

A GENERIC REVISION OF THE FAMILY TYDEIDAE (ACARI : ACTINEDIDA)

III. ORGANOTAXY OF THE LEGS *

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PHANEROTAXY
TYDEID LEG
ANABASIS

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

PHANÉROTAXIE
PATTE DE TYDÉIDAE
« ANABASE »

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

Legs generally comprise six segments in Tydeidae. These are the trochanter, femur, genu, tibia, tarsus and apotele¹. 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

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

Tydeidae. For instance, genera II, III and IV of Pretideinae are nude. This parallel regression is a good sign of conformity.

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

A. APOTELE (Figure 1).

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

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

Because of their setal derivation, lateral claws² and the empodium are birefringent and have a root and a development³ similar to that of a seta. The lateral 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 which arises a rather large excrescence which expands into a real claw in some genera or species like the "true" claws; it is birefringent.

The cotyloid cavities are connected with two

condylophores which are very much developed in Pronematinæ. 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 Pronematinæ. Pronematinæ are interesting because apotele I is very much reduced or even lost. Such a phenomenon is known in some other actinidid families and has been studied extensively by GRANDJEAN (1966) in two species of Staurobatidae (Oribatida). As in the latter family, two steps in regression of the apotele have been observed in Tydeidae. The first step is seen in some adults of the genera *Naudea*, *Pausia* and *Pronecupulatus* as well as in larvae of *Metapronematus* and *Homeopronematus*. Only the larva of *Homeopronematus* was studied in depth because it alone was prepared in lactic acid. The size of the apotele is reduced but the empodium remains obvious. A close study shows that, in addition to the empodium, every element of a normal apotele is present: the two lateral claws which are vestigial, the basilar sclerite, and even the condylophores. Therefore, as in the oribatid *Staurobates schusteri*, the apotele is assumed to have retained its mobility. The major difference when compared to the usual leg I of tydeids is the great development of the tarsal eupathidia, exactly as in Staurobatidae. The second step in regression of the apotele is the complete disappearance of the segment. This is associated with the disappearance of the condylophores belonging to tarsus I as in *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 appear on tarsus I, but a substantial lengthening of the existing eupathidia is noticed. According

2. The french word "ongle" used by GRANDJEAN is translated as "claw". The set of three "ongles" is called "griffes" 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.

3. The development of a claw has been followed in several larvae, beginning with their formation in the prelarval apoderm. Initially, they are, like a seta, very clear and with no root. In Oribatida, claws are subject to vertitions (GRANDJEAN, 1961).

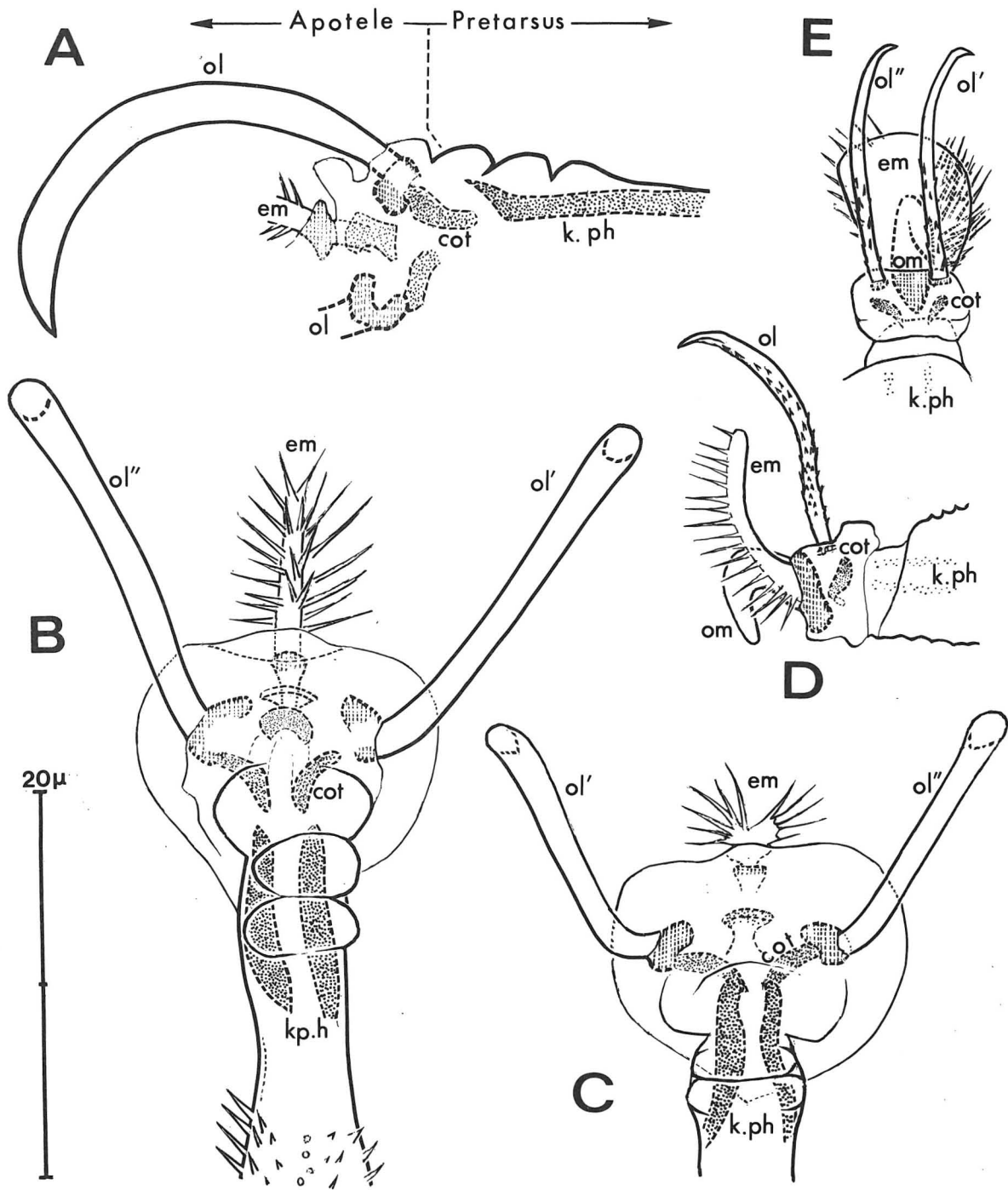


FIG. 1 : Apotele. *Proctotydaeus schistocercae* : lateral (A) and dorsal (B) views of apotele IV of a male, dorsal view of apotele II of a tritonymph (C). *Pretydeus lwioirensis* : lateral (D) and dorsal (E) views of apotele I of a tritonymph.

to Grandjean, this lengthening precedes and even "causes" the loss of the apotele, which becomes quite unable to assume its usual function.

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

B. TARSUS (figure 2).

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

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

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

$$(ft', (tc), (p), (u)), ft'', ((it), v''), v' (1)$$

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

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

$$(ft', (p), (u)), tc'', tc', ft'', ((it), v''), v' (2)$$

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

		(ft)	(tc)	(it)	(p)	(u)	(v)
I	1.	EE	EE	EE	EE	NN	NN
	2.	EE	EE	EE	EE	NN	—N
	3.	EE	EE	EE	EE	NN	—
	4.	EN	EE	EE	EE	NN	—
	5.	NE	EE	NN	EE	NN	NN
	6.	NN	EE	NN	EE	NN	NN
	7.	NE	EE	NN	EE	NN	—N
	8.	NN	EE	NN	EE	NN	—N
	9.	NE	EE	—	EE	NN	NN
	10.	NN	EE	—	EE	NN	NN
	11.	NE	EE	—	EE	NN	—
	12.	NN	EE	—	EE	NN	—
	13.	N—	EE	—	EE	NN	—
	PF	100 99	100 100	40 40	100 100	100 100	22 40
	ESF	11 84	100 100	11 11	100 100	— —	— —
II	1.	NE	—	—	NE	NN	—
	2.	NN*	—	—	EN	NN	—
	3.	NN	—	—	NE	NN	—
	4.	NN	—N	—	NE	NN	—
	5.	NN	NN	—	NN	NN	—
	6.	NN	—N	—	NN	NN	—
	7.	NN*	—	—	NN	NN	—
	PF	100 100	26 36	—	100 100	100 100	—
	ESF	— 7	—	—	2 12	—	—
III-IV	1.	N—	NN	—	NN	NN	—
	2.	N—	—N	—	NN	NN	—
	3.	N—	—	—	NN	NN	—
	4.	E—	—	—	NN	NN	—
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 %).

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

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

$$p'', p', (tc), ft'', ft', (it) (3)$$

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

Table I also prompts other comments about eupathidia. The eupathidial character of (*it*)

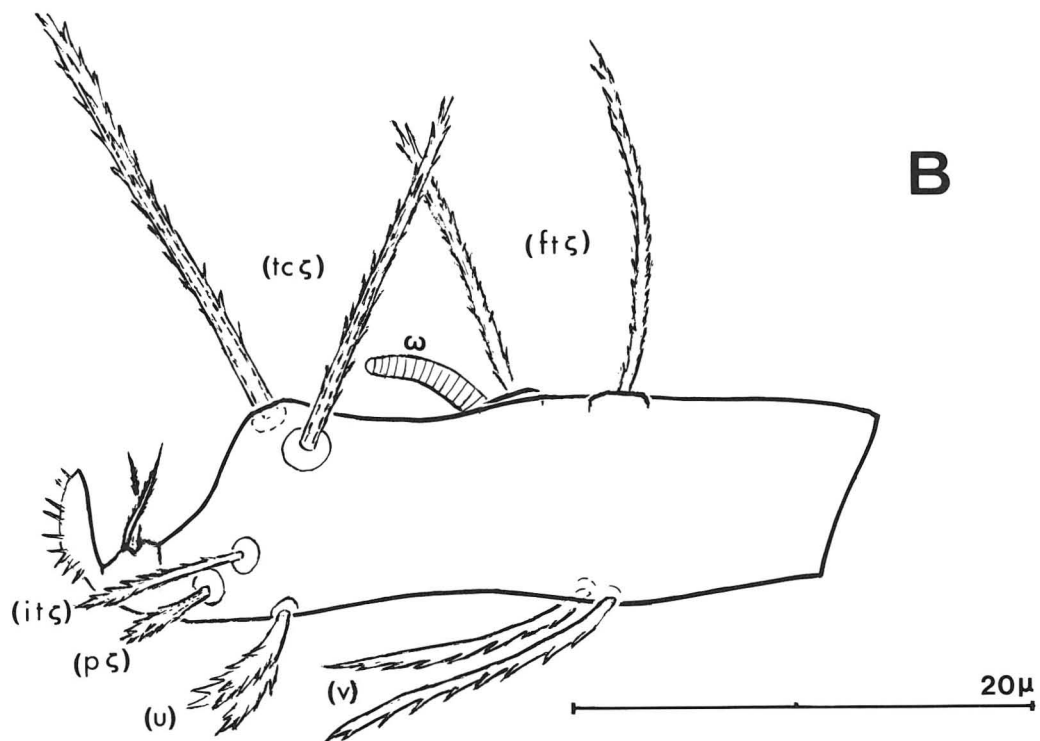
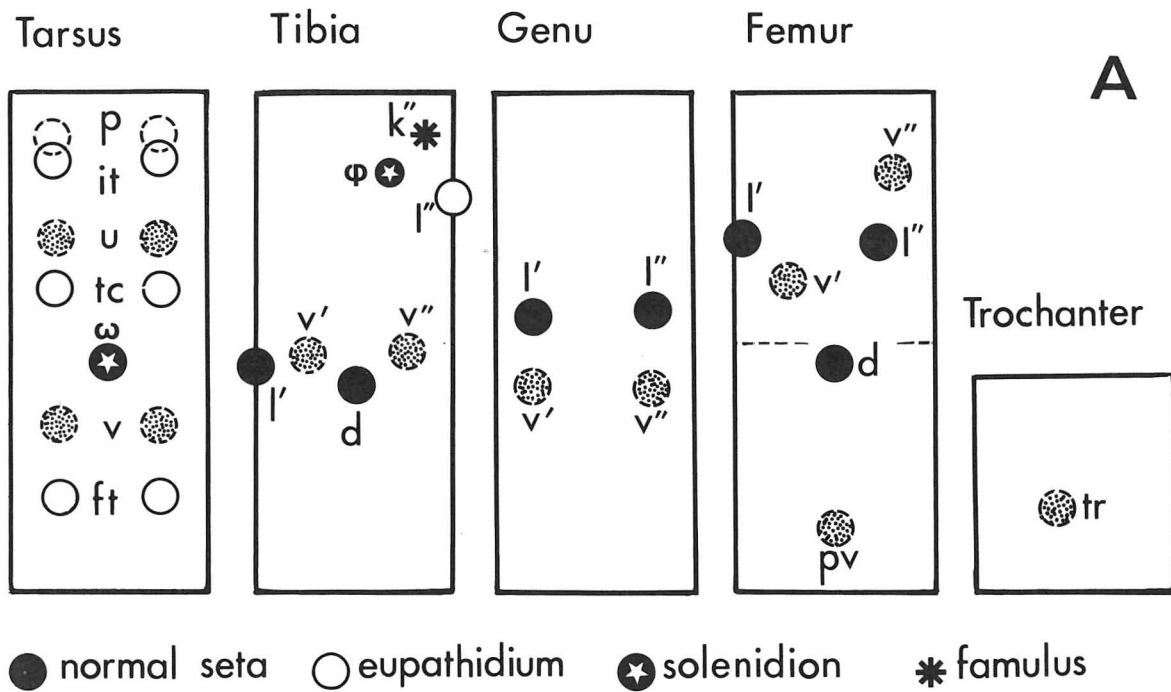


FIG. 2 : Leg segment phanerotaxy in Tydeidae. Diagram of a leg segment phanerotaxy in dorsal view (archetype) (A) ; antiaxial view of tarsus I of *Meyerella marshalli* (tritonymph) (B).

seems stronger in Meyerellinae and 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 heretofore 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 ($tc\zeta$) 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), $tc''\zeta$, $p'\zeta$, (v). Both interpretations 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 is situated at the typical position of tc'' . In addition, a distal pair of setae is found on the ventral side and another pair, (ft), on the dorsal side apparently completes the count. Closer study, however, shows that there are two additional setae, rather small and slender, and inserted near the eupathidium occupying the loca-

tion of tc'' . These two setae have to be named and the only consistent formula becomes :

(ft), (tc) both undersized, ($p\zeta$), (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 3). 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"⁴.

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 insertion of tc'' begin to amalgamate with the insertion of $p''\zeta$. The next phase is the anabasis of $p'\zeta$ as in *Prelorryia indionensis* or *Tydaelolus* : (tc) are vestigial but both share the same insertion with ($p\zeta$). The last step involves the complete disappearance of (tc). This may be the case in *Homeopronematus vidae* whose (tc) could not be found⁵. 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.

4. From $\alpha\nu\alpha$, meaning both upward and backward, and $\beta\alpha\nu\epsilon\iota\nu$, 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, Erythraeidae, Bdellidae and Caeculidae) or second as in Tydeidae.

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

Table II summarizes data on fundamental chaetotaxy of each tarsus.

TABLE II. — FUNDAMENTAL CHAETOTAXY OF TARSI.

		(ft)	(tc)	(it)	(p)	(u)	(v)
I	1.	NN	N* N*	— —	EE	NN	NN
	2.	NN	N* N*	— —	EE	NN	— N
	3.	NN	N* N*	— —	EE	NN	— —
	4.	NN	— ? — ?	— —	EE	NN	— —
II	1.	NN	— —	— —	NE	NN	— —
	2.	NN	— —	— —	NN	NN	— —
III-IV	1.	N —	— —	— —	NN	NN	— —
	PF	100 50	7 7	— —	100 100	100 100	4 7
	ESF	— —	— —	— —	25 29	— —	— —

Symbols : the same as in the previous table.

■ *Ontogeny of the setae.* As far as is known, the fastigials become eupathidial at the deutonymphal stage. Seta *ft*" disappears in *Apoloryia 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 tritonymph and on tarsi III and IV in the adult. There is, therefore a metameric delay in the acquisition of the eupathidial state from leg I to IV. These setae seem to be eustatic which is the usual state of fundamental setae (GRANDJEAN, 1942 : 238).

The tectals become eupathidial on tarsus I of the protonymph. Seta *tc*" appears on tarsus II at the tritonymphal stage in *Meyerella marshalli* and *Proctotydaeus schistocercae* while both tectals, (*tc*), appear together in the deutonymph of *Paratydaeus* and *Tydaeus frequens*, and in the tritonymph of *Paratriophtydeus*. Setae (*tc*) exist on tarsi III and IV at the adult stage in *Microtydeus* and *Tydaeus* but not in the deutonymph (unfortunately, their tritonymphs are unknown). In *Coccotydaeus*, (*tc*) appear at the deutonymphal stage on tarsus III but are delayed to the tritonymph on tarsus IV. The unpaired tectal seta, *tc'*, is formed at the deutonymphal stage on tarsus III of *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 : (N N) — (ξ N) — (ξ ξ) — (ξ ξ) ; (— —) — (N N) — (ξ ξ) — (ξ ξ) ; (? ?) — (? ?) — (N N) — (ξ ξ) and (— —) — (— —) — (N N) — (N N). From formula (3) (page 168), this arrangement permits more precision in arriving at eupathidial priorities :

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

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

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

■ *Parallel homology* 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 ω I is present in every species and, as far as ontogenies are known, is eustatic from the larva ; ω II 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 Pronematinæ, a feature which

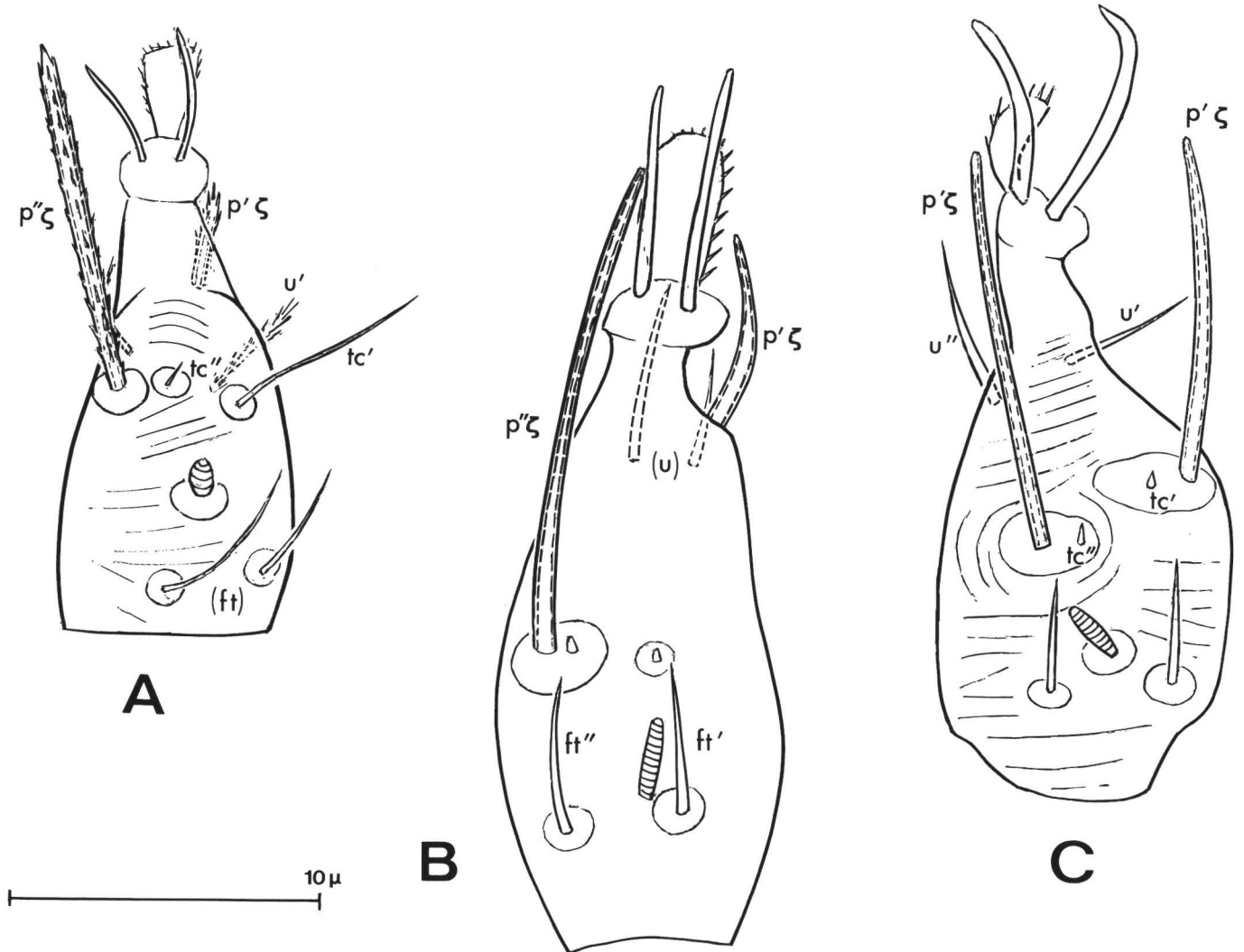


FIG. 3 : Anabasis. Tarsus I of larva of *Metatriophtydeus* sp. (A), *Orthotydeus* sp. (B) and *Prelorryia indionensis* (C).

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 ω I 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*.

C. TIBIA.

The study of the tibia is more difficult than that of the tarsus because the relative locations of the tibial setae often are poorly defined. The archetype (figure 2) includes five normal setae of which one may be eupathidial, a famulus k'' 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 setae always occurs on a segment and that the setae are quite independent, then the number of different possible formulae describing the four legs rises to 625. If the above assumptions are followed, the number of possible formulae between the two observed extremes : (5-3-2-2) and (2-1-1-1) (table IV), is still high : 48. With the inclusion of one additional assumption ; i.e. that a segment may not carry more setae than a more anterior segment, the number of possibilities drops to 25. However, formula 8 of table IV cannot be included in the set. A last assumption may be added here : there is a priority between the setae, simple (i.e. amphistasy and eustasy do not coexist) and absolute. The number of possible formulae is then reduced to eight. Of these eight formulae, one has not been observed and is missing in table IV, (3-2-2-1) while formulae 8 and 9 do not belong to the set of eight. This mathematical exercise shows clearly that setal loss on the tibiae is not a stochastic phenomenon.

However a leg setal tabulation⁶ 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 Tydaolinae ; i.e. they are not homologous. Figure 4 depicts the

homologies and chaetotactic regression of the tibial five-setae verticil. In the case of tibia I, the designation used at starting may be interpreted as a notation ; for tibiae II-IV, however, designation still remains the only means of defining a seta.

TABLE IV. — CHAETOTACTIC FORMULAE OF THE FOUR TIBIAE.

	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

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

6. This term is taken from VERCAMMEN-GRANDJEAN (1971).

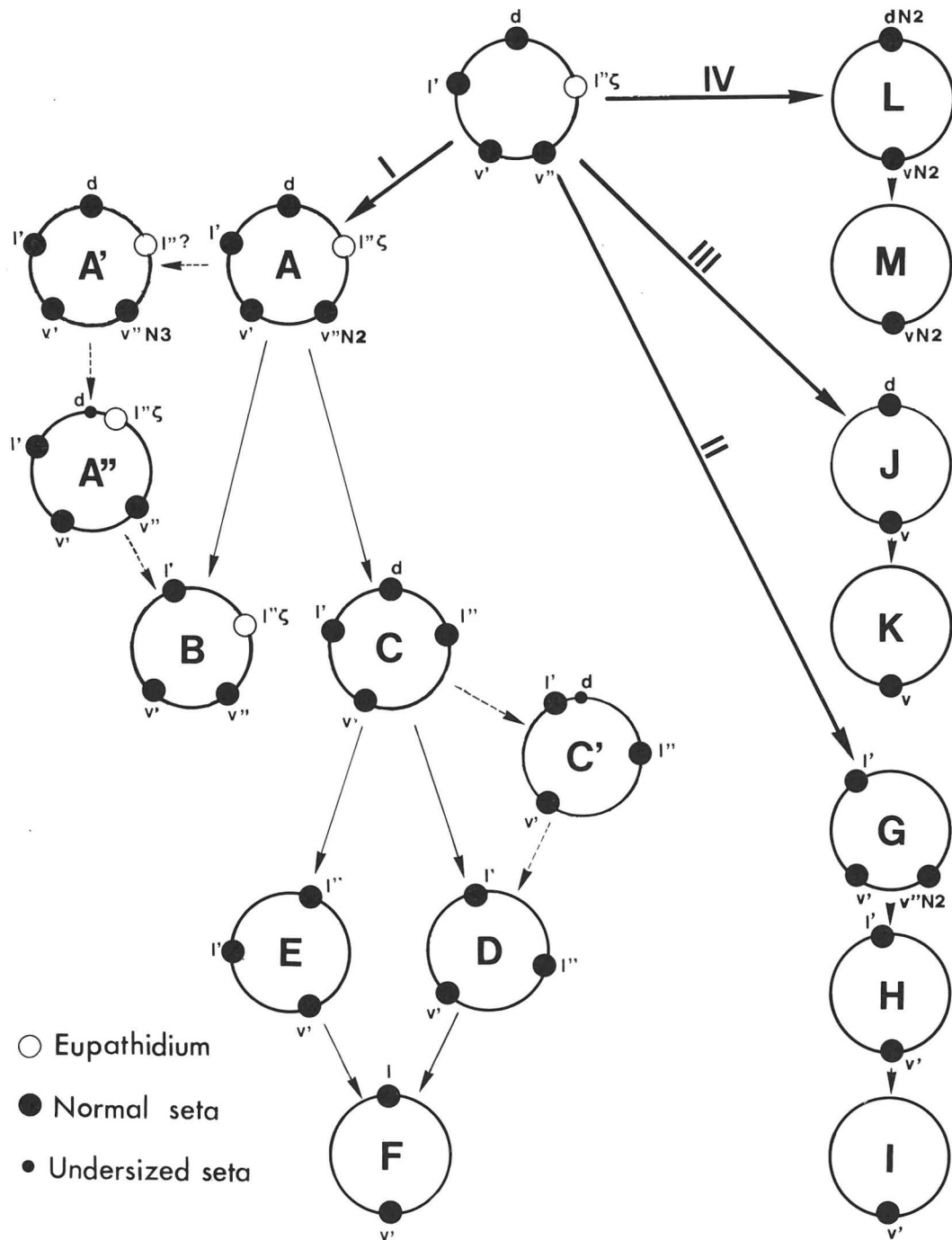


FIG. 4 : Schematic regressive pattern in tibial chaetotaxy in Tydeidae.
 Roman figures refer to the four legs.

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

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

Among the normal setae, k'' deserves special attention. This seta is hollow and is present in every species and stase. It is likely a famulus and should be homologous to k'' in the family Caeculidae. The seta is situated dorsoantiaxially but is slightly more antiaxial and a bit more distal than solenidion ϕI^7 . In *Pseudotydeus perplexus*, seta k'' forms a cluster with $l''\zeta$ as in *Ereynetes* as described by GRANDJEAN (1939) ; it is slender and lies side by side with the setae except at the tip, so that it is difficult to see.

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

D. GENU.

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

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

7. However, an exception is known in the generic unit T1 where these positions are reversed.

TABLE V. — GENUAL CHAETOTACTIC FORMULAE.

	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

E. FEMUR (figure 2).

The femur is special in that it consists of two primary segments : a basi- and a telofemur⁸, 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 generic character, but it has not been thoroughly studied. Observations have revealed that the joint between basi- and telofemora IV is vanishing, even in Meyerellinae and Triophtydeinae. In these subfamilies, there is a degree of flexibility at each leg joint except for the interfemoral junction where flexion does not appear to occur. If strong pressure is exerted on leg IV, then it is possible to elicit flexion even at the interfemoral joint. However, the flexion is less pronounced than at other joints. This difference in degree of flexibility is easy to understand when leg segment musculature is studied⁹.

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 segment¹⁰ 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 action¹¹ 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 femur¹². In *Eotydeus*, the major stress joint is situated 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 disadvantageous¹³,
- 2°) the muscle is regressive and much thinner than other leg muscles.

The inefficiency of this arrangement is all the more important in that the joint is proximal and should be a major stress point. The joint is thus vanishing. In *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

8. Or, respectively, a femur 1 and a femur 2 after the nomenclature of VAN DER HAMMEN (1970).

9. 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.

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

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

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

13. Except when the angle of flexion is null or close to zero.

joint may be located by the presence of the 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.

Table VI summarizes the femur chaetotactic formulae. The richest is (6-4-3-2) and the most regressive is (2-2-1-1). Once again, the 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.

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

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 setae, *pv*, seems to be easy to recognize. This seta is the strongest on leg IV and among the strongest on the other legs.

All the setae of femur IV are formed in the deutonymph, as are those of genu and tibia IV. This sudden appearance of all the setae at the same stage is surprising. It implies that all the setae are delayed in appearance as eustatic setae or, conversely, that the setae are eustatic at the deutonymphal stage. 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 chaetotaxy¹⁴. GRANDJEAN (1946) pointed out this denudation of the protonymphal leg IV in mites and interpreted it as a precursory sign of the disappearance of the leg.

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

F. TROCHANTER.

Table VII summarizes the data regarding the trochanteral chaetotactic formulae. Of the total of 16 possible formulae, only six are known to exist. This means that a priority list based on table VII may be induced. This list is (*tr* III, *tr* I, *tr* II, *tr* IV). It must be pointed out that formula 4 does not fit with this list. The different ontogenies reveal that the setae are all amphistatic. The seta *tr* III always appears first except after the disappearance of seta *tr* II; then, *tr* I seems to become as strong as *tr* III.

14. The case of the trochanter is a bit different as explained later.

TABLE VII. — TROCHANTER CHAETOTACTIC FORMULAE.

	1	a	2 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.

It must be pointed out that setae do not normally appear at the adult stage ; they are formed at the latest in the tritonymph¹⁵. 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.

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