from Vercammen-Grandjean (1971).

appears in the tritonymph. Seta $\underline{v}''$ is thus amphistatic. Likewise, a seta disappears from the lateroparaxial area at each stase. However, the missing setae is $\underline{d}$ rather than $\underline{l}'$ as might be expected. Figure 9 A' and A'' explain this circumstance and refer respectively to $\underline{Ereynetes}$ a (Grandjean, 1939) and to $\underline{Pseudotydeus\ perplexus}$. A' is similar to A except that $\underline{v}''$ is delayed to the tritonymph. A'' differs from A' in that $\underline{d}$ is reduced. Seta $\underline{d}$ may consequently be supposed to become unable to assume its role because of its reduced size, and in light of the movement of $\underline{l}''\mathcal{S}$, which seemingly is usurping its location. Seta $\underline{l}''$ in $\underline{Pseudotydeus}$ 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 $\underline{l}''$ to substitute for $\underline{d}$ 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 $\underline{Metatriophtydeus}$ (figure 9 B), the same assumption may be made for $\underline{d}$, but in this case seta $\underline{d}$ completely disappears and $\underline{l}'$ substitutes for $\underline{it}$. Theoretically, the substitution of $\underline{d}$ by $\underline{l}'$ is as likely as by $\underline{l}''$. Moreover, such a substitution has been observed as will be described in the following paragraph.

Figure 9 C depicts another regressive step : the complete absence of $\underline{v}''$ from all stases, but with seta $\underline{d}$ still present. Such a pattern is found in $\underline{Coccotydaeolus}$, $\underline{Microtydeus}$, and $\underline{Tydaeolus}$... However, one species, $\underline{Tydaeolus\ frequens}$ (Grandjean, 1938) shows, once again, the reduction of $\underline{d}$ (figure 9 C'). Here again, movement of a lateral setae is observed, but in this case, it is seta $\underline{l}'$ which movesto the dorsal face while $\underline{l}''$ retains its
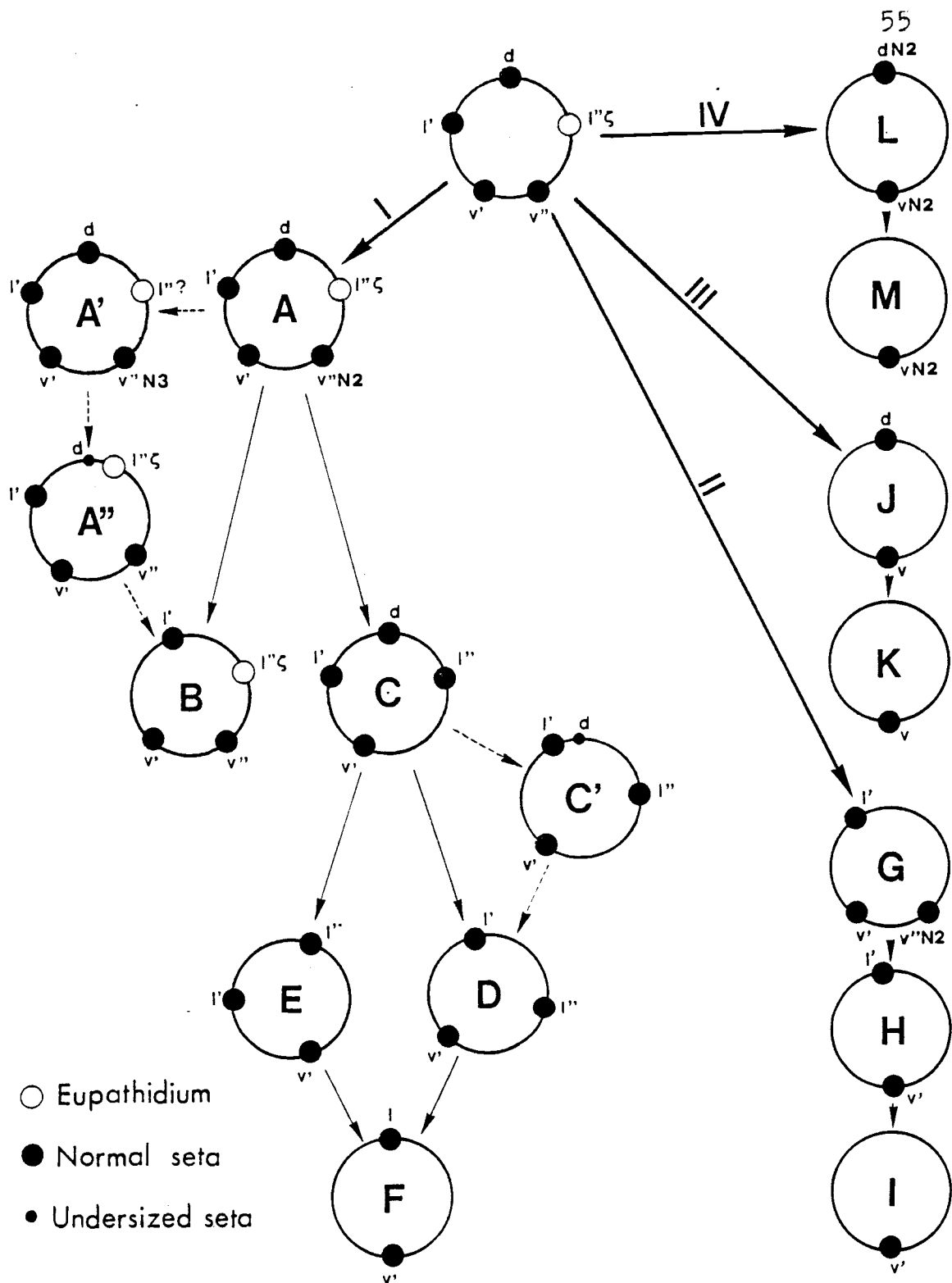
Figure 9 : Schematic regressive pattern in tibial chaetotaxy in Tydeidae. Roman figures refer to the four legs.

typical position in relation to v'. To go from
figure 9 C' to D requires only the loss of seta d.
Figure 9 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 9 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 9 F).

In tibia II, the richest formula includes three setae
whose designations are l', v', v"N2 (figure 9 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 9 H) and, lastly,
l' drops out (figure 9 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 9 J, K, L, M).
Both tibia 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 φI (27). In
Pseudotydeus perplexus, seta k" forms a cluster with l"♀

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(27) However, an exception is known in the generic unit Tl
where these positions are reversed.

as in <u>Ereynetes</u> 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, φ I and φ II. The latter exists only in
Meyerellinae and is recessed. Solenidion φ 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 <u>Pseudotydeus</u>. Solenidial recession is
typical in mites and sometimes precedes their
disappearance. However, such a phenomenon could also be
adaptative as Zacharda (1979) hypothetizes 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 (page 52)
is again applied to the genu, there are 160 possible
formulae between the abovementioned 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

TABLE V. GENUAL CHAETOTACTIC FORMULAE

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
I	4	4	4	4	4	3	3	3	3	3	3	3	2	2	2	2	2	1
II	4	4	4	3	2	3	3	3	2	2	2	1	2	2	1	1	0	1
III	3	2	1	2	1	2	2	1	2	2	1	1	2	1	1	0	0	0
IV	1	1	1	3	0	2	1	0	2	1	1	1	1	1	1	0	0	0

TABLE VI. FEMORAL CHAETOTACTIC FORMULAE

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
I	6	6	5	5	5	5	5	5	4	4	4	3	3	3	3	3	3	3	2
II	4	3	4	4	4	3	2	2	4	4	2	3	3	3	3	2	2	1	2
III	3	3	3	3	1	1	3	1	3	1	2	2	2	1	1	2	1	1	1
IV	2	2	3	2	3	2	3	3	2	3	2	2	1	1	0	1	1	0	1

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 the 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.

E. Femur (figure 7)

The femur is special in that it consists of two
primary segments : a basi- and a telofemur (28), which
usually are fused following a proregressive evolution
(Grandjean, 1952, 1954). van der Hammen (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 used generic character, but it has not been
throughly 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

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(28) or, respectively, a femur 1 and a femur 2 after
the nomenclature of van der Hammen (1970).

musculature is studied (29).

Each joint from the tarsus to the basifemur is
monovalent as explained by van der Hammen (1970). Several
muscles originate from the ventral and proximal area of
a segment (30) 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 (31)
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
(32). In Eotydeus, the major stress joint is situated

(29) The musculature of three specimens was studied : an
Eotydeus adult and a Meyerella adult in cavity slide and
a paratype of Apotriophtydeus wilkesi in permanent slide
Only leg IV was examined closely.

(30) The tendons could not be seen. In any case, their
attachments must be more distal than the distal end of
their muscles.

(31) More precisely, what is briefly called "line of
action" refers to the line of action of the useful
component of the muscular vector force.

(32) The trochanter is unimportant in this context since
its joint with the femur is bivalent and devoted to
forward and backward movement.

between the femur and genu (i.e. the primitive telofemur-genu joint). The position is 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 (33),

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

The efficiency 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 Eotydeus, the interfemoral muscle has dropped out entirely. The migration to the ventral side of the muscle acting on 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 joint may be located by the presence of the dorsal condyle as observed, for instance, in Proctotydaeus pyrohippeus. The presence of a joint membrane with no striation also aids in its location. 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.

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(33) except when the angle of flexion is null or close to zero.

Table IV summarizes the femur chaetotactic formulae.
The richest is (6-4-3-2) and the most regressive is
(2-2-1-1). Once again, the mathematical approach to the
tarsus and tibia may be applied here. Between the two
extreme formulae, noted above, there are 135 possible
setal combinations 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.

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 the poorest in Triophtydeinae
and , in one case, femur II is the poorest (Apotriophtydeus).
Australotydeus kirstenae also has the minimum number of
setae on the third femur. This is in opposition 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 seta, _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
deutonymph, as are those of genu and tibia IV. This sudden
appearance of all the setae at the same stase is
surprising. It implies that all the setae are delayed in
appearance as eustatic setae or, conversely, that the
setae are eustatic at the deutonymphal stase. Neither
explanation seems satisfactory, since such a regularity
in the behavior of the setae of all the species observed
is unlikely. An explanation based on the phenomenon of
deficiency (Grandjean, 1951) would be more cogent. The
protonymphal level of Tydeidae may be regarded as being
deficient with regard to femoral, genual and tibial
chaetotaxy (34). Grandjean (1946) pointed out this
denudation of the protonymphal leg IV in mites and
interpreted it as a percursory sign of the disappearance
of the leg.

Lastly, sexual dimorphism is observed on femur IV
of adult Pronematinae. The males bear a dorsal spiniform
excressence at the distal edge of the femur which is
absent in the female. (figure 16 D and E)

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

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(34) The case of the trochanter is a bit different as
explained later.

induced. This list is ($\underline{tr}$ III, $\underline{tr}$ I, $\underline{tr}$ II, $\underline{tr}$ IV). It
must be pointed out that formula 4 does not fit with this
list. The different ontogenies reveal that the setae are
all amphistatic. The seta $\underline{tr}$ III always appears first
except after the disappearance of seta $\underline{tr}$ II ; then, $\underline{tr}$ I
seems to become as strong as $\underline{tr}$ 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 (35). 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.

TABLE VII. TROCHANTER CHAETOTACTIC FORMULAE

	1	2 a	b	c	3 a	b	4	5	6
I	1N2	1N2	1N2	1N3	1N2	1N2	1	0	0
II	1N2	1N2	1N2	1N3	0	0	0	0	0
III	1N1*	1L	1N1	1N1	1N1	1N2	0	1	0
IV	1N3	0	0	0	0	0	0	0	0

✗ The larva is unknown.

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(35) Two exceptions are known, ($\underline{tc}$)III and IV are formed
in the $\underline{Meyerella\ bifurcatus}$ adult as is $\underline{tc}$"IV in $\underline{Homeo}$-
$\underline{pronematus\ vidae}$.

CHAPTER IV : GNATHOSOMA

The gnathosoma represents a highly evolved and
specialized body region and includes two main segments :
the cheliceral frame and the infracapitulum (Grandjean,
1957 ; van der Hammen, 1968, 1970 ; Coineau, 1974) (36).
The gnathosoma of Tydeidae was described by Grandjean
(1938). A paragraph will be devoted to both segments
while a third one will deal with taenidia.

A. Infracapitulum

A ventral view of the gnathosoma presents a few
interesting points. Since there is no sclerite, no
boundary is obvious between the mentum and genae. There
are always two subcapitular setae, scl and sc2. In ventral
orientation, the lateral lips appear as thick lobes which
meet in the ventral commissure of the mouthparts. Usually,
two pairs of adoral setae, (ad1) and (ad2), arise close to
the tip of the infracapitulum. These are difficult to see
because they are small, recumbent and likely eupathidial.
Dorsally, the preoral cavity is covered by the labrum. The
three commissures are far anterior with the result that
the lips form a long duct called a propharynx (37).
In Australotydeus kirstenae, a large species, the lips
seem to end with some small teeth. The dorsal wall is the

(36) The precheliceral segment is not taken into account
here. According to van der Hammen (1970), a part of what
is usually called infracapitulum should be included with
that segment.

(37) I proposed this word earlier (1977) to designate
such a preoral cavity.

cervix whose shape is standard. In <u>Meyerella</u>, the
cheliceral grooves are very deep while the capitular
saddle is slightly convex.

The infracapitular epimeron bears as appendages the
palps whose shape is characteristic in Tydeidae. They are
divided into four segments : trochanter, femorogenu, tibia
and tarsus. The phanerotaxy is simple. The trochanter is
nude and the femorogenu bears two setae : a dorso-genual
(<u>dg</u>) and a dorso-femoral (<u>df</u>). The former drops out in
only three species : <u>Tydides ulter</u>, <u>Pseudotydeus perplexus</u>,
and <u>Coccotydaeolus bakeri</u> ; the latter is always present.
The tibia also bears two setae : <u>t'</u> and <u>t"</u>. One of them
drops out in Pronematinae and in some tydeine genera. It
would seem that <u>t'</u> is the setae which is missing, but this
is not certain.

The palp tarsus has a solenidion, ω which tends to be
recessed. It is often difficult to find and sometimes
impossible to see in a permanent mount. The paleotrichy of
the palp tarsus includes eight setae of which four are
eupathidial : (<u>pς</u>), <u>acmς</u>, <u>dς</u>, <u>l'</u>, <u>l"</u>, <u>v</u> and <u>ba</u>. This
situation is found in <u>Meyerella</u>, but the chaetotaxy is
fundamentally similar throughout the family. The following
differences occur in the other genera : <u>d</u> becomes normal ;
(<u>pς</u>) and <u>acmς</u> progressively become a multiple eupathidium ;
<u>ba</u> becomes vestigial. The eupathidia are located and arise
in such a way that they are directed forward when the palp
is in its normal position. (figures 10, 14A, 17B, 20J, 21B)

The dorsal setae, <u>d</u>, is only eupathidial in <u>Meyerella</u>
In other genera, it is often ornate, serrate (<u>Metatrioph-
tydeus</u>), trifurcate (<u>Pseudotydeus</u>) or bifurcate (<u>Australo-
tydeus</u>). The three anterior eupathidia become fused to
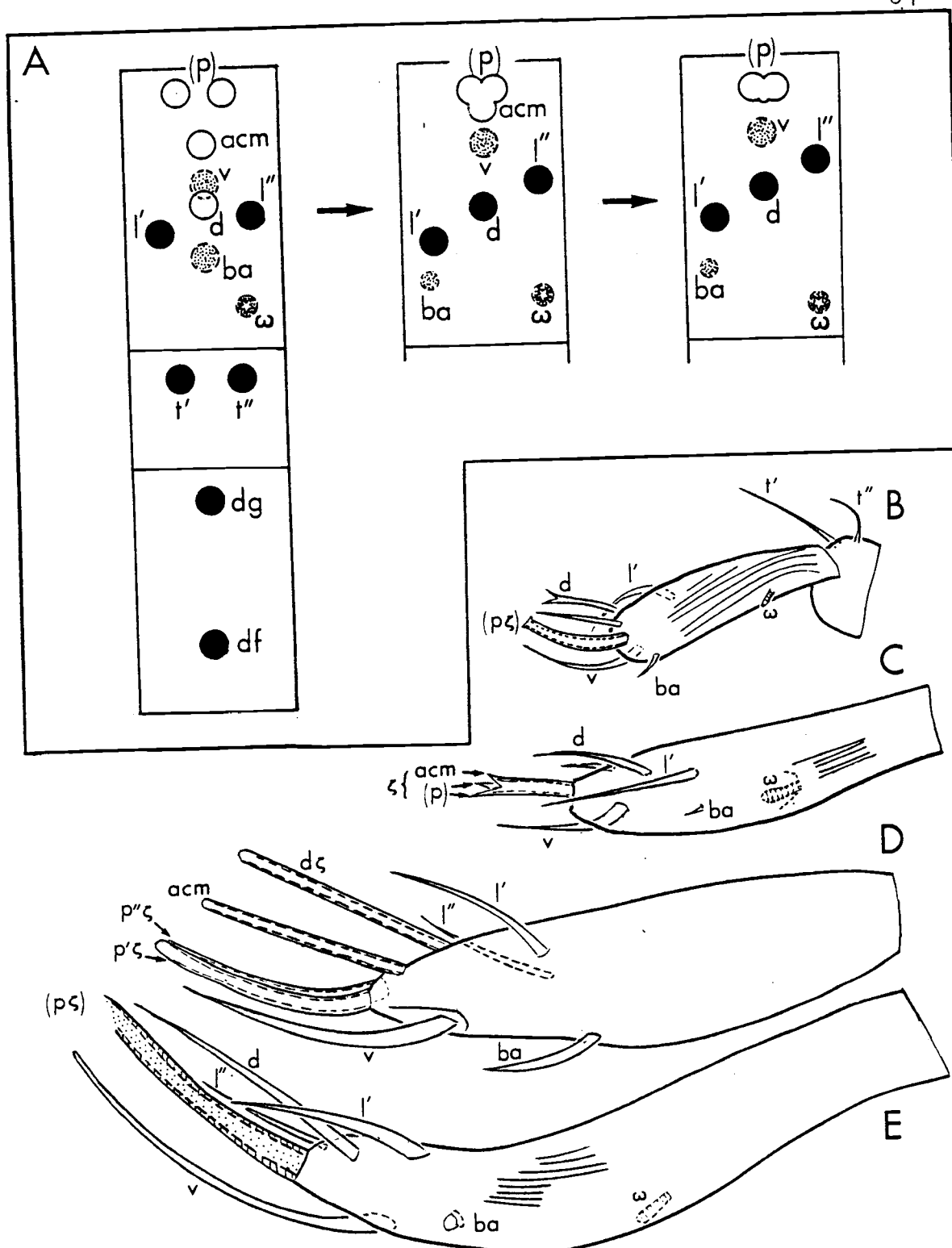form a tridentate multiple eupathidium. This is

Figure 10 : Palp segment phanerotaxy in the Tydeidae. Diagram (dorsal view) with evolution of the tarsus (A) (symbols as in figure 7A) ; palptarsus of _Tydeus tridactylus_ (B), _Paratriophtydeus coineaui_ (C), _Meyerella bifurcatus_ (C) and _Lasiotydeus krantzi_ (D).

particularly obvious in Triophtydeinae whose three tines
are still equal and well separated. In Paratriophtydeus,
Microtydeus, and Pseudotydeus, the three tines illustrate
progressive coalescence ; the tine acm is smaller than
the others and tends to form a small spine on the back
side of a double eupathidium, (pζ). In Prototydeinae, it
is possible to distinguish the three tines, but in
Tydeinae, there remains only a single large eupathidium
which seems double but, in fact, is triple. The terminal
eupathidium of Pronematinae is similar to that of Tydeinae.
Such an enlarged and modified eupathidium could conceivably
produce silk, as does the terminal palpal eupathidium of
spider mites. Seta ba is more or less spiniform but quite
obvious in Tydeinae and Prototydeinae although it is often
"forgotten" in the published formulae. In Triophtydeinae,
ba is small or even vestigial. It is also small in Procto-
tydaeus pyrohippeus. In Lasiotydeus krantzi, a large
species, ba is not difficult to see although it is
vestigial. It still likely exists in Microtydeus as a
vestige. As for the other genera, I am unable to state
whether ba really drops out or is still vestigial.
Tydaeolus is very regressive in this respect, as there
remain only v, d and the terminal eupathidium whose three
tines are still distinguishable.

The palp phanerotactic formulae are as follows
(numbers represent tarsus, tibia, femorogenu, trochanter ;
numbers in parentheses refer to solenidia) :

    8(1)-2-2-0 with four simple eupathidia,
    6(1)-2-2-0 with a multiple eupathidium and ba present,
    6(1)-1-2-0
    5(1)-2-2-0 with a multiple eupathidium and no ba,
    5(1)-1-2-0

5-6(1)-2-1-0 ba doubtful,

   5(1)-1-1-0

   3(1)-2-2-0

No variation has been observed through ontogeny.

B. The cheliceral frame

The chelicerae are very advanced and fused in great part. Moreover, there is no well defined limit between the cheliceral sheath and the chelicerae. The latter comprise only two elements : the apotele or digitus mobilis and the "principal segment" consisting of five fused primary segments : trochanter, femur, genu, tibia and tarsus. The digitus mobilis is articulated with the principal segment and bears a stylet which is birefringent and hollow. The stylet may be more or less slender but the basic structure remains constant. In some genera (Meyerellinae and Triophtydeinae) there are some signs of the fixed digit. Over the digit(s), there is fleshy extension of the principal segment which contains several muscles and other structures described by Grandjean (1938). The principal segment bears an antiaxial excressence in some Triophtydeinae.

C. Taenidia

There are two pairs of taenidia : the podocephalic canals and the peritremes. The podocephalic canals of Tydeidae were described by Grandjean in 1938. Each canal is bordered by two laterocoxal (or supracoxal) setae, eI and ep which are always present in every species and stase. They originate at the cheliceral vault and their course is standard and constant throughout the family. Each canal runs on the surface of the body but the two

lips are in touch. At its posterior extremity, the canal runs internally and receives a small affluent ductus, dg3. The connection with a coxal gland is difficult to establish (38).

The other taenidia are the peritremes which also originate from the cheliceral vault where the four stigmata open. The tracheal ducts, (trα), open in the cheliceral vault by the stigmata (sti). The tracheal ducts (trπ), run up before opening in the cheliceral vault by two stigmata so closely associated that they may be considered as only one, stπ. This opening is extended forward and upward by two fused peritremes, vs, which form what Grandjean (1938) called the vestibulum. These peritremes which are fused on the sagittal plane run up between the chelicerae and open on the dorsal face at the neostigma, n.st..

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(38) The only one coxal gland observed was found within coxa II of a Meyerella. No connection with the podocephalic canal could be established.

CHAPTER V : SYSTEMATICS AND
GENERAL CLASSIFICATION

An extensive review of the role and purpose of
sytematics is obviously beyond the field of this work.
However, no classification may be advanced without some
comments regarding the metholology used and its foundation.

A. Preliminary comments

Purpose and meaning of systematics. In the first
chapter, I claimed that evolution follows a hierarchical
strategy. Consequently, the living world may be
comprehended as a hierarchy of open systems. In my opinion
and in this frame, the aim of systematics is to represent
that structure, i.e. what are the systematic relations
between the elements constituting these systems. This point
of view is not widely considered, but has recently been
developed by Griffiths (1974) : "The task of a scientific
systematics is not to introduce order into the manifold
of particular phenomena, but to investigate and represent
their intrinsic order" (Hennig, 1950 quoted by Griffiths).
The concept of time is of course essential in such an
approach as in any biological field. To deny time amounts
to excluding systematics from the biological sciences and
confining it within a logico-mathematical framework
(Sokal's (1974) system is an example).

The taxon as a holon. In the framework of the theory
of organization levels, a taxon is considered as a holon
and handled as such. This implies that the taxon must be
comprehended as a whole, and not merely as the sum of its

elements. If a taxon is considered as an Aristotelian class or as an independent logical complex, it does not have these relationships to its elements, but rather it is characterized by the fact that all statements about it can be transformed into statements about its elements (Carnap, 1967 : 9). A class is therefore defined as "the extension of property" (ibidem : 57). The later interpretation cannot be accepted here. Latter, in this work, a species will be described by the following statement " $\male$: 4($\underline{ge}$) (occurrence 100%) - $\female$: 3($\underline{ge}$) (occurrence : 17,5%)". It is obvious that such a statement is irrelevant for any particular individual, since it refers to the species as a system and not as a class sharing common characteristics with its constituents. The latter concept ignores variations among individuals. Grandjean's work, on the contrary, calls attention to these variations in his studies on mites.

Taxa and stases. Aristotelian philosophy is the source of the persistent and prejudicial notion that only mature individuals are important for classification since individuals do not fully manifest the essence of the species until they reach maturity (Griffiths, 1974). The prejudice is all the more important since each stase, according to Grandjean, follows its own phylogeny. Therefore systematics must be based on the entire ontogeny or at least on two extremes stases (the larvae and adults for example) (39).

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(39) Some classifications are based on the larvae, such as the nepophylogeny of Vercammen-Grandjean (1969). This is relevant to some extent, insofar as larvae may be more advanced than adults in many respects.

Cladistic analysis. As already explained in Chapter I,
the evolution of holons is influenced by two main groups
of factors : its canons and the contingencies of the
environment (40). Chaetotactic patterns are canonical
and are more or less independent from environmental factors
as noted by Grandjean and Gisin (1967). However, this
independence is relative as shown by the concept of an-
homologous tautergy. Based on what is understood about
the rules governing chaetotactic pattern (41), the
cladistic approach may be quite useful. Therefore, Camin
and Sokal's (1965) method was chosen as a tool for
building phylogenies. On the other hand, some non-
chaetotactic features seem more linked to the contingencies
of the environment and are thus believed to be adaptive.
The extension of the eupathidia in Pronematinae or the
development of paraproctal suckers are examples. Nothing is
known about the rules governing the appearance of these
structures ; they are assumed to be irreversible. However,
such adaptive characteristics may be useful to better
characterize an evolutionary trend even if the rules and
environmental conditions governing such an evolution are
unknown. The only one restriction is that an evolutionary
trend established in this way may not go against a canon.

Camin and Sokal's method. This method is strong and
consistent as long as the preliminary assumptions are
accepted. Two of these assumptions are not taken into
account here. The first concerns use of the minimum

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(40) This point of view is parallel with the concept of
"anagenesis" and "cladogenesis". (Gama, 1971)

(41) Contrary to what Mayr (1969) states, it does not
matter that the chaetotactic evolution is regressive.

number of evolutionary steps in establishing a phylogeny.
This assumption is derived from Maupertuis' philosophical
axiom "of least action" or parsimony. Taxa whose
subdivisions have parallel evolutions are poorly handled
by this method since it tends to blend the elements from
different subdivisions in order to retain the minimum
number of steps. Unfortunately, parallel evolutions seem
to occur fairly frequently among mites. The Maupertuis
axiom does not actually imply a minimum number of steps
but rather the repeated use of the same canons throughout
different branches of a cladogram. The problem above arises
partly because the characters used are supposedly equal.
Yet to each systematic level belongs a special set of
characters and this exactly describes the theory of
organization levels. The study of the canons allows
a posteriori weighting of these characters. Therefore, Camin
and Sokal's method was used after having imposed some
priority among the characters used. Nevertheless, this
method remains debatable, not because of its lack of
consistency, but because it depends too much on the number
of characters used and the number of species available.
However, the method is heuristic in that it provides ideas
about gaps between the different O.T.U.'s (Operational
Taxonomic Unit).

Classification. As noted by Mayr (1974), the cladistic
analysis does not necessarily imply a cladistic
classification. The reconstitution of a phylogeny is a
deductive process and a cladogram is supposed to call up
the story of a group. Such a process is therefore
susceptible to falsification, according to Popperian
philosophy (Kitts, 1974). This is not a case of

classification which is essentially a matter of convention.
A genus is separated from other taxa of the same rank by a
decided gap (Mayr, 1969) but no one has ever defined the
width of such a gap. Consistency within a group is the
only rule. The problem arises from the fact that words are
discrete units and are used to describe continuous
phenomena.

B. The subfamilial level

The solenidiotaxy of the Tydeidae is greatly reduced
and consists of only five solenidia : palpal ω, ωI, ωII,
φI, and φII. Clearly, only very strong solenidia have
persisted and these apparently are eustatic. Solenidion φII
exists only in Meyerella and always is recessed ; φI is
more common, but sometimes is also recessed ; ω II is
seldom absent and ω I is always present. The strength of
these solenidia and their special nature suggests that they
can be a useful criterion for distinguishing the tydeid
subfamilies. (42)

Lyrifissures number four pairs in Tydeidae except in
Tydeus and some other genera. The canons regulating
lyrifissures are not well known, but they seem eustatic.
In any case, their presence is certainly not stochastic,
and their disappearance within the family is somewhat
surprising. Absence of lyrifissures (ip) (figure 3 D)
separates Tydeus and other genera from the rest of the
Tydeidae.

Genital acetabula are eustatic. The tritonymphal
acetabular pair is missing in all the Tydeidae. The

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(42) An exception will be made for ω II which disappears
only in a few specimens for which it would be premature
to create a subfamily.

regression continues in some genera which lose one or two
pairs of genital acetabula.

The disappearance of apotele I or at least its
regression and the concomitant elongation of the adjacent
eupathidia seems to be another subfamilial criterion. While
this phenomenon has occured in several families (even
among Oribatida), it is not common. Certainly it is
doubtful that it occurs more than once among the tydeid
subfamilies.

The shape of the dehiscence line of the prodorsum
(figure 2) is another useful subfamilial character even
if some intermediate cases exist between the procurved and
the recurved types. The number of eyes could be another
good criterion but further information is necessary on this
point. There are three eyes in Meyerella, Apotriophtydeus,
and Metatriophtydeus, and only two in Tydeus and
Lasiotydeus. No eyes were seen in Homeopronematus.

Some other chaetotactic characters are of interest.
A case in point is the coxisternal or epimeric chaetotaxy.
The epimeric chaetotaxy is (3-1-4-3) and has been seen
only in Tydaeolinae, and in Australotydeus. Either seta
3d drops out (Meyerella, Metatriophtydeus...) or 4c is
absent (Tydeus). Seta 12 is especially interesting in that
it has been observed only in the genus Australotydeus
(figure 3 A). It is not only absent in other Tydeidae, but
also in the tydeoid family Ereynetidae and apparently in
the Paratydeidae. It is thus a special and primitive
character, the presence of which makes it necessary to
classify Australotydeus apart from the other tydeid genera.
Anabasis is simple in several genera but double in others.
Other characters may be of value in better describing
subfamilies, but what is important is the set of criteria

selected above and expressed in figure 11 . These criteria
distinguish seven subfamilies, all of which are new since
no subfamilies were created in previous revisions. These
are the Australotydeinae, Meyerellinae, Triophtydeinae,
Tydeinae, Pretydeinae, Pronematinae and Tydaeolinae.

An interpretation of the general phylogeny (43) of
Tydeidae as an amalgam of these subfamilies is proposed in
figure 11. The number of evolutionary steps sensu Gisin
(1967) (44) is expressed in the ordinate. This scale rests
only on organotactic characters, such as phanerotaxy and
idiotaxy, i.e. on discrete or discontinuous characters
(Grandjean, 1951) as well as on apotele I. Some characters
of an adaptative nature could be introduced in a third
dimension but such characters are more difficult to
quantify even arbitrarily. Of course, the selected scale
is also arbitrary and the resulting pattern is all the
more relative.

Subfamilies are represented by terminal leaf-like
expansions. Each expansion has a lower and an upper limit
which respectively represents the number of evolutionary
steps of the less and the more advanced species in
respect to organotaxy. The width of the expansion was
determined in such a manner that its area is more or less
proportional to the number of species described in the
subfamily (45). Since the subfamilies are well advanced in

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(43) In this particular case, it is not too wrong to speak
about the general phylogeny of Tydeidae as long as
phylogenies of different stases are in harmony. Of course,
the prelarva is calyptostatic.

(44) Contrary to the opinion of Griffiths (1974), it is
not immaterial as to whether one uses time or evolutionary
steps as the ordinate. The resulting diagrams are somewhat
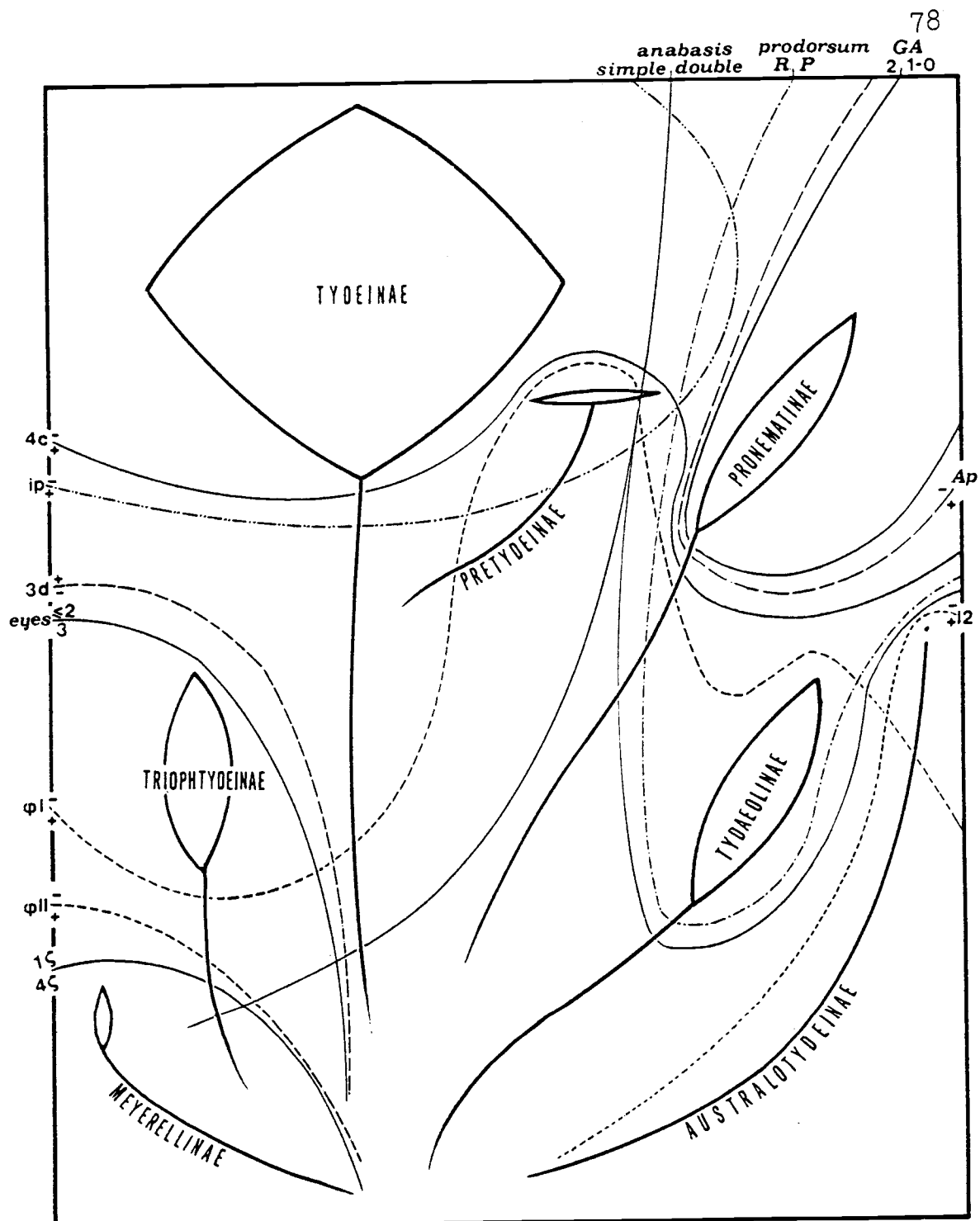different due to different points of view in data analysis.

Figure 11 : Hypothetical phylogeny of subfamilies of Tydeidae. "Contour" lines delimit the occurrence of certain characters used in defining the subfamilies (special abbreviations : GA : genital acetabula ; Ap : apotele I ; R : recurved ; P : procurved ; 1ς and 4ς refer to the palp eupathidia ; + : present ; - : absent (or reduced when apotele I is concerned)).

their own directions on the basis of the criteria used, it
is difficult to determine how they may have begun their
own evolution. It is the reason why the origins of the
different subfamilies are expressed as free entities in
the diagram. The diagram also has "contour" lines which
delimit the presence of certain characters used in
defining the subfamilies.

The different subfamilies may be described as follows:

Australotydeinae n. subfam.

Prodorsum recurved (46) ; setae (12) present on the
opisthosoma (unique) (figure 3 A) ; four pairs of
lyrifissures ; two pairs of genital acetabula, eugenitals
present at least in σ, longitudinal progenital aperture
in σ, progenital depression in nymphs, cis-acetabulal
area absent in nymphs ; epimeric formula (3-1-4-3) in the
adults, coxal organ present ; femora IV fused, setae
tr I, II and III present in adults, two solenidia on the
legs (ω I, ω II), five eupathidia on tarsus I, none on
other segments ; terminal eupathidium at the tip of the
palp tarsus seemingly double.

Paraproctal suckers are well developed in the only
one species known. (figure 14C)

Meyerellinae n. subfam.

Prodorsum recurved with three eyes ; four pairs of
lyrifissures (figure 3 C) ; two pairs of genital acetabula,

(45) Only the species mentioned in the revisions of Baker
and Kuznetzov, and those amply described before or
subsequently , are taken into account here.

(46) This does not refer to the shape of the prodorsum but
to the shape of the dehiscence line and the location of
the prodorsal setae as explained in chapter II.

eugenitals present in ♀ and ♂, longitudinal progenital
aperture ; progenital groove in nymphs with cis-acetabulal
area ; epimeric formula (3-1-3-3) in adults, femur IV
divided, four solenidia on the legs (ω I, ω II, φ I, φ II)
(unique), eight eupathidia on tarsus I, one on tibia I and
another on tarsus II ; four distinct eupathidia at the
tip of the palp tarsus (unique).

The Meyerellinae is the only subfamily with setae
tr IV but their appearance is delayed until the
tritonymphal stase ; their total disappearance in some
species would not be surprising. The subfamily may also be
characterized by its particular leg chaetotactic regression
as described in chapter III.

Pretydeinae n. subfam.

Prodorsum recurved ; opisthosoma with three pairs of
lyrifissures (ip absent) ; two pairs of genital acetabula,
eugenitals present only in ♂, longitudinal progenital
aperture in ♂, recumbent-H shaped in ♀, no cis-acetabulal
area in nymphs but a sign of the anterior apex of the
progenital chamber ; epimeric formula (3-1-4-2) in adults,
coxal organ present ; femora IV undivided ; leg chaetotaxy
reduced ; genua II, III and IV nude, tr I, II and III
present in adults ; three solenidia on the legs, ω I, ω II
and φ I (the latter absent in one case), slightly recessed
particularly φ I ; at the most five eupathidia on tarsus I,
eupathidia absent on the other leg segments ; simple or
double anabasis ; multiple eupathidium at the tip of the
palp tarsus, with three terminal tines.

The anagenesis of the Pretydeinae is characterized by
the appearance of the empodial claw as in some Tydeinae.

Pronematinae n. subfam.

Prodorsum procurved, no eyes at least in one genus, sensilla may be clublike ; four pairs of lyrifissures ; two to zero pairs of genital acetabula, no eugenitals or genitals, progenital aperture varying from a five-branches shape to a transverse split, cis-acetabulal area in nymphs absent or very reduced ; paraproctal suckers often well developed ; epimeric formula (3-1-4-2) in adults ; apotele I with vestigial claws or absent ; pretarsi II, III and IV with strong condylophores ; femur IV divided or undivided ; tr III always present in adults and tr IV always lacking ; three solenidia on the legs (ω I, ω II and φ I) ; generally, five eupathidia on tarsus I, very long ; in a few cases, a eupathidial seta on tarsus II ; double anabasis ; terminal eupathidium of the palp tarsus seemingly double ; only one seta on the palp tibia.

The regression of apotele I could be interpreted as being recent. However, femur IV is still divided in several pronematine genera and seta p' II of Parapronematus has retained the eupathidial condition. This indicates that the subfamily began its "palpian evolution" pretty early. The different location of the progenital aperture in $\male$ and $\female$, the structure of genitalia and the presence of a dorsal excrescence on femur IV suggest that true mating may occur among pronematinae. Direct sperm transfer is highly advanced strategy when compared to reproduction by means of spermatophores as has been observed in Tydeinae (Schuster, 1970). Such a difference would be quite important from an evolutionary standpoint.

Several pronematine species have been taken on insects, and certain adaptive characters suggest this type of relationship ; i.e. slender pretarsi, strong

condylophores, paraproctal suckers, and pulvillus.

Triophtydeinae n. subfam.

Prodorsum recurved with three eyes ; four pairs of lyrifissures ; two pairs of genital acetabula, eugenitals in ♀ and ♂ , progenital aperture longitudinal in ♂ and recumbent-H shaped in ♀ , cis-acetabulal area present in nymphs ; epimeric formula (3-1-3-3) in adults ; femur IV generally divided ; (it) present on tarsus I in adults but not always eupathidial, three other pairs of eupathidia on tarsus I ; often with other eupathidia on tibia I, and on tarsi II, III and IV ; simple anabasis ; two solenidia on the legs (ω I and ω II) ; triple eupathidium at the tip of the palptarsus.

As in Meyerellinae, the subfamily is characterized by its special leg chaetotactic regression as explained in chapter III. It is noteworthy that most members of the Triophtydeinae are found in the Arctic or Antarctic realms or in particularly uncogenial environments such the cortical medium on trees.

Tydaeolinae n. subfam.

Prodorsum procurved with probably two eyes, sensillum sometimes clublike ; four lyrifissures ; two pairs of genital acetabula, eugenitals present only in ♂ ; progenital aperture longitudinale in ♂ , recumbent-H shaped in ♀ , cis-acetabulal area absent in nymphs ; epimeric formula (3-1-4-3) in adults ; leg chaetotaxy rich ; (it) present but not eupathidial in adults, at most, five eupathidia on tarsus I, eupathidia absent on other segment, femur IV undivided ; setae tr I, II and III present in adults ; three solenidia on legs (ω I, ω II and φ I) ;

double anabasis ; trifurcated eupathidium at the end of the palp tarsus.

As in the Tydeidae, the subfamily is cosmopolitan and occurs in diverse habitats such as soil, plants and birds. The paraproctal lips are always smooth.

Tydeinae n. subfam.

Prodorsum recurved with two eyes ; opisthosoma with three pairs of lyrifissures (ip absent) ; two pairs of genital acetabula, eugenitals only in ♂ , progenital aperture longitudinal in ♂ ; without a cis-acetabulal area in nymphs ; epimeric formula (3-1-4-2) in adults, coxal organ present ; leg chaetotaxy reduced ; at maximum, with five eupathidia on tarsus I, eupathidia absent on other segments ; setae tr II and IV absent, others may sometimes be absent ; two solenidia on the legs (ωI and ωII, latter missing in a few cases ; simple anabasis ; terminal eupathidium of the palp tarsus seemingly double.

The anagenesis of the Tydeinae is characterized by the appearance of the empodial claw in some genera, the development of paraproctal suckers or the lengthening of chelicera in others. The subfamily is cosmopolitan and occurs in many habitats including soil, plants, birds, and mammals.

Based on the data gathered, other subfamilial classifications for the Tydeidae could be proposed : Meyerellinae and Triophtydeinae could be combined as a single group, as could the Tydeinae and Pretydeinae. On the other hand, the Pronematinae and Tydaeolinae seem quite distinct in all aspects. Australotydeus has the typical habitus of a tydeine, but the two groups differ in organotaxy.

C. Generic level

Even after having applied the Camin and Sokal
approach, the problem of defining the genera of Tydeidae
is not solved. Indeed, several classifications may be built
on a single genealogical tree. Moreover, this genealogy is far
from being finalized and needs further inputs on new
species and on the ontogeny of already described species.
Certainly the most predictable character states used in
cladistic analyses of tydeid subfamilies were derived
from leg chaetotaxy. As a consequence, grouping species
with too different chaetotaxies seemed a debatable option.
Therefore, generic units heve been defined by a
particular chaetotaxy (defined on all the stases when
possible) and on certain related chaetotactic characters
(47). As a result, the number of genera has been increased
substantially, although some previously recognized genera
have been united. Some arguments could be advanced against
this extensive division at the generic level.
Strandtmann (1967) feels there are too many tydeid genera,
but such a statement is without meaning as long as generic
criteria are not defined. In fact, the problem is more
a matter of the magnitude of the gaps between the genera
than a matter of number.

Mayr (1969) states that "splitters" almost without
exception classify characters rather than groups of
organisms. Inasmuch as a taxon is recognized by a
particular combination of characters, and since a set of
characters express the individuality of a taxon,

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(47) A related chaetotactic character would be one which is
not significant at a generic level. For instance, ft" I may
be eupathidic or not, in almost every group . This is
obviously not a generic charcter.

this statement is difficult to accept. It is true that some genera in the classification presented here are monospecific, especially in the Triophtydeinae. However, it is not surprising that this primitive group is represented only by a few species representing different genera which probably were much richer in earlier times. A great number of tydeid species probably remain to be discovered, even in the Triophtydeinae, so that there is little chance that any genus will remain monospecific for long.

It is felt that chaetotaxy provides a sound basis for that generic division in the Tydeidae, at least at our present state of knowledge. The gaps between the genera proposed are based on particular chaetotaxies;i.e. they are of the "all of none" type. It should be remembered also that every change in the adult often means changes through ontogeny, i.e. through several stases. This does not mean that a great number of specific variations may not be played on a single chaetotactic theme, or that several adaptive characters may not arise from a single chaetotactic pattern.

The subfamilies and genera of Tydeidae are listed below. The Australotydeinae is a very special subfamily (see diagnosis on page 79), and is monogeneric and monospecific. The Meyerellinae comprises only one genus, Meyerella, with three species. The special shape of the bifurcate idiosomal setae (figure 19) is not considered a subfamilial character. The generic unit (M1) (48) has a

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(48) To describe a new genus from one or two specimens is felt to be inadvisable except when the specimen(s) exhibit very special characteristics. However, it may be useful to indicate the existence of its chaetotactic pattern. Therefore, some generic units are acknowledged but are not officially described.

habitus similar to that of <u>Triophtydeus</u>, and will be
described later. At the present time, the Pretydeinae
comprise only five species distributed in two new genera
which differ in their solenidiotaxy and anabasis. It would
have been pointless to create a subfamily for <u>Prelorryia</u>,
which differs from the four other species in these
characters. Reducing the above criteria to the specific
level also would not provide a consistent solution.
Therefore, it was necessary to create two genera. The
Pronematinae illustrate many new chaetotactic formulae,
and others must be expected when new species are discovered
The genus <u>Proctotydaeus</u> is returned to the Tydeidae, from
which it was removed by Baker (1965). Fain and Evans
(1966) pointed out that the genus was closely related to
the Tydeidae. The Triophtydeinae comprise new genera.
Many of them are represented by species from Antarctica
described by Strandmann (1967), who was unable to key them
out with Baker's (1965) key. Other problems arose in that
any species with three eyes and an undivided femur IV was
assigned to the genus "<u>Triophtydeus</u>" regardless of the
chaetotaxy. The genus "<u>Triophtydeus</u>" is not included in this
treatment since its chaetotaxy is unknown. The type, which
is in the Oudemans collection at Leiden, is in need of
remounting before additional study will be possible. Since
a synonymy is easier to correct than an homonymy, it is
considered advisable not to use "<u>Triophtydeus</u>" until the
generic type can be studied again. The Tydaeolinae is a
quite homogenous subfamily. Only the genera <u>Pseudotydeus</u>
and <u>Lasiotydeus</u> seem somewhat atypical. Both are discussed
in the next chapter. Some new tydaeoline genera are
described because of the diversity of their leg chaetotaxy.
The Tydeinae represent the biggest tydeid subfamily.

Unfortunately, their systematic history is extremely
confused. A single genus was found to include several
species with different -sometimes very different-
chaetotaxies, while species with identical chaetotaxy were
distributed in several genera. This confusion arose
because of adherence of many recent workers to the old
generic concept of Canestrini, Berlese, Thor and Oudemans,
a concept which was based mainly, or only, on variations
in skin ornementation. The systematics of the Tydeidae has
been completely reorganized in this interpretation.

Australotydeinae : Australotydeus Spain 1969.

Meyerellinae :   Meyerella Baker 1968,
                      (+ one generic unit, M1).

Pretydeinae :   Pretydeus n. gen.,
                      Prelorryia n. gen...

Pronematinae :   Apopronematus n. gen.,
                      Homeopronematus n. gen.,
                      Metapronematus n. gen.,
                      Naudea Meyer & Rodrigues 1965,
                      Parapronematus Baker 1965,
                      Pausia Kuznetzov & Livshitz 1972,
                      Proctotydaeus Berlese 1911 sensu Fain &
                                   Evans 1966,
                      Pronecupulatus Baker 1965,
                      Pronematulus Baker 1965,
                      Pronematus Canestrini 1886 sensu Baker
                                   1965.

Triophtydeinae : Apotriophtydeus n. gen..,

Metatriophtydeus n. gen.,

Pretriophtydeus n. gen.,

Teletriophtydeus n. gen.,

(+ one generic unit : TR1).

Tydaeolinae :   Aesthetydeus n. gen.,

Coccotydaeolus Baker 1965,

Lasiotydeus Berlese 1908, sensu Baker
1965,

Metatydaeolus n. gen.,

Microtydeus Thor 1931, sensu Baker 1965,

Paratriophtydeus Baker 1965,

Paratydaeolus n. gen.,

Primotydeus n. gen.,

Pseudotydeus Baker & Delfinado 1974,

Tydaeolus Berlese 1910, sensu Baker 1965,

Tyndareus Livshitz & Kuznetzov 1972,

(+ one generic unit, G1).

Tydeinae :   Afrotydeus Baker 1970,

Apolorryia n. gen.,

Eotydeus Kuznetzov 1973,

Homeotydeus n. gen.,

Idiolorryia n. gen.,

Krantzlorryia n. gen.,

Metalorryia n. gen.,

Neolorryia n. gen.,

Orthotydeus n. gen.,

Perafrotydeus n. gen.,

Tydeus Koch 1835, n. comb.,

Tydides Kuznetzov 1975,

(+ two generic units, TY1 and TY2).

Generic descriptions and keys are presented in chapter VI.

D. Infrageneric or specific level

Some new genera are monospecific but, as noted earlier, for most of them, this is not likely to be a permanent situation. A great number of new tydeid species is expected to be described. The old systematics was an obstacle to such an achievement because of its lack of consistency.

At the present time, for each taxon described by a particular chaetotactic formula, a great deal of variation may be expected in the condition of chelicerae, empodia, setae,and striations, and in the clustering of certain setae... For example, in the collection kindly sent by Dr. Marshall, several species were labelled as "Coccotydaeolus sp." based on the old classification. These species were extracted from different types of litter and are distinctive in their pattern and density of striation, setal shape, and sensilla.. All of these characters will have to be considered in the future for proper species identification.

Dr. Marshall's collection also is interesting from an ecological point of view in that it reveals that the Tydeidae may be expected to occur in a particular habitat type, as already suggested by André (1975, 1979). But, once again, serious ecological studies require precise specific identification, or at least, they must rest on strong generic concepts. Misidentifications of tydeids have had some interesting zoogeographical consequences. For instance, Tydaeolus frequens is thought to occur in many locations throughout the world. However, the drawings of the sensillum published by Weis-Fogh (1948)and Wood (1965) suggest that there are, in fact, several species. It is

significant that the minute size of seta 1" on tibia I of _Tydaeolus frequens_ as described by Grandjean (1938) has never since been recorded in other collections of this "species".

CHAPTER VI : GENERIC DESCRIPTIONS
AND KEYS

The genera of Tydeidae are ranked alphabetically and
described below. The descriptions are followed by :
    1°) a key to the stases,
    2°) a key to the subfamilies valid for any stase, and
    3°) a key to the genera only valid for the adults.

Certain conventions have been used in drafting the
descriptions. Only generic information is utilized ; i.e.
characters common to all the Tydeidae (as the supracoxal
setae for instance) are not mentioned. Utilization of the
terms "procurved" and "recurved" in reference to the
prodorsum does not refer to its shape but rather to the
shape of the dehiscence line and the location of the
prodorsal setae, as explained in chapter II. If there are
no modifying comments regarding the prodorsum, it should
be assumed to be normal, with four pairs of setae present
(($p1$), ($p2$), ($p3$) and (s)). The number of eyes is noted
when it is known.

A variety of information is included under the term
"opisthosoma". The number of pairs of dorsal setae is
noted under "dorsal chaetotaxy" and followed by the names
of missing setae in parentheses (except for seta 13, which
is never present in Tydeidae). The number of lyrifissures
is listed under "poroidotaxy" ; it is not deemed
necessary to identify the missing lyrifissure since only
(ip) is likely to disappear. "Genital organotaxy" is
described by a series of formulae preceded by the
abbreviation of the stase involved (Ad, T, D, P or L). The
adult formula comprises three values separated by hyphens :
the number of eugenitals, genitals and aggenitals (eu –

ge - ag). If a setal number differs between sexes, both values are given and separated by a comma ; the first refers to the female (for example : (eu ♀ , eu ♂ - ge-ag)). For the nymphs, only the number of genitals and aggenitals (ge - ag) are mentionned ; the convention relative to sexual variation, as noted above, is applied where necessary. The number of pairs of genital acetabula in the adult also is noted, but only if other than two. Lastly, the epimeral formula is presented and the presence of coxal organs is mentioned when necessary.

Leg chaetotaxies are indicated by a series of conventional formulae preceded by the abbreviation of the stase. Eupathidia are then listed in ontogenic notation (49) and the number of solenidia is given. The palp is described by the conventional formula and some additional comments. Further information on essential particulars may conclude the description.

Species that should belong to a particular genus according to published accounts but have not been studied here are mentioned under the heading "other species".

Similarly, species of special but not exceptional morphological interest which are represented by only one or two specimens are described as "generic units" (G.U.), and listed at the end of the generic diagnoses.

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(49) This means that the stase at which the seta becomes eupathidial is indicated when necessary.

A. Generic descriptions

Aesthetydeus new genus

-DESCRIPTICN : Strandtmann (1967).

-SYNONYM : Tydeus (sensu Strandtmann 1967).

-SPECIES STUDIED : A. Setsukoae (Strandtmann 1967)
(monotypic), 1 ♂ paratype (Antarctica), 2 ♀ labelled
" N. Victoria Land, Possession Is. 150m, Antarctica,
Nov. 8.1964, Gressit" and nymphs labelled "Bishop
Museum, Antarctica Possession I. D. XI. 64, Single
large stone, J.L. Gressitt".

-DIAGNOSIS : Prodorsum : procurved. Opisthosoma :
dorsal chaetotaxy : 10 (12 and h1 missing) ; poroido-
taxy : 4 ; genital organotaxy : Ad(0,5-6-4), T(4-4),
D(2-2) `; epimeral formula : (3-1-4-3). Legs :
chaetotaxy : I(10-5-4-4-1) II(6-2-4-4-1) III(5-2-2-
3-1) IV(5-2-1-2-0) in the adults and tritonymphs ;
eupathidia on tarsus I : (tc) and (p) ; solenidiotaxy :
3 ; femur IV undivided. Palp : 6(1)-2-2 with ba well
developped and a terminal eupathidium apparently
double.

Afrotydeus Baker 1970

-DESCRIPTION : Baker (1970).

-SYNONYM : Tydeus (Afrotydeus) Baker 1970 (in part)

-SPECIES STUDIED : A. kenyensis Baker 1970, 1 ♀ holo-
type (Kenya) ; Afrotydeus sp. 3 ♀ + 1 deutonymph
labelled "on tree, Turrialba, Costa Rica, April 3,
1959, E.W. Baker Coll." NM NH n° 3189.

-DIAGNOSIS : Prodorsum recurved. Opisthosoma : dorsal
chaetotaxy : 10 (12 and h1 missing) ; poroidotaxy :

3 ; genital organotaxy : Ad(0-4-4), D(0-2) ; epimeral
formula : (3-1-4-2) ; coxal organ. Legs : chaetotaxy :
I(8-4-3-3-1) II(6-2-2-1-0) III(5-2-1-1-0) IV(5-2-1-
0-0) in the deutonymph and adult ; eupathidia on
tarsus I : ft", (tc), (p) ; solenidiotaxy : 2 ;
femur IV undivided. Palp : (6-2-2) + ω , with a double
eupathidium at the tip of the tarsus. Other features :
as in Perafrotydeus but unlike the other Tydeinae,
the paraproctal suckers are well developed. Seta l'
on the tibia is slender with a small root.

-OTHER SPECIES : likely some other species belonging
to the subgenus Afrotydeus as defined by Baker 1970.

Apolorryia new genus

-DESCRIPTION : Baker (1968b).

-SYNONYM : Lorryia (Baker 1968b in part).

-SPECIES STUDIED : A. congoensis (Baker 1968)
(monotypic), ♀ holotype and paratype (Zaïre).

-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 9 (12, h1 and h2 missing) ;
poroidotaxy : 3 ; reticulate pattern ; genital
organotaxy : (0-3-3) ; epimeral formula : (3-1-4-2) ;
coxal organ. Legs : chaetotaxy : I(7-3-1-2-0) II(6-1-
1-2-0) III(5-1-0-1-0) IV(5-1-0-1-0) ; eupathidia on
tarsus I : (tc) and (p) ; solenidiotaxy : 2 ; femur IV
undivided. Palp : (5?-1-2) + ω with a double
eupathidium at the tip of the tarsus.

Apopronematus new genus

-SPECIES STUDIED : A. bakeri n. sp. (monotypic), 3 ♀ +
1 tritonymph.

-DIAGNOSIS : <u>Prodorsum</u> : procurved. <u>Opisthosoma</u> :
dorsal chaetotaxy : 11 (<u>12</u> missing) ; poroidotaxy : 4 ;
genital organotaxy : Ad(0-0-3), T(0-3), no genital
acetabula ; epimeral formula : (3-1-4-2). <u>Legs</u> : no
apotele I ; chaetotaxy : I(8-4-2-3-1) II(6-2-2-3-1)
III(5-2-1-2-1) IV(5-2-1-1-0) ; eupathidia on tarsus I :
(<u>p</u>) and (<u>tc</u>) ; solenidiotaxy : 3 ; femur IV seemingly
divided. <u>Palp</u> : (5-1-2) $+\omega$ with a double eupathidium
at the tip of the tarsus.

-DESCRIPTION of <u>A</u>. <u>bakeri</u> (50) : the species is
described by figures 12 and 13 . <u>Material</u> 3 ♀ labelled
"Paicines, Calif. - Hilltop Plot, Ex Pinot noir Bark,
IV - 24- 1969, coll. D. Kinn", 1 tritonymph labelled
"Napa Valley, winery, St Helena, Calif. I - 26 - '70 -
Ex. Grape Bark, var. : Sauvignon vert Coll. O. Kinn".

<u>Apotriophtydeus</u> new genus

-DESCRIPTION : Strandtmann (1967).

-SYNONYMS : <u>Tydeus</u> (<u>sensu</u> Strandtmann 1967), <u>Trioph-</u>
<u>tydeus</u> (Baker 1970).

-SPECIES STUDIED : <u>A</u>. <u>erebus</u> (Strandtmann 1967) : 1
tritonymph paratype (Antarctica), 1 ♂ labelled "Moss
and lichen - Tottan Mts - Z92H - T.J. Tilbrook -
1965" ; <u>A</u>. <u>wilkesi</u> (Strandtmann 1967) : 1 tritonymph
paratype (Antarctica), 2 ♂ labelled "Bishop Museum -
Dufek Rge - Pensacolas Flotation - Loc. 67 - 82° 37S
52° 56W - II - XII - 1965 - O.R. Wilkes" and

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(50) This species is named for Dr. E. W. Baker who has
worked extensively on Tydeidae and who has very kindly
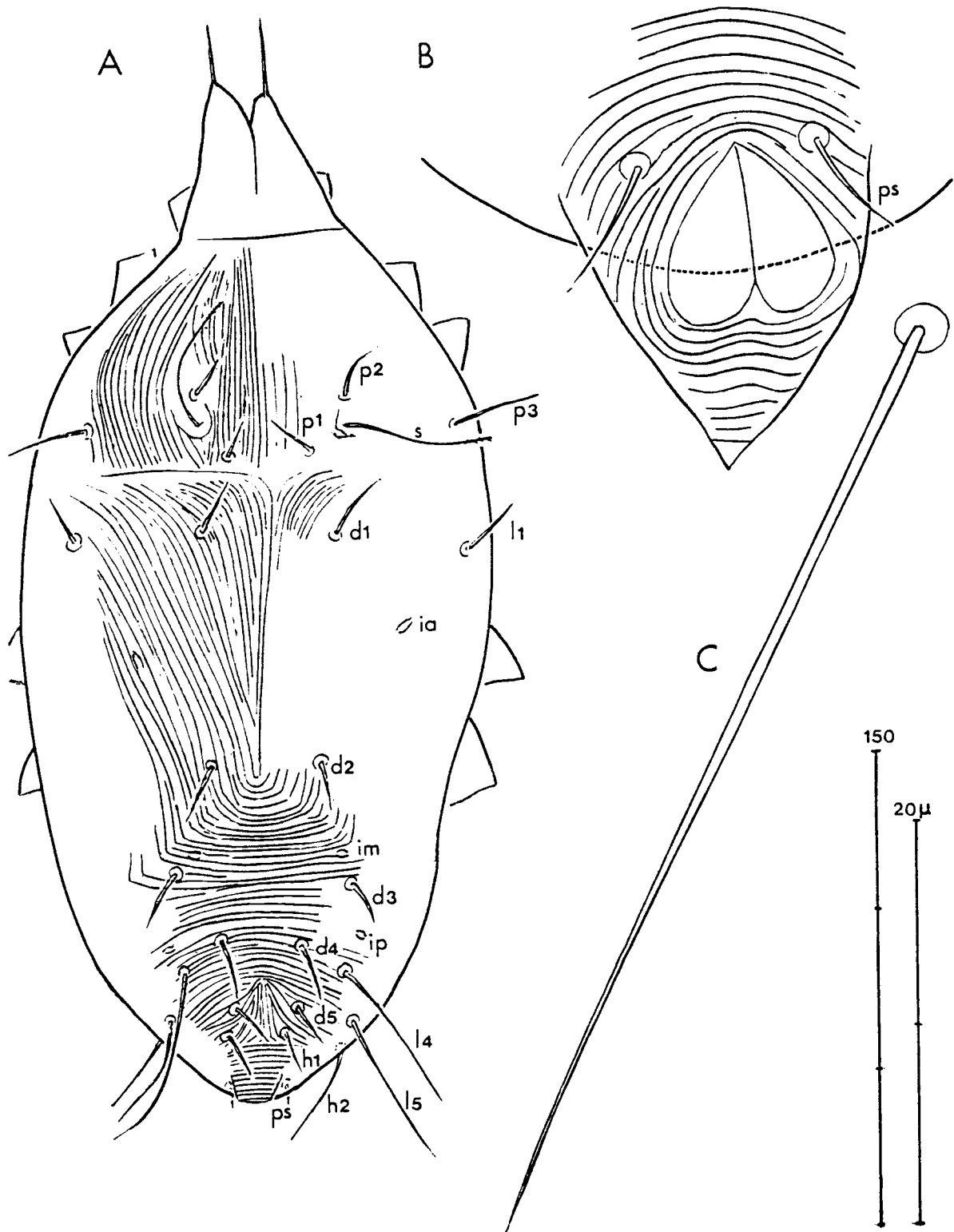sent me a great number of type specimens for study.

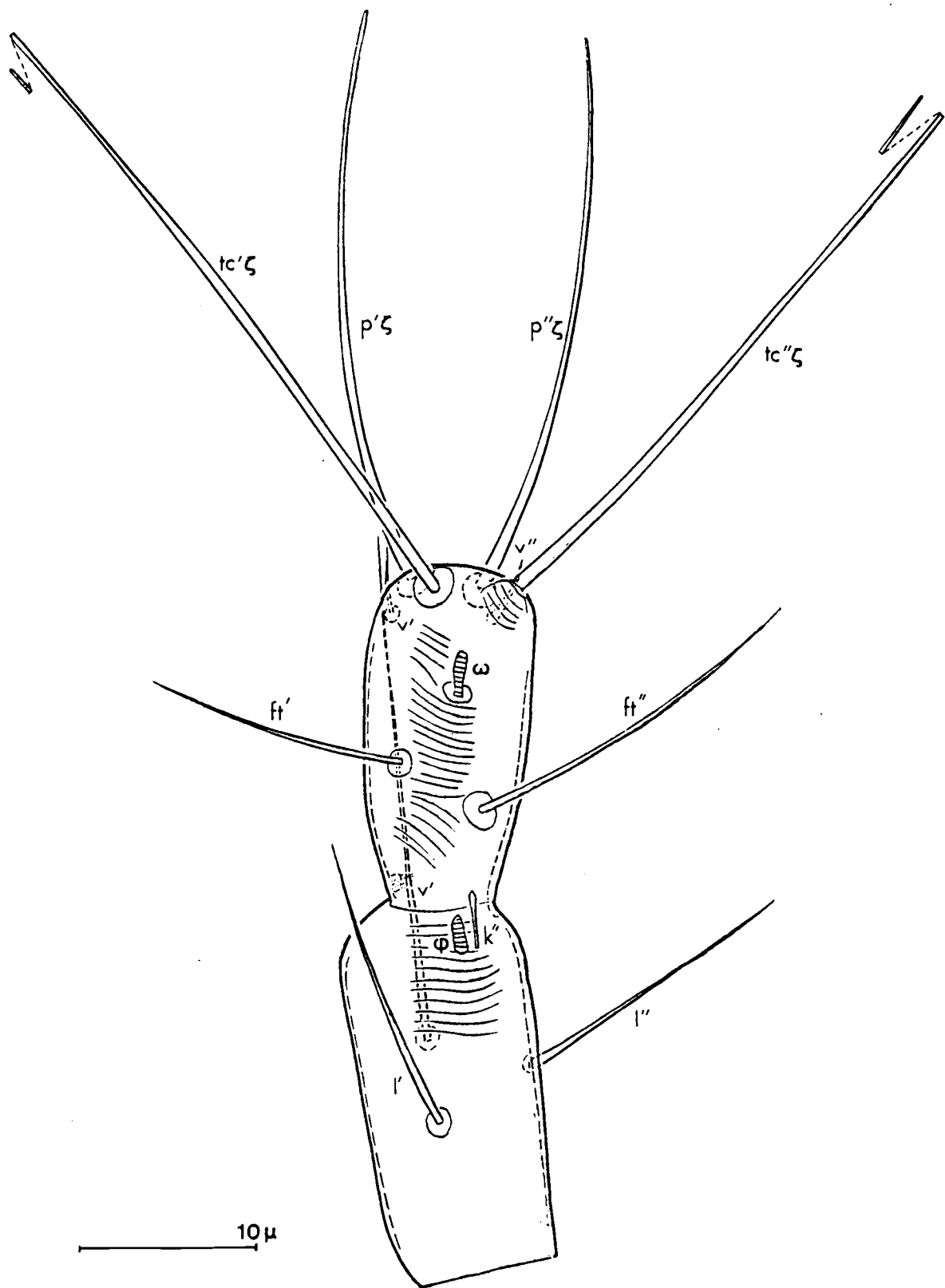Figure 12 : Apopronematus bakeri. Dorsal habitus (A) ; "tail" and anal area of tritonymph (B) ; seta 15.

Figure 13 : Apopronematus bakeri. Tarsus and tibia I.

"Bishop Musem – Antarctic, Loc. 108, 1830 m – Summit Dufeck range – 82°38S 52°20W – Flotation – 26 Dec. 1965 – O. R. Wilkes" ; A. alaskensis (Baker 1965) ♀ and ♂ types (Alaska).

-DIAGNOSIS : Prodorsum : recurved ; three eyes. Opisthosoma : dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy : 4 ; genital organotaxy : Ad(2,6-6-5), T(4-4) ; epimeral formula : (3-1-3-3). Legs : chaetotaxy : I(11-5-3-5-1) II(6-3-2-4-1) III(5-2-2-3-1) IV(5-2-2-(1-2)-0) ; eupathidia variable (see below) ; solenidiotaxy : 2 ; femur IV divided. Palp : (6-2-2) + ω with a triple eupathidium at the tip of the tarsus.

-FURTHER COMMENTS : The species are easily distinguished on the basis of eupathidia. A. alaskensis has the maximum eupathidial number ; i. e. eight on tarsus I ((ft), (tc), (it) and (p)), two on tarsus II (ft" and p") and one on tarsi III and IV, ft . A. erebus has the same condition minus ft"II, ft III and ft IV. A. wilkesi has only five eupathidia ((tc I), (p I) and p"II). A. wilkesi and A. erebus are thus two species contrarily to the opinion of Rounsevell (1977). Lastly, Strandtmann (1967) described a typical form of "Tydeus tilbrooki" and a variety. The typical form belongs to the new genus Pretriophtydeus while the variety has the chaetotaxy described above. The eupathidia of this variety are (tc I), (p I), ft" II, p'II, ft III and ft IV. Only one specimen was available for this study but a redescription should be undertaken since the variety is "variable" according to Strandtmann (1967).

-OTHER SPECIES : none.

Australotydeus Spain 1969 (Figure 14)

-DESCRIPTION : Spain (1969).

-SPECIES STUDIED : Australotydeus kirstenae Spain 1969
(monotypic) : 1 ♂ paratype, 1 tritonymph paratype
(New Zealand).

-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 11 setae (hl missing) ; poroido-
taxy : 4 ; genital organotaxy : Ad(0,3-4-6), T(4-4) ;
epimeral formula : (2-1-4-3) ; coxal organ present.
Legs : chaetotaxy : I(10-5-3-5-1) II(6-2-3-3-1)
III(5-2-1-1-1) IV(5-2-0-2-0) ; eupathidia on tarsus I
ft", (tc) and (p) ; solenidiotaxy : 2 ; femur IV
entire. Palp : (6-2-2)+ω, with d bifurcate and with
large double terminal eupathidium. Other features :
two large paraproctal suckers, progenital depression
in the tritonymph, dorsal setae of idiosoma hollowed
(except (ps)).

Coccotydaeolus Baker 1965

-DESCRIPTION : Baker (1965).

-SPECIES STUDIED : C. krantzi Baker 1965 : 1 ♀ holotype
(California) ; C. bakeri Wood 1965 : 1 ♀ holotype
(Yorkshire, Great-Britain) ; Coccotydaeolus sp. : 1♀
labelled "2C - 6 - 60, Ex Acer Mull, Morgan Arboretum,
P.2. Canada, Hoger's 17 - 7 - 63, Gurr's 24 - 7 - 63,
coll. V. Marshall".

-DIAGNOSIS : Prodorsum : procurved ; the species
studied have clublike sensilla. Opisthosoma : dorsal
chaetotaxy : 11 (12 missing) ; poroidotaxy : 4 ;
genital organotaxy : (0,?-3-4) ; epimeral formula :
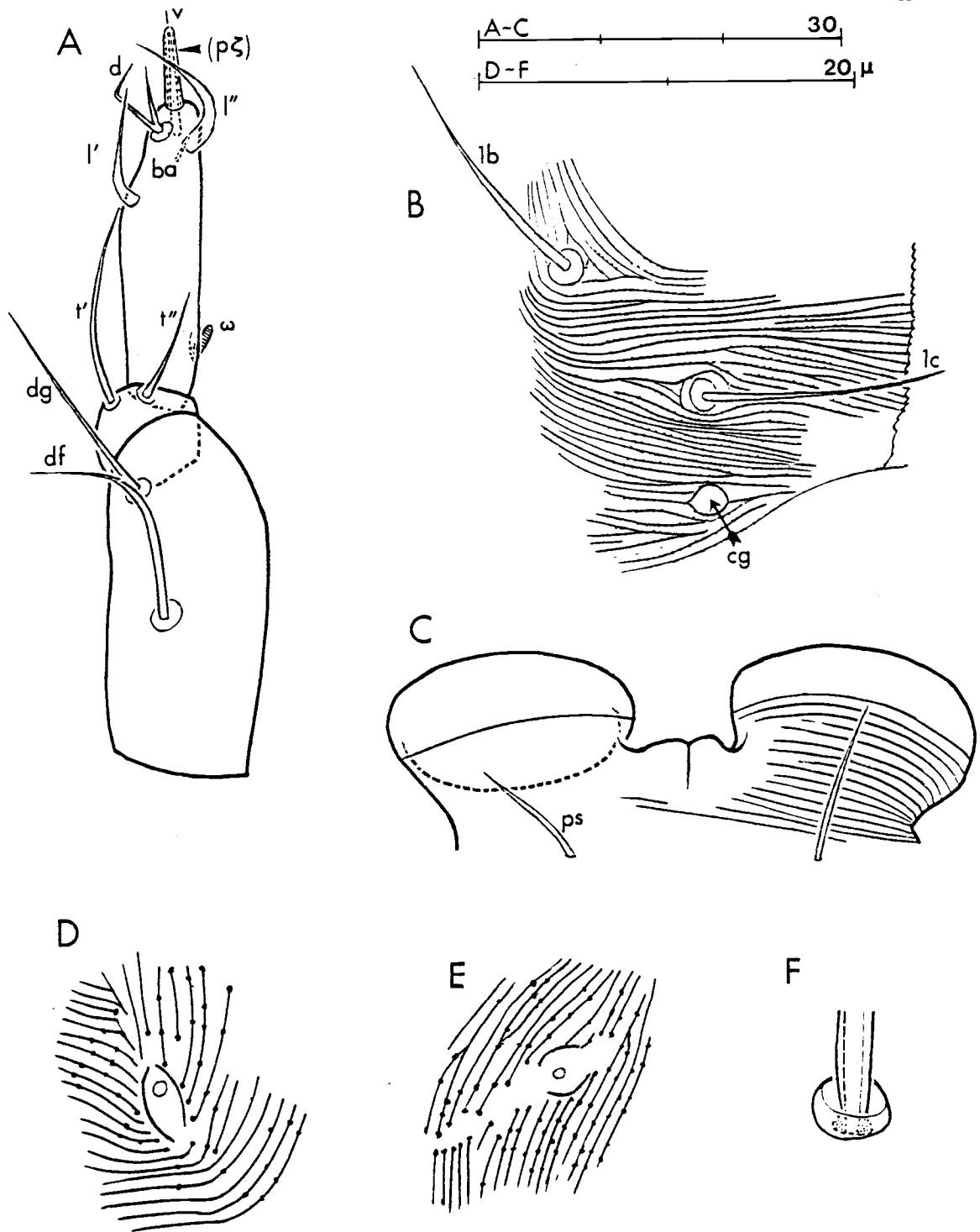(3-1-4-2). Legs : chaetotaxy : I(12-5-4-4-1) II(8-2-

Figure 14 : <u>Australotydeus kirstenae</u>. Palp (A) ; coxal (D) organ (B) ; paraproctal suckers (C) ; lyrifissures <u>ip</u> and <u>ih</u> (E) ; insertion of seta <u>12</u> (F).

2-3-1) III(7-2-1-2-1) IV(7-2-0-2-0) ; eupathidia on
tarsus I : (<u>tc</u>), (<u>p</u>) and sometimes (<u>ft"</u>) ;
solenidiotaxy : 3 ; femur IV undivided. <u>Palp</u> : (5-2-2)
or (5-2-1) + ω with a triple eupathidium at the tip
of the tarsus.
-OTHER SPECIES : none.

<u>Eotydeus</u> Kuznetzov 1973

-DESCRIPTION : Kuznetzov (1973).
-SYNONYM : <u>Tydeus</u> (<u>Eotydeus</u>) (Kuznetzov 1973).
-SPECIES STUDIED : <u>Eotydeus</u> sp. : 1 ♀ labelled "29 -
IV - 62 ex. Balsam fir duff, Maynooth, Ont. Coll.
J.H. Martin, Canada Dpt. Forestry & Rural Development".
-DIAGNOSIS : <u>Prodorsum</u> : recurved. <u>Opisthosoma</u> : dorsal
chaetotaxy : 10 (<u>12</u> and <u>h1</u> missing) ; poroidotaxy : 3 ;
genital organotaxy : (0-2-3) ; epimeral formula :
(3-1-4-2) ; coxal organ. <u>Legs</u> : chaetotaxy : I(8-4-
3-3-1) II(6-2-2-3-0) III(5-2-1-2-1) IV(5-2-1-1-0) ;
eupathidia on tarsus I : <u>ft"</u>, (<u>tc</u>), (<u>p</u>) ;
solenidiotaxy : 2 ; femur IV entire. <u>Palp</u> : (6-2-2) +
ω with a double eupathidium at the end of the tarsus.
-OTHER SPECIES : <u>Eotydeus</u> <u>mirabilis</u> Kuznetzov 1973.

<u>Homeopronematus</u> new genus

-DESCRIPTION : Schruft (1972).
-SYNONYM : <u>Pronematus</u> (Schruft 1972).
-SPECIES STUDIED : <u>H</u>. <u>staercki</u> (Schruft 1972) : several
individuals without specific label ; <u>H</u>. <u>vidae</u> n.sp.
-DIAGNOSIS : <u>Prodorsum</u> : procurved ; no eyes.

Opisthosoma : dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy : 4 ; genital organotaxy : Ad & T(0-0-4,1), D(0-2,?), P(0-0) ; one pair of genital acetabula ; epimeral formula : Ad, T & D(3-1-4-2) P(3-1-4-0), L(3-1-2). Legs : no apotele I but the larva which has an apotele I with vestigial claws ; chaetotaxy : I(8-4-3-3-1) II(6-2-3-3-1) III(6-2-2-2-1) IV(6-2-1-2-0) in the adults and tritonymphs ; deutonymph with one seta less on tarsi III and IV (tc") and with no trI, trII ; the protonymph as the deutonymph except IV(5-0-0-0-0) ; larval chaetotaxy : I(6-4-3-3-0) II(6-2-3-3-0) III(5-2-2-2-0) ; eupathidia on tarsus I : ft", (tc), (p) ; double anabasis in the larva : solenidiotaxy : 3 ; femur IV entire. Palp : (5-1-2) + ω with a double eupathidium at the tip of the tarsus.

-DESCRIPTION of H. vidae n. sp. (51) (figures 15 and 16). H. vidae is distinguished from H. staercki by the density of striation ; the shape and length of the idiosomal setae. Material : $\male$, $\female$, and nymphs in a vial labelled "Tydeidae ex lab culture, Univ. Calif. Berkeley, 24 - III - 78, M.A. Hoy" ; 1 $\female$ labelled "Christian Brothers, Napa Co, Calif., IV - 3 - '69, ex cut canes of Zinfandel grape, coll. R.L. Doutt, D.N. Kinn".
-OTHER SPECIES : none.

Homeotydeus new genus

-DESCRIPTION : Baker (1970).

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(51) The species is named for Mrs V. Krantz whose hospitality during my sojourn at Oregon State University was greatly appreciated.
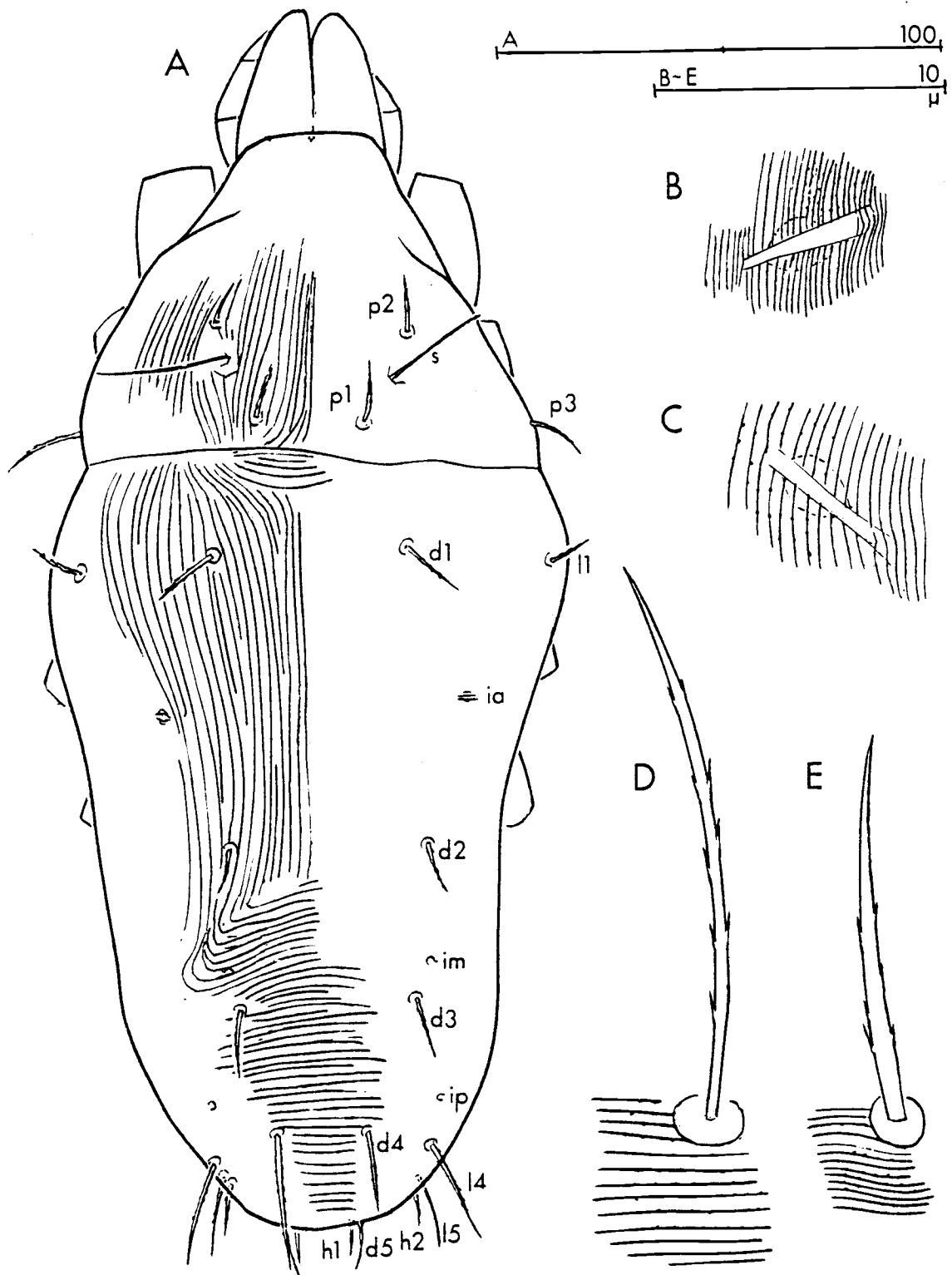
Figure 15 : Homeopronematus vidae. Dorsal habitus (A) ; lyrifissure ia (left) (C) and seta l1 (D). Homeo- pronematus staercki : lyrifissure ia (right) (B) and seta l1 (E).
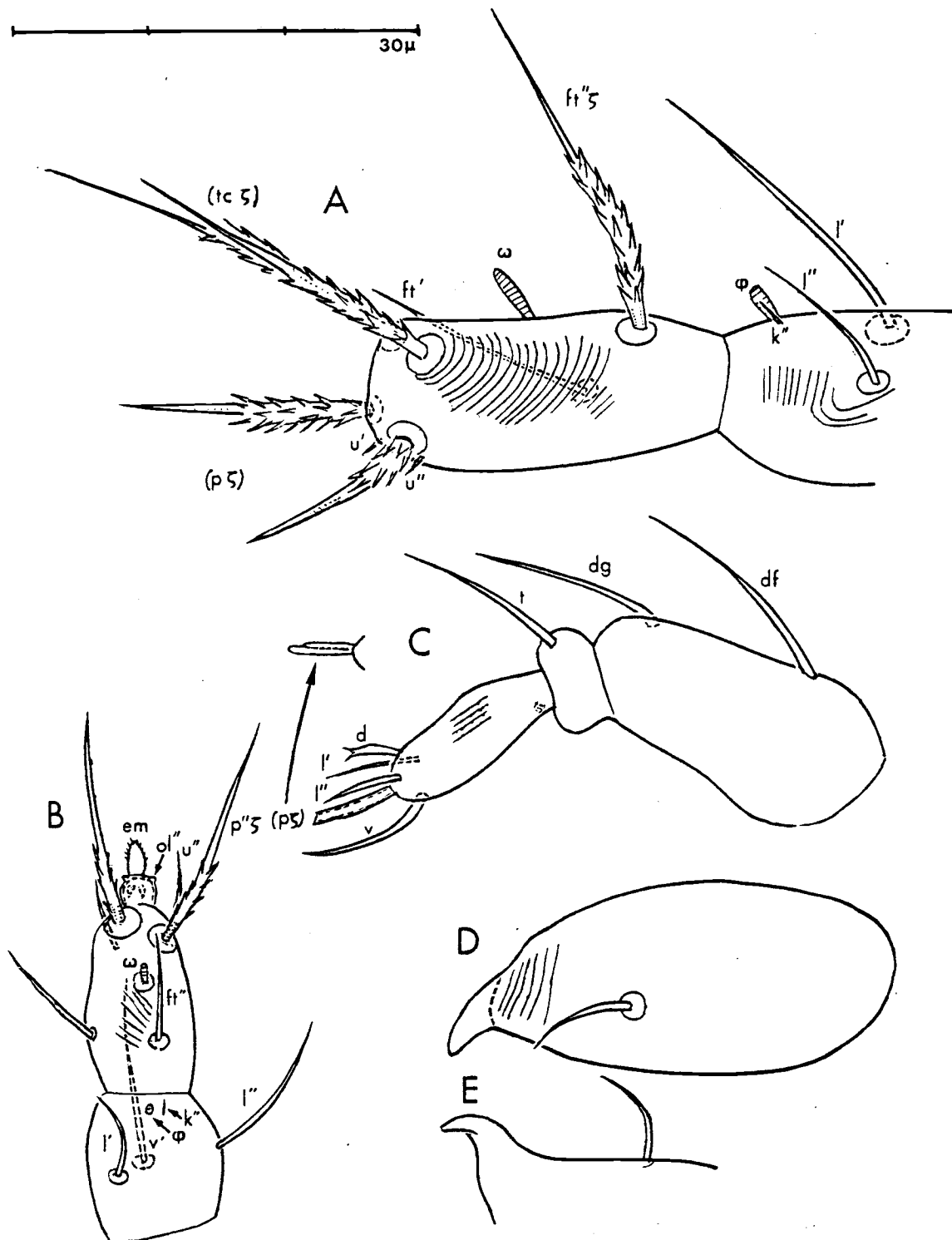
Figure 16 : Homeopronematus vidae. Tarsus and tibia I of adult (A) and larva (B) ; palp in antiaxial view (C) ; femur IV of male in dorsal (D) and antiaxial (E) views.

-SYNONYMS : <u>Lorryia</u> (Baker 1944b) ; <u>Paralorryia</u>
(Baker 1965, 1968d in part) ; <u>Tydeus</u> (Baker 1970 in
part).

-SPECIES STUDIED : <u>H</u>. <u>cumbrensis</u> (Baker 1944),♀type ;
<u>H</u>. <u>shawi</u> (Baker 1943), ♀paratype of <u>Melanotydeus</u>
<u>brachipalpus</u> synonymized with <u>Tydeus</u> <u>shawi</u> by Baker
(1970) ; <u>H</u>. <u>arthurbakeri</u> (Baker 1944),♀paratype. It
must be pointed out that all the species were
collected from   high altitudes in Mexico.

-DIAGNOSIS : <u>Prodorsum</u> : recurved. <u>Opisthosoma</u> :
dorsal chaetotaxy : 10 (<u>12</u> and <u>h1</u> missing) ; poroido-
taxy : 3 ; genital organotaxy : (0-4-6) ; epimeral
formula : (3-1-4-2) ; coxal organ. <u>Legs</u> : chaetotaxy :
I(8-4-3-3-0) II(6-2-2-3-0) III(5-2-1-1-1) IV(5-2-
1-1-0) ; eupathidia on tarsus I : (<u>tc</u>), (<u>p</u>) and
sometimes (<u>ft"</u>) ; solenidiotaxy : 2 ; femur IV entire.
<u>Palp</u> : (6-2-2) +ω with a double eupathidium at the
tip of the tarsus.

<u>Idiolorryia</u> new genus

-DESCRIPTION : Baker (1968b).
-SYNONYM : <u>Lorryia</u> (Baker 1968 in part).
-SPECIES STUDIED : <u>I</u>. <u>macquillani</u> (Baker 1968),
(monotypic) : ♀ holotype (Ireland) + tritonymph (same
data) ; <u>Idiolorryia</u> sp. : ♀ and tritonymph from bark,
Ruette - StMard (Belgium).
-DIAGNOSIS : <u>Prodorsum</u> : recurved. <u>Opisthosoma</u> :
dorsal chaetotaxy : 9 (<u>12</u>, <u>h1</u> and <u>h2</u> missing) ;
poroidotaxy : 3 ; genital organotaxy : Ad(0,?-6-4),
T(2-4) ; epimeral formula : (3-1-4-2) ; coxal organ.
<u>Legs</u> : chaetotaxy : I(8-4-2-3-0) II(6-1 or 2-1-3-0)

III(5-1-1-2-1) IV(5-1-1-1-0) ; eupathidia on tarsus I: ft", (tc), (p) ; solenidiotaxy : 1 ; femur IV entire. Palp : (6-1-2) + ω with a double eupathidium at the end of the tarsus. Other feature : gnathosoma elongate with movable chelae very long and straight ; palpal tarsus long and slender, as are the setae it bears. Reticulate striation.

Krantzlorryia new genus (52)

-DESCRIPTION : Baker (1968b).

-SYNONYM : Lorryia (Baker 1968b in part).

-SPECIES STUDIED : K. grewia (Baker 1968) (monotypic) : 1 ♀ holotype (Zaire).

-DIAGNOSIS : Prodorsum : recurved. Opisthosoma : dorsal chaetotaxy : 10 (12 and h1 missing) ; reticulate striation ; poroidotaxy : 3 ; genital chaetotaxy : (0-6-4) ; epimeral formula (3-1-4-3) ; coxal organ. Legs : I(8-3-2-2-0) II(6-2-1-2-0) III(5-2-0-1-1) IV(5-2-0-1-0) ; eupathidia on tarsus I : (tc), (p) ; solenidiotaxy : 2 ; femur IV undivided. Palp : (6-1-2) + ω with a double eupathidium at the end of the tarsus.

Lasiotydeus Berlese 1908 sensu Baker 1965

-DESCRIPTION : Baker (1965).

-SPECIES STUDIED : L. krantzi Baker 1965 : ♀ holotype (California) ; L. krantzi ♀ and ♂ labelled "77 - IX -

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(52) This genus is named for Dr. G.W. Krantz, under whom this work was achieved.

20 , ex K - 76 - C 3A, coll. V.G. Marshall, Canadian
forestry service" from Kamloops, B.C., Canada..

-DIAGNOSIS : Prodorsum : recurved or slightly
procurved, two eyes. Opisthosoma : dorsal chaetotaxy :
11 (12 missing) ; poroidotaxy : 4 ; genital organo-
taxy : (0,4-6-4) ; epimeral formula : (3-1-4-3).
Legs : chaetotaxy : I(12-5-4-6-1) II(8-2-4-4-1)
III(7-2-3-3-1) IV(7-2-1-2-0) ; eupathidia on tarsus
I : (tc) and (p) ; solenidiotaxy : 3 ; femur IV
entire. Palp : (6-2-2) with ba vestigial and a
terminal eupathidium apparently double. Other feature:
a well developed empodial claw.

-REMARKS : This genus is closely related to Primotydeus.
Its habitus recalls a Tydeinae as does its empodial
claws, palp eupathidium, and the prodorsal
chaetotactic pattern.

-OTHER SPECIES : L. volaticus Livshitz 1973.

Metalorryia new genus

-DESCRIPTION : Baker (1968b).
-SYNONYM : Lorryia (Baker 1968b in part).
-SPECIES STUDIED : M. armaghensis (Baker 1968) :
tritonymph, holotype (Ireland) ; specimens (adult,
trito- and deutonymph from Belgium).
-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 10 (12 and h1 missing) ; poroido-
taxy : 3 ; reticulate striation ; genital organotaxy :
Ad(0,4-6-4), T(4-4) D(2-2) ; epimeral formula : (3-1-
4-2) ; coxal organ. Legs : chaetotaxy : I(8-3-2-3-0)
II(6-2-1-2-0) III(5-2-1-1-1) IV(5-2-1-1-0) in the
adult, trito- and deutonymph ; eupathidia : ft', (tc),

(p) ; solenidiotaxy : 2 ; femur IV entire. Palp :
(6-1-2) + ω with a double eupathidium at the end of
the palp.

-OTHER SPECIES : likely M. magdalenae (Gerson 1968).

Metapronematus new genus

-DESCRIPTION : Treat (1970).

-SYNONYM : Pronematus (Treat 1970).

-SPECIES STUDIED : M. leucohippeus (Treat 1970)
(monotypic) : 2 ♀ paratype, one tritonymph paratype
(Massachusetts). A larva was described by Treat but,
unfortunatelly, was lost.

-DIAGNOSIS : Prodorsum : procurved. Opisthosoma :
dorsal chaetotaxy : 10 (12 and hl missing) ; poroido-
taxy : 4 ; genital organotaxy : Ad & T(0-0-3) ; one
pair of genital acetabula ; epimeral formula : Ad &
(3-1-4-2), L(3-1-1). Legs : apotele I with no,or at
least reduced, claws in the larva ; apotele I absent
in the tritonymph and adult ; chaetotaxy : I(8-4-3-
3-1) II(6-2-3-3-1) III(6-2-2-2-1) IV(5-2-1-1-0) in
the tritonymph and adult ; in the larva : I(6-4-3-3-
0) II(6-2-3-3-0) III(5-2-2-2-0) ; eupathidia on
tarsus I : ft", (tc) and (p) ; larva with double
anabasis ; solenidiotaxy : 3 ; femur IV undivided.
Palp : (5-1-2) with a double eupathidium at the tip
of the tarsus.

Metatriophtydeus new genus

-DESCRIPTION : Wood (1965).

-SYNONYM : Triophtydeus (Wood 1965 ; André 1975).

-SPECIES STUDIED : M. lebruni n. sp. (all stases) ;
M. craveni (Wood 1965) : ♀ holotype and paratype ;
Metatriophtydeus sp. : 2 ♀ labelled "L. Martini
winery, St Helena, Napa Co., Calif., I - 15 - 70, Ex.
Budscale : var. Sauvignon Vert. Coll. : D. Kinn" and
"Martini vineyards, St Helena, Calif. VII - 10 - 69,
Ex Sauvignon vert, coll. D. Kinn) and 1 larva
labelled "Christian Brothers, Napa Co., Calif., IV -
3 - 69, Ex cutcanes of Zinfandel grape, coll. R.L.
Doutt, D.W. Kinn".

-DIAGNOSIS : Prodorsum : recurved ; three eyes.
Opisthosoma : dorsal chaetotaxy : 11 setae (12
missing) ; poroidotaxy : 4 ; genital organotaxy :
Ad(2,6-6-5or4), T(4-4), D(2-2), P(0-1) ; epimeral
formulae : Ad & T(3-1-3-3), D(3-1-3-2), P(3-1-2-0),
L(3-1-2). Legs : chaetotaxy : I(10-5-3-5-1) II(6-2-2-
4-1) III(5-1-2-1-1) IV(5-2-2-(1-2)-0) in adult and
tritonymph, deutonymph : idem but I(10-4-3-4-0)
II(6-2-2-4-0), protonymph : I(8-4-3-4-0) II(6-2-2-4-
0) III(5-1-2-1-1) IV(5-0-0-0-0), larva : same chaeto-
taxy as the protonymph but without leg IV ; eupathidia
on tarsus I : (ft N2), (tc N1), (it N3), (p), on
tarsus II : ft"N3, p", on tarsus III : ft Ad, and IV :
ft N3 ; solenidiotaxy : 2 ; femur IV undivided. Palp :
(6-2-2) +ω with a triple eupathidium on the tarsus.

-DESCRIPTION of Metatriophtydeus lebruni n. sp. (53)
(figure 17). Organotaxy defined in the generic
description ; five pairs of aggenitals in the adult
(instead of four pairs in M. craveni). The presence

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(53) This species is called for Dr. Ph. Lebrun, who
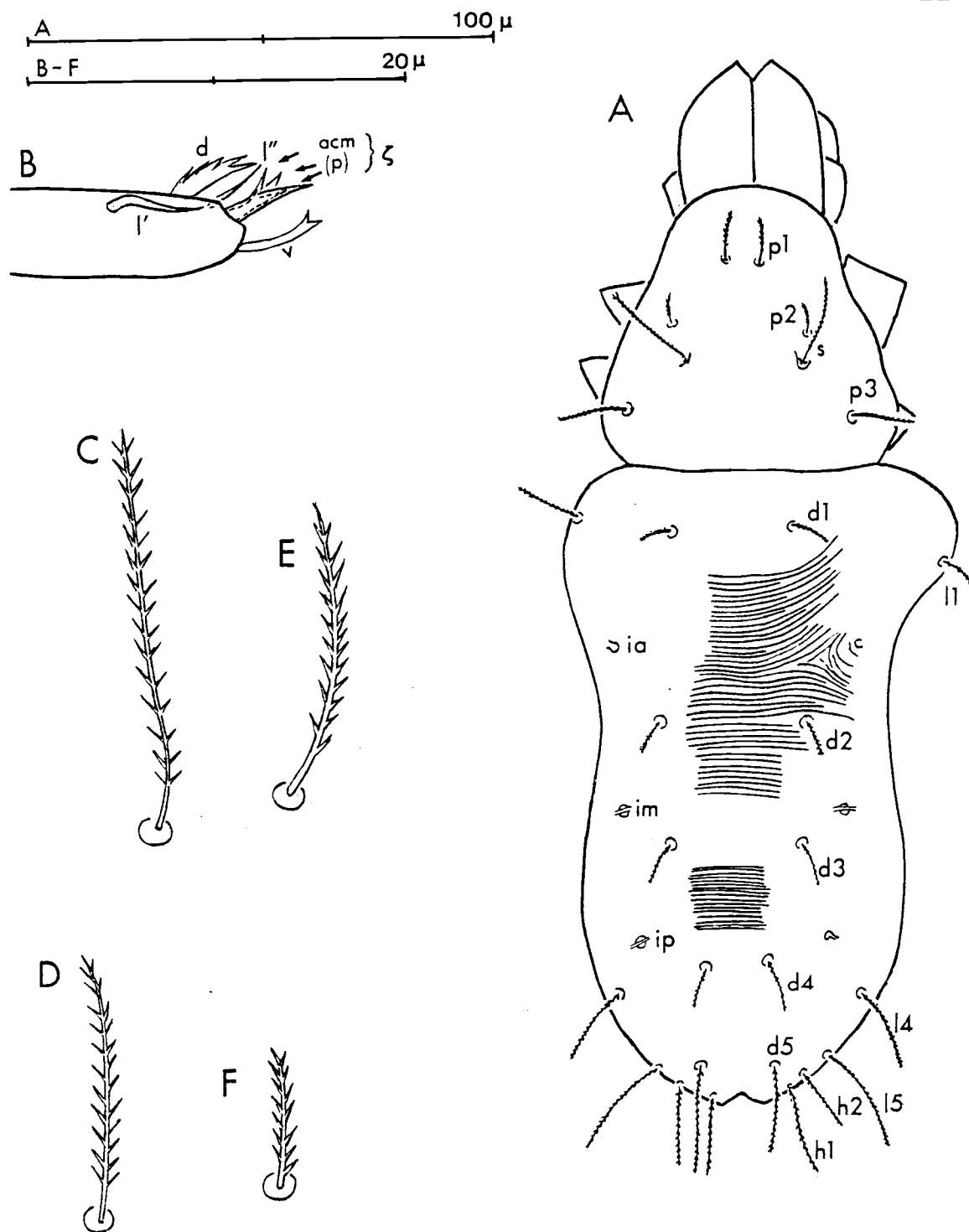introduced me to mites and their ecology.

Figure 17 : <u>Metatriophtydeus</u> <u>lebruni</u>. Dorsal habitus (A) ; tip of the <u>palptarsus</u> (B) ; setae <u>14</u> (C) and <u>p3</u> (D). <u>Metatriophtydeus</u> <u>craveni</u> : setae <u>14</u> (E) and <u>p3</u> (F).

of (ps) is vertitionel. Material : all the stases
collected in Belgium (Ruette and St Mard) on bark of
different tree species (the ecology of M. lebruni
is defined by André in 1975 (under the old name
"Triophtydeus") and 1979.
-OTHER SPECIES : M. flatus (Livshitz 1973).

Metatydaeolus new genus

-SPECIES STUDIED : Metatydaeolus sp. A : 2   labelled
"Ex Aspen Mull, Morgan Arboretum, P.2. Canada, 15 -
VI - 65, Coll. J.R. Hill" ; Metatydaeolus sp. B : 1
labelled "20 - 6 - 60 H-A, Tsuga Mor, Morgan
Arboretum, P.2., Canada, Coll. V. Marshall" ;
Metatydaeolus joannis n. sp..
-DIAGNOSIS : Prodorsum : procurved ; clublike
sensillum. Opisthosoma : dorsal chaetotaxy : 11 (12
missing) ; poroidotaxy : 4 ; genital organotaxy :
(0-4-3) ; epimeral formula : (3-1-4-3). Legs :
chaetotaxy : I(12-5-4-4-1) II(8-2-4-4-1) III(7-2-2-
3-1) IV(7-2-1-2-0) ; eupathidia on tarsus I : ft",
(tc), (p) ; solenidiotaxy : 3 ; femur IV undivided.
Palp : (5-2-2) +ω with a triple eupathidium.
-DESCRIPTION of Metatydaeolus joannis (54) (figure 18)
Organotaxy as described above. Material : 3 ♀ (one in
bad state) labelled "22 - 8 - 60 L+F, Ex Fagus mor,
Morgan Arboretum, P.2. Canada, Coll. V. Marshall".
-OTHER SPECIES : none.

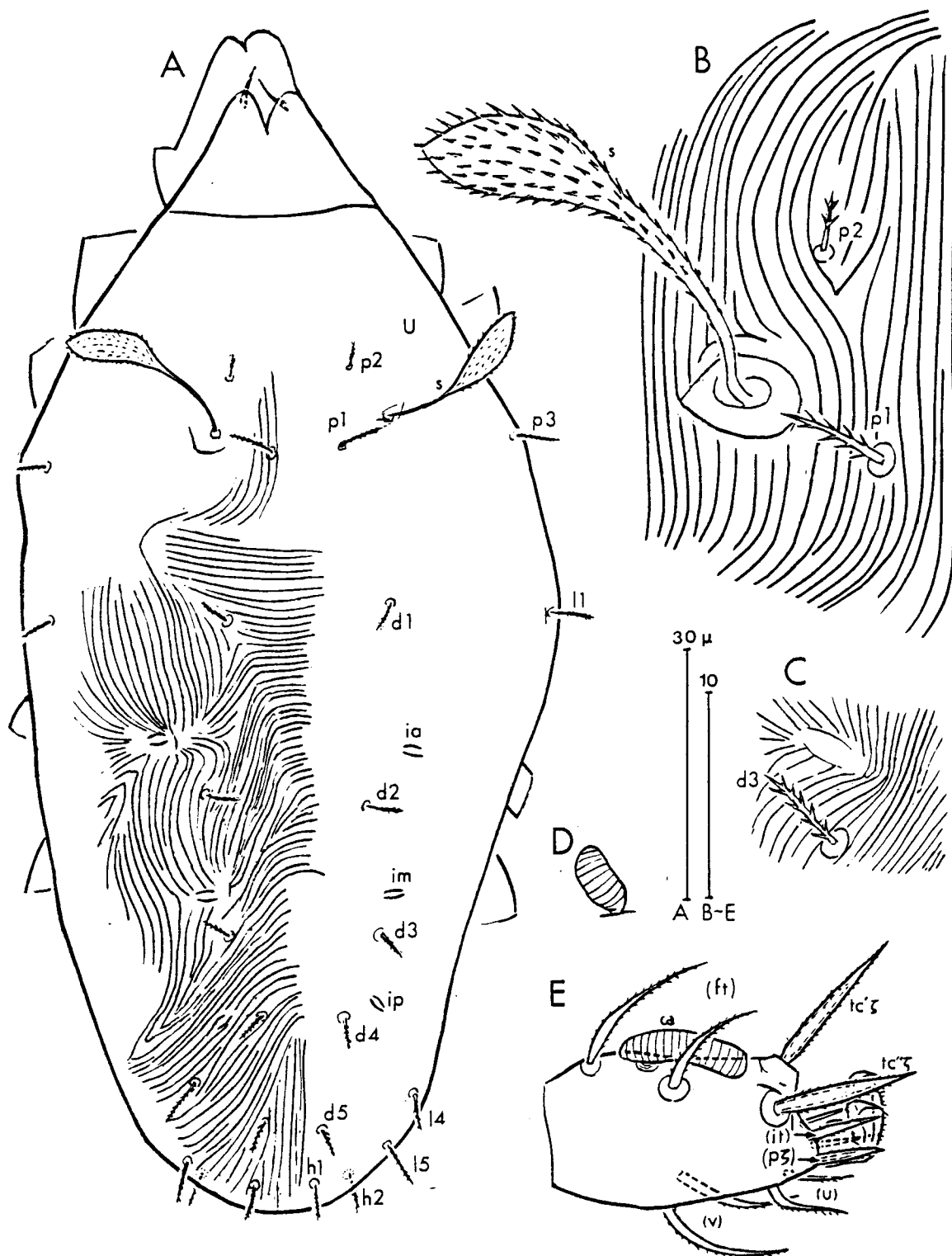
(54) This species is named for my father, Jean André.

Figure 18 : <u>Metatydaeolus joannis</u>. Dorsal habitus (A) ;
detail of prodorsum (B) and of opisthosoma (C) ;
solenidion ωII (D) and tarsus I in antiaxial view (E).

<u>Meyerella</u> Baker 1968

 -DESCRIPTION : Baker (1944), Baker (1968).

 -SYNONYM : <u>Tydeus</u> (Baker 1944b).

 -SPECIMENS STUDIED : <u>M</u>. <u>bifurcatus</u> Baker 1944 : 1♀
 holotype (Mexico) ; <u>M</u>. <u>marshalli</u> n. sp. (♀ and
 the three nymphs).

 -DIAGNOSIS : <u>Prodorsum</u> : recurved. <u>Opisthosoma</u> :
 dorsal chaetotaxy : 11 setae (<u>12</u> missing) ; poroido-
 taxy : 4 ; genital organotaxy : Ad(4-6-5), T(4-4),
 D(2-2), P(0-1) ; epimeral formulae : Ad & T(3-1-3-3),
 D(3-1-3-2), P(3-1-2-0).. <u>Legs</u> : chaetotaxy : I(12-6-4-
 5-1) II(7-3-3-4-1) III(7 or 5-2-2-3-1) IV(7 or 5-2-
 3-(1-2)-1) in the adult, in the tritonymph : idem
 but tarsi III and IV always with only five setae, in
 deutonymph : tarsus II with only six setae and no
 <u>tr</u> IV, in the protonymph : I(12-5-4-5-0) II(6-2-2-4-
 0) III(5-2-2-3-1) IV(5-0-0-0-0), eupathidia on tarsus
 I : (<u>ft</u> N2), (<u>tc</u>), <u>it</u>'N2, <u>it</u>"N3, (<u>p</u>) and on tarsus II :
 p" ; solenidiotaxy : 4 ; femur IV divided. <u>Palp</u> :
 (8-2-2) +ω with four tarsal eupathidia.

 -DESCRIPTION of <u>Meyerella</u> <u>marshalli</u> n. sp. (55).
 Organotaxy is defined in the generic description.
 Tarsus III and IV with five setae in the adults.
 Figures 19, 20 illustrate the new species. It differs
 from <u>M</u>. <u>bifurcatus</u> in the following characters : <u>d4</u>
 bifurcate rather than simple, the shape of the palp
 eupathidia are different (compare figures 1CC and
 20C), shape of the opisthosomal setae (compare figures

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(55) This species is named for Dr. V.G. Marshall whose
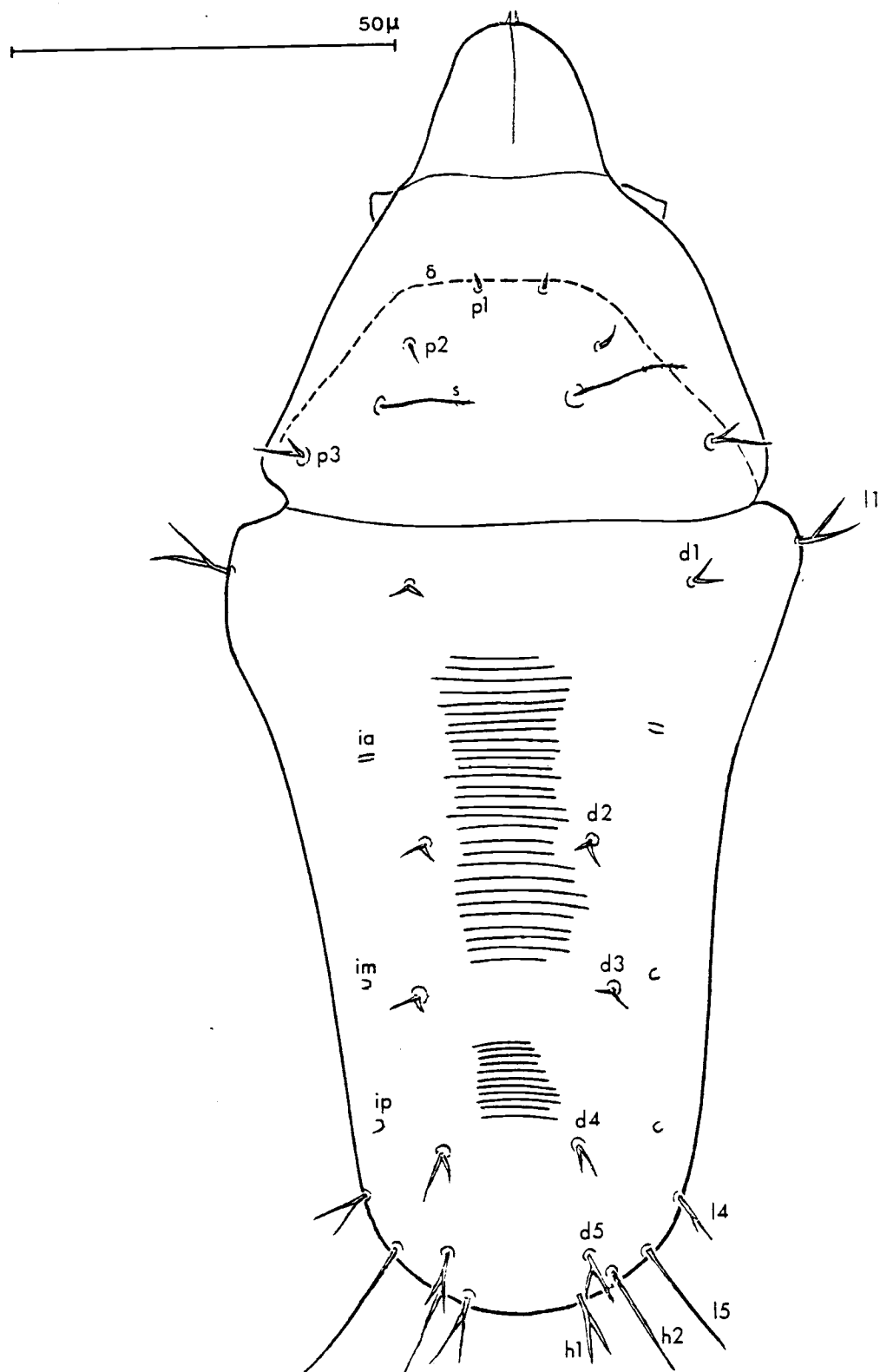help during this study was greatly appreciated..

Figure 19 : Meyerella marshalli dorsal habitus of a
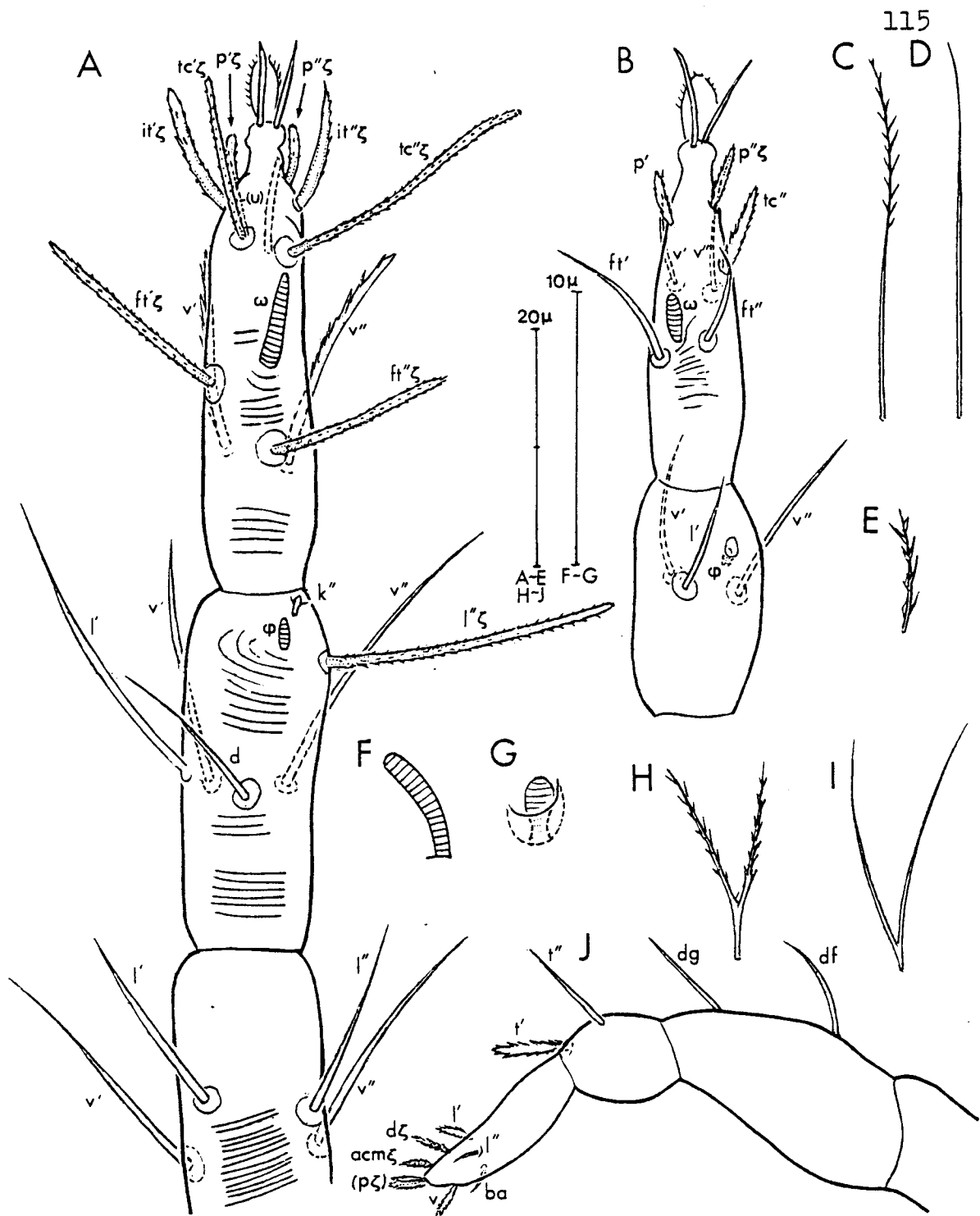deutonymph.

Figure 20 : Meyerella marshalli. Tarsus, tibia and genu I in dorsal view (A) ; tarsus and tibia II in dorsal view (B); sensillum (C) ; seta 1a (E), solenidia φI (F) and φII (G), seta hl (H) and palp in antiaxial view (J). Meyerella bifurcatus : sensillum (D) and seta hl (I).

2OH and I), 1a serrate rather than smooth, with five
setae on tarsi III and IV in adult rather than seven.
The description is based on the three nymphs and a ♀
found in the Dr. Marshall's collection. The labels
give as information the date (16 - V - 76) or (77 -
9 - 20) and a code number (K-D-75-#1A, K-D-75-#2A,
K-76-D : 2A, K-76-D : 5A, K-76-D : 6A or K-76-C : 5A).
All the slides bear the following : "Coll. V.G.
Marshall. Canadian Forestry Service". The mites were
collected in Kamloops, B.C., Canada.
-OTHER SPECIES : M. petua Livshitz 1972 (which has
also 14 simple).

Microtydeus Thor 1931, sensu Baker 1965
    -DESCRIPTION : Baker (1965).
    -SPECIES STUDIED : Microtydeus beltrani Baker 1944 :
    ♀ paratype (Mexico) ; Microtydeus subterraneus
    Wood 1965 : ♀ holotype + paratype (Yorkshire, Great
    Britain) ; Microtydeus sp. : 1 ♀ labelled "Host Parus
    caeruleus, Loc. Nijmegen, Date 7 - VI - 73,
    Lukoschus coll" ; Microtydeus sp. : ♀ (in Evernia
    prunastri on Populus, St Mard, Belgium, Sept. 1974) ;
    Microtydeus spp. : ♀ , deuto- and tritonymph, larva
    (ex litter, mull... Morgan Arboretum, P.2., Canada,
    Coll. V.G. Marshall).
    -DIAGNOSIS : Prodorsum : procurved. Opisthosoma :
    dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy : 4 ;
    genital organotaxy : Ad(0,?-2-3), D(0-2), P(0-0) ;
    epimeral formula : Ad(3-1-4-3), D(3-1-4-2), P(3-1-
    3-0), L(3-1-2). Legs : chaetotaxy : I(11-5-4-6-1)
    II(8-2-4-4-1) III(7-2-1-3-1) IV(7-2-1-2-0) in the

adults ; deutonymph as the adults but with two setae
less on tarsi ((it) on tarsus I and (tc) on the other);
protonymph : I(9-5-4-6-0) II(6-2-4-4-0) III(5-2-1-
3-1) IV(5-0-0-0-0) ; larva as the protonymph but
minus leg IV and with double anabasis and (tc)
vestigials on tarsus I ; eupathidia on tarsus I :
ft"N2, (tc N1), (p) ; solenidiotaxy : 3 ; femur IV
undivided. Palp : 6(1)-2-2 with ba vestigial and a
triple terminal eupathidium.
-OTHER SPECIES : Microtydeus bellus Livshitz and
Kuznetzov 1973.

Naudea Meyer and Rodrigues 1965

-DESCRIPTION : Meyer and Rodrigues (1965).
-SPECIES STUDIED : none.
-DIAGNOSIS : (according to Meyer & Rodrigues 1965 as
well as Baker & Delfinado 1976) : Prodorsum :
recurved. Opisthosoma : dorsal chaetotaxy : 10 (12
and hl missing) ; poroidotaxy : ? ; genital
organotaxy : (0-0-4) ? ; epimeral formula : (3-1-4-2).
Legs : chaetotaxy : I(8-4-3-3-1) II(7-2-3-3-1) III(7-
2-2-2-1) IV(7-2-1-(1-1)-0) ; solenidiotaxy : 3 ;
femur IV divided.Palp : (5-1-2). Other features :
claws vestigials or absent on apotele I.
-REMARK : The only one species : Naudea richinda Meyer
and Rodrigues 1965 was not available for this study.

Neolorryia new genus

-DESCRIPTION : Baker (1968b).
-SYNONYM : Lorryia (Baker 1968b in part).

-SPECIES STUDIED : N. boycei Baker 1968 : 1 ♀ holotype
with a trito- and a deutonymph (Mexico) ; N. pandana
Baker 1968 : 1 ♀ holotype (Hawaii).

-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 9 ($\underline{12}$, $\underline{h1}$ and $\underline{h2}$ missing) ;
poroidotaxy : 3 ; reticulate pattern ; genital
organotaxy : Ad(0,?-4 or 5-4), T(3-4), D(1-2) ;
epimeral formula : (3-1-4-2) ; coxal organ. Legs :
I(8-3-2-2-0) II(6-1-1-2-0) III(5-1-0-1-1) IV(5-1-
0-1-0) in the adult, trito- and deutonymphs ;
eupathidia on tarsus I : $\underline{ft''}$, ($\underline{tc}$), ($\underline{p}$) : solenidio-
taxy : 2 ; femur IV entire. Palp : (6?-1-2) + ω , with
a double eupathidium at the tip of the tarsus.

-OTHER SPECIES : none.

Orthotydeus new genus

-DESCRIPTION : Marshall (1970).

-SYNONYM : Lorryia (Marshall 1970).

-SPECIES STUDIED : O. lindquisti (Marshall 1970)
(monotypic) : 1 ♂ from Chalk River Ontario, Pine
litter, coll. V.G. Marshall.

-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 10 ($\underline{12}$ and $\underline{h1}$ missing) ;
poroidotaxy : 3 ; genital organotaxy : Ad(0,4-6-4),
D(2-2) ; epimeral formula : (3-1-4-2) ; coxal organ.
Legs : chaetotaxy : I(8-4-3-3-1) II(6-2-2-2-0)
III(5-2-1-1-1) IV(5-2-1-1-0) ; eupathidia on tarsus
I : $\underline{ft''}$, ($\underline{tc}$), ($\underline{p}$) ; solenidiotaxy : 2 ; femur IV
undivided. Palp : (6-2-2) + ω , with a double
eupathidium at the end of the tarsus.

Parapronematus Baker 1965

-DESCRIPTION : Baker (1965).

-SPECIES STUDIED : P. acaciae Baker 1965 : 1 ♀ holotype
(Zaire) ; P. geminus Meyer and Rodrigues 1966 : 2
specimens from South-Africa sent by Meyer (slide n°
AcY 70/533 and AcY 467/273).

-DIAGNOSIS : Prodorsum : procurved ; (p2) undersized
or missing. Opisthosoma : dorsal chaetotaxy : 9 (12,
h1, ps missing) ; poroidotaxy : 4? ; genital
organotaxy : (0-0-3) ; only one pair of genital
acetabula ; epimeral formula : (3-1-4-2). Legs :
no apotele I ; chaetotaxy : I(8-3-2-3-1) II(6-2-2-3-
0) III(5 or 6-2-2-2-1) IV(5 or 6-2-1-1-0) ;
eupathidia on tarsus I, ft', (tc), (p) and on tarsus
II, p' ; solenidiotaxy : 3 ; femur IV entire. Palp :
(5-1-2) with a double eupathidium at the tip of the
tarsus.

-OTHER SPECIES : P. citri Salviejo 1969.

Paratriophtydeus Baker 1965

-DESCRIPTION : Baker (1965).

-SYNONYM : Tydeus (Baker 1943).

-SPECIES STUDIED : P. protydeus : ♀ holotype (Mexico) ;
P. plummeri : ♂ holotype (Mexico) ; Paratriophtydeus
sp. : ♀ and ♂ labelled "Anaktaouk Pass, Alaska VI -
12 - 68, ex clump of Claytonia" Paratriophtydeus sp. :
5 labelled "14 - X - 68 Ex pine duff, Maynooth
Ont. Hoyer's 1 - XI - 68 Coll J. Martin" ; Paratri-
ophtydeus coineaui n. sp. : ♀,♂, trito- and
deutonymphs.

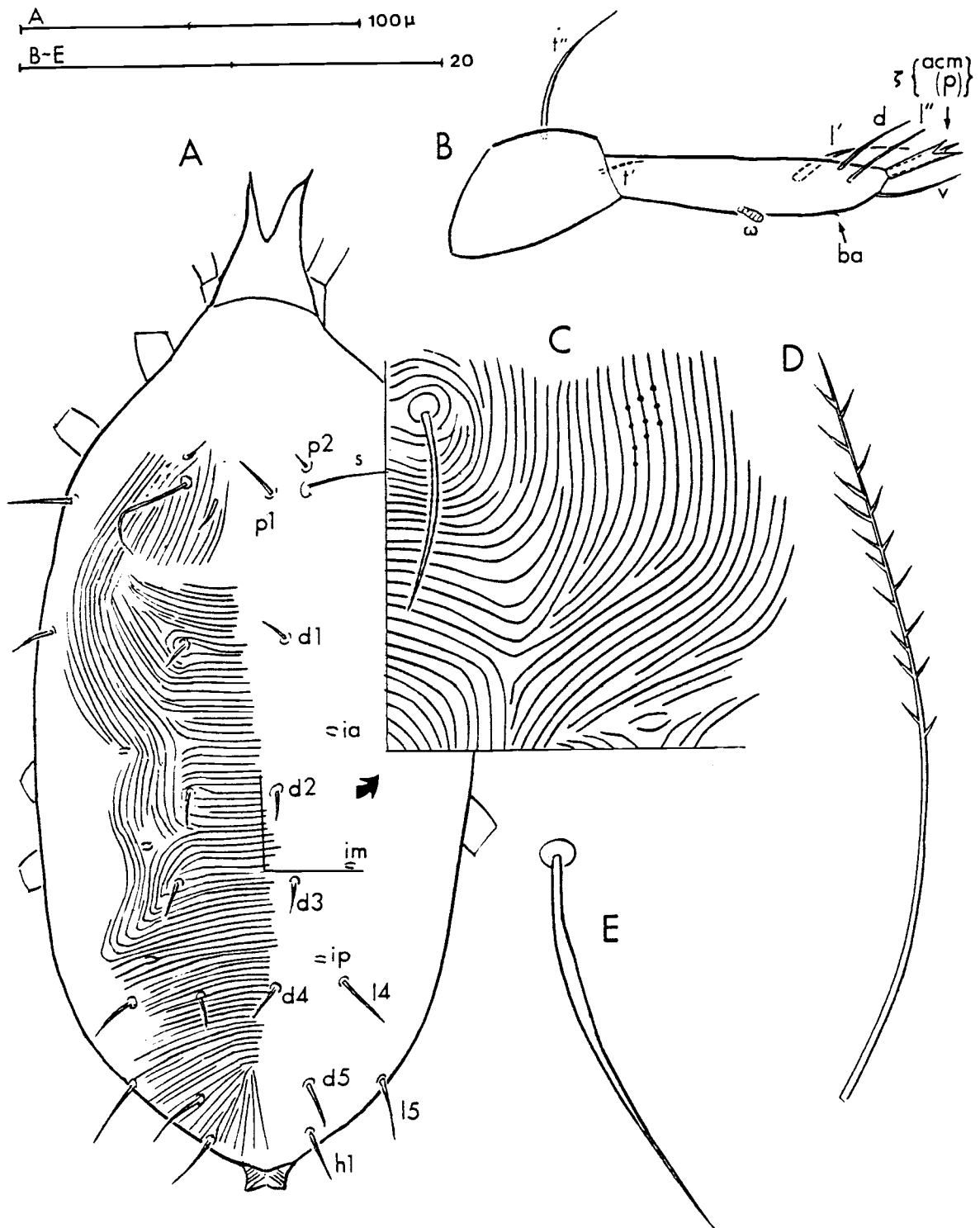-DIAGNOSIS : Prodorsum : procurved. Opisthosoma :

Figure 21 : _Paratriophtydeus coineaui_. Dorsal habitus (A) ; palp in antiaxial view (B) ; detail of opistho-soma (C) ; sensillum (D) ; seta _l5_ (E).
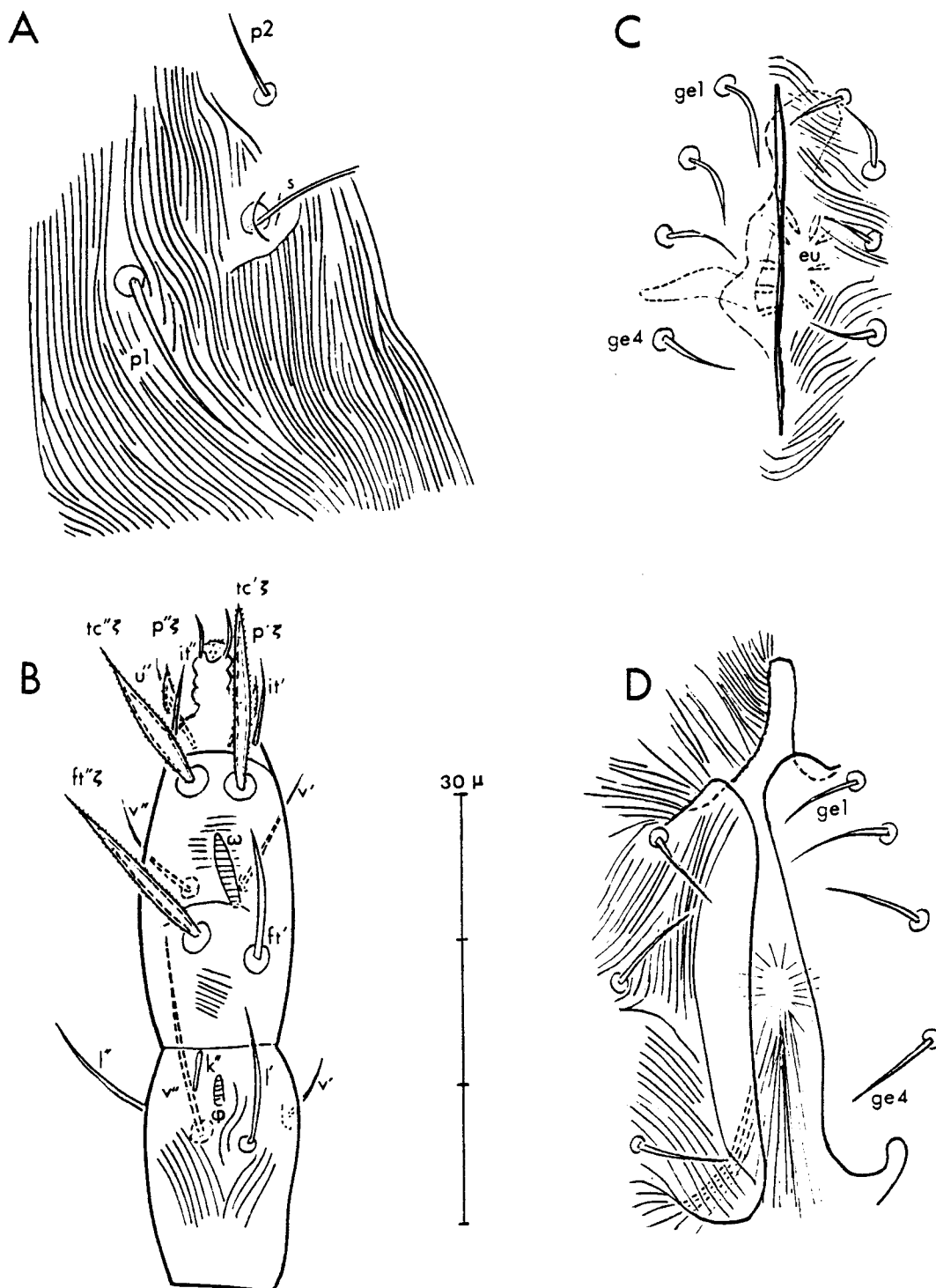
Figure 22 : <u>Paratriophtydeus coineaui</u>. Detail of pro-dorsum (A) ; tarsus and tibia I in dorsal view (B) ; genital area of male (C) and female (D).

dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy :
4 ; genital organotaxy : Ad(0,4 or 5-3,4-4), T(1-4),
D(0-2) ; epimeral formula : Ad & T(3-1-4-3), D(3-1-
4-2). Legs : chaetotaxy : I(12-5-4-6-1) II(8-2-4-4-1)
III(7-2-2-3-1) IV(7-2-1-2-0) in the adults and
tritonymphs ; deutonymph similar to the adults but
with two setae less on each tarsus ((it) on tarsus I
and (tc) on the other) ; eupathidia on tarsus I : ft",
(tc), (p) ; solenidiotaxy : 3 ; femur IV entire.
Palp : (5 or 6-2-2)+ω with a triple eupathidium at the
tip of the tarsus. Other features : sensilla simple
or clublike.

-DESCRIPTION of Paratriophtydeus coineaui n. sp.
(figures 21, 22) (56). Organotaxy as described above ;
5 pairs of eugenitals in males ; vertition of genitals
in female : with 4 genitals on a genital lip
(frequency = 0,175) ; males always with four pairs of
genitals. Seta ba is vestigial. Material : 20 ♀ , 7 ♂ ,
2 tritonymphs, 1 deutonymph labelled "Winnipeg, Man.
Ex Wheat. Coll. R.N. Sinha Oct. 20 1969", some slides
are dated "Nov. 13 1968".

-OTHER SPECIES : none.

Paratydaeolus new genus

-DESCRIPTION : Wood (1965).
-SYNONYM : Coccotydeus (Wood 1965).
-SPECIES STUDIED : P. loadmani (Wood 1965): ♀ holotype
(Great Britain) ; P. lukoschusi n. sp. : ♀ , trito-

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(56) The species is named for Dr. Y. Coineau who welcomed
me into his laboratory at Banyuls-sur-Mer (France).

and deutonymphs, larva ; <u>Paratydaeolus</u> sp. : 7 adults, 2 trito- and 1 protonymphs labelled "Ex Sexsmith, Alberta, Hoyer's 21 - X - 68, Coll. R.N. Sinha".

-DIAGNOSIS : <u>Prodorsum</u> : procurved ; the sensilla clublike. <u>Opisthosoma</u> : dorsal chaetotaxy : 11 (<u>12</u> missing) ; poroidotaxy : 4 ; genital organotaxy : (0,?-3-4), T(1-4), D(0-2), P(0-1) ; epimeral formula : Ad & T(3-1-4-3) or (3-1-4-2), D(3-1-4-2), P(3-1-3-0) L(3-1-2). <u>Legs</u> : I(12-5-4-6-1) II(8-2-4-3-1) III(7-2-1-3-1) IV(7-2-1-2-0) in adults and tritonymphs ; tarsus I with only 10 setae and tarsus IV with 5 in deutonymphs; protonymph : I(10-5-4-6-0) II(6-2-4-3-0) III(5-2-1-3-1) IV(5-0-0-0-0) ; larva : I(8?-5-4-6-0) II(6-2-4-3-0) III(5-2-1-3-1) with double anabasis ; eupathidia on tarsus I : <u>ft</u>"N2, (<u>tc</u> N1), (<u>p</u>) ; solenidiotaxy : 3 ; femur IV entire. <u>Palp</u> : (5-2-2) + ω with a triple eupathidium at the tip of the palp.

-DESCRIPTION of <u>P</u>. <u>lukoschusi</u> (57). Organotaxy is defined in the generic description. Figures 2B and 23 describe the species. <u>Material</u> : 5 ♀ , 2 tritonymphs, 5 deutonymphs and 1 larva labelled : "Host <u>Parus</u> <u>caeruleus</u> ; Loc. Nijmegen ; Date 7 - VI - 73 ; Lukoschus Leg."

-OTHER SPECIES : <u>P</u>. <u>expressus</u> (Kuznetzov 1973) and <u>P</u>. <u>lanceoclaviger</u> (Livshitz 1973) (they differ from <u>P</u>. <u>lukoschusi</u> by the lenght and the shape of setae and the shape of sensillum).

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(57) This species is named for Dr. F. Lukoschus who kindly sent me his collection of Tydeidae.
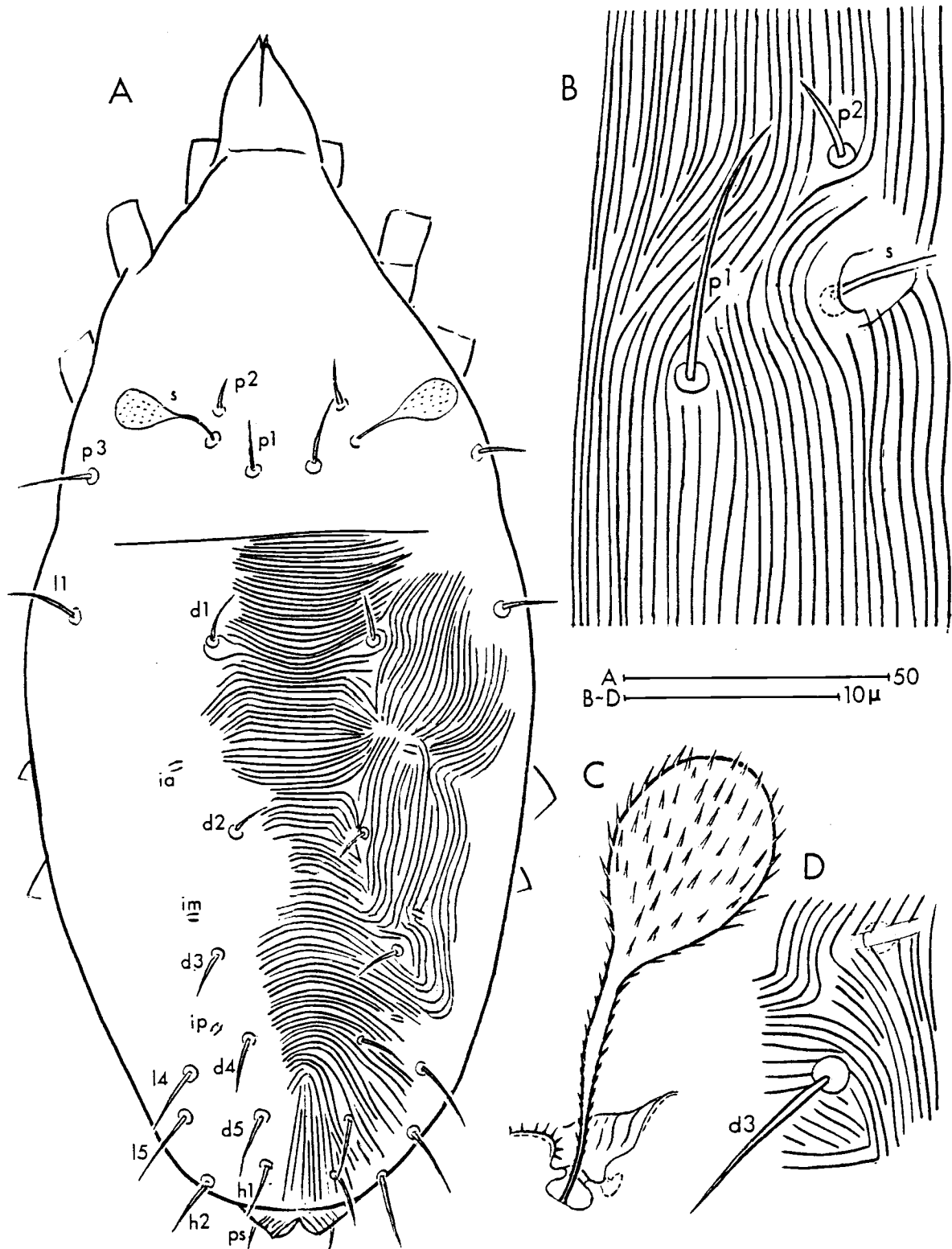
Figure 23 : <u>Paratydaeolus lukoschusi</u>. Dorsal habitus (A); detail of prodorsum (B) ; sensillum and bothridia (C) ; detail of opisthosoma (D).

Pausia Kuznetzov and Livshitz 1972

-DESCRIPTION : Kuznetzov and Livshitz (1972).

-SPECIES STUDIED : P. magdalenae (Baker and Delfinado 1976) : 1 ♀ holotype (Greece/Boston).

-DIAGNOSIS : Prodorsum : procurved. Opisthosoma : dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy : 4 ; genital organotaxy : (0,?-0-4) ; epimeral formula : (3-1-4-2). Legs : no apotele I ; chaetotaxy : I(8-4-3-3-1) II(6-2-3-3-1) III(6-2-2-2-1) IV(5-2-1-(1-1)-0) ; eupathidia on tarsus I : ft", (tc), (p) ; solenidiotaxy : 3 ; femur IV divided. Palp : (5-1-2) + ω with a double eupathidium at the end of the tarsus (figure 4F).

-OTHER SPECIES : Pausia taurica Kuznetzov 1972.

Perafrotydeus new genus

-SYNONYM : Tydeus (Afrotydeus) Baker (1970 in part).

-SPECIES STUDIED : P. meyerae Baker 1970 (monotypic) : 1 tritonymph in pupation , holotype (Kenya).

-DIAGNOSIS : Prodorsum : recurved. Opisthosoma : dorsal chaetotaxy : 10 (12 and h1 missing) ; poroidotaxy : 3 ; genital organotaxy : Ad(0-4-4), T(2-4) ; epimeral formula : (3-1-4-2) ; coxal organ. Legs : chaetotaxy : I(8-4-4-3-1) II(6-2-2-1-0) III(5-2-1-1-0) IV(5-2-1-0-0) in the adult ; tritonymph similar but with no tr I and with nude femur III ; eupathidia on tarsus I : (tc) and (p) ; solenidiotaxy : 1 ; femur IV undivided. Palp : (6-2-2) + ω with a double eupathidium at the tip of the tarsus. Other features : as in Afrotydeus, paraproctal suckers well developed and l' on tibia I slender and with a small root.

Prelorryia new genus

-DESCRIPTION : Baker (1968b).

-SYNONYM : Lorryia (Baker 1968b).

-SPECIES STUDIED : P. indionensis (Baker 1968)
(monotypic) : 1 ♀ holotype (Java).

-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 9 (12, h1 and h2 missing) ;
poroidotaxy : 3 ; genital organotaxy (0-?,6-4) ;
epimeral formula : Ad(3-1-4-3) ; coxal organ. Legs :
chaetotaxy : I(8-4-2-3-1) II(6-2-0-3-1) III(5-2-0-
1-1) IV(5-2-0-0-0) in the adult ; larva : I(8-4-2-3-
0) II(6-2-0-3-0) III(5-2-0-1-0) ; eupathidia on
tarsus I : ft", (tc), (p) in the adult ; double
anabasis with (tc) vestigial in the larva (figure 8C);
solenidiotaxy : 2 ; femur IV entire. Palp : (6-2-2) +
ω, with a triple eupathidium at the end of the
tarsus.

Pretriophtydeus new genus

-DESCRIPTION : Strandtmann (1967, 1970).

-SYNONYM : Tydeus (Strandtmann 1967), Triophtydeus
(Baker 1970)

-SPECIES STUDIED : P. tilbrooki (Strandtmann 1967)
(typical form) : 1 tritonymph paratype (Antarctica),
1tritonymph labelled "Bishop Museum, Antarctica,
Norsel pt. - Anvers I - ex Alaskozetes - exoskeleton
cender rock - 9-I-1966 - J. Strong", 1 ♀ labelled
"Bishop Museum - Antarctica - Norsel Pt. - Anvers I -
lichen incrused Moss - 3-XI-65 - J. Strong".

-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 11 setae (12 missing) ; poroido-

taxy : 4 ; genital organotaxy : Ad(2,6-6-4), T(4-4) ;
epimeral formula : (3-1-3-3). Legs : chaetotaxy :
I(12-5-3-5-1) II(7-3-2-4-1) III(5-2-2-3-1) IV(5-2-2-
(1-2)-0) ; eupathidia on tarsus I : (ft), (tc), (it),
(p), on tarsus II, ft" and p", and on tarsi III and
IV, ft ; solenidiotaxy : 2 ; femur IV divided. Palp :
(6-2-2) + ω with a triple eupathidium on the tarsus.
-OTHER SPECIES : (The varietal form of "Tydeus
tilbrooki" should belong to the genus Apotriophtydeus)

Pretydeus new genus

-DESCRIPTION : Baker (1968b, d), Marshall (1970).
-SYNONYMS : Retetydeus (Baker 1944c, 1947) ; Lorryia
(Baker 1944b, 1947, 1965, 1968b, 1970 in part) ;
Paralorryia (Baker 1968d in part).
-SPECIES STUDIED : P. hondurensis (Baker 1968) : ♀
holotype (Honduras) ; P. doddsi (Baker 1944) : ♀
holotype, ♂ and tritonymph paratypes (Mexico) ;
P. lwiorensis (Baker 1965) : 1 ♀ holotype and 2
tritonymphs (Zaire) (figure 6D, E) ; P. kevani
(Marshall 1970) : 1 ♀ holotype and paratypes (deuto-
nymph, tritonymph, larva and prelarva) (Man. Canada).
-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 10 (12 and hl missing) ; poroido-
taxy : 3 ; genital organotaxy : Ad(0,4-6-4), T(4-4),
D(2-4) ; epimeral formula : Ad & T(3-1-4-3) D(3-1-4-2)
L(3-1-2) ; coxal organ. Legs : chaetotaxy : I(8-4-2-
3-1) II(6-2-0-3-1) III(5-2-0-1-1) IV(5-1-1-1-0) in
the adult and tritonymph ; deutonymph similar but
without trI and trII ; larva : I(8-4?-?-?-?) II(6-2-
0-?-?) III(5-2-?-?-?) ; eupathidia on tarsus I : ft"

(not always), (tc), (p) ; simple anabasis in the
larval stase with (tc) vestigials ; solenidiotaxy :
3 (φI partly recessed) ; femur IV entire. Palp : (6-
2-2) +ω with a triple eupathidium at the tip of the
tarsus. Other feature : empodial claws well developed.

-REMARK : The genital chaetotaxy of P. lwiorensis is
variable in tritonymphs ; four different formulae
were observed on two specimens : (3-4) (2-4?) (4-4)
and (4-3).

-OTHER SPECIES : Maybe P. panitae (Baker 1968),
P. marcandrei (Baker 1968)... (i.e. the group
"lwiorensis" of Baker (1968b)).

Primotydeus new genus

-SPECIES STUDIED : Primotydeus strandtmanni n. sp. (58)
(monotypic) $\female$ and $\male$, tritonymph and deutonymph.

-DIAGNOSIS : Prodorsum : procurved. Opisthosoma :
dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy :
4 ; genital organotaxy : Ad(0,5-2,6-4), T(2-4),
D(1-2) ; epimeral formula : Ad & T (3-1-4-3),
D(3-1-4-2).. Legs : chaetotaxy : I(12-5-4-6-1) II(8-2-
4-4-1) III(7-2-3-3-1) IV(7-2-1-2-0) in the adults
and tritonymph ; deutonymph similar but with two
setae less on each tarsus ((it) on tarsus I and (tc)
on the other) and with no tr II ; eupathidia on tarsus
I : ft", (tc), (p) ; solenidiotaxy : 3 ; femur IV
entire. Palp : (6-2-2) +ω with ba vestigial and a

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(58) This species is named for Dr. R.W. Strandtmann who
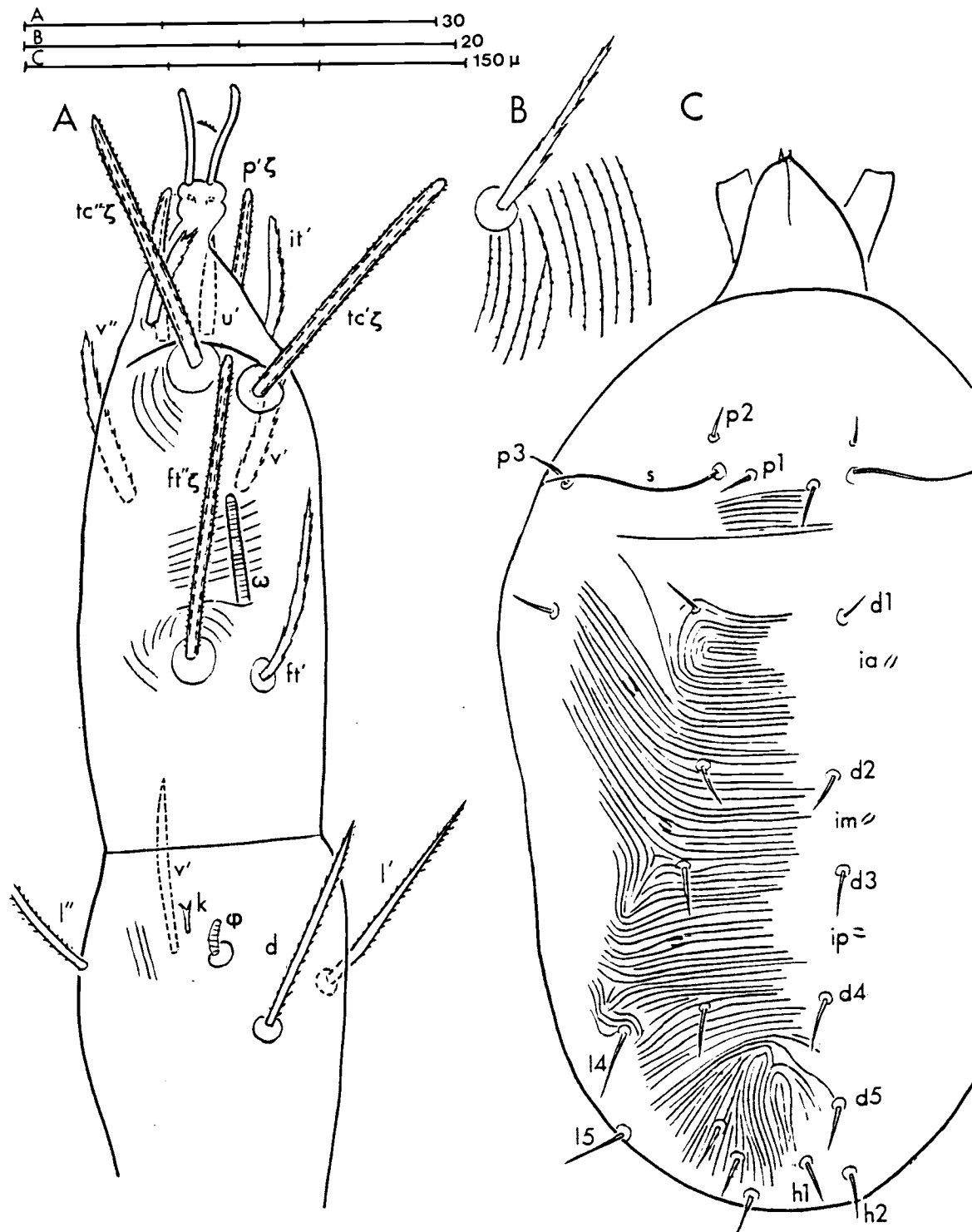kindly sent me a collection of Tydeidae for this study.

Figure 24 : _Primotydeus strandtmanni_. Tarsus and tibia I in dorsal view (A) ; seta _p2_ (B) ; dorsal habitus (C).

triple eupathidium at the tip of the tarsus.

-DESCRIPTION of <u>Primotydeus strandtmanni</u> n. sp. (figure 24). Organotaxy as described above. <u>Material</u> : 4 ♀ , 3 ♂ , 1 deuto- and 1 tritonymph labelled "Nuwak, Alaska, Snow Bunting Nest, 12-VII-67 R.W.S.".

<u>Proctotydaeus</u> Berlese 1911 <u>sensu</u> Fain and Evans 1966

-DESCRIPTION : Fain and Evans (1966)

-SYNONYM : <u>Pronematus</u> (Baker and Wharton 1952 ; Treat 1961) ; <u>Pronematulus</u> (Treat 1967, 1970) ; <u>Oriola</u> (Baker 1968) ; <u>Oriolella</u> (Baker 1969).

-SPECIES STUDIED : <u>Proctotydaeus schistocercae</u> Fain and Evans 1966 : ♀ , ♂ , trito- and deutonymphs, larva (all paratypes) ; <u>P</u>. <u>pyrohippeus</u> (Treat 1961) : two adults labelled."Ex right tympanic recess of <u>Acronycta dactylina</u> Grote ♂ , at light, Tyringham, Mass., 19 July 1963, A.E. Treat leg." and "in left tympanic recess of <u>Acronycta morula</u> G & R, 70-32 ♀ , Tyringham Mass, 27 July 1970" and a larva labelled "reared from egg found on 71-6 ♂ , <u>Acronycta dactylina</u> (Grote), Tyringham Mass., 29 June to 10 July 1971" ; <u>P</u>. <u>farbae</u> (Baker 1968) : 1 ♂ holotype ; <u>Proctotydaeus</u> sp. (description of this species by Flechtmann and Camargo still in press) (figures 4C ; 6A, B, C).

-DIAGNOSIS : <u>Prodorsum</u> : procurved. <u>Opisthosoma</u> : dorsal chaetotaxy : 11 (<u>12</u> missing) ; poroidotaxy : 4 ; genital organotaxy : Ad(0-0-4), T(0-4), D(0-2) ; only one pair of genital acetabula ; epimeral formula : Ad, T, D(3-1-4-2), L(3-1-2). <u>Legs</u> : no apotele I ; chaetotaxy : I(8-4-3-3-1) II(7-2-3-3-1) III(7-2-2-2-

1) IV(7-2-1(1-1)-0) in the adults and tritonymphs ;
deutonymph similar minus <u>tr</u> I and <u>tr</u> II, <u>tc"</u> II,
(<u>tc</u>) III and (<u>tc</u>) IV ; larva : I(6-4-3-3-0) II(6-2-
3-3-0) III(5-2-2-2-0) ; eupathidia on tarsus I : <u>ft"N2</u>
(<u>tc</u>), (<u>p</u>) ; anabasis in the larva ; solenidiotaxy :
3. <u>Palp</u> : (4 or 5-1-2) with a double eupathidium at
the tip of the tarsus. <u>Other feature</u> : femur IV
divided or not ; paraproctal more or less developed ;
sensilla clublike in the species described by
Flechtmann and Camargo (in press).

—OTHER SPECIES : <u>P</u>. <u>rusticus</u> (Meyer and Rodrigues 1965),
<u>P</u>. <u>oblongus</u> (Kuznetzov 1973), <u>P</u>. <u>galapagosensis</u> Fain
and Evans 1965.

—REMARKS : Most of the known species of <u>Proctotydaeus</u>
have been found associated with insects (gallery of
bark beetle, bee-hive, phoretic on Lepidoptera or
Orthoptera). <u>P</u>. <u>rusticus</u> (found on <u>Gossypium</u>) and
<u>P</u>. <u>oblongus</u> (found on a Greek nut tree) are
exceptions. These species are involved in special
adaptations to their environment. This genus is a
good example of the variations played by the
evolutionary process on a chaetotactic theme.

<u>Pronecupulatus</u> Baker 1944

   —DESCRIPTION : Baker (1944a, 1965).
   —SPECIES STUDIED : <u>P</u>. <u>anahuacensis</u> Baker 1944 (mono-
      typic) : 1 ♀ holotype and 1 protonymph found on the
      same tree but later by Baker.
   —DIAGNOSIS : <u>Prodorsum</u> : procurved. <u>Opisthosoma</u> :
      dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy :
      4? ; genital organotaxy : Ad(?) (holotype twisted),

P(0-0), epimeral formula : Ad(?), P(1-3-3-0). Legs :
no apotele I ; chaetotaxy : I(8-4-3-3-1) II(6-2-1-3-
1) III(5-2-1-2-1) IV(5-2-1-2-0) in the adult ; I(8-
4-3-3-1) II(6-2-1-3-0) III(5-2-1-2-0) in the
protonymph ; eupathidia on tarsus I : ft' (not in
the protonymph), (tc), (p) ; solenidiotaxy : 3 ;
femur IV entire. Palp : ? (in too bad a state).

Pronematulus Baker 1965

   -DESCRIPTION : Baker (1965).
   -SPECIES STUDIED : P. vandus Baker 1965 (monotypic) :
   ♀ holotype (Florida).
   -DIAGNOSIS : Description : recurved. Opisthosoma :
   dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy :
   4 ; genital organotaxy : (0-0-4) ; epimeral formula :
   (3-1-4-2). Legs : no apotele I ; chaetotaxy : I(8-4-
   3-3-1) II(7-2-2-3-1) III(6-2-2-2-1) IV(6-2-1-2-0) ;
   eupathidia on tarsus I : ft", (tc), (p) ; solenidio-
   taxy : 3 ; femur IV seemingly divided. Palp : (5-2-2)
   with a double eupathidium at the tip of the tarsus.

Pronematus Canestrini 1886 sensu Baker 1965

   -DESCRIPTION : Baker (1965), Baker (1968).
   -SPECIES STUDIED : P. ubiquitus (McGregor 1932) : 2
   specimens from the collection of Dr. M.K.P. Meyer
   (South Africa, found on plants) (slides AcY 76/351
   and AcY 77/473) and P. rykei Meyer and Rodrigues
   1965 : three specimens sent by Dr. Meyer from South
   Africa (slides AcY 74/456, AcY 74/260 and AcY 74/
   224).

-DIAGNOSIS : <u>Prodorsum</u> : procurved. <u>Opisthosoma</u> :
dorsal chaetotaxy : 10 (<u>12</u> and <u>hl</u> missing) ;
poroidotaxy : 4 ; genital organotaxy : (0-0-4) ;
epimeral formula : (3-1-4-2). <u>Legs</u> : no apotele I ;
chaetotaxy : I(8-4-3-3-0) II(6-2-3-3-0) III(5-2-2-2-
1) IV(5-2-1-2-0) ; eupathidia on tarsus I : <u>ft"</u>, (<u>tc</u>),
(<u>p</u>) ; solenidiotaxy : 3 ; femur IV undivided. <u>Palp</u> :
(5-1-2).

-OTHER SPECIES : undetermined.

<u>Pseudotydeus</u> Baker and Delfinado 1974

-DESCRIPTION : Baker and Delfinado (1974).

-SPECIES STUDIED : <u>P</u>. <u>perplexus</u> Baker and Delfinado
1974 (monotypic) : 1 tritonymph paratype (Ohio).

-DIAGNOSIS : <u>Prodorsum</u> : recurved. <u>Opisthosoma</u> :
dorsal chaetotaxy : 11 (<u>12</u> missing) ; poroidotaxy :
4 ; genital organotaxy : T(4-4) ; epimeral formula :
(3-1-4-3). <u>Legs</u> : chaetotaxy : I(12-6-4-6-1) II(7-2-
3-3-1) ; eupathidia on tarsus I : <u>ft'</u>, (<u>tc</u>), (<u>p</u>) and
on tibia I (<u>1"</u>) ; solenidiotaxy : 3   (φ I recessed) ;
femur IV entire. <u>Palp</u> : (5-1-1) + ω with a triple
eupathidium at the tip of the tarsus. <u>Other feature</u> :
there are two clusters, one (ωI-<u>ft</u>') on tarsus I and
(k"-1"5) on tibia I ; the species has a long tail
like caudal extension overhanging an inward fold.

-REMARK : <u>Pseudotydeus</u> was considered the type genus
of a new subfamily by Baker and Delfinado. This
opinion is not followed here. It must be pointed out
that the clusters observed in this species exactly
coincide with a description of a member of the tydeoid
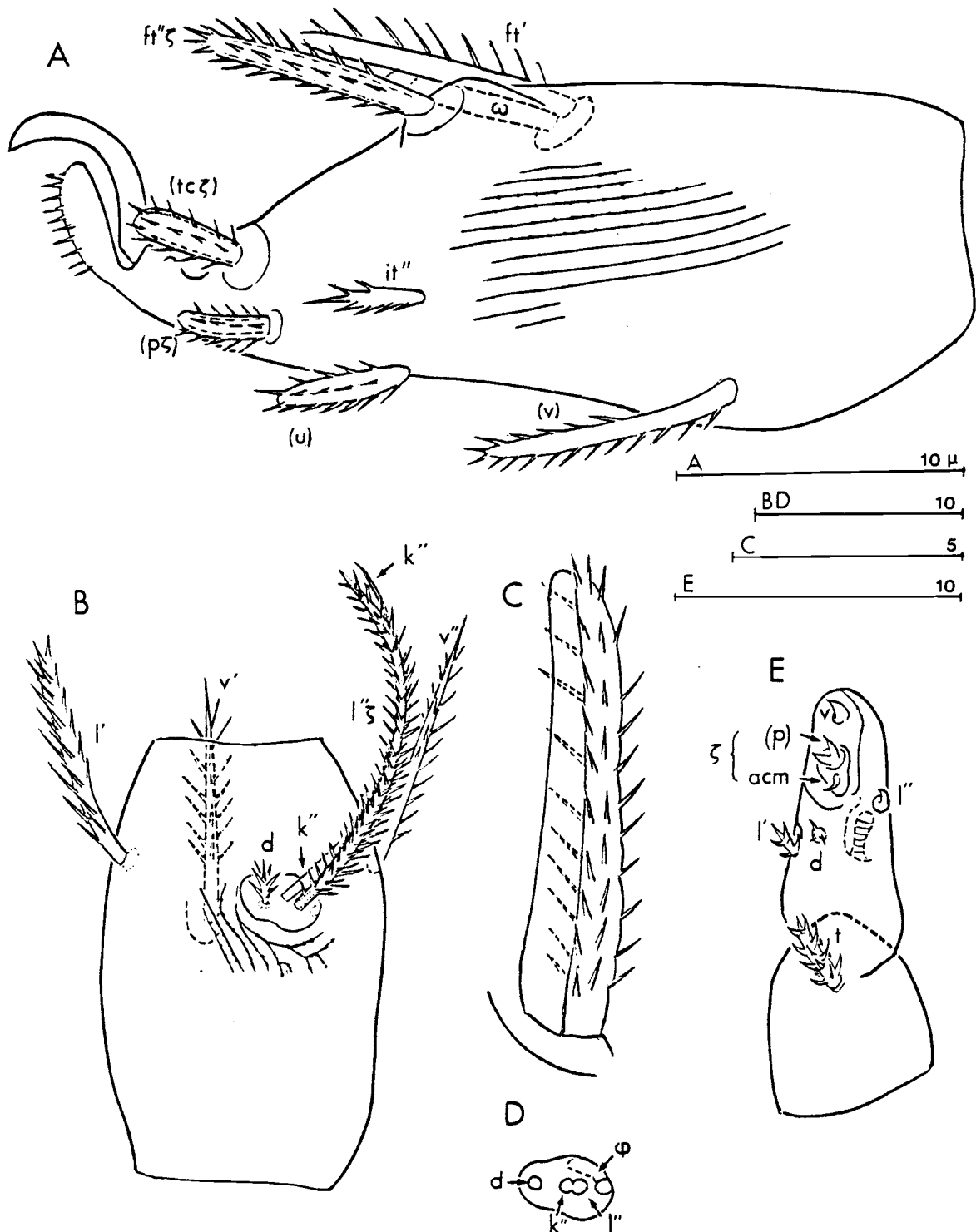family Ereynetidae by Grandjean (1939) (figure 25).

Figure 25 : _Pseudotydeus perplexus_. Tarsus I in antiaxial view (A) ; tibia I in dorsal view (B) ; cluster (ωI-ft') in antiaxial view (C) ; location of φI, with setae not drawn (D) ; palp in dorsal view (E).

Teletriophtydeus new genus

- -DESCRIPTION : Strandtmann (1967).
- -SYNONYM : <u>Tydeus</u> (Strandtmann 1967), <u>Paratriophtydeus</u> (Baker 1970)
- -SPECIES STUDIED : <u>T</u>. <u>wadei</u> (Strandtmann 1967) (monotypic) : 1 tritonymph and 1 ♂ paratypes (Antarctica).
- -DIAGNOSIS : <u>Prodorsum</u> : recurved, no bothridia. <u>Opisthosoma</u> : dorsal chaetotaxy : 11 (<u>12</u> missing) ; poroidotaxy : 4 ; genital organotaxy : Ad(4,6-6-5), T(4-4) ; epimeral formula : (3-1-3-3). <u>Legs</u> : chaetotaxy : I(10-6-3-4-0) II(6-3-1-4-0) III(5-2-1-3-1) IV(5-2-1-2-0) ; eupathidia on tarsus I : <u>ft'</u>, (<u>tc</u>), (<u>it</u> N3), (<u>p</u>) ; solenidiotaxy : 2 ; femur IV divided. <u>Palp</u> : (6-2-2) + ω with a triple eupathidium at the tip of the tarsus.

Tydaeolus Berlese 1910 <u>sensu</u> Baker 1965

- -DESCRIPTION : Baker (1965).
- -SYNONYMS : <u>Tydeus</u> (Berlese 1910), <u>Coccotydeus</u> (Thor 1931, 1933 ; Baker and Wharton 1952).
- -SPECIES STUDIED : <u>Tydaeolus</u> <u>tenuiclaviger</u> (Thor 1931) <u>sensu</u> Baker 1965 ; <u>Tydaeolus</u> sp. (from different fungi (<u>Penicillium</u>, <u>Trichoderma</u>, <u>Absidia</u>), Winnipeg, Man. Canada, coll. H.A.H. Wallace or R.N. Sinha) ; <u>Tydaeolus</u> sp. : labelled "<u>Parus</u> <u>caeruleus</u> ; Loc. Nijmegen, Date 7-VI-73, Lukoschus Leg.".
- -DIAGNOSIS : <u>Prodorsum</u> : procurved ; clublike sensillum· <u>Opisthosoma</u> : dorsal chaetotaxy : 11 (<u>12</u> missing) ; poroidotaxy : 4 ; genital organotaxy : Ad(0,?-2-4) ; epimeral formula : (3-1-4-3). <u>Legs</u> : (ontogeny after

Grandjean 1938) : I(11-5-4-6-1) II(8-2-4-4-1) III(7-
2-2-3-1) IV(7-2-1-2-0) in the adults ; deutonymphs
with two setae less on each tarsus, (it) on tarsus I
and (tc) on the other ; protonymph : I(9-5-4-6-0)
II(6-2-4-4-0) III(5-2-2-3-1) IV(5-0-0-0-0) ; larva :
I(7?-4-4-6-0) II(6-2-4-4-0) III(5-2-2-3-0) with
double anabasis ; eupathidia on tarsus I : ft"N2,
(tc N1), (p) ; solenidiotaxy : 3 ; femur IV entire..
Palp : apparently only three setae on the tarsus,
among which is the triple eupathidium, and the
solenidion. However, Kuznetzov and Livshitz (1972)
give the formula (5(1)-2-2).
-OTHER SPECIES : Tydaeolus frequens (Grandjean 1938),
Tydaeolus shaeroclaviger Kuznetzov 1972..

Tydeus Koch 1835 new combination

-SYNONYMS : Tydeus Koch 1835 sensu Baker 1968 (in
part) ; Lorryia Oudemans 1925 sensu Baker 1968 (in
part), Paralorryia Baker 1965 (in part), Tydulosus
Canestrini 1886 sensu Baker 1965.
-SPECIES STUDIED : T. raphignathoides (Berlese 1910)
sensu Baker 1968 : labelled "from Apple, Bramley,
Richhill, Co. Down, Ireland, 3-2-61, collector M.J.
MacQuillan, Tritonymph" ; T. reticulata Oudemans
1928:"from rt. tympanic recess of ? Feltia sp.
killed by spider. Tyringham Mass, 9 october 1954, A.E.
Treat, Det. E.W. Baker" ; T. bedfordiensis (Evans
1952) : 1 ♀ paratype (Great-Britain) (in addition,
numerous specimens from Dr. Marshall's collection
(Canada) and mine (Belgium)) ; T. turrialbensis
(Baker 1968) : 1 ♀ holotype (Costa-Rica), the three

nymphs and the larval paratype ; <u>T</u>. <u>tridactylus</u>
(Weiss-Fogh 1948 : 2 ♀ and 1 ♂ , deutonymphs
(holotype and paratypes) (Danmark) ; <u>Tydeus</u> sp. :
specimens from grape, Tessino, Switzerland ; three
other species from Belgium which will be described
elsewhere.

-DIAGNOSIS : <u>Prodorsum</u> : recurved ; two eyes.
<u>Opisthosoma</u> : dorsal chaetotaxy : 10 (<u>12</u> and <u>hl</u>
missing) ; poroidotaxy : 3 ; genital organotaxy :
Ad(0,4-6-4), T(4-4), D(2-2), P(0-1) ; epimeral
formulae: Ad, T & D(3-1-4-2), P(3-1-3-0), L(3-1-2) ;
coxal organ.. <u>Legs</u> : chaetotaxy : I(8-4-3-3-1) II(6-2-
2-3-0) III(5-2-1-2-1) IV(5-2-1-1-0) in the adult,
trito- and deutonymphs ; protonymph with no <u>tr</u> I,
sometimes with no <u>tr</u> III, and with only five tarsal
setae on the fourth leg ; larva : I(8-4-3-3-0) II(6-2-
2-3-0) III(5-2-1-2-0) ; eupathidia on tarsus I :
<u>ft</u>" N2, (<u>tc</u> N1), (<u>p</u>) ; simple anabasis with (<u>tc</u>)
vestigials in the larva ; solenidiotaxy : 2 ; femur
IV undivided. <u>Palp</u> : (6-2-2) + ω with a double
eupathidium at the tip of the tarsus. <u>Other feature</u> :
the integument may be merely striated, partly or
entirely reticulate or exhibit a "basketweave"
pattern. A third unpaired empodial claw may be
inconspicuous or obvious.

-REMARKS : A number of generic entities have been
synonymized here with <u>Tydeus</u> on the basis of
chaetotaxy and ontogeny. However, the expanded genus
may not necessarily be homogenous, since only a few
ontogenies are known. For instance, <u>T</u>. <u>tridactylus</u>

is classified here in _Tydeus_ but the genital formula
of its tritonymph is (2-4) rather than (4-4).

-OTHER SPECIES : According to the literature, about
200 species should belong to the genus _Tydeus_.
However, further information must be gathered in order
to clarify the status of many of these. For instance,
Grandjean's (1938c) description of the leg
chaetotaxy of _T. viviparus_ (Thor) coincides with that
described above for the genus except that the larva
exhibit a double anabasis. This may constitute a
specific difference.

Tydides Kuznetzov 1975 (monotypic)

-DESCRIPTION : Kuznetzov (1975).

-DIAGNOSIS : (according to Kuznetzov 1975) _Prodorsum_ :
recurved. _Opisthosoma_ : dorsal chaetotaxy : 10 (_12_
and _hl_ missing) ; poroidotaxy : ? ; genital
organotaxy : (?-3-4) ; epimeral formula : (3-1-4-2) ;
coxal organ ?. _Legs_ : chaetotaxy : I(8-4-3-3-0)
II(6-2-2-3-0) III(5-2-1-2-1) IV(5-2-1-1-0) ;
eupathidia on tarsus I : _ft"_, (_tc_), (_p_) ;
solenidiotaxy : 2 ; femur IV entire. _Palp_ : (5-2-1) +
ω , with a double eupathidium at the tip of the
tarsus.

-REMARK : _Tydides_ _ulter_ Kuznetzov 1975 was not
available for this study.

Tyndareus Livshitz and Kuznetzov 1972

-DESCRIPTION : Livshitz and Kuznetzov (1972).

-DIAGNOSIS : (according to Livshitz and Kuznetzov 1972)

Prodorsum : procurved. Opisthosoma : dorsal chaeto-
taxy : 11(12 missing) ; poroidotaxy : 4? ; genital
organotaxy : (?-6-4) ; epimeral formula : (3-1-4-3).
Legs : chaetotaxy : I(10 or 12-5-4-5-1) II(8-2-4-4-1)
III(7-2-2-3-1) IV(7-2-1 or 0-2-0) ; (it) is missing
or not on tarsus I ; eupathidia on tarsus I : ft",
(tc), (p) ; solenidiotaxy : 3 ; femur IV entire.
Palp : (5-2-2) + ω .

-REMARK : The two species, Tyndareus eloquens
Livshitz 1972 and Tyndareus rostratus Kuznetzov 1972,
were not available for this study.

Generic Unit : G1 (Tydaeolinae)

Only 1 ♀ labelled "Nawak Alaska, 12-VII-67, R.W.S,
Snow bunting nest".

-DIAGNOSIS : Prodorsum : procurved. Opisthosoma :
dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy :
? ; genital organotaxy : (0-2-3) ; epimeral formula :
(3-1-4-3). Legs : chaetotaxy : I(12-5-4-6-1) II(8-2-
4-4-1) III(7-2-3-3-1) IV(7-2-1-2-0) ; five eupathidia
on tarsus I : ft", (tc), (p) ; solenidiotaxy : 3 ;
femur IV entire. Palp : (6-2-2) +ω, with a triple
eupathidium at the tip of the tarsus.

Generic Unit : M1 (Meyerellinae)

Among the specimens of Metatriophtydeus lebruni
collected in Belgium (Ruette - St Mard), a protonymph
was found with a recessed solenidion on tibia II. It
is thus a member of the Meyerellinae although the
habitus coincides with that of the Triophtydeinae.

The idiosomal setae are not bifurcate as in Meyerella.
-DIAGNOSIS : Prodorsum : recurved ; three eyes.
Opisthosoma : dorsal chaetotaxy : 11 (12 missing) ;
poroidotaxy : 4 ; genital organotaxy : (0-1) and
only one pair of diachile slots in the progenital
groove ; epimeral formula : (3-1-2-0). Legs :
chaetotaxy : I(10-5-4-4-0) II(6-3-2-4-0) III(5-2-2-
2-1) IV(5-0-0-0-0) ; eupathidia on tarsus I : (tc)
and (p) and on tarsus II : p" ; solenidiotaxy : 4 ;
femur IV entire. Palp : (5-2-2) with a triple
eupathidium at the end of the palp.

Generic Unit M1 (Triophtydeinae)

The following generic unit diagnosis is based on two
specimens (1 ♀ and 1 ♂). Kindly sent by Dr. R.L.
Smiley, U.S. National Museum, labelled "Inglis Motneka
Kiwifruit leaves, 20-11-75 and 24-11-75".
-DIAGNOSIS : Prodorsum : recurved. Opisthosoma :
dorsal chaetotaxy : 11 (12 missing) ; poroidotaxy :
4 ; genital organotaxy : (2,6-6-5) ; epimeral formula :
(3-1-3-3). Legs : chaetotaxy : I(10-5-3-5-1) II(6-2-
2-4-1) III(5-1-2-1-1) IV(5-2-2-(1-2)-0) ; eupathidia
on tarsus I : (ft), (tc), (it) and (p), on tibia I :
1" and on tarsus II : ft" and p" ; solenidiotaxy :
2 ; femur IV divided. Palp : (6-2-2) + ω, with a triple
eupathidium at the tip of the tarsus.

Generic Unit TY1 (Tydeinae)

4 ♀ labelled "on Berlinia sp., Stanleyville, Belg
Congo, April 18. 1955, E.W. Baker coll., n°33".

-DIAGNOSIS : <u>Prodorsum</u> : recurved. <u>Opisthosoma</u> :
dorsal chaetotaxy : 9 (<u>12</u>, <u>h1</u> and <u>h2</u> missing) ;
poroidotaxy : 3 ; genital organotaxy : (0-6-4) ;
epimeral formula : (3-1-4-2) ; coxal organ present.
<u>Legs</u> : chaetotaxy : I(8-4-3-3-1) II(6-2-2-3-0)
III(5-2-1-2-0) IV(5-2-1-1-0) ; four eupathidia on
tarsus I : (<u>tc</u>) and (<u>p</u>) ; solenidiotaxy : 2 ; femur
IV entire. <u>Palp</u> : (6-2-2) + ω , with a double
eupathidium at the end of the tarsus.

Generic Unit TY2 (Tydeinae)

1 ♂ + 1 ♀ labelled "Oregon Benton Co. near Rock Creek,
Corvallis watershed, Ex Moss & Litter on Fir Stump,
11-13-76, Coll R.D. Sanders".

-DIAGNOSIS : <u>Prodorsum</u> : recurved ; <u>Opisthosoma</u> :
dorsal chaetotaxy : 10 (<u>12</u>, <u>h1</u> missing) ; poroidotaxy :
3 ; genital organotaxy : (0,4-6-4) ; epimeral formula:
(3-1-4-2) ; coxal organ present. <u>Legs</u> : chaetotaxy :
I(8-4-3-3-0) II(6-2-2-3-0) III(5-2-1-2-1) IV(5-2-
1-1-0) ; eupathidia on tarsus I : <u>ft</u>", (<u>tc</u>) and (<u>p</u>) ;
solenidiotaxy : 1 ; femur IV entire. <u>Palp</u> : (6-1-2) +
ω , with a double eupathidium at the end of the
tarsus.

B. Key to the stases

1.-Calyptostasis . . . . Prelarva

   -"Normal" stase 2

2.-Three pairs of legs . . . . Larva

   -Four pairs of legs 3

3.-Dehiscence line, δ , on prodorsum ; genital

   acetabula, if present, exposed ; pro-

   genital aperture absent . . . . Nymph . . 4

   -Dehiscence line absent ; with a progenital

   chamber (sheltering genital acetabula when

   they exist) opening through a progenital

   chamber . . . . Adult

4.-Legs IV with only five setae, all arising

   on the tarsus ; epimeral formula (3-1-2-

   0) or (3-1-3-0) ; no more than one pair

   (eventually fused) of diachile slots . . Protonymph

   -At least six setae on leg IV ; epimeron IV

   with two or three setae 5

5.-Epimeral formulae (3-1-3-2) or (3-1-4-2) ;

   at most, with two pairs of genital setae

   and two pairs of aggenitals . . . . Deutonymph (59)

   -Epimeral formulae (3-1-3-3), (3-1-4-3) or

   (3-1-4-2) . . . . Tritonymph (59)

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(59) In our present state of knowledge, it is impossible to distinguish between deuto- and tritonymphs in every case. Couplet 5, however, permits separation in most instances. The epimeral formula (3-1-4-2) is common to both nymphs, but the number of aggenital setae generally differs between the two stases. The key does not provide adequate information for certain genera, such as Homeopronematus male or Eotydeus where genital chaetotaxy regression occurs even in the adults. Further information on the ontogeny of these genera is required.

C. Key to the subfamilies of Tydeidae (any stase)

1.-Leg solenidiotaxy : four ; four terminal
   eupathidia at the tip of the palptarsus . . Meyerellinae
  -Leg solenidiotaxy : three or less ;
   multiple eupathidia at the tip of the
   palp tarsus 2
2.-Leg solenidiotaxy : three 3
  -Leg solenidiotaxy : two or less 5
3.-Apotele I absent or, at least, without
   claws or with vestigial claws ;
   eupathidia very long on tarsus I ; genital
   setae absent, number of genital acetabula
   varying from two pairs to none . . . . . . Pronematinae
  -Apotele I normal ; genital setae present
   at least commencing with the tritonymphal
   stase ; two pairs of genital acetabula
   commencing with the deutonymph 4
4.-Genua II, III and IV nude ; three pairs
   of lyrifissures . . . . Pretydeinae (Pretydeus)
  -Genu II with at least two setae ;
   genu III with at least one setae ;
   four pairs of lyrifissures . . . . Tydaeolinae
5.-Palptibia with two setae ; genu II, III
   and IV nude ; multiple eupathidium at
   the end of the palp with three small
   tines . . . . Pretydeinae (Prelorryia)
  -Without the above combination of
   characters ; double or triple
   eupathidium at the end of the palptarsus 6
6.-Four pairs of lyrifissures ; setae 12
   present on the opisthosoma (fig. 3A). .Australotydeinae

-Three or four pairs of lyrifissures ;
setae 1̲2̲ absent 7

7.-Three pairs of lyrifissures ; at most
three setae on femur I ; two eyes . . . . . Tydeinae

 -Four pairs of lyrifissures ; at least,
four setae on femur I ; three eyes. . . Triophtydeinae

D. Key to the genera (adults only)

1.-Tarus I with 12 setae 2

 -Tarsus I with 11 setae or less 11

2.-Tibia I with six setae (one of them
being eupathidial and another being
the famulus) and one solenidion ;
tibia II also with a solenidion . . . . . . Meyerella

 -without the above combination of
characters 3

3.-Tibia I with six setae (one of them
being an eupathidium clustered with
the famulus) ; solenidion φ I
recessed ; φ II absent . . . . Pseudotydeus

 -Tibia I with five setae 4

4.-Prodorsum recurved, (p̲1̲) clearly
anterior to (p̲2̲) ; femur IV divided . . Pretriophtydeus

 -Prodorsum procurved, (p̲1̲) either
between (p̲2̲) and (s̲) or posterior
to (s̲) ; femur IV not divided 5

5.-(p̲1̲) located posteriorly to (p̲2̲)
but anterior to (s̲) ; strong double
eupathidium at the end of the palp
tarsus 6

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        -(pl) located between or posterior
         to sensilla ; triple eupathidium
         at the end of the palp . . . . . . . . . . . . . . . . 7
   6.-Femur I with six setae ; genu III
         with three setae . . . . . . . . . . . . Lasiotydeus
        -Femur I with five setae ; genu III
         with two setae . . . . . . . . . Tyndareus (rostratus)
   7.-Genu III with three setae ; six
         pairs of genital and four pairs
         of aggenital setae . . . . . . . . . . . . . Primotydeus
        -Genu III with one or two setae . . . . . . . . . . 8
   8.-Genu III with two setae ;
         femur II with four setae . . . . . . . . . . . . . 9
        -Genu III with one seta ;
         femur II with three setae . . . . . . . . . . . 10
   9.-Femur I with four setae . . . . . . . Metatydaeolus
        -Femur I with six setae . . . . . . . Paratriophtydeus
  10.-Femur I with six setae : femur
         III with three setae . . . . . . . . . Paratydaeolus
        -Femur I with four setae ; femur
         III with two setae . . . . . . . . . Coccotydaeolus
  11.-Tarsus I with 11 setae . . . . . . . . . . . . . 12
        -Tarsus I with 10 setae or less . . . . . . . . . 14
  12.-Prodorsum recurved ; femur IV
         divided . . . . . . . . . . . . . . . Apotriophtydeus
        -Prodorsum procurved ; femur IV
         not divided . . . . . . . . . . . . . . . . . . 13
  13.-Three pairs of aggenital setae ;
         genu III with one seta . . . . . . . . . Microtydeus
        -Four pairs of aggenital setae ; genu
         III with two setae . . . . . . . . . . . Tydaeolus
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14.-Tarsus I with ten setae 15

   -Tarsus I with eight setae or less 19

15.-Tarsus I with a pair of ventrals

      (v) but without iterals (it) ; genu

      II with three or four setae 16

   -Tarsus I with a pair of iterals (it)

      but without ventrals (v) ; genu II

      with one or two setae 18

16.-Prodorsum recurved ; 12 present on

      opisthosoma . . . . Australotydeus

   -prodorsum procurved ; 12 absent 17

17.-Tarsi III and IV with seven setae ;

      femur I with five setae . . . . . Tyndareus (eloquens)

   -Tarsi III and IV with five setae ;

      femur I with four setae . . . . Aesthetydeus

18.-Genua II, III and IV with only

      one seta . . . . Teletriophtydeus

   -Genua II, III and IV with two setae . Metatriophtydeus

19.-Apotele I with vestigial claws or

      with no claws ; or apotele I absent 20

   -Apotele I present and normal 30

20.-Apotele I absent 21

   -Apotele I with vestigial claws or with

      no claws ; femur IV divided 28

21.-Four pairs of aggenital setae 22

   -Three pairs of aggenital setae, or

      less. 25

22.-Tarsi II, III and IV with seven

      setae . . . . Proctotydaeus

   -Tarsi II and IV with six setae or

      less ; femur IV not divided 23

23.-Tarsus II with seven setae ; genu II
    with two setae . . . . <u>Pronematulus</u>
   -Tarsus II with only six setae ;
    genu II with three setae 24

24.-Trochanters I and II with no setae ;
    Tarsi III and IV with five setae . . . . <u>Pronematus</u>
   -Trochanter I and II with one setae ;
    Tarsi III and IV with six setae .. . <u>Homeopronematus</u>♀

25.-Only one pair of aggenital setae . . <u>Homeopronematus</u>♂
   -Three pairs of aggenital setae 26

26.-Genua I and II with three setae ;
    genu III with two setae . .. . <u>Metapronematus</u>
   -Genua I and II with two setae 27

27.-(<u>p2</u>) reduced or absent on the
    prodorsum ; genu III with two setae ;
    trochanter II nude . . . . <u>Parapronematus</u>
   (<u>p2</u>) normal ; genu and trochanter II
   with one setae . . . . <u>Apopronematus</u>

28.-Tarsi II, III and IV with seven setae . . . <u>Naudea</u>
   -Tarsi II, III and IV with at most
    six setae 29

29.-Tarsus III with six setae ; genu II
    with three setae and genu III with
    two setae . . . . <u>Pausia</u>
   -Tarsus II with five setae ; genua II
    and III with only one setae . . . . <u>Pronecupulatus</u>

30.-Genua II, III and IV nude ; trochanter
    II with one seta 31
   -At least one seta on genu II ;
    trochanter II nude 32

31.-Solenidion φ I present on tibia I . . . <u>Pretydeus</u>
   -Solenidion φ I absent . . . . <u>Prelorryia</u>

-Trochanter IV with no seta ; three
  pairs of genital and aggenital setae . . . <u>Apolorryia</u>

CONCLUSIONS

As emphasized by Athias-Henriot (1975), the
elaboration of identification tools has nothing in
common with systematic investigations. "For the first
procedure, clearly visible morphological details are
important. The second one requires a correct morphological
understanding of the body components and an exhaustive
study of their distribution and variability throughout the
members of the whole group." (Athias-Henriot, 1975 : 106).
An exhaustive study of organotactic characteristics of the
family Tydeidae is presented in chapters II to IV of this
work. The data collected were subjected to cladistic
analyses in order to construct a consistent phylogeny
and classification for the family. The resulting scheme
does not pretend to be free of error, especially in regard
to the manner of weighting the characters used. However,
at the very least, a frame of reference has been provided
for future studies.

Future work on tydeid systematics may be oriented
in one of two ways : either downward to the generic and
specific levels, or upward to the superfamilial level.
Many species will have to be redescribed either because
of the poor quality of the first description, or because
immatures were neglected. Such a study could be achieved
by individual in-depth reviews of the proposed subfamilies
or even of genera. The other possibility for a meaningful
approach to future study of tydeid systematics is through
an examination of the superfamily Tydeoidea. Krantz (1978)
grouped three other families with the Tydeidae in the
Tydeoidea : the Ereynetidae, Paratydeidae, and Iolinidae.

I have studied only a few specimens of Ereynetidae,
Paratydeidae, and Iolinidae. On the basis of this
limited study, however, some features are already obvious.
The Paratydeidae are clearly distinct from Tydeidae ; the
peritremes of the former group are more developed and their
solenidiotaxy is notably richer. However, the notation
proposed here for the Tydeidae should be applicable to
the Paratydeinae as well. The Ereynetidae pose a problem
in that I am unable to demonstrate any differences
between them and the Tydeidae. The so-called ereynetal
organ of tibia I of Ereynetidae (designation still used
by Fain 1964) was identified long ago as solenidion φI
(Grandjean, 1939). This solenidion is deeply recessed in
adult ereynetids but, in the larval stase, it does not
differ from a recessed solenidion of tydeids. The soleni-
diotaxy of Ereynetidae is richer than that of the tydeid
subfamily Tydeinae but poorer than that of Meyerellinae.
The ereynetid chaetotaxy is surprisingly similar to that
of the Tydeidae, even as regards the eupathidia.
Paraproctal suckers are common to both families. A
distinctive clustering of (ωI-ft') and (k"-l"ζ) which
has been observed both in an __Ereynetes__ species and in
__Pseudotydeus__. The number of genital acetabula is
virtually identical in both families (the tydeid
subfamily Pronematinae is an exception). Poroidotaxy is
also similar. Therefore, it is likely that the two
families will have to be amalgamated ar at least reorganized
along other lines. It would be necessary to study the
Ereynetidae in depth and to apply a cladistic approach
simultaneously to genera that presently are assigned to
the Tydeidae or Ereynetidae. The Iolinidae, from which

the genus _Proctotydaeus_ has been withdrawn, comprises only
the genus _Iolina_. At first sight, Iolinidae could be
included in the Tydeoidea as proposed by Krantz (1978).
Differences may be found on the gnathosoma (palpsegments
fused, styliform chelicerae).

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APPENDICES

Appendix I : Glossary of special terms

AMPHISTASY : the quality of state of being amphistatic (ant. eustasy).

AMPHISTATIC : not appearing at a particular stase (ant. eustatic).

ANABASIS : migration of either or both proral setae of tarsus to the position on the tectal setae (see figure 8).

ANHOMOLOGOUS TAUTERGY : repetition through ontogeny of a particular morphological character of (a) well defined organ(s) when the organs bearing this character are not the same from one stase to another but apparently keep the same location on the animal (adapted from Grandjean, 1964 : 170).

ANOMALY : individual and exceptional variation of any nature, almost always unilateral, to which no evolutionary significance may be attributed in the present state of knowledge (Grandjean, 1972 : 455).

ATRICHOSY : state or quality of an area or of a segment that has lost all of its setae.

CHAETOTAXY : see organotaxy.

DESIGNATION : a nomenclature system not based on idionymy but generally resting on location (cf. notation).

DISJUNCTION : distal migration of either member of a setal pair on a leg segment.

ERROR : variation of all or none (see anomaly, vertition).

EUSTASY : the quality or state of being eustatic (ant. amphistasy).

EUSTATIC : appearing at a particular stase (ant. amphistatic).

IDIONYMIC : relating to a particular organ as distinct from other organs of the same nature. Consequently, an idionymic organ may be named ; for example, a pair of setae is called "prorals" since they may be distinguished from all other tarsal setae, even when they migrate.

IDIONYMY : the quality or state of being idionymic.

NEOTRICHY : state or quality of being neotrichial (ant. prototrichy).

NEOTRICHIAL : referring to an area, a segment or an animal some setae of which are secondarily formed (ant. prototrichial).

NOTATION : a nomenclative system based on idionymy (cf. designation).

ORGANOTAXY : Distribution pattern or "taxy" of organs - specifically their number and their location. Organotaxy comprises chaetotaxy (setae), phanerotaxy (setiform organs), solenidiotaxy (solenidia), poroidotaxy(lyrifissures), sigillotaxy (muscle insertions), and adenotaxy (glands).

ORTHOTRICHY : state or quality of being orthotrichial.

ORTHOTRICHIAL : referring to an area, a segment or an animal the setae of which keep their primitive and original location.

PALECTRICHY : state or quality of being paleotrichial.

PALEOTRICHIAL : referring to a prototrichial area, segment
or animal which keeps all the primitive setae.

PARALLEL HOMOLOGY : an hypothesis referring to a primitive
state where each leg segment is supposed to be
identical on all four legs.

PHANEROTAXY : see organotaxy.

POROIDOTAXY : see organotaxy.

PRIORITY LIST : a method for ranking setae according to
their frequences of occurrence, in the normal or
eupathidial state, from the strongest (high
frequencies) to the weakest (low frequencies).
Grandjean (1942) distinguished four types of priority
lists ontogenetic, vertitional, metameric, and
phylogenetic.

PROTOTRICHY : state or quality of being prototrichial
(ant. neotrichy).

PROTOTRICHIAL : referring to an area, a segment or an
animal the setae of which are primitive (ant.
neotrichial).

SIGILLOTAXY : see organotaxy.

SOLENIDIOTAXY : see organotaxy.

VERTITION : a fundamentally unilateral "all or none"
variation in an idionymic organ which is observed in
individuals of the same species and at the same stase,
which may be considered to have an evolutionary
significance (from Grandjean, 1972 : 455).

Appendix II : List of abbreviations
and symbols

acm : anteroculminal seta (palptarsus) ;

ad1, ad2 : adoral seta ;

ag1 to ag5 : aggenital setae ;

ba : basal seta (palptarsus) ;

cot : cotyloid cavities ;

cpc : podocephalic canal ;

d : dorsal seta (on a leg segment) ;

d1 to d5 : first five setae of the paraxial aligment of
the dorsal face of opisthosoma ;

das : disjugal - abjugal - sejugal furrow;

dg : dorsogenual seta (palpgenu) ;

dg3 : third ductus of podocephalic canal ;

eI and ep : supracoxal spines (on legI and palp) ;

em : empodium ;

eu1 to eu6 : eugenital setae ;

ft : fastigial seta (tarsus) ;

ge1 to ge6 : genital setae ;

h1, h2 : setae of segment H ;

H : segment anterior to the pseudanal segment (PS) ;

ia, im, ip and ih : lyrifissures ;

it : iteral seta (tarsus) ;

k" : famulus ;

k.ph : condylophore ;

l : lateral seta (on a leg segment) ;

l1 to l5 : first five setae of the antiaxial alignment of
the dorsal face of opisthosoma.

ma, mb1, mb2, mc, md, mds, me, mes : dorsal sigilla on
                                       opisthosoma ;

n.st. : neostigma ;

N1, N2, N3 : the three nymphs ;

ol : lateral claw ;

om : empodial claw ;

p : proral seta (tarsus) ;

p1 to p3 : prodorsal setae ;

ps : pseudanal seta ;

pv : proximoventral seta (femur) ;

s : sensillum ;

sc1 and sc2 : subcapitular setae ;

smd : furrow posterior to das ;

sti and stπ : stigmata (anti- and paraxial) ;

t : seta on palptibia ;

tc : tectal seta (tarsus) ;

tr : trochanteral seta ;

tr α, tr π : anti- and paraxial tracheae ;

u : unguinal seta (tarsus) ;

v : ventral seta (on appendages) ;

vs : vestibulum ;

α : antiaxial ;

δ : dehiscence line ;

ζ : eupathidial ;

π : paraxial ;

φ : tibial solenidion ;

ω : tarsal solenidion ;

1a, 1b, 1c, 2a, 3a, 2b, 3c, 3d, 4a, 4b, 4c : epimeral setae.